Quantification of genetic diversity for drought adaptation in a reference collection of common bean (*Phaseolus vulgaris* L.)

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Declaration

I declare that this thesis hereby submitted by me for the degree Philosophiae Doctor in Plant Breeding at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I further cede copyright of the thesis in favour of the University of the Free State.

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Dedication

To my son, Sunfree

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List of abbreviations and acronyms

SI units

cm	centimetre
g	gramme
Ha	hectare
hrs	Hours
kg	kilogramme
kg ha^{-1}	kilogramme per hectare
kPa	kilopascal
L	Litre
m	Metre
ml	millilitre
mm	millimetre
mM	milliMolar
Ng	Nanogramme
nM	nanoMolar
U	Unit
V	Volts
^{o}	degree
^{o}C	degrees Celsius
%	percent
µl	microlitre
µg	microgramme
µm	micrometre
µM	microMolar

Abbreviations

A	Andean
ABA	Absiscic acid
(AG)n	Adenine – guanine repeats

ALS	Angular leaf spot
AM	Association mapping
AMOVA	Analysis of molecular variance
ANOVA	Analysis of variance
(AT)n	Adenine – thymine repeats
Bp	Base pair
C	Carbon
CA	Cytosine – adenine
CAPs	Cleaved amplified polymorphic sequences
CBB	Common bacterial blight
cDNA	Complementary deoxyribonucleic acid
CIAT	International Centre for Tropical Agriculture
cM	centiMorgan
D	Durango
D1	Durango 1
D2	Durango 2
DII	Drought intensity index
DAB	Drought Andean beans
DAP	Days after planting
dCAPs	Derived cleaved amplified polymorphic sequences
DF	Days to flowering
D.f	Degrees of freedom
DLB	Dead leaf dry biomass
DM	Days to maturity
DNA	Deoxyribonucleic acid
dNTP	deoxyribonucleotide triphosphate
DREB	Dehydration responsive element binding protein
DSI	Drought sensitivity index
D’	Standardised disequilibrium coefficient
E	East
ECSA	East, Central and Southern Africa

EDTA	Ethylenediaminetetraacetic
EST	Expressed sequence tag
F_0	Fluorescence yield in the absence of photosynthetic light
F_1	First filial generation
F_2	Second filial generation
FAM	Blue fluorescent dye
FAO	Food and Agriculture Organisation
F_{IS}	Measure of inbreeding in subgroups
F_{IT}	Measure of inbreeding in the entire group
F_M	Maximum fluorescence when a highest intensity of light is applied on leaves
F_{ST}	Measure of the identity of individuals within subgroups compared to other individuals in other subgroups
F_T	Continuous fluorescence yield in non-actinic light
F_V	Variable fluorescence
G	Genotype
GA	Guanine – adenine
GxE	Genotype by environment
GLB	Green leaf dry biomass
GLM	General linear model
GM	Geometric mean
GxT	Genotype by treatment interaction
H	Huevo de huanchaco
H_e	Gene diversity
H_o	Observed heterozygosity
IML	Interactive matrix language
K	Number of subpopulations
K^+	Potassium ion
LA	Leaf area
LB	Dry leaf biomass at mid pod filling stage
LD	Linkage disequilibrium
LEA	Late embryogenesis abundant

LSD	Least significance differences
M	Mesoamerican
M1	Mesoamerica 1
M2	Mesoamerica 2
MAF	Minor allelic frequency
MAS	Marker-assisted selection
Masl	metres above sea level
Mb	Million base pairs
MCMC	Markov chain Monte Carlo
Min	Minute
MRD	Mean root diameter
M.S	Mean square
MT	Metric tonnes
N	North
N	Nitrogen
NED	Yellow fluorescent dye
NERICA	New rice for Africa
NG	Nueva Granada
NG1	Nueva Granada 1
NG2	Nueva Granada 2
NJ	Neighbour joining
OA	Osmotic adjustment
OH^-	Hydroxyl group
P	Peru
P100	100-seed weight
PB	Dry pod biomass at mid pod filling stage
PCoA	Principal coordinate analysis
PCR	Polymerase chain reaction
PE	Photosynthetic efficiency
PET	Red fluorescent dye
pH	Acid-base balance of a solution

PIC	Polymorphic information content
PL	Pod length at maturity
PP	Number of pods per plant
PR	Percentage reduction
PVC	Polyvinyl chloride
PWUE	Photosynthetic water use efficiency
Q	Population structure
QPM	Quality protein maize
QTL	Quantitative trait loci
QTLxE	Quantitative trait loci by environment
QY	Quantum yield
R	Pearson's correlation coefficient
r^2	Coefficient of determination
RFLP	Restriction fragment length polymorphism
RIL	Recombinant inbred line
RV	Root volume
S	South
SB	Dry stem biomass at mid pod filling stage
SCMR	Chlorophyll content
SCOND	Stomatal conductance
sec	Second
SNP	Single nucleotide polymorphism
SPAD	Chlorophyll content
S.S	Sum of square
SSCP	Single strand conformation polymorphism
SSR	Simple sequence repeat
STR	Short tandem repeat
T	Treatment
Taq	*Thermus aquaticus*
TASSEL	Trait Analysis by Association, Evolution and Linkage
TB	Total dry biomass at mid pod filling stage

TE	Transpiration efficiency
TE_C	Transpiration efficiency of carbon gain
TE_N	Transpiration efficiency of N gain
TR	Transpiration ratio
TRB	Total root biomass
TRL	Total root length
$TRL_{0.5mm}$	Total root length with diameter 0-0.5 mm
TRL_{1mm}	Total root length with diameter 0.5-1 mm
TxS	Treatment by soil depth level
UNESCO	United Nations Educational, Scientific and Cultural Organisation
USA	United States of America
US$	United States of America dollar
UTR	Untranslated regions
VIC	Green fluorescent dye
VRD	Visual rooting depth
W	West
WS	Water stressed
WUE	Water use efficiency
w/v	Weight of solute per volume of solvent
WW	Well watered

Chapter 1

General introduction

Common bean (*Phaseolus vulgaris* L.) accounts for half of the food legumes consumed in the world (McClean *et al*. 2004) and impacts on agriculture, the environment, human nutrition and health (Broughton *et al.* 2003; Graham and Vance 2003). The crop adds biodiversity in agriculture through positive roles in crop rotations and intercropping with cereals and many other crops. The ability of common bean to fix atmospheric nitrogen in the soil (Serraj 2004) plays a significant role in the structure of ecosystems and sustainability of agriculture.

In some parts of the world, notably Rwanda and Burundi, common bean provides 15% and more than 30% of the daily energy and protein requirements, respectively. In these communities animal protein is limited due to a lack of animals to cull or exorbitant prices, leaving common bean as the best substitute which was thus nick named 'the poor man's meat'. In addition to their protein content supremacy, common bean has a unique combination of nutrients, including vitamins and minerals, essential to human health and functioning (Broughton *et al.* 2003).

Recently, apart from being dominantly a subsistence crop, common bean has begun to fetch higher market prices than other staple crops, making it an important source of income for farmers. Of the total production in Africa, 40% is marketed annually at a value of US$452 million (Katungi *et al.* 2010). This benefit is now rapidly being taken up by seed houses, traders and farmers in both large scale and small farming areas. Today beans are found in large supermarkets and open markets.

After being subjected to two parallel domestication events on the American continent (Sauer 1993), common bean spread to different parts of the world through European traders (Gentry 1969). Evidence from different genetic markers, namely morphological markers, isozymes (Singh *et al.* 1991), seed storage protein profiles (Gepts *et al.* 1986)

and molecular markers (Beebe *et al.* 2000; Blair *et al.* 2006; 2007) show the availability of two primary gene pools in common bean, an Andean gene pool, consisting of large seeded genotypes (≥ 40 g 100^{-1} seed), which is native to the Andes mountains of South America and a Mesoamerican gene pool, containing small seeded genotypes (≤ 25 g 100 $seed^{-1}$), which originated from Central America and Mexico (Singh *et al.* 1991). Another group of medium seeded (≥ 25 ≤ 40 g 100 $seed^{-1}$) genotypes do exist, but largely as a result of crop improvement programmes, selection of Durango populations (Diaz and Blair 2006) and germplasm exchange between and within the two gene pools (Beebe *et al.* 2001).

Worldwide common bean production stood at 23 million metric tonnes (MT) in 2007 (FAOSTAT 2008) with smallholder farmers in third world countries contributing two-thirds of this production. In Africa, cultivation of common bean is mainly done by women on small pieces of land (Broughton *et al.* 2003).

Globally common bean is produced under variable environmental conditions, leaving the crop to face a wide array of both biotic and abiotic constraints. Production of common bean is predominantly rainfed in developing countries and 60% of cultivated beans suffer from water deficit at some stage during their growth (Singh 2001; Beebe *et al.* 2010). Drought in coexistence with high temperatures and solar radiation is the most threatening abiotic constraint to survival and productivity of crops (Chaves *et al*. 2003). The realised yields under drought stress will only be 20-30% of the genetic potential of improved varieties (Wortmann *et al*. 1998).

Sub-Saharan Africa is likely to face more frequent drought episodes due to the predicted climate changes (IPPC 2007). The future challenges of bean production in Africa will therefore be related to lower rainfall and high temperatures (Sivakumar *et al.* 2005). The widespread and devastating effects of drought are already felt by smallholder farmers in common bean growing areas. During the last decade, yield losses of over 300 000 MT of beans have been experienced annually in Africa due to drought (Amede *et al.* 2004). Due to a lack of social protection from governments, smallholder farmers in developing

countries end up selling their livestock and other valuable assets to meet their daily food requirements and other basic needs (Ceccarelli *et al.* 1991).

Drought is complex and there are as many possible definitions as there are users of water (Blum 2011). In this study, drought is defined as the shortage of available water, which includes rainfall and stored soil moisture in quantity during the reproductive and maturity phases of common bean. Water deficit restricts the expression of the full genetic yield potential of crops. The major cause of water deficit in bean growing areas in Africa is low and unevenly distributed rainfall (Lunze *et al.* 2011).

Drought management through supplementary irrigation has been an option to increase realisable yields but few smallholder bean growers have access to irrigation water and equipment due to the prohibitive initial costs and monthly charges. Moreover, water reservoirs like dams, rivers and even boreholes are often insufficient for use by humans, livestock and for irrigating crops. The development of drought adapted common bean varieties is a practical and economic approach to minimise crop failure and improve food and nutrition security in bean growing areas (Rao 2001; Beebe *et al.* 2008). This seed based technology is easier and cheaper to transfer to farmers than more complex knowledge based agronomic practices. However, yield gaps between realised yield and potential yield need to be addressed to improve and sustain bean yields in smallholder systems (Lunze *et al.* 2011).

In other crops, mostly cereals, productivity under water stress has been enhanced through constant innovations such as molecular breeding (Cattivelli *et al.* 2008; Ribaut *et al.* 2010). However, molecular breeding interventions have not been well developed in common bean, especially for abiotic stresses. Though progress has been made through conventional breeding based on selecting high yielding genotypes under drought, it has been slow and difficult and often affected by high error variance, significant interactions of genotype by environment (GxE), quantitative trait loci (QTL)-by-environment (QTLxE), low heritability and epistatic interaction among genes (Zondervan and Cardon 2004). Yu and Buckler (2006) suggested genetic mapping and molecular characterisation

of functional loci as useful tools to facilitate genome aided breeding for crop improvement, and targeting complex traits such as drought tolerance.

Genome wide association mapping is an attractive and good starting point in dissecting complex traits such as drought tolerance in common bean. This method utilises a mapping population which represents diversity in all basic collections and does not require prior knowledge on loci controlling the trait and speeds up QTL fine mapping which can be corrected for, based on population structure. It offers an opportunity to simultaneously look at highly heritable traits that can be correlated with high yield under drought conditions (Yu and Buckler 2006).

The objectives of this study were to:

- Identify sources of drought tolerance from the reference collection held at the International Centre for Tropical Agriculture (CIAT) for use in future bean breeding programmes and/or as finished products.
- Improve genetic and physiological understanding of drought tolerance in different gene pools of common bean through the genetic and physiological characterisation of the CIAT reference collection and a subset of this collection and other parental genotypes commonly used in breeding programmes.
- Establish the role of deep rooting, root length and root biomass distribution as well as mean root diameter and root density in improving grain yield under terminal drought environments in a selected few Andean and Mesoamerican genotypes from the reference collection.
- Determine the genetic structure and diversity in a reference collection of common bean using simple sequence repeat (SSR) marker data.
- Identify simply inherited markers in close proximity to genes affecting drought tolerance. Marker associations can involve discovery of candidate genes if linkage disequilibrium is at a short distance.

References

Amede T, Kimani P, Ronno W, Lunze L, Mbikay N. 2004. Coping with Drought: Strategies to Improve Genetic Adaptation of Common bean to Drought-Prone Regions of Africa. CIAT Ocasional Publication Series no. 38. Cali, Colombia. pp. 3-26.

Beebe SE, Rao IM, Blair M, Acosta-Gallegos JA. 2010. Phenotyping common beans for adaptation to drought. In: Ribaut JM, Monneveux P (Eds.) Drought Phenotyping in Crops: From Theory to Practice. Generation Challenge Program Special Issue on Phenotyping. pp. 311-334.

Beebe SE, Rao IM, Cajiao C, Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. Crop Science 48:582-592.

Beebe S, Renjifo J, Gait'an-Solis E, Duque MC, Tohme J. 2001. Diversity and origin of Andean landraces of common bean. Crop Science 41:854-862.

Beebe S, Skroch PW, Tohme J, Duque MC, Pedraza F, Nienhuis J. 2000. Structure of genetic diversity among common bean landraces of Middle American origin based on correspondence analysis of RAPD. Crop Science 40:264-273.

Blair MW, Fregene MA, Beebe SE, Ceballos H. 2007. Marker assisted selection in common beans and cassava. In: Guimaraes E, Ruane J, Scherf B, Sonnino A, Dargie J (Eds.) Marker Assisted Selection. Current Status and Future Perspectives in Crops, Livestock, Forestry and Fish. FAO Rome. pp. 81-116.

Blair MW, Giraldo MC, Buendia HF, Tovar E, Duque MC, Beebe SE. 2006. Microsatellite marker diversity in common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 113:100-109.

Blum A. 2011. Drought resistance and its improvement. In: Plant Breeding for Water-limited Environments. Springer New York, Dordrecht Heidelberg, London. pp. 53-152.

Broughton WJ, Hernandez G, Blair M, Beebe S, Gepts P, Vanderleyden J. 2003. Beans (*Phaseolus* spp); model food legumes. Developmental Plant Soil Science 99:55-128.

Cattivelli L, Rizza F, Badeck F, Mazzucotelli E, Mastrangelo AM, Francia E, Maré C, Tondelli A, Stanca AM. 2008. Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. Field Crops Research 105:1-14.

Ceccarelli S, Acevedo E, Grando S. 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits and architecture of genotypes. Euphytica 56:169-185.

Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought-from genes to the whole plant. Functional Plant Biology 30:239-264.

Diaz LM, Blair MW. 2006. Race structure within the Mesoamerican gene pool of common bean (*Phaseolus vulgaris* L.) as determined by microsatellite markers. Theoretical and Applied Genetics 114:143-154.

FAOSTAT. 2008. FAO statistical databases. Available at http:faostat.fao.org/ (accessed 19 January 2009) FAO, Rome.

Gentry HS. 1969. Origin of common bean. *Phaseolus vulgaris*. Economic Botany 23:55-69.

Gepts P, Osborn T, Rashka K, Bliss F. 1986. Phaseolin-protein variability in wild forms and landraces of common bean (*Phaseolus vulgaris*): Evidence for multiple centers of domestication. Economic Botany 40:451-468.

Graham PH, Vance CP. 2003. Legumes. Importance and constraints to greater use. Plant Physiology 131:872-877.

IPCC. 2007. http://www.ipcc-data org. (accessed 17 September 2009).

Katungi E, Farrow A, Mutuoki T, Gebeyehu S, Karanja D, Alamayehu F, Sperling L, Beebe S, Rubyogo J.C, Buruchara R. 2010. Improving common bean productivity: An Analysis of socioeconomic factors in Ethiopia and Eastern Kenya. Baseline Report Tropical legumes II. Centro Internacional de Agricultura Tropical – CIAT. Cali, Colombia.

Lunze L, Buruchara R, Ugen MA, Nabahungu L, Rachier GO, Ngongo M, Rao I, Abang MM. 2011. Integrated soil fertility management in bean-based cropping systems of Eastern, Central and Southern Africa. In: Whalen J (Ed.) Soil Fertility. INTECH Open Access Publisher, Rijeka, Croatia. pp. 315-318.

McClean P, Gepts P, Kami J. 2004. Genomics and genetic diversity in common bean. In: Wilson RF, Stalker HT, Brummer EC (Eds.) Legume Crops Genomics. AOCS Press, Champaign, Illinois. pp. 60-82.

Rao IM. 2001. Role of physiology in improving crop adaptation to abiotic stresses in tropics. The case of common bean and tropical forages. In: Pessaraki M (Eds.) Handbook of Plant and Crop Physiology. Marcel Dekker, New York, USA. pp. 583-613.

Ribaut J-M, de Vicente CM, Delannay X. 2010. Molecular breeding in developing countries. Challenges and perspectives. Current Opinion in Plant Biology 13:1-6.

Sauer JD. 1993. Historical Geography of Crop Plants: A selected Roster, Boca Raton, USA, CRC Press. pp. 23-31.

Serraj R. 2004. Symbiotic nitrogen fixation: challenges and future prospects for application in tropical agro ecosystems. Oxford and IBH, New Delhi, India. pp. 76-84.

Singh SP. 2001. Broadening the genetic base of common bean cultivars: A review. Crop Science 41:1659-1675.

Singh SP, Gepts P, Debouck D. 1991. Races of common bean (*Phaseolus vulgaris*, Fabaceae). Economic Botany 45:379-396.

Sivakumar MVK, Das HP, Brunini O. 2005. Impacts of present and future climate variability and change on agriculture and forestry in the arid and semi arid tropics. Climate Change 70:31-72.

Wortmann C, Kirkby R, Eledu C, Allen D. 1998. Atlas of common bean production in Africa. CIAT publication no. 297. Cali Colombia. pp. 32-37.

Yu J, Buckler ES. 2006. Genetic association mapping and genome organisation of maize. Current Opinion in Biotechnology 17:155-160.

Zondervan KT, Cardon LR. 2004. The complex interplay among factors that influence allelic association. Nature Review Genetics 5:89-100.

Chapter 2

Literature review

2.1 Common bean

Common bean is a widely cultivated grain legume crop in tropical and sub-tropical areas of the world (FAO statistic 2004). Over 3.5 million hectares are planted under common bean in East, Central and southern Africa (ECSA) each year (PABRA 2008). The crop belongs to the Fabaceae (Leguminosae) family and is widely adapted to a wide range of environments, found around 52^{o}N to 32^{o}S in humid tropics, in the semi-arid tropics and even in the cold climatic regions (Islam *et al.* 2002). Common bean is a short day tropical legume species which requires between 200-400 mm of soil moisture to complete its life cycle, depending on soil, climate and cultivar (Allen *et al*. 2000). Optimum crop production requires temperatures of between 21-24^{o}C during the growing season and soil pH of between 6.3-6.7.

The preferred common bean types vary in size, colour and shape from region to region. The seed is the most widely used part of common bean. Developing countries from sub-Saharan Africa, Latin America and Asia are the leading producers of common bean grain in the world (Miklas and Singh 2007). In many developing countries common bean is grown by resource poor smallholder farmers on small pieces of land rarely exceeding 1.5 hectares (PABRA 2008). In sub-Saharan Africa female farmers are custodians of this crop. Most of smallholder production is rainfed and under low input agriculture. Often, in smallholder farmers' fields, a multiple of both biotic and abiotic stresses interact simultaneously and have a negative influence on common bean yield.

In sub-Saharan Africa, 73% of common bean production takes place in environments subject to moderate to severe water deficits (Katungi *et al.* 2010). Common bean is sensitive to water deficits (Kavar *et al.* 2008) and yields obtained in sub-Saharan Africa are below the yield potentials of the varieties. Crops experiencing drought are usually more susceptible to weeds, insects and diseases which increase yield losses (Reddy *et al.*

2004). Notably aphid attack and root rots caused by *Macrophomina phaseolina* (Tassi) Goid are more pronounced in common bean under drought conditions.

Production mainly relies on rainfall except in small irrigation schemes found in low lying areas where irrigation is applied to utilise the favourable temperatures after the rainy season (Lunze *et al.* 2011). Common bean is normally planted three to four months before the end of the rainy season in sub-Saharan Africa. Common bean is more prone to a multitude of diseases and pests when planted during the start of the season. In addition, common bean will mature during the peak of the rainy season if planted during the start of the rainy season. Harvesting of the crop is impossible when it is raining and the grain is of poor quality due to contamination from pests and diseases. More frequently late plantings subject common bean to terminal drought (Lunze *et al.* 2011).

2.2 Common bean in the human diet and nutrition

Common bean is mainly grown for human consumption and in some countries it is one of the food security crops providing protein, fibre and income to more than 100 million people in Africa (Kimani *et al.* 2001). Common bean is mainly consumed as a mature grain in most parts of the world. Immature seeds, young pods and leaves are also consumed as a vegetable by some communities in sub-Saharan Africa and Latin America.

Common bean is a highly nutritive and relatively low cost protein food. The unit cost of legume protein is 50%, 70% and 75% cheaper in Brazil, Egypt and Rwanda respectively, compared to that of meat (Miklas and Singh 2007). The common bean grain provides an important source of protein (22-25%) in the form of phaseolin, vitamins (foliate) and minerals (calcium, copper, iron, magnesium, manganese and zinc) for human diets, especially in developing countries (Broughton *et al.* 2003). The high protein content complements the carbohydrate rich foods consumed in Africa. In Burundi, Rwanda and Uganda common bean provides 40%, 31% and 15% of the daily intake of total protein, respectively (Buruchara 2007).

Between 25% and 40% of women in sub-Saharan Africa and Latin America suffer from anaemia caused by iron deficiencies (FAO Statistic 2010). Common bean production and consumption can lower the effects of anaemia in these two regions. In addition, common bean is also a folk medicine in developed countries where it is used to lower cholesterol levels, and minimises incidences of cancer risks (Myers 2000), diabetes as well as heart diseases (Hangen and Bennink 2003) in humans. Common bean is therefore part of the diet of diabetic patients (Jenkins *et al.* 2003).

Apart from being an important protein source in sub-Saharan Africa, common bean is also ranked third after maize and cassava in supplying carbohydrates (Wortmann *et al.* 1998). The seed contains both carbohydrates (60%) and dietary fibre (Broughton *et al.* 2003). The timing of common bean's contribution to the diet is important. Their short growth cycle ensures that smallholder farmers also have leaves, green pods and mature grain as food during critical times of food shortages, especially before the maturity of cereal crops.

2.3 Common bean in cropping systems

Common bean fits in a wide range of cropping systems where the crop can be grown as a monocrop, intercrop with cereals or other crop species and as a relay crop. In East and Central Africa, 23% of the production area is monocropped and 77% under associations with different crops (Katungi *et al.* 2010). Monocropping is dominant in southern Africa with only 47% of the production area assigned to intercropping with other crops (Kimani *et al.* 2001; Katungi *et al.* 2010). Common bean has been widely used in rotations with cereals and other crops worldwide. In this cropping system, common bean has the capacity to break disease and pest cycles usually associated with cereals. This is more cost effective by minimising the use of chemicals and pesticides, thereby reducing pollution of the environment (Lunze *et al.* 2011).

Intercropping is a common practice in sub-Saharan Africa and provides the opportunity for farmers to maximise the returns from their pieces of land in a single season. Relay cropping furthermore ensures that there is maximum utilisation of land and

diversification of agriculture at smallholder farm level. The ability to fix atmospheric nitrogen (N) for subsequent crops has made common bean a valuable crop in many smallholder cropping systems. Improved sorghum yields of between 40-57% were reported in East Africa when sorghum was in rotation with climbing beans (Wortman 2001). The source of N for the sorghum was from atmospheric N fixed in the soil by beans. Lunze and Ngongo (2011) found that climbing beans have the capacity to fix between 16-42 kg ha^{-1} of atmospheric N per season and this could even be increased with good agronomic and cultural practices. In general, climbing beans have been reported to increase cereal yields by 25-40% in the eastern region of Central Africa (Lunze *et al.* 2011). In this region farmers have no capacity to purchase inorganic fertilisers, neither do they have enough animals to supply organic fertiliser in the form of manure. As a result, common bean acts as a source of N supply to primary cereal crops. Hence common bean is important in improving soil health and maintaining soil fertility.

2.4 Common bean as an income generating crop

Total world production for common bean is not well captured in Africa due to confusion with other legumes in some data and lack of capacity by government and developmental partners to make assessment in some countries (Beebe *et al.,* 2013). Statistics provided (FAO statistic 2010) give a worldwide insight into the economic and societal importance of common bean. In 2010 alone, 18.7 million MT of grain were produced from 27.7 million hectares in 148 countries. In sub-Saharan Africa, production is mainly for household consumption with only a third of the output sold on open markets (CIAT 2008; FAO Statistics 2010; Katungi *et al.* 2010). A large volume of common bean is also traded through the informal markets between neighbouring countries, in city markets and among smallholder farmers. Millions of US dollars are generated through formal and informal trading and has improved lives of many farmers, traders and consumers. In Ethiopia, common bean contribute 9.5% of the total export value from agriculture and is ranked third among the agricultural export commodities (FAO Statistics 2010). Common bean fetches a higher price than that of many cereal crops in both formal and informal markets making it a lucrative crop to grow in many smallholder farming communities (CIAT 2008; Katungi *et al.* 2010).

2.5 Drought and its effects on common bean

Drought, by definition, is the shortage of available water, which includes rainfall and stored soil moisture in quantity and distribution during the crop's life cycle (Amede *et al.* 2004; Blum 2011). Drought is the most devastating abiotic constraint with far reaching effects. Due to drought, people become poor by selling off their assets and some even starve to death. The FAO statistics (2004) indicate that drought was the greatest cause of food relief emergencies between 2003 and 2004, surpassing conflicts, flooding and economic problems.

Worldwide, losses due to drought amount to hundreds of millions US dollars annually due to a reduction in crop productivity and crop failure. Annual yield losses of up to 71 000; 119 800 and 100 400 metric tons (MT) were recorded in common bean by Wortman *et al.* (1998) that were associated with early, mid- and late season drought, respectively, in Central and southern Africa.

Drought also negatively affects the symbiotic interaction of common bean roots with specific soil borne bacteria, the rhizobia, which allow plants to fix atmospheric N (Dita *et al.* 2006). This leads to a reduced supply of N for protein production which is the critical seed product of the plant and consequently lowers crop yields (Purcell and King 1996). Little to no N will be fixed in the soil when severe drought conditions prevail during the common bean growth cycle (Dita *et al.* 2006).

Drought is often accompanied by high temperatures and with aluminium toxicity in acid soils (Butare *et al.* 2011). Under these conditions, aluminium toxicity reduces root elongation and limits the capture and use of water and nutrients by crops, hence amplifying the effects of drought. In Africa, 73% of common bean is produced in environments prone to drought (Buruchara 2007). Recent climatic models predict that global climate change will leave a large portion of the world's agricultural lands more prone to drought (Pan *et al.* 2002; Beebe *et al.* 2011). As rainfall becomes more limiting for agricultural productivity, the enhancement of drought tolerance in crops becomes a novel approach.

Drought occurrence, its duration and magnitude during the crop life cycle vary from place to place and from time to time (Amede *et al.* 2004). Drought can occur throughout the life cycle of the crop or at any stage of crop growth and development. Severe effects occur when drought sets in during early plant establishment, vegetative expansion, flowering and grain filling stages (Rao 2001). Three distinct categories of drought were defined by Ludlow and Muchow (1990) as early season, intermittent and terminal depending on where it occurs during crop development.

2.5.1 Early season drought

Early season drought might occur due to the delayed onset of rain that signals the beginning of the planting season. This has a negative effect on yield because crops might complete their growth cycles in another season which might not be conducive for normal growth of the crop. Another situation for early season drought is that rain does come but is inadequate for seed germination or might only be enough for seed germination and crop establishment but inadequate for seedling growth and development. Early season drought causes poor seed germination and poor plant stand in the field. Seedling elongation and expansion growth are affected (Shao *et al.* 2008). In two other grain legumes, soybean (Specht *et al.* 2001) and cowpea (Manivannan *et al.* 2007), stem length was reduced under early season drought. As expected, yield obtained after early season drought is lower than when soil moisture is adequate for plant growth. In the worst case scenario all planted seed rot in the soil and no germination occurs. Farmers are forced to replant when adequate moisture is available. This is a waste of resources which are already scarce for smallholder farmers who normally depend on rainfed agriculture (Amede *et al.* 2004).

2.5.2 Intermittent drought

Intermittent drought is a result of climatic patterns of sporadic rainfall that causes intervals of drought at varying intensities during the vegetative phases of crop growth. Depending on intensity and frequency of occurrence, crops become stunted in growth and the leaf area development becomes reduced. Leaf senescence and leaf drop are also common. Legume crops such as common bean and cowpea become prone to aphid attack

when subjected to intermittent drought. These pests suck plant sap from the stems and leaves and in the process reduce photosynthesis. Diseases such as root rots use this dry spell to infect the roots and impair water and nutrient extraction from the soil. The nature of this drought is unpredictable and also lowers crop yields. Intermittent drought has been frequently reported in common bean production areas of East and Central Africa (Amede *et al.* 2004; Blair *et al.* 2010).

2.5.3 Terminal drought

Terminal drought occurs when the crop encounters moisture stress during the reproductive stages due to an early ceasing of rains during the rainy season. In lowland tropical environments terminal drought occurs when crops are planted at the beginning of a dry season. Crops rely mainly on stored soil moisture for growth during the critical flowering and pod filling periods. This type of drought is more critical in common bean since the crop is planted late. Terminal drought is becoming more frequent due to reduction in the duration of the rainy season, especially in common bean producing areas of southern Africa (Beebe *et al.* 2011).

Drought occurring two weeks before flowering, at flowering and at reproductive phases are considered to have devastating effects on common bean yield (Lizzana *et al.* 2006). Drought for longer than 12 days during flowering and grain filling stages was the most damaging in reducing seed yield of common bean (Webber *et al.* 2006). Flower and pod abortions as well as leaf senescence are major phenomena observed when common bean is under terminal drought stress. The number of pods per plant has been singled out as the most important yield component that is mainly affected by drought stress during flowering in grain legumes and can reduce final grain yield up to 70% depending on the duration and intensity of the stress period (Amede *et al.* 2004).

Drought tolerance is a complex trait since it is measured in terms of crop yield. Yield is influenced by many traits and genes (Porch *et al*. 2009). In this sense, a multitude of physiological and biochemical processes take place within plant cells to alleviate the effects of drought (Blum 1988). Genes and traits interact to determine the overall crop

response to the variable nature of the drought (Ceccarelli *et al.* 1991) and hence call for the understanding of the genetic, physiological and morphological mechanisms employed by plants to withstand drought. Understanding mechanisms of drought tolerance forms the basis of developing drought tolerant crop varieties (Zhao *et al.* 2008).

2.6 Molecular response to drought stress

There are multiple primary sensors that sense the initial stress signal and alter the expression of a large number of genes. Water stress activates a large array of genes that enhance drought tolerance. These genes produce two broadly classified gene products. The first group is comprised of gene products that directly protect cells against stress. These include chaperons, LEA (late embryogenesis abundant) proteins, osmoprotectants, detoxifying enzymes, free radical scavengers and various proteases (Reddy *et al.* 2004). Osmoprotectants are responsible for maintaining the turgor pressure of plant cells. Detoxification enzymes such as catalase, superioxide dismutase and hydrolase enable cellular, physiological and biochemical metabolism to occur without disruptions. Lipid peroxidation was high in leaves of 14-day old common bean plants subjected to drought and an increased activity of catalase and superoxide-dismutase to neutralise the harmful effects of peroxides was observed only in tolerant genotypes (Zlatev *et al.* 2006; Nemeskéri *et al.* 2010). Other proteins such as osmotin and chaperons function in the protection of macromolecules from disintegration in plant cells (Nemeskéri *et al.* 2010).

The second group of gene products includes transcription factors, secondary messengers, phosphatases and kinases which regulate the function of other genes in response to water deficit. Examples of transcription factors include dehydration responsive element binding protein (DREB), protein kinases and proteinases (Agarwal *et al.* 2006). DREB proteins are considered important transcription factors that induce a set of drought stress related genes and impart stress tolerance to plants. DREB genes have been identified in common bean but their importance to drought tolerance needs to be demonstrated (Galindo *et al.* 2003). Once the DREB genes are found to determine drought resistance functions in common bean, then gene-based marker-assisted selection (MAS) might be feasible

(Ishitani *et al.* 2004). Products of gene expression cause a number of changes in the physiological and metabolic processes of plants when stressed by drought.

2.7 Drought tolerance mechanisms

Plants have developed a number of physiological and metabolic strategies to proof themselves against drought stress. Broadly, these strategies may be classified into three groups namely drought escape, drought avoidance and drought tolerance. Drought tolerance is an important trait in common bean production considering a reduction in rainfall, expansion of production areas and increasing input costs such as irrigation. Incorporation of one or all of the drought tolerance mechanisms into cultivated varieties to stabilise yield under drought conditions need to be considered. In common bean, seed yield is widely used as a selection tool for drought tolerance (Beebe *et al.* 2008).

2.7.1 Drought escape

Drought escape is defined as the ability of a plant to complete its life cycle before severe soil and plant water deficits occur (Amede *et al.* 2004). The mechanism involves early flowering and maturity. Drought escape is desirable and has proven to be useful in legume crops. Over the last few decades, breeding programmes in both cereals and legumes worldwide have been breeding for earliness as a way of minimising crop losses to terminal drought stress (Lunze *et al.* 2011). Nleya *et al.* (2001) cited early maturity as one of the components of terminal drought avoidance in common bean. However, early maturity is associated with low yield. Drought shortens the grain filling period resulting in smaller seed and low yields. The seed filling duration is under genetic control and is sensitive to water deficit (Rao 2001).

The earliness trait in common bean has several benefits in sub-Saharan Africa where the crop can provide the first food and first marketable product before harvesting of cereal crops. In addition to escaping drought, early maturing genotypes also escape diseases and pests which are associated with terminal drought (Butare *et al.* 2011). Araus *et al.* (2002) noted that breeding for early flowering and maturity has made the most important contribution to drought tolerance.

2.7.2 Drought avoidance

Plants adjust their metabolic and physiological processes once they sense drought, in order to adapt to the changing environment. Dehydration avoidance and dehydration tolerance are two main mechanisms used by plants for survival under drought stress. These mechanisms ensure that the plant maintains higher water status during periods of drought stress, either by efficient water absorption from roots or by reducing transpiration from aerial parts (Levitt 1980). Transpiration causes dehydration in plant cells. In response to drought stress, plants change their leaf anatomy and morphology to minimise water loss. In addition, stomata are also closed to minimise water loss.

2.7.2.1 Transpirational control under drought stress

In order to minimise water loss through transpiration notable changes in leaf anatomy and morphology occur. Leaf rolling occurs in common bean and other plant species as a way of reducing absorption of radiation by the leaf. The leaf surface or area becomes reduced and leaves close their stomata (Nemeskéri *et al.* 2010). Transpiration through the epidermis or cuticles of leaves is also lowered under water stress conditions.

2.7.2.2 Stomatal conductance

Plants close their stomata in response to water deficits as a way of preventing water loss through transpiration. The closing of stomata under drought stress conditions is largely under hormonal influence. Stomatal closure is regulated by absiscic acid (ABA), a hormone produced in the roots. Drought stress promotes the accumulation of ABA in the leaf and xylem vessels which promotes the efflux of potassium (K+) ions from the guard cells (Liu *et al.* 2003). This results in the loss of turgor pressure of leaf cells leading to stomatal closure. Drought tolerance in common bean was achieved by maintenance of high leaf water potential (Amede and Schubert 2003; Santos *et al.* 2009). The high leaf water potential was a result of stomatal regulation and higher root length density and weight.

Other studies in *P. vulgaris* showed that tolerant cultivars tend to exhibit a faster stomatal closure in response to decreasing soil water potential than susceptible cultivars (Lizzana

et al. 2006). Stomata regulation was also demonstrated in other experiments in *P. vulgaris* where tolerant genotypes exhibited higher rates of stomatal conductance in the morning, but lower rates at midday and during the afternoon (Pimentel *et al.* 1999). Stomatal conductance has potential as a surrogate physiological trait for selecting drought tolerant common bean genotypes considering the non-destructive nature of the measurement and availability of precise instruments for the measurement of the trait. Stomatal conductance is directly measured from leaves with a porometer. However, the porometer is slow in taking measurements and could result in biased estimates if a large trial is under consideration. Leaf temperature or canopy temperature depression can be used to indirectly measure stomatal conductance. A linear relationship has been found between canopy temperature depression, leaf temperature and stomatal conductance in faba bean (Khan *et al.* 2007).

2.7.2.3 Cuticular transpiration

Cuticular transpiration also contributes to the total leaf conductance to water vapour. However, under optimal conditions when stomata are open, cuticular conductance generally contributes a negligible fraction of total conductance. Cuticular transpiration becomes important under water stressed environments when the stomata close. In water stressed environments, the cuticular component of leaf epidermal conductance may exceed the stomatal conductance (Boyer *et al.* 1997). Hence, selection for lower epidermal conductance could allow improved survival of leaves under drought stress. Lower epidermal conductance is a desirable trait for drought tolerance (Hufstetler *et al.* 2007).

2.7.2.4 Reduced leaf growth and leaf drop

The ABA produced during drought stress restricts shoot growth and leaf expansion. Reduced leaf expansion and leaf rolling characteristics are beneficial under water stress as less leaf area is exposed to the sun, resulting in reduced transpiration. In many plants, including common bean, accelerated senescence of leaves and abscission of older leaves is also part of reducing the leaf area exposed to transpiration, particularly under terminal drought stress. Tardieu (1996) suggested that the senescing and abscission of leaves

under drought stress allows an organised translocation of resources to the developing seeds.

2.7.2.5 Leaf pubescence

Leaf pubescence increases irradiation reflectance from the leaf, resulting in lower leaf temperatures under high irradiance. In common bean, leaf pubescence decreased water loss by evaporation and enhanced transpiration resistance (Nemeskéri *et al.* 2012). Similar observations were made in soybean were dense pubescence reduced leaf temperature, restricted transpirational water loss and enhanced photosynthesis (Manavalan *et al.* 2009). This was due to lower radiation penetration into the canopy. Large white hairs in sunflower or the development of a wax bloom in sorghum can decrease leaf temperature and transpiration.

2.7.2.6 Leaf movement and orientation

Leaf rolling and paraheliotrophy, defined as the movement of leaves to align themselves parallel to incident light, decrease the irradiation load on the crop canopy. This helps in reducing leaf temperature and subsequent water loss. Common bean showed leaf movement as a way of avoiding incident light under drought conditions (Wentworth *et al.* 2006). Common bean leaves were capable of making a 90^0 rotation with respect to their original position depending on the duration of the water stress (Lizzana *et al.* 2006).

2.7.2.7 Water extraction under drought stress

One of the important components of the dehydration avoidance mechanism is the capability of roots to acquire water from deep soil layers (Passioura 1977; Amede *et al.* 2004). In common bean, a deep root system which helps reach the lower soil layers where water is available has been advocated (Sponchiado *et al.* 1989; Nemeskéri *et al.* 2010). An extensive fibrous root system can also be useful in common bean for foraging sub-soil surface moisture and nutrients such as phosphorus (Beebe *et al.* 2008; Manavalan *et al.* 2009). These nutrients also help to maintain good plant health. Root tips sense the moisture in soil and direct their tissues in the direction of moisture. Root length, diameter and mass as well as the ability of roots to penetrate compacted soil layers

become important under drought stress (Amede *et al.* 2004; Ho *et al.* 2005; Vallijodan and Nguyen 2006). The rooting ability is important for crops growing under terminal drought conditions.

Studies by Sponchiado *et al.* (1989) showed a significant correlation of deep rooting with shoot growth and seed yield in common bean. Rao (2001) also found deep rooting an important trait for drought avoidance in Mesoamerican common bean. The high yielding ability of a CIAT bred Mesoamerican genotype, BAT477, under drought conditions was attributed to deep rooting (White and Castillo 1992) as well as larger water absorption efficiency. Roots were also proven to be beneficial for yield under terminal drought stress in chickpea (Kashiwagi *et al.* 2004). Drought stressed soybean showed an increase in root length in the subsoil compared to irrigated plants (Manavalan *et al.* 2009). However, there exists a need to better understand how root traits contribute to drought tolerance.

Improving plant characteristics that are responsible for water extraction from the soil and minimising water loss through the leaves offer promising avenues of improving drought resistance in crops (Serraj and Sinclair 2002). These traits are considered to be the major traits of interest to expand production of common bean to presently uncropped areas and post-rainy fallows in Africa.

2.7.2.8 Osmotic adjustment

The synthesis of osmoprotectants and osmolytes is one mechanism that has been used by drought tolerant plants to adapt to drought stress. During this process plants accumulate solutes that help cells maintain their hydrated states and therefore function to provide tolerance against drought. The osmoprotectants include amino acids (proline and citrulline), onium compounds (glycine betaine), monosaccharide (fructose) and sugar alcohols (mannitol and pinitol). These molecules are broken down in plant cells once drought is over (Serraj and Sinclair 2002).

Osmotic adjustment (OA) has been shown to make a small to no contribution to drought tolerance in common bean (Amede and Schubert 2003). In their study, solute

accumulation was a direct effect of water loss and growth inhibition. Serraj and Sinclair (2002) also noted that OA has little value in increasing crop yield under drought stress but is crucial for plant survival. The removal of water from the cell membrane disrupts the normal bilayer structure and results in the cell membrane becoming porous and non-selective. The osmoprotectants prevent interaction between harmful ions and cellular components by replacing water around these compounds, thereby protecting against destabilisation during water stress. The hydroxyl (OH^-) group of alcohols substitutes OH^- groups of water to maintain the hydrophilic interactions with membrane lipids and proteins (Serraj and Sinclair 2002).

Drought stress within the lipid bilayer may also result in displacement of membrane proteins and contributes to loss of membrane integrity, disruption of cellular compartmentalisation and loss of activity of enzymes which are membrane based. The osmoprotectants are highly soluble in water and act as a substitute for water molecules during the period of drought stress. The hydrophilicity of osmoprotectants helps maintain turgor pressure and water content of cells and protect against water loss from leaves under drought stress (Amede and Schubert 2003).

2.7.2.9 Water use efficiency

Water use efficiency (WUE) is another important trait for attaining high yield in crops grown under terminal drought conditions (Passioura 1977). WUE contributes towards drought avoidance in plants. The little water extracted from the soil is used efficiently towards high yield (Ravi *et al.* 2011). WUE explains the relationship between a plants' assimilate production rate and the rate at which it loses water to the atmosphere. In cropping systems, improving WUE assures increased crop productivity under limited soil moisture (Richards *et al.* 2002). WUE has been measured in four different ways. These include photosynthetic water use efficiency (PWUE), transpiration efficiency of carbon (C) gain (TE_C), transpiration efficiency of N gain (TE_N) and transpiration ratio (TR).

PWUE compares the exchange of carbon dioxide and water vapour between photosynthesising leaves and the immediate environment. TE_C describes the WUE in

relation to C accumulation as dry matter compared to transpired water. TE_N defines the WUE in relation to N accumulation in dry matter compared to transpired water. The water loss could be measured in days, weeks or months. The TR describes the relationship between the transpired water and synthesis of a given amount of dry matter. Transpiration efficiency (TE) is one of the popularly used methods of measuring WUE in plants. TE has been estimated through proxy traits such as the SPAD chlorophyll meter reading, specific leaf area and carbon isotope discrimination ratio ($\delta^{13}C$) (Ravi *et al.* 2011). A better understanding of this trait will result in the ability to produce plants that are able to remain productive, even under limited water supplies.

2.8 Seed yield

Seed yield acts as the main criterion for selection of drought tolerant varieties in common bean. A comparison of crop yield in stressed and irrigated fields have been applied to quantify the stress response to identify tolerant genotypes. The statistical tools to estimate tolerance for these two treatments vary widely including geometric means (Singh 1995), percentage loss in grain yield (Beebe *et al.* 1997) and deviation from regression of stressed yields on unstressed yields (Ramírez-Vallejo and Kelly 1998). Many breeding programmes target a high yield potential under drought stress.

Drought experienced during early reproductive growth reduces yield, through reduced number of pods and seeds per hectare (Manavalan *et al.* 2009). ABA can move to reproductive structures causing pod abortion via inhibition of cell division in young ovaries (Liu *et al.* 2003). Drought experienced during seed filling could affect the seed growth rate by reducing photosynthesis and therefore the supply of assimilate available to the seed, ultimately affecting seed size.

Using seed yield in selecting drought tolerant genotypes is easy, however, seed yield is severely affected by GxE interactions and environments. The heritability for seed yield has been reported to be low under drought conditions (Beebe *et al.* 2008). Yield components and other traits such as WUE, transpiration and harvest index that are highly correlated to seed yield under drought could be used as yield proxy traits. Drought affects

yield proxy traits in an antagonistic manner resulting in negative correlations between these traits. Consequently, their wider application in selecting superior genotypes under drought stress is limited because of these negative correlations (Beebe *et al.* 2008).

2.9 Dehydration tolerance

Dehydration tolerance is the ability of a plant to maintain plant function in a dehydrated state (Blum 2005). 'Resurrection' plants employ this tolerance mechanism and other plants become dormant to avoid drought stress. Stem reserves have been found to support a high yield under drought stress (Plaut *et al.* 2004; Blum 2005). Stem reserve utilisation permits filling of grains even when photosynthesis is inhibited by drought stress during the reproductive cycle of the plant. Photosynthates stored in stems are converted into soluble sugars and transported into the grains during drought stress (Blum 2005).

In common bean, a higher mobilisation of assimilates from both leaves and stems to the grain have been an important trait contributing to high yields under water stress conditions in Mesoamerican beans. Race Mesoamerica line G21212 produces high yields under water stress conditions due to its ability to mobilise a higher amount of photosythates to the seed (Rao 2001). Remobilisation of assimilates to the head supported a high yield in sunflower grown under drought environments (Manavalan *et al.* 2009).

The major condition required for a higher mobilisation of assimilates to grains during drought stress is that the plant establishes a huge aerial biomass before the grain filling stage. Improved growth rates before flowering cause an increase in stem biomass which acts as carbohydrate reserve for future use (Shearman *et al.* 2005). A high plant biomass under water limited conditions is a desirable character. However, drought reduces plant fresh and dry weights (Farooq *et al.* 2009). Drought reduced plant biomass in soybean (Specht *et al.* 2001) and common bean (Wu *et al.* 2008). A high yield under water stressed environments is a function of aerial biomass accumulation and partitioning of assimilates to grains (Kage *et al.* 2004). However, Blum (2005) defines this type of tolerance as a rarely effective drought resistance mechanism since it is found in the embryo of the seed and vanishes as soon as the plant germinates.

2.10 Drought tolerance in common bean

Breeding for drought tolerance in common bean has a long history in CIAT and some national programmes in Latin America (Beebe *et al.* 2009). Hybridisation of germplasm of the Durango race adapted to the dry highlands in Mexico with the small seeded germplasm types of the Mesoamerican race from lowland Central America has been done to improve drought tolerance in common bean (Beebe *et al.* 2009). SER21, SEA5 and SEN21 breeding lines are products between Durango and Mesoamerica inter-racial crosses that were found to have drought tolerance in Africa, Colombia and Puerto Rico (CIAT 2004, Porch *et al.* 2009). SEA5 was also found to possess deep roots which could aid its good performance under drought conditions (CIAT 2004). The recurrent selection method was followed in developing drought tolerant lines. Improved drought resistance in interracial crosses combining Durango and Mesoamerican races were also reported by Schneider *et al.* (1997). In Mexico, native Durango germplasm always give high yields under drought (Beebe *et al.* 2009). Deep rooting, stem reserve remobilisation (Rao 2001), early maturity (Nleya *et al.* 2001) and pod harvest index (Beebe *et al.* 2009) are considered useful traits in improving drought tolerance in common bean.

2.11 Reference collection of common bean

More than 29 000 domesticated and 13 000 wild accessions of common bean are kept at CIAT in Cali, Colombia (Broughton *et al.* 2003). These were collected from the primary, secondary and tertiary centres of common bean domestication. Landraces are still the backbone of agricultural systems in unfavourable environments (Laurentin 2008) and contain a high level of readily usable genetic variation. The value of landraces as sources of drought tolerance has been reported in barley (Pswarayi *et al.* 2008). However, despite the availability of a large amount of germplasm, only a limited number of these accessions have been used in crop improvement programmes. Large accession sizes are difficult to manage and evaluate during field trials (Glaszmann *et al.* 2010).

Brown (1989a; b) proposed the use of core collections as a strategy to evaluate large accession sizes, to promote use of germplasm and to facilitate the study of the genetic diversity in landraces. Core collections are usually 10% of the entire germplasm

collection that represents the collection's variability (Brown 1989b). A reference collection is a sub-set of a core collection and represents the genetic resources of a crop (Glaszmann *et al.* 2010). A reference collection is a manageable and cost effective entry point into germplasm collections for identifying parental genotypes with new sources of stress tolerance.

A common bean core collection has been compiled at CIAT and constitutes 1 441 accessions obtained as genetically representative of the total collection (Tohme *et al.* 1995). There are 1 072 accessions on which there is complete information. These are from Mesoamerica, Mexico, Costa Rica, El Salvador, Guatemala, Honduras and Nicaragua. Collections from the Andean countries of Colombia, Ecuador, Peru, Bolivia and Argentina were also included. These countries are considered to be the primary centres of diversity of common bean (Tohme *et al.* 1995). A reference collection in common bean was developed from the CIAT core collection using available information on accessions, including the origin and geographical distribution, characterisation and evaluation data. The reference collection of common bean consists of 202 accessions and maintains a well balanced representation of the Andean and Mesoamerican gene pool.

2.12 Genetic diversity in common bean

Common bean was domesticated in at least two centres of origin (Acosta-Gallegos *et al.* 2007) on the American continent. The two centres of origin are the Mesoamerican and Andean regions of America. These centres of origin are associated with the two known gene pools in common bean namely the Mesoamerican and Andean gene pools. Major differences between gene pools include seed size, phaseolin (seed storage protein) patterns, plant morphology, isozymes and molecular profiles with different molecular marker types. Andean beans are large seeded ($\geq$ 40 g 100 seed weight^{-1}) whilst Mesoamerican beans are small ($\leq$ 25 g 100 seed weight^{-1}) to medium ($\geq 25 \leq 40$ g 100 seed weight^{-1}) sized.

Polymorphisms also exist within each gene pool expressed by huge differences in seed sizes and colours, growth habits and different ecological adaptation within each

domesticated gene pool (Singh *et al.* 1991a; Beebe *et al.* 2000). A group of related landraces which consist of morphologically similar cultivars and that share the same agro-ecological adaptation, constitute a race (Singh *et al.* 1991a; b). This group differs from other races in the allelic frequencies at specific isozyme or microsatellite loci (Singh *et al.* 1991c; Blair *et al.* 2007). Genetic variability is important in developing improved varieties and broadening the genetic base against biotic and abiotic stresses in commercial varieties.

2.12.1. Genetic diversity within the Mesoamerican gene pool

Singh *et al.* (1991a) identified three races namely Durango (D), Jalisco and Mesoamerica (M) in the Mesoamerican pool. Race Durango originated from dryland Mexico, an area receiving 350 mm or less annual rainfall. Race Durango possesses some traits which are highly associated with high yield under drought conditions. These genotypes are early maturing, have a high harvest index, produce high shoot biomass and in general have a high yield potential under drought and low soil fertility conditions. The majority of genotypes from this race have type III indeterminate prostrate or climbing growth habits and S or Sd phaseolin (Díaz and Blair 2006). Indeterminacy promotes high shoot biomass production which is related to high yield. This race has been an important source of useful drought resistance genes in many breeding programmes (Terán and Singh 2002).

Blair *et al.* (2006) found that Durango and Jalisco races always grouped together in the panel and represented the same race using microsatellite markers. This confirmed earlier results from Beebe *et al.* (2000) and McClean *et al.* (2004) who detected no morphological and geographical origin differences between these two races. Races Durango and Jalisco should be classified in one group since additional information suggested they shared a common chloroplast DNA pattern and Mexico as the country of origin (Beebe *et al.* 2013).

Race Mesoamerica is the most popular and widely grown type of common bean. This race is native to the warm lowlands of Central America (Singh *et al.* 1991a) and has the longest history of genetic improvement. Genotypes from this race have relatively small

seeds which are adapted to a range of hot, humid to moderate climates in the tropics and sub-tropics (Díaz and Blair 2006). The predominant phaseolin type is S but Sb and B are also found in this group (Singh *et al*. 1991a). The race is further subdivided into sub-races reflecting plant architecture and seed type (Beebe *et al.* 2000). Sub-race Mesoamerica 1 is mostly composed of small black seeded beans with type II growth habits while sub-race Mesoamerica 2 is composed of diverse seed colour classes (red, white and carioca), most with a prostrate type III growth habit (Beebe *et al*. 2000).

An additional race for the Mesoamerican pool, Guatemala, was determined by Beebe *et al.* (2001) based on AFLP molecular profiling. Race Guatemala (G) comes from Guatemala and the neighbouring Mexican state of Chiapas and contains genotypes mostly with an indeterminate climbing growth habit and small seed size similar to race Mesoamerica (Beebe *et al*. 2000). Race Guatemala was also identified as a distinct group by Blair *et al.* (2006) using SSR markers on the core collection of common bean. This race is now widely regarded as an importance group in common bean genetic resources.

2.12.2 Genetic diversity within the Andean gene pool

Three races exist within the Andean gene pool namely Nueva Granada (NG), Chile (C) and Peru (P) (Singh *et al.* 1991a). Nueva Granada originated in low to medium elevation [650-1850 metres above sea level (masl)] of the northern Andes with a moderately cool climate. Nueva Granada has been further subdivided into two sub-races, namely Nueva Granada 1(NG1) and Nueva Granada 2 (NG2). Race Nueva Granada represents the most widely cultivated Andean race grown at both mid-altitude elevations of the Andes and Africa as well as sub-tropical regions of Brazil, Mexico and the Caribbean as well as temperate climates of North America and Europe (Matthew Blair, personal communication, October 2009). Seed sizes vary from medium to large and most varieties have bush type I or II growth habits.

Race Peru originated from Argentina, Bolivia and Peru but is now also found in Ecuador and Colombia (Matthew Blair, personal communication, October 2009). This group contains climbing beans which are adapted to highlands (> 2000 masl).

Race Chile is an indigenous landrace of Chile, with medium-sized, round to oval seeds with pale colours. Genotypes within this race have prostrate type III growth habits. These are often found at higher latitudes in Turkey, Iran and China (Blair *et al.* 2006).

2.13 Molecular markers in plant breeding programmes

The continuous development and use of DNA-based markers have improved crop breeding efficiency and enhanced world agricultural productivity (Ribaut *et al.* 2010). In Africa, success stories on the use of molecular markers include rice, through the new rice for Africa (NERICA) varieties and maize through quality protein maize (QPM) varieties (Stafford 2009). In common bean, molecular markers are primarily used for genetic mapping and diversity studies and to a lesser extent in gene discovery and marker-assisted selection (MAS) for fungal and bacterial diseases (Blair *et al.* 2010). A molecular marker is an identifiable DNA sequence that is associated with part of the genome and transmitted by the standard laws of Mendelian inheritance from one generation to the other. Various types of DNA markers were developed since the late 1980's and have evolved rapidly with advances in molecular biology science. However, the majority of DNA-based markers have shown growing limitations in chromosomal coverage, time frames, ease of use, information generated and cost effectiveness. Microsatellite or SSR and single nucleotide polymorphism (SNP) analyses have found their niche in plant genetic studies based on their properties.

2.13.1 Simple sequence repeats

'Ever since their discovery in the early 1980's, the ubiquitous occurrence of microsatellites – also referred to as short tandem repeats (STRs) or simple sequence repeats (SSRs) – has puzzled geneticists. Understanding STRs is important if we wish to understand how genomes are organized and why most genomes are filled with sequences other than genes' (Ellegren 2004).

SSRs are tandem repeat units of short nucleotide motifs of two to six base pairs (bp) long and measure size polymorphisms (Powell *et al.* 1996) as well as motif type polymorphisms (Cordoba *et al.* 2010) among individuals. Variances among SSRs exist

depending whether they are composed of one repeat type or the repeat units are interrupted by nucleotides different from those making the core repetitions (Cordoba *et al.* 2010). They are randomly and uniformly spread all over the genome of plants and animals (Varshney *et al.* 2005) ensuring good genome coverage and could be located in introns or exons (Blair *et al.* 2009), though fewer SSR loci are found in exons than introns (Blair *et al.* 2008).

SSRs are inherited in a Mendelian fashion and are multi-allelic polymerase chain reaction-(PCR) based marker types. SSRs usually detect single loci and are specific to a particular position in the genome. The most abundant SSRs in plant species are $(AT)_n$ or $(AG)_n$ repeats. In common bean, the di-nucleotide (AT) motif is more abundant than any other SSR class (Blair *et al.* 2008; Cordoba *et al.* 2010). This group of markers is informative with high polymorphic information contents (PICs), even between closely related lines (Gupta *et al.* 1999). In common bean, SSRs have shown the relatedness of race Durango and Jalisco in race structure studies (Díaz and Blair 2006; Blair *et al.* 2007). These races have previously been grouped as two separate races of the Mesoamerican origin by Singh *et al.* (1991a; b; c). Genetic diversity in common bean landraces from the two gene pools is now better understood through the use of microsatellite markers (Blair *et al.* 2006). A further application of microsatellite markers in common bean has led to the construction of a genome wide, simple sequence framework map based on an inter-genepool cross (Blair *et al.* 2003).

Other merits of microsatellites are that they are co-dominant and accessible to other research laboratories via published primer sequences. Published sequences (Yu *et al.* 1999; Blair *et al.* 2003) and microsatellite enriched libraries for GA or CA repeat containing sequences (Buso *et al.* 2006) have been the major sources of SSR markers widely used in common bean.

However, SSRs are less suitable for association studies because of the occurrence of homoplasy and the possibility of SSRs of different sizes being embedded in identical haplotypes. The mapping resolution would also be reduced, because microsatellites are

multi-allelic and identify chromosomal regions that are too large for identification of the causal locus. In addition, SSR loci are prone to mutations thought to emanate from replication slippages or mistakes in DNA replication repair mechanisms (Ellegren 2004).

2.13.2 Single nucleotide polymorphisms

SNPs represent the smallest unit of genetic variation between individuals and are the most common type of alleles found within and between varieties of a crop species. SNPs are genetically stable with low mutation rates making them suitable for studying complex genetic traits and as a tool for understanding genome evolution (Stephen *et al.* 2005). They are highly available as differences of individual nucleotides between individuals and every SNP in a single copy DNA is a potentially useful marker (Stephen *et al.* 2005).

SNPs may fall in exons, introns or the inter-genic regions. When present in the coding sequences, they may or may not determine the mutant phenotype due to degeneracy of the genetic code but will show 100% association with the trait and will therefore be useful for molecular breeding and gene isolation. Also, SNPs that reside in introns might have a role in transcription and are considered important as well (Zondervan and Cardon 2004).

In diploids, SNPs are bi-allelic and provide exact allele information that can be described in a binary alphanumeric manner according to the nucleotide present (Zondervan and Cardon 2004). This allows direct comparison of data collected across time and in different laboratories and using different assay chemistries and platforms. Their bi-allelism makes them easy to score in high throughput genotyping assays. SNPs assays do not require DNA separation by size and are easier to locate in most single copy regions of the genome than SSRs (Rafalski 2002). Their lower genotyping error rate makes them essential in marker assisted breeding and other plant genetic applications (Rafalski 2002).

Pioneering studies for SNP frequency in common bean showed one SNP in every 88 bp in introns for 10 accessions of cultivated and wild bean (Mesoamerican and Andean) (Gaitan-Solis *et al.* 2008) and one SNP in every 387 bp in an inter gene pool comparison

of G19833 (Andean) and Negro Jamapa (Mesoamerican) (Ramírez *et al.* 2005). In other studies between BAT93 and Jalo EEP558 which are parents of the community mapping population, McConnell *et al.* (2007) detected SNPs for 65% of the genes and a SNP was observed on every 375 nucleotide. Of these SNPs, approximately 42% were in introns, 40.3% in exons and 17.2% in the 3'- untranslated regions (UTR). Therefore, SNPs are more abundant in introns of common bean.

Their abundance in both animal and plant genomes, the reduction in cost of assaying and the increased throughput of SNP assays have made these markers attractive for high resolution fine mapping of QTL and linkage disequilibrium (LD) based association mapping (Slate *et al.* 2009). Association mapping is a recent method used to detect statistical correlations between SNP markers and agronomic traits from a population of individuals with unknown pedigree and relations (Rafalski *et al.* 2010).

2.14 Association mapping as a potential tool in common bean genomics

Association mapping or LD is a powerful technique used in population genetics to analyse statistical correlations between genotypes mostly using individual SNPs or SNP haplotypes determined in a collection of individuals and the phenotypes of the same individuals (Rafalski 2010). Haplotypes are combinations of three or more linked SNP markers on a single chromosome. The power of detecting relationships between phenotypic variation and genetic polymorphisms lies in the LD between alleles of the same chromosome resident in different loci (Zondervan and Cardon 2004; Breseghello and Sorrells 2006). LD is the non-random co-inheritance of alleles at separate loci located on the same chromosome (Mackay and Powell 2007) usually sharing the same history of mutation and recombination.

LD examines the physical size of chromosomal regions on which all pairs of adjacent loci are always inherited together (Stich 2006) and determines the marker density required for association mapping. However, the length and decay of LD varies depending on the mating system of a crop as well as relatedness of genotypes within sub-populations used in the association analysis (Blair *et al.* 2010).

In addition, LD is also non-uniform across the genome and is greatly influenced by the physical locations of alleles along the chromosome (Rafalski 2010). Certain regions of chromosomes have higher LD due to reduced recombination or effects of selection (Flint-Garcia *et al.* 2003). Variability in recombination along the chromosome depends on the chromosomal region since crossover is higher in euchromatin than heterochromatin segments (Lichten and Goldman 1995; Mezard 2006). Crossing over could also be avoided when parts of widely related genomes exist together in a genome and results in a slow decay of chromosomal regions in a genotype (Blair *et al.* 2010).

2.14.1 Linkage disequilibrium in common bean

Not much is available in literature on the extent of LD in common bean (Kwak and Gepts 2009). Initial indirect analysis showed a large extent of LD, which runs over a few centiMorgans (cM) (Papa *et al.* 2007). Population structure has been singled out as the greatest contributor to the observed high levels of LD in common bean (Rossi *et al.* 2009). Race structures present in each gene pool and bottle necks encountered during domestication led to different allele frequencies occurring in a diverse common bean population. Rossi *et al.* (2009) using restriction fragment length polymorphisms (RFLPs) found a higher and slower decaying LD in domesticated Andean than Mesoamerican populations. Similar results were found for the wild Andean versus the wild Mesoamerican beans (Rossi *et al.* 2009). Andean beans were exposed to a significant bottle neck during domestication hence high levels of LD. Intensive selection limits the genetic diversity around a locus and results in an increased LD around selected genes (Rossi *et al.* 2009).

Statistical methods have been developed to avoid spurious associations caused by population structure (Pritchard *et al.* 2002) and a modest number of genetic markers ranging between 50 and 100 have been proposed to evaluate the population structure in subpopulations (Ralfaski 2010). The size of the experimental population can also affect the size of LD and larger germplasm collections provide more power and in practice at least 100 to 500 individuals are needed (Ralfaski 2010).

2.14.2 Advantages of association mapping over traditional linkage mapping

Assembling the experimental population in association mapping is fast since it utilises existing cultivars, lines or landraces and in some cases historical phenotypic data. The nature of the experimental populations in association mapping offers broad genetic variation in a more representative genetic background and one is not, as in the case of linkage mapping, limited to the marker and trait loci that happen to differ between the two parents (Kraakman *et al.* 2006). Linkage analysis can only identify QTL from the phenotypic diversity generated from a controlled cross and often represents only a small fraction of the phenotypically relevant variation in a species. However, association mapping evaluates many alleles or thousands of polymorphisms at all loci simultaneously compared to two alleles at a time in linkage mapping; hence, association mapping facilitates the study of many traits with the same genotypic data (Oraguzie *et al.* 2007; Belo *et al.* 2008). This simultaneous manipulation of several chromosomal regions (QTL) offers great opportunity of increasing the genetic gains in crops in the near future by using marker-assisted breeding in the identification and combining of many QTL in a short period of time (Yu *et al.* 2006; Zhu *et al.* 2008).

A higher resolution might be attained in association mapping because of the use of a thousand of meiosis events accumulated in the breeding history of the lines (Holland 2007). Resolutions of 10-20 cM have been reported in traditional linkage mapping (Holland 2007) primarily because recombination did not have enough time to shuffle the genome into small fragments. Only two cycles of recombination would have occurred in F_2 populations and a few cycles of recombination in the case of recombinant inbred line (RIL) populations. In addition, the precise location of alleles within a very small chromosomal region is impossible with linkage analysis since recombination within such a small region may not be available in an examined finite population (Mackay 2001; Neale and Savolainen 2004). However, association mapping has a bigger chance of finding alleles that are in LD controlling traits of interest. The linked inheritance will only persist for very closely linked polymorphisms.

Despite the numerous advantages of association mapping over linkage analysis, the power of association mapping can be strongly reduced by population structure or the relatedness between individuals (Mezmouk *et al.* 2011). Population structure arises from the unequal distribution of alleles among subpopulations of different ancestries. Construction of an association mapping panel involves sampling genotypes from different subpopulations with different allele frequencies which creates linkage disequilibrium (Soto-Cerda *et al.* 2012). Strong statistical programmes are required to efficiently control panel population structure. Another challenge in association mapping analysis is the inability to detect rare alleles at some loci (Mezmouk *et al.* 2011). Myles *et al.* 2009 reported that a high percentage of alleles are rare meaning that they are present in too few individuals to warrant detection in an association mapping study.

2.14.3 Approaches used in association mapping

Association mapping uses one of two approaches: candidate gene sequencing or whole genome scanning of natural populations (Rafalski 2002). Under the candidate gene approach, candidate genes are selected based on prior information from different analyses such as mutation, biochemical pathways or linkage analysis. The standing hypothesis in this study would be that 'there are correlations between DNA polymorphisms in gene A and the trait of interest'. Whole genome scanning involves testing for association on most segments of the genome, by genotyping densely distributed genetic marker loci covering all chromosomes (Rafalski 2010). The hypothesis for genome wide scanning would be that 'one or more of the genetic loci being considered is either causal for the trait or in LD with the causal locus'. No prior information about candidate genes is required and one stands a chance of detecting unknown loci.

2.14.4 Assembling the population for association mapping

The efficiency and accuracy of the association analysis partly lies with the population used during analysis. The population used for association analysis should represent the whole diversity (species wide, including all races) of the crop that is adaptable to the target testing environments.

2.14.4.1 Steps followed in association mapping

The steps followed in association mapping were outlined by Abdurakhmonov and Abdukarimov (2008):

- Selection of a group of individuals from a natural population or germplasm collection
- Phenotyping of the selected population groups
- Genotyping of all individuals in the population groups with available markers
- Assessment of population structure and kinship. The degree of relatedness of individuals in the population needs to be determined prior to association analysis
- Statistical analyses to reveal marker-trait associations are run using information obtained from population structure, genotypic/haplotypic and phenotypic data.

2.14.5 Calculations and measurements of linkage disequilibrium in plants

Several software packages have been developed to test for association between SNP variations in crops. One of the most frequently used programmes is Trait Analysis by Association, Evolution and Linkage (TASSEL). Two different models can be used in TASSEL depending on population structure and objectives of the test:

- TASSEL general linear model (Yu and Buckler 2006): This is a single regression model that assumes a structured association.

- TASSEL mixed linear model (Kraakman *et al.* 2006; Yu *et al.* 2006): This is a multiple regression model that provides estimates for the false discovery rate (Kraakman *et al.* 2006) and a unified mixed model approach (Yu *et al.* 2006).

The basic component of all LD statistics is the difference between the observed and expected haplotype frequencies at polymorphic loci and the frequent measures are D' and r^2 (Abdurakhmonov and Abdukarimov 2008). Pearson's correlation coefficient (r) explains the predictive value of the allelic state at one polymorphic locus on the allelic state at another polymorphic locus while r^2 measures the correlation between the alleles at two loci and provides a summary of both the recombination and mutation history. D' is the standardised disequilibrium coefficient which mainly measures recombination history and is useful to assess the probability of historical recombination in a given population.

The r^2 is the most informative and widely used tool in association mapping (Myles *et al.* 2009; Oraguzie *et al.* 2007).

2.14.6 Prospects of association mapping in common bean

Cytogenetically, common bean is a true diploid with 11 chromosomes. The flowers are cleistogamous and this predominantly self-pollinating annual crop has a small genome size of between 450 and 650 million base pairs (Mb) (Bennett and Leitch 1995; McClean *et al.* 2004). The chromosomes have been reported to be extremely small (around 2 µm) with similar morphologies (Mok and Mok 1977; Cheng and Bassett 1981; Fonseca *et al.* 2010) and nearly all loci are single copy (McClean *et al.* 2004).

The reproductive nature of common bean reduces opportunities for recombination and introduction of rare alleles into the genome. Consequently, complex patterns of population structure and relatedness have been generated (Myles *et al.* 2009) as found in gene pools and race structures in common bean. The small chromosomes and genome size permits the use of a moderate number of markers evenly distributed across the genome in association analysis. Studies elsewhere have demonstrated the potential of association mapping in identifying and characterising loci associated with different complex traits in true breeding crops (Kraakman *et al.* 2006).

2.15 Conclusions

Improvements in yield and tolerance to biotic and abiotic stresses in any crop rely on the genetic diversity of parental sources. The broadest genetic diversity for cultivated crops resides in landraces and yet these have not been widely exploited in most common bean breeding programmes (Singh 2001).The current study offers the first opportunity to search for sources of drought tolerance in a large set of Andean and Mesoamerican landraces from different countries. This set of landraces is a subset of the CIAT core collection and termed a reference collection. Previous experiments in common bean as cited in the literature review indicated that studies on drought tolerance were confined to Mesoamerican genotypes particularly those from races Durango and Mesoamerica. Broadening the genetic base for Andean genotypes is also important considering that they are widely cultivated in sub-Saharan Africa. In the current study all known races in

common bean except race Chile formed the materials of the experiments. Deep rooting and other root characteristics which contribute to drought tolerance of crops were also less studied in Andean landraces and elite materials, hence the current study offers an opportunity to study root traits of Andean genotypes under drought stress.

The current study is the first to utilise genome wide association mapping for drought tolerance in common bean and would possibly reveal some marker-trait associations which would form the first point for fine mapping of drought tolerant traits in common bean. Predictions from climate change models indicate that drought will be more prevalent in the near future. Plant breeding, through novel breeding techniques should help to minimise the negative effects of drought in common bean. In addition, the current study utilises a large number of SSR markers against a set of common bean genotypes and is instructive on the value of obtaining bigger marker sets. A large number of markers were employed in the current study to saturate the common bean genome with the aim of defining the population structure more accurately. Population structure forms the basis for genome wide association or for the discovery of marker-trait associations in candidate gene analysis. Thus, a better understanding of genetic structure, response of common bean to drought and use of molecular markers through MAS for drought tolerance in common bean would likely provide increased productivity and high returns in future.

2.16 References

Abdurakhmonov IY, Abdukarimov A. 2008. Application of association mapping to understanding the genetic diversity of plant germplasm resources. International Journal of Plant Genomics 27:1-18.

Acosta-Gallegos JA, Kelly JD, Gepts P. 2007. Pre-breeding in common bean and use of genetic diversity from wild germplasm. Crop Science 47:44-59.

Agarwal PK, Agarwal P, Reddy MK, Sopory SK. 2006. Role of DREB transcription factors in abiotic and biotic stress tolerance in plants. Plant Cell Reports 25:1263-1274.

Allen RG, Yonts CD, Wright JL. 2000. Irrigation to maximize bean production and water use efficiency. In: Bean Research, Production and Utilization. Proceedings of the Idaho Bean Workshop. Singh SP (Ed.) University of Idaho, Moscow. pp. 71-92.

Amede T, Kimani P, Ronno W, Lunze L, Mbikay N. 2004. Coping with drought: strategies to improve genetic adaptation of common bean to drought-prone regions of Africa. CIAT Occasional Publication Series 38:1-39.

Amede T, Schubert S. 2003. Mechanisms of drought resistance in grain legumes: II. Stomatal regulation and root growth. Ethiopian Journal of Science 26:137-144.

Araus JL, Slater GA, Reynolds MP, Royo C. 2002. Plant breeding and water relations in C_3 cereals: what should we breed for? Annals of Botany London 89:925-940.

Beebe S, Lynch J, Galwey N, Tohme J, Ochoa I. 1997. A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica 95:325-336.

Beebe SE, Rao IM, Cajio C, Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favourable environments. Crop Science 48:582-592.

Beebe S, Rao IM, Blair MW, Butare L. 2009. Breeding for abiotic stress tolerance in common bean: present and future challenges. In: Proceedings of the 14th Australian Plant Breeding & 11th SABRAO Conference, 10-14 August 2009, Brisbane, Australia. pp. 307-319.

Beebe S, Ramirez J, Jarvis A, Rao IM, Mosquera G, Bueno JM, Blair M. 2011. Genetic improvement of common beans and the challenges of climate change. In: Yadav SS, Redden RJ, Hatfield JL, Lotze-Campen H, Hall AE (Eds.) Crop Adaptation to Climate Change. John Wiley & Sons, Ltd., Published by Blackwell Publishing Ltd. pp. 356-369.

Beebe SE, Rao IM, Blair MW, Acosta-Gallegos JA. 2013. Phenotyping common beans for adaptation to drought. Plant Physiology 4:1-20.

Beebe S, Renjifo J, Gait'an-Solis E, Duque MC, Tohme J. 2001. Diversity and origin of Andean landraces of common bean. Crop Science 41:854-862.

Beebe S, Skroch PW, Tohme J, Duque MC, Pedraza F, Nienhuis J. 2000. Structure of genetic diversity among common bean landraces of Middle American origin based on correspondence analysis of RAPD. Crop Science 40:264-273.

Belo A, Zheng P, Luck S, Shen B, Meyer DJ, Li B, Tingey S, Rafalski A. 2008. Whole genome scan detects an allelic variant of *fad2* associated with increased oleic acid levels in maize. Molecular Genetics and Genomics 279:1-10.

Bennett MD, Leitch IJ. 1995. Nuclear DNA amounts in angiosperms. Annals of Botany London 76:113-116.

Blair MW, Buendia HF, Giraldo MC, Metais I, Peltier D. 2008. Characterization of AT-rich microsatellites in common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 118:56-64.

Blair MW, Díaz LM, Buendía HF, Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 119:955-972.

Blair MW, Díaz JM, Hidalgo R, Díaz LM, Duque MC. 2007. Microsatellite characterisation of Andean races of common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 116:29-43.

Blair MW, Giraldo MC, Buendia HF, Trovar E, Duque MC, Beebe S. 2006. Microsatellite marker diversity in common bean (*Phaseolus vulgaris* L). Theoretical and Applied Genetics 113:100-109.

Blair MW, Pedraza F, Buendia HF, Gaita'n-Solis E, Beebe SE, Gepts P, Tohme J. 2003. Development of a genome wide anchored microsatellite map for common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 107:1362-1374.

Blair MW, Prieto S, Diaz LM, Buendia HF, Cardona C. 2010. Linkage disequilibrium at the APA insecticidal seed protein locus of common bean (*Phaseolus vulgaris* L.) BioMedical Central Genomics 10:79-93.

Blum A. 1988. Plant Breeding for Stress Environments. CRC Press, Boca Raton, Florida. pp. 23-30.

Blum A. 2005. Drought resistance, water use efficiency and yield potential – are they compatible, dissonant or mutually exclusive? Australian Journal of Agricultural Research 56:1159-1168.

Blum A. 2011. Drought resistance and its improvement. In: Plant breeding for water-limited environments. Springer New York, Dordrecht Heidelberg, London. pp. 53-152.

Boyer JS, Wong SC, Farquhar GD. 1997. Carbon dioxide and water vapor exchange across leaf cuticle (epidermis) at various water potentials. Plant Physiology 114:185-191.

Breseghello F, Sorrells MS. 2006. Association mapping of kernel size and milling quality in wheat (*Triticum aestivum*) cultivars. Genetics 172:1165-1177.

Broughton WJ, Hernandez G, Blair M, Beebe S, Gepts P, Vanderleyden J. 2003. Beans (*Phaseolus* spp); model food legumes. Developmental Plant Soil Science 99:55-128.

Brown AHD. 1989a. The case of core collections. In: Brown AHD, Frankel OH, Marshal DR, Williams JT (Eds.) Use of Plant Genetic Resources. Cambridge University, Press UK. pp. 24-27.

Brown AHD. 1989b. Core Collections: A practical approach to genetic resources management. Genome 31:818-824.

Buruchara R. 2007. Background information on common bean (*Phaseolus vulgaris* L). Biotechnology, Breeding and Seed systems for African crops. http://www.africancropsnet/rockefeller/crops/beans/index.htm.

Buso GSC, Amaral PS, Brondani RPV, Ferreira ME. 2006. Microsatellite markers for the common bean *Phaseolus vulgaris*. Molecular Ecology Notes 6:252-254.

Butare L, Rao IM, Lepoivre P, Polania J, Cajiao C, Cuasquer JB, Beebe S. 2011. New sources of resistance in *Phaseolus* species to individual and combined aluminum toxicity and progressive soil drying stresses. Euphytica 181:385-404.

Ceccarelli S, Acevedo E, Grando S. 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits and architecture of genotypes. Euphytica 56:169-185.

Cheng SS, Bassett MJ. 1981. Chromosome morphology in common bean (*Phaseolus vulgaris* L.) at the diplotene stage of meiosis. Cytology (Tokyo) 46:675-684.

CIAT. 2004. Bean Project Annual Report. CIAT, Cali, Colombia. pp. 55-56.

CIAT. 2008. Annual Report. Outcome line SBA-1. Improved beans for the developing world. pp. 39-65.

Cordoba JM, Chavarro C, Schlueter JA, Jackson SA, Blair MW. 2010. Integration of physical and genetic maps of common bean through BAC-derived microsatellite markers. BioMedical Central Genomics 11:436-451.

Díaz LM, Blair MW. 2006. Race structure within the Mesoamerican gene pool of common bean (*Phaseolus vulgaris* L.) as determined by microsatellite markers. Theoretical and Applied Genetics 114:143-154.

Dita MA, Rispail N, Prats E, Rubiales D, Singh KB. 2006. Biotechnology approaches to overcome biotic and abiotic stress constraints in legumes. Euphytica 147:1-24.

Ellegren H. 2004. Microsatellites: simple sequences with complex evolution. Nature Reviews Genetics 5:435-444.

FAO statistic. 2004. http://faostat.fao.org/site/408/default.aspx (accessed 1 November 2009).

FAO statistic. 2010. http://faostat.fao.org (accessed 16 November 2012)

Farooq M, Basra SMA, Wahid A, Cheema ZA, Cheema MA, Khaliq A. 2009. Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). Crop Science 194:325-333.

Flint-Garcia SA, Thornsberry JM, Buckler ES. 2003. Structure of linkage disequilibrium in plants. Annual Review of Plant Biology 54:357-374.

Fonseca A, Ferreira J, dos Santos TRB, Mosiolek M, Bellucci E, Kami J, Gepts P, Geffroy V, Schweizer D, dos Santos KGB, Pedrosa-Harand A. 2010. Cytogenetic map of common bean (*Phaseolus vulgaris* L.). Chromosome Research 10:1007-1018.

Gaitan-Solis E, Choi IY, Quigley C, Cregan P, Tohme J. 2008. SNP in common bean: Their discovery and genotyping using a multiplex detection system. The Plant Genome 1:125-134.

Galindo L, Blair MW, Beebe S, Ishitani M, Tohme J. 2003. Development of a molecular marker: DREB for drought tolerance in common bean. In: Annual Report, Biotechnology Research Project, CIAT, Cali, Colombia. pp. 177-179.

Glaszmann JC, Kilian B, Upadhyaya HD, Varshney RK. 2010. Accessing genetic diversity for crop improvement. Current Opinion in Plant Biology 13:1-7.

Gupta PK, Varshney RK, Sharma PC, Ramesh B. 1999. Molecular markers and their applications in wheat breeding. Plant Breeding 118:369-390.

Hangen LA, Bennink MR. 2003. Consumption of black beans and navy beans (*Phaseolus vulgaris*) reduced azoxymethane-induced colon cancer in rats. Nutrition Cancer 44:60-65.

Ho MD, Rosas JC, Brown KM, Lynch JP. 2005. Root architectural tradeoffs for water and phosphorous acquisition. Functional Plant Biology 32:737-748.

Holland JB. 2007. Genetic architecture of complex traits in plants. Current Opinion in Plant Biology 10:156-161.

Hufstetler EV, Boerma HR, Carter TE, Earl HG. 2007. Genotypic variation for three physiological traits affecting drought tolerance in soybean. Crop Science 47:25-35.

Ishitani M, Rao I, Wenzl P, Beebe S, Tohme J. 2004. Integration of genomics approach with traditional breeding towards improving abiotic stress adaptation: Drought and aluminum toxicity as case studies. Field Crops Research 90:35-45.

Islam FMA, Basford KE, Redden RJ, Beebe S. 2002. Preliminary evaluation of the common bean core collection at CIAT. Plant Genetics Resources Newsletter 145:29-37.

Jenkins DJA, Kendall CWC, Marchie A, Jenkins AL, Augustin LSA, Ludwig DS, Barnard ND, Anderson JW. 2003. Type 2 diabetes and the vegetarian diet. Journal of Clinical Nutrition 78:610-616.

Kage H, Kochler M, Stűtzel H. 2004. Root growth and dry matter partitioning of cauliflower under drought stress conditions: measurements and simulation. European Journal of Agronomy 20:379-394.

Kashiwagi J, Krishnamurthy L, Upadhyaya HD, Krishna H, Chandra S, Vadez V, Serraj R. 2004. Genetic variability of drought avoidance root traits in the mini core germplasm collection of chickpea (*Cicer arietinum* L.). Euphytica 146:213-222.

Katungi E, Farrow A, Mutuoki T, Gebeyehu S, Karanja D, Alamayehu F, Sperling L, Beebe S, Rubyogo J.C, Buruchara R. 2010. Improving common bean productivity: An Analysis of socioeconomic factors in Ethiopia and Eastern Kenya. Baseline Report Tropical legumes II. Centro Internacional de Agricultura Tropical – CIAT. Cali, Colombia.

Kavar T, Maras M, Kidric M, Sustar-Vozlic J, Meglic J. 2008. Identification of genes involved in the response of leaves of *Phaseolus vulgaris* to drought stress. Molecular Breeding 21:159-172.

Khan HR, Link W, Hocking TJH, Stoddard FL. 2007. Evaluation of physiological traits for improving drought tolerance in faba bean (*Vicia faba* L.) Plant and Soil Science 292:205-217.

Kimani PM, Buruchara R, Ampofo K, Pyndji M, Chirwa RM, Kirkby R. 2001. Breeding beans for smallholder farmers in East, Central and Southern Africa: Constraints, achievements and potential. PABRA Millenium Workshop, Arusha, Tanzania. pp.76-79.

Kraakman ATW, Martinez F, Mussiraliev B, van Eeuwijk FA, Niks RE. 2006. Linkage disequilibrium mapping of morphological, resistance and other agronomically relevant traits in modern spring barley cultivars. Molecular Breeding 17:41-58.

Kwak M, Gepts P. 2009. Structure of genetic diversity in the two major gene pools of common bean (*Phaseolus vulgaris* L. Fabaceae). Theoretical and Applied Genetics 118:979-992.

Laurentin H. 2008. Data analysis for molecular characterisation of plant genetic resources. Genetic Resources and Crop Evolution 8:58-71.

Levitt J. 1980. Water stress, dehydration and drought injury. In: Responses of Plants to Environmental Stresses. Volume II, Academic Press, London. pp. 213-216.

Lichten M, Goldman ASH. 1995. Meiotic recombination hotspots. Annual Review of Genetics 29:423-444.

Liu F, Andersen MN, Jensen CR. 2003. Loss of pod set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. Functional Plant Biology 30:271-280.

Lizzana C, Wentworth M, Martinez JP, Villegas D, Meneses R, Murche EH, Pastenes C, Lercari B, Vernieri P, Harton P, Pinto M. 2006. Differential adaptation of two varieties of common bean to abiotic stress. Journal of Experimental Botany 57:685-697.

Ludlow MM, Muchow RC. 1990. A critical evaluation of traits for improving crop yields in water limited environments. Advances in Agronomy 43:107-157.

Lunze L, Buruchara R, Ugen MU, Nabahungu L, Rachier GO, Ngongo M, Rao I, Abang MW. 2011. Intergrated soil fertility management in bean based cropping systems of Eastern, Central and Southern Africa. In: Whalen J (Ed.) Soil Fertility. INTECH Open Access Publisher, Rijeka, Croatia. pp. 315-318.

Lunze L, Ngongo M. 2011. Potential nitrogen contribution of climbing bean to subsequent maize crop in rotation in South Kivu Province of Democratic Republic of Congo. In: Bationo A, Waswa B, Kihara J, Kimetu J (Eds.) Innovations as Key to the Green Revolution in Africa. Springer Science, Dordrecht, The Netherlands. pp. 677-681.

Mackay L. 2001. The genetic architecture of quantitative traits. Annual Review of Genetics 33:303-339.

Mackay L, Powell W. 2007. Methods for linkage disequilibrium mapping in crops. Trends in Plant Science 12:57-63.

Manavalan LP, Guttikonda SK, Tran LP, Nguyen HT. 2009. Physiological and molecular approaches to improve drought resistance in soybean. Plant Cell Physiology 50:1260-1276.

Manivannan P, Jaleel CA, Kishorekumar A, Sankar B, Somasundaram R, Sridharan R, Panneerselvam R. 2007. Changes in antioxidant metabolism of *Vigna unguiculata* (L.) Walp. by propiconazole under water deficit stress. Biointerfaces 57:69-74.

McClean P, Kami J, Gepts P. 2004. Genomics and genetic diversity in common bean. In: Wilson RF, Stalker HT, Brummer EC (Eds.) Legume Crop Genomics. AOCS Press, Champaign, IL. pp. 60-82.

McConnell MD, Mamidi S, Rossi M, Lee RK, McClean PE. 2007. A gene-based linkage map of common bean (*Phaseolus vulgaris* L.). Plant and Animal Genome 15:745-757.

Mezard C. 2006. Meiotic recombination hotspots in plants. Biochemical Society Transactions 34:531-534.

Mezmouk S, Dubreuil P, Bosio M, Décousset L, Charcosset A, Praud S, Mangin B. 2011. Effect of population structure corrections on the result of association mapping tests in a complex maize diversity panels. Theoretical Applied Genetics 122:1149-1160.

Miklas P.N, Singh S.P. 2007. Common bean: Pulses, Sugar and Tuber Crops. C Kole (Ed.) Genome Mapping and Molecular Breeding in Plants. Springer-Verlag, Berlin pp.111-134.

Mok DWS, Mok MC. 1977. Monosomics in common bean (*Phaseolus vulgaris*). Theoretical and Applied Genetics 49:145-149.

Myers JR. 2000. Tomorrow's snap bean cultivars. In: Singh SP (Ed.) Bean Research, Production and Utilization. Proceedings of the Idaho Bean Workshop. University of Idaho, Moscow, ID. pp. 39-51.

Myles S, Peiffer J, Brown PJ, Ersoz ES, Zhang Z, Costich DE, Buckler ES. 2009. Association mapping: Critical considerations shift from genotyping to experimental design. The Plant Cell 21:2194-2202.

Neale DB, Savolainen O. 2004. Association genetics of complex traits in conifers. Trends in Plant Science 9:325-330.

Nemeskéri E, Sárdi E, Remenyik J, Kószegi B, Nagy P. 2010. Study of defensive mechanism against drought in French bean (*Phaseolus vulgaris* L.) varieties. Acta Plant Physiology 32:1125-1134.

Nleya TM, Slinkard AE, Vandernberg A. 2001. Differential performance of pinto bean under varying levels of soil moisture. Canadian Journal of Plant Science 81:233-239.

Oraguzie NC, Rikkerink EHA, Gardiner SE, de Silva HN. 2007. Association mapping in plants. Springer, Tokyo and New York. pp. 277.

PABRA. 2008. Supporting nutrition and health, food security, environmental stresses and market challenges that will contribute to improve the livelihood and create income of resource poor smallholder families in sub-Saharan Africa. PABRA, CIAT, Kampala, Uganda. pp. 44-65.

Pan XY, Wang YF, Wang GX, Cao QD, Wang J. 2002. Relationship between growth redundancy and size inequality in spring wheat populations mulched with clear plastic film. Acta Phytoecology Sinica 26:177-184.

Papa R, Bellucci E, Rossi M, Leonardi S, Rau D, Gepts P, Nanni L. 2007. Tagging the signatures of domestication in common bean (*Phaseolus vulgaris*) by means of pooled DNA samples. Annals of Botany 100:1039-1051.

Passioura J. 1977. Grain yield, harvest index and water use of wheat. Journal of Australian Agricultural Science 43:117-120.

Pimentel C, Herbert G, da Silva JV. 1999. Effects of drought on oxygen evolution and stomatal conductance of beans at the pollination stage. Environmental and Experimental Botany 42:155-162.

Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW. 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Research 86:185-198.

Porch TG, Ramirez VH, Santana D, Harmsen EW. 2009. Evaluation of common bean for drought tolerance in Juana Diaz, Puerto Rico. Agronomy and Crop Science 195:328-334.

Powell W, Machray GC, Provan J. 1996. Polymorphism revealed by simple sequence repeats. Trends in Plant Science 1:215-222.

Pritchard JK, Stephens M, Donnelly P. 2002. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

Pswarayi A, van Eeuwijk FA, Ceccarelli S, Grando S, Comadran J, Russell JR, Pecchion N, Tondelli A, Akar T, Al-Yassin A, Benbelkacem A, Quabbou H, Thomas WT, Romagosa I. 2008. Changes in allele frequencies in landraces, old and modern barley cultivars of marker loci close to QTL for grain yield under high and low input conditions. Euphytica 163:435-447.

Purcell LC, King CA. 1996. Drought and nitrogen source effects on nitrogen, seed growth and yield in soybean. Journal of Plant Nutrition 19:969-993.

Rafalski JA. 2002. Applications of single nucleotide polymorphisms in crop genetics. Current Opinion in Plant Biology 5:94-100.

Rafalski JA. 2010. Association genetics in crop improvement. Current Opinion in Plant Biology 13:174-180.

Ramírez M, Graham MA, Blanco-Lopez L, Silvente S, Medrano-Soto A, Blair MW, Hernández G, Vance CP, Lara M. 2005. Sequencing and analysis of common bean ESTs. Building a foundation for functional genomics. Plant Physiology 137:1211-1227.

Ramírez-Vallejo P, Kelly JD. 1998. Traits related to drought resistance in common bean. Euphytica 99:127-136.

Rao IM. 2001. Role of physiology in improving crop adaptation to abiotic stresses in tropics. The case of common bean and tropical forages. In: Pessaraki M (Ed.) Handbook of Plant and Crop Physiology. Marcel Dekker, New York, USA. pp. 583-613.

Ravi K, Vadez V, Isobe S, Mir RR, Guo Y, Nigam SN, Gowda MVC, Radha-Krishnan T, Bertioli DJ, Knapp SJ, Varshney RK. 2011. Identification of several main-effect QTLs and a large number of epistatic QTLs for drought tolerance related traits in groundnuts (*Arachis hypogaea* L.). Theoretical and Applied Genetics 122:11119-1132.

Reddy AR, Chaitanya KV, Vivekanandan M. 2004. Drought induced responses of photosynthesis and antioxidant metabolism in higher plants. Journal of Plant Physiology 161:1189-1202.

Ribaut J-M, de Vicente CM, Delannay X. 2010. Molecular breeding in developing countries. Challenges and perspectives. Current Opinion in Plant Biology 13:1-6.

Richards RA, Rebetzke GJ, Condon AG, van Herwaarden AF. 2002. Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. Crop Science 42:111-121.

Rossi M, Bitocchi E, Bellucci E, Nanni L, Rau D, Attene G, Papa R. 2009. Linkage disequilibrium and population structure in wild and domesticated populations of *Phaseolus vulgaris* L. Evolutionary Applications 23:1-19.

Santos MG, Ribeiro RV, Machado EC, Pimentel C. 2009. Photosynthetic parameters and leaf water potential of five common bean genotypes under mild water deficit. Plant Biology 53:229-236.

Schneider KA, Rosales-Serna R, Ibarra-Perez F, Cazares-Enríquez B, Acosta-Gallegos JA, Ramírez-Vallejo P, Wassimi N, Kelly JD. 1997. Improving common bean performance under drought stress. Crop Science 37:43-50.

Serraj R, Sinclair TR. 2002. Osmolyte accumulation: Can it really help increase crop yield under drought conditions? Plant Cell Environment 25:335-341.

Shao HB, Chu LY, Shao MA, Abdul Jaleel C, Hong-Mei M. 2008. Higher plant antioxidants and redox signaling under environmental stresses. Comparative plant biology 331:433-441.

Shearman VJ, Sylvester-Bradley R, Scott RK, Foulkes MJ. 2005. Physiological processes associated with wheat yield progress in the UK. Crop Science 45:175-185.

Singh SP. 2001. Broadening the genetic base of common bean cultivars: A review. Crop Science 41:1659-1675.

Singh SP. 1995. Selection for water stress tolerance interracial populations of common bean. Crop Science 35:118-124.

Singh SP, Gepts P, Debouck D. 1991a. Races of common bean (*Phaseolus vulgaris*, Fabaceae). Economic Botany 45:379-396.

Singh SP, Gutiérrez JA, Molina A, Urrea U, Gepts P. 1991b. Genetic diversity in cultivated common bean: II. Marker based analysis of morphological and agronomic traits. Crop Science 31:23-29.

Singh SP, Nodari R, Gepts G. 1991c. Genetic diversity in cultivated common bean. I. Allozymes. Crop Science 31:19-23.

Slate J, Gratten J, Beraldi D, Stapley J, Hale M. 2009. Gene mapping in the wild with SNPs: Guidelines and future directions. Genetica 136:97-107.

Specht JE, Chase K, Macrander M, Graef GL, Chung J, Markwell JP, Germann M, Orf JH, Lark KG. 2001. Soybean response to water. A QTL analysis of drought tolerance. Crop Science 41:493-509.

Sponchiado BN, White JW, Castillo JA, Jones PG. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Experimental Agriculture 25:249-257.

Soto-Cerda BJ, Cloutier S. 2012. Association Mapping in Plant Genomes. Genetic Diversity in Plants, Mahmut Caliskan (Ed.) InTech pp. 433-454.

Stafford W. 2009. Marker Assisted Selection (MAS): Key Issues for Africa. The African Centre for Biodiversity, South Africa. pp. 26-30.

Stephen R, Schoof H, Mayer K. 2005. Plant Marker – a database of predicted molecular markers from plants. Theoretical and Applied Genetics 103:1010-1023.

Stich B. 2006. A new test for family based association mapping with inbred lines from plant breeding programs. Theoretical and Applied Genetics 113:1121-1130.

Tardieu F. 1996. Drought perception by plants. Do cells of droughted plants experience water stress? Plant Growth Regulation 20:93-104.

Terán H, Singh SP. 2002. Comparison of sources and lines selected for drought resistance in common bean. Crop Science 42:64-70.

Tohme J, Jones P, Beebe S, Iwananga M. 1995. The combined use of agroecological and characterization data to establish the CIAT *Phaseolus vulgaris* core collection. In: Hodgkin T, Brown AHD, van Hintum JL, Morales EAV (Eds.) Core Collections of Plant Genetic Resources. International Plant Genetic Resources Institute (IPGRI). A Wiley-Sayce Publication. pp. 95-107.

Vallijodan B, Nguyen HT. 2006. Understanding regulatory networks and engineering for enhanced drought tolerance in plants. Current Opinion in Plant Biology 9:1-7.

Varshney RK, Graner A, Sorrells ME. 2005. Genic microsatellite markers in plants: features and applications. Trends in Biotechnology 23:48-55.

Webber M, Barnett J, Finlayson B, Wang M. 2006. Pricing China's Irrigation Water. Working Paper, School of Anthropology, Geography and Environmental Studies, The University of Melbourne, Victoria, Australia. pp. 56-59.

Wentworth M, Murchie EH, Gray JE, Villegas D, Pastenes C, Pinto M, Horton P. 2006. Differential adaptation of two varieties of common bean to abiotic stress. II. Acclimation of photosynthesis. Journal of Experimental Botany 57:699-705.

White JW, Castillo JA. 1992. Evaluation of diverse shoot genotypes on selected root genotypes of common bean under soil water deficits. Crop Science 32:762-765.

Wortmann CS. 2001. Nutrient dynamics in a climbing bean and sorghum crop rotation in the Central African highlands. Nutrient Cycling in Agroecosystems 61:267-272.

Wortmann C, Kirkby R, Eledu C, Allen D. 1998. Atlas of common bean production in Africa. CIAT publication no. 297. Cali Colombia. pp. 32-37.

Wu QS, Xia RX, Zou YN. 2008. Improved soil structure and citrus growth after inoculation with three arbuscular mycorrhizal fungi under drought stress. European Journal of Soil Biology 44:122-128.

Yu J, Buckler ES. 2006. Genetic association mapping and genome organisation of maize. Current Opinion in Biotechnology 17:155-160.

Yu J, Pressor G, Briggs WH, Vroh-Bi I, Yamasaki M, Doebley JF, McMullen MD, Gaut BS, Nielsen DM, Holland JB, Kresovich S, Buckler ES. 2006. A unified mixed model method for association mapping that accounts for multiple levels of relatedness. Nature Genetics 38:203-208.

Yu K, Park SJ, Poysa V. 1999. Abundance and variation of microsatellite DNA sequences in beans (*Phaseolus* and *Vigna*). Genome 42:27-34.

Zhao CX, Guo LY, Jaleel CA, Shao HB, Yang HB. 2008. Prospects for dissecting plant-adaptive molecular mechanisms to improve wheat cultivars in drought environments. Comparative Plant Biology 331:579-586.

Zhu C, Gore M, Buckler ES, Yu J. 2008. Status and prospects of association mapping in plants. The Plant Genome 1:5-20.

Zlatev Z, Lidon F, Ramalho J, Yordanov I. 2006. Comparison of resistance to drought of tree bean cultivars. Plant Biology 50:389-394.

Zondervan KT, Cardon LR. 2004. The complex interplay among factors that influence allelic association. Nature Review Genetics 5:89-100.

Chapter 3

Field evaluation of yield, yield components, physiological traits and leaf, stem and pod biomass under irrigated and rainfed treatments

3.1 Abstract

Drought tolerant varieties combined with good agronomic practises have the potential to increase crop productivity under marginal areas. The objectives of this study were to identify sources of drought tolerance, traits that are correlated to yield under terminal drought and understand the physiological mechanisms of drought tolerance in a reference collection of common bean. The reference collection consisted of a total of 202 landrace genotypes of Andean and Mesoamerican origins. Experiments were laid out as 11x11 Mesoamerican and 9x9 Andean lattices and replicated three times under irrigated and terminal drought conditions at CIAT-Palmira (site 1) and Harare Research Station (site 2). At both locations drought stress reduced yield, total shoot biomass at mid-pod filling stage, 100-seed weight, pod length and number of pods per plant. Grain yield was reduced by 22% (site 1) and 53% (site 2) in Andean trials and 23% (site 1) and 40% (site 2) in Mesoamerican trials. Treatments and genotypes had significant effects ($P \leq 0.001$) on yield and genotypic main effects made large contributions to the variability of most traits measured across locations in both trials. High geometric means for grain yield and low drought susceptibility index values were observed in races Durango sub-race 1 and Nueva Granada sub-race 1 at both locations and demonstrated that sources of drought tolerance could be found in these two races for Mesoamerican and Andean genotypes respectively. BAT477, DOR390, G11721, G5142 and PVA1111 had high geometric means for grain yield across the two locations and could serve as sources of drought tolerance. Positive and significant correlations between 100-seed weight, number of pods per plant and total shoot biomass at mid-pod fill with yield were observed under terminal drought at both locations. Canopy temperature depression was significantly correlated with yield under terminal drought in Mesoamerican trials at CIAT-Palmira. In conclusion, the current study demonstrated the possibility of evaluating large sets of genotypes under field conditions to facilitate selection for drought tolerant genotypes.

3.2 Introduction

Drought is a worldwide agricultural problem affecting 60% of total common bean production and is especially severe in eastern and southern Africa as well as certain parts of Mexico and Brazil, which are major producers (Graham and Vance 2003). Worsening the situation is the fact that climate change predictions associate southern Africa with hot and dry spells in the near future. In this region, common bean is an important source of protein and micronutrients essential for human health as well as income generation at farm level. Unfortunately, common bean is prone to drought compared to other legume crops grown in southern Africa.

Common bean losses to drought primarily depend on the onset of drought (early, intermittent and terminal), intensity (severe, moderate) and duration (Terán and Singh 2002). Huge losses have been recorded when common bean is affected by drought during the reproductive stages (Casquero *et al.* 2006). Reported yield reductions in pinto bean exposed to drought during the reproductive growth stages are 80% (Urrea *et al.* 2007). One feature observed in drought prone areas is the shortening of the rainy season, exposing common bean to much more terminal drought. However, even in the areas of bimodal rainfall intermittent drought has become a more serious problem. In sub-Saharan Africa, yield losses (MT) due to early, intermittent and terminal drought were 71 000, 119 800 and 100 400 respectively (Wortmann *et al.* 1998). The current study examined yield losses due to terminal drought at research sites in Colombia and Zimbabwe.

Yield, yield components and biomass accumulation are the main traits affected by drought in common bean (Asfaw *et al.* 2012; Blair *et al.* 2012). Seed yield has been used as a measure of drought tolerance in many common bean experiments since it represents the harvestable product (Ramírez-Vallejo and Kelly 1998). Beebe *et al.* (2008) proposed the use of other attributes such as pod harvest index in selecting common bean genotypes tolerant to drought stress. Asfaw *et al.* (2012) used measures of photosynthate accumulation and mobilisation as traits to characterise drought tolerance. A high shoot biomass accumulation towards flowering (Blum 2005), early maturity and phenotypic plasticity (Nleya *et al.* 2001) were reported to support high yield under drought stress

conditions. The characterisation of these traits conferring drought tolerance and defining how they work under drought would be useful in breeding programmes.

Improvement for both biotic and abiotic stress tolerance relies on the genetic diversity in crop species. The use of core collections have been proposed (IPGRI 2000) but consist of too many genotypes for field studies. A total of 1440 genotypes constitute the core collection of common bean and represent the genetic diversity found in this species and 600 of these have been genotypically characterised (Blair *et al.* 2009).

For drought phenotyping to be carried out with a manageable sample, a reference collection of common bean comprising of 202 genotypes was constituted using molecular markers to represent the greatest diversity of cultivated common bean prevailing in the core collection (CIAT 2008). Screening of germplasm under targeted drought conditions is a requirement for the identification of drought tolerance traits (Khan *et al.* 2007).

The objectives of this study were to:

- Identify sources of drought tolerance in the CIAT reference collection through characterisation of phenotypic traits under rainfed and irrigated conditions at CIAT-Palmira in Colombia and Harare Research Station, Zimbabwe for future breeding programmes.
- Identify traits that are correlated with yield under terminal drought stress conditions.
- Improve the physiological understanding of drought tolerance in common bean through characterisation of shoot traits that are correlated to high yield under terminal drought.

3.3 Materials and methods

3.3.1 Sites for field experiments

CIAT-Palmira in Colombia and Harare Research Station in Zimbabwe were used for the field experiments.

3.3.1.1 CIAT-Palmira, Colombia

CIAT-Palmira lies at an altitude of 965 masl with latitude 3°29'N and longitude of 76°21'W. Soils are mollisol defined as fine silty, mixed isohyperthermic Aquic Hapludoll. Trials were planted in soil with a pH of 7.6. Weather parameters recorded during the growing season of the common bean trials are presented in Table 3.1.

Table 3.1 Temperature, rainfall and evaporation experienced at CIAT-Palmira, Colombia, during the growing season of common bean trials in 2009

Climatic factor	Month			
	June	July	August	September
Mean maximum temperature, °C	30.09	32.17	32.06	33.67
Mean minimum temperature, °C	19.25	19.09	19.71	19.73
Total rainfall, mm	1.39	0.25	0.95	0.00
Evaporation, mm	4.07	6.38	5.44	6.63

3.3.1.2 Harare Research Station, Zimbabwe

Harare Research Station is at an altitude of 1 506 masl and latitude 31°03'E with longitude of 17°48'S. It has Rhodic Notisol soils (FAO/UNESCO classification) which are deep to very deep, dark reddish brown clays over well drained, dark red structured clays which exhibit nitic features. The field used for the field experiment had a soil pH of 7.2 and a slope of less than 1%. Table 3.2 presents weather parameters experienced during the growing season of the common bean trial in Zimbabwe.

Table 3.2 Temperature, rainfall and evaporation experienced at Harare Research Station during the growing season of the common bean trials in 2009

Climatic factor	Month			
	February	**March**	**April**	**May**
Mean maximum temperature, ^{o}C	26.01	26.37	26.44	24.87
Mean minimum temperature, ^{o}C	14.74	14.47	12.16	9.75
Total rainfall, mm	94.70	32.00	10.50	7.10
Evaporation, mm	40.00	36.32	16.13	8.00

3.3.2 Plant material for field experiments

The reference collection was divided into two major groups according to centre of domestication namely Andean and Mesoamerican. Genotypes were placed in separate experiments according to this grouping. Genotypes within each gene pool were further divided into races based on agro-morphological characters (Singh *et al.* 1991) and as reflected by polymorphisms using molecular markers (Blair *et al.* 2007). The Andean genotypes were grouped into races Nueva Granada, with two sub-races, Nueva Granada 1 (NG1) and Nueva Granada 2 (NG2), Peru and Chile (Table 3.3). Mesoamerican genotypes were classified into races Durango, with two sub-races, Durango 1 (D1) and Durango 2 (D2), Guatemala (G) and Mesoamerica which also had two sub-races, Mesoamerica 1 (M1) and Mesoamerica 2 (M2) (Table 3.4). In this study, a total of 81 Andean and 121 Mesoamerican genotypes were evaluated under rainfed and irrigated conditions at CIAT-Palmira and Harare Research Station.

Table 3.3 Andean genotypes grouped according to their race classification with their principal characteristics and country of origin

Genotype	Race	Phaseolin type	Growth habit	Country of origin
G1836	NG1	T	II	Costa Rica
G1938	NG1	T	II	Mexico
G738	NG1	T	I	Guatemala
G1688	NG1	T	II	Brazil
G3157	NG1	T	I	Guatemala
G5625	NG1	T	I	Mexico
G17076	NG1	T	I	Ecuador
G18942	NG1	T	I	Brazil
G18255	NG1	T	I	Cuba
G17070	NG1	T	I	Ecuador
G11957	NG1	T	III	Mexico
G13094	NG1	T	I	Mexico
G16115	NG1	T	I	Peru
G11982	NG1	T	I	Mexico
G7776	NG1	T	I	Ecuador
G5273	NG1	T	I	Mexico
G5142	NG1	T	I	Mexico
G22247	NG1	T	I	Dominican Republic
G4001	NG1	T	I	Costa Rica
G2875	NG1	T	I	Mexico
G9846	NG1	T	I	Ecuador
G2563	NG1	T	I	Ecuador
G21210	NG1	T	I	Colombia
G6639	NG1	TM	I	Haiti
G7945	NG1	TM	I	Haiti
G4906	NG1	CA	I	Colombia
G4534	NG1	CA	I	Peru
AND1005	NG2	T	II	Colombia
G1678	NG2	T	II	Brazil
G16110A	NG2	T	II	Peru
G16346	NG2	T	IIB	Ecuador
G13595	NG2	T	III	Colombia
G13911	NG2	T	III	Ecuador
G13910	NG2	T	III	Ecuador
G17168	NG2	T	IN	Ecuador
G18264	NG2	T	III	Dominician Republic
G11759A	NG2	T	IIA	Peru
G14253	NG2	T	II	Peru
G12517	NG2	T	III	Peru
G16104E	NG2	T	I	Peru
G5708	NG2	T	I	Colombia

Table 3.3 continued

Genotype	Race	Phaseolin type	Growth habit	Country of origin
G6873	NG2	T	I	Brazil
G5170	NG2	T	I	Brazil
G7895	NG2	T	I	Peru
G9855	NG2	T	IIB	Ecuador
PVA1111	NG2	T	I	Colombia
G9335	NG2	T	III	Brazil
G23829	NG2	T	II	Peru
G4644	NG2	T	I	Colombia
G5034	NG2	T	I	Brazil
G11585	NG2	T	I	Peru
G9603	NG2	T	III	Brazil
G11564	NG2	T	IIA	Ecuador
G11512	NG2	T	I	Ecuador
G11727	NG2	T	III	Peru
G5849	NG2	H	III	Chile
G4672	NG2	CA	III	Colombia
G2567	P	T	II	Ecuador
DRK47	P	T	I	Colombia
G12529	P	T	III	Peru
G14016	P	T	II	Colombia
G22147	P	T	I	Peru
G23604	P	T	II	Peru
G4494	P	T	I	Colombia
PVA773	P	T	I	Colombia
G2686	P	T	I	Peru
G4739	P	T	II	Peru
G4547	P	H	I	Colombia
G4721	P	H	II	Peru
G19833	P	H	III	Peru
G11521	P	C	I	Ecuador
G8209	P	C	IIIB	Peru
SEQ1003	Check	-	I	Breeding line
CAL96	Check	-	I	Breeding line
G19860	Check	-	III	Breeding line
SEQ1027	Check	-	I	Breeding line
SAB258	Check	-	I	Breeding line
G19842	Check	-	II	Breeding line
SAB645	Check	-	I	Breeding line
CAL143	Check	-	I	Breeding line
AFR619	Check	-	I	Breeding line

P - Peru; NG1 - Nueva Granada 1; NG2 - Nueva Granada 2; T - Tender green; C - Contender; H - Huevo de huanchaco; TM - Tender green and Middle America hybrid; CA - Contender and Ayacucho hybrid; - represents unkown phaseolin type

Table 3.4 Mesoamerican genotypes grouped according to their race classification with their principal characteristics and country of origin

Genotype	Race	Phaseolin type	Growth habit	Country of origin
G1957	M2	Sd	III	Guatemala
G801	M2	S	III	Nicaragua
G803	M2	Sd	III	El Salvador
G1358	M2	Sd	III	Mexico
G1264	M2	S	II	Mexico
G1977	M2	Sb	III	Guatemala
G17649	M2	S	III	Guatemala
G4258	M2	S	III	Guatemala
G12806	M2	S	II	Mexico
G7952	M2	S	III	Mexico
G7038	M2	B	III	Brazil
G5733	M2	B	III	Jamaica
G5712	M2	S	III	Guatemala
G3990	M2	Sb	II	Costa Rica
G4280	M2	Sb	III	Mexico
G14163	M2	S	III	Mexico
G16849A	M2	Sd	III	Guatemala
G18141	M2	Sd	III	Haiti
G15641	M2	Sb	III	Mexico
G11721	M2	B	II	Peru
G7863	M2	Sb	III	Honduras
G7765	M2	B	IIB	Colombia
G7761	M2	Sb	III	Mexico
G18157	M2	B	III	Haiti
G18451	M2	S	III	Nicaragua
G18454	M2	S	II	Nicaragua
G3005	M2	Sb	II	Guatemala
G3178	M2	Sd	III	Guatemala
G3217	M2	Sd	II	Guatemala
G3142	M2	Sb	III	Guatemala
G3017	M2	Sd	III	Guatemala
G3185	M2	Sb	III	Guatemala
G3586	M2	S	III	Mexico
G2093	M1	Sd	II	Nicaragua
G955	M1	Sd	III	Costa Rica
DOR364	M1	S	II	El Salvador
G2199	M1	S	III	Guatemala
G17648	M1	Sd	III	Guatemala
G12778	M1	B	II	Brazil
G5694	M1	B	II	USA

Table 3.4 continued

Genotype	Race	Phaseolin type	Growth habit	Country of origin
G5036	M1	S	II	Brazil
G6450	M1	B	II	Ecuador
G3661	M1	S	III	El Salvador
G4206	M1	S	II	Brazil
G4002	M1	Sb	II	Costa Rica
G4495	M1	B	II	El Salvador
G4637	M1	S	III	Colombia
G16835	M1	S	III	Mexico
G2445	M1	S	III	Mexico
G2348	M1	S	III	Mexico
G2352	M1	Sb	III	Mexico
G2137	M1	S	III	Nicaragua
G7932	M1	S	III	El Salvador
G15416	M1	S	III	Brazil
G19204	M1	B	II	Haiti
G21212	M1	B	III	Haiti
G18147	M1	B	III	Haiti
G3595	M1	B	III	Colombia
G3545	M1	Sd	II	Mexico
G2997	M1	B	III	Guatemala
G3593	M1	Sd	II	Mexico
G1328	G	S	III	Mexico
G1356	G	S	II	Mexico
G5653	G	S	III	Ecuador
G4730	G	B	III	Peru
G16401	G	Sb	III	Mexico
G16072	G	S	III	Mexico
G16400	G	Sd	III	Mexico
G2277	G	S	IIIB	Mexico
G2660	G	Sb	III	Mexico
G22787	G	B	II	Mexico
G278	D2	M	III	Mexico
G753	D2	S	III	Guatemala
G14737	D2	H	III	Peru
G22044	D2	M	IIIB	Mexico
G4278	D2	M	III	Mexico
G3331	D2	Sd	III	Mexico
G3334	D2	Sb	III	Mexico
G13578	D2	B	II	Brazil
G11057	D2	M	III	Mexico
G12796	D2	M	III	Mexico
G4822	D2	S	II	Brazil
G7742	D2	M1	III	Mexico

Table 3.4 continued

Genotype	Race	Phaseolin type	Growth habit	Country of origin
G4017	D2	Sb	III	Brazil
G3936	D2	S	III	Costa Rica
G3807	D2	Sb	I	Brazil
G16026	D2	M1	III	Mexico
G15685	D2	M	III	Mexico
G11656A	D2	S	III	Guatemala
G14914	D2	S	III	Mexico
G19012	D2	M	III	Mexico
G1797	D1	M	III	Mexico
G10945	D1	S	III	Mexico
G18440	D1	Sd	III	Mexico
G2379	D1	T	III	Peru
G13177	D1	M	III	Mexico
G7602	D1	S	III	Mexico
G4342	D1	M	III	Mexico
G13696	D1	M	III	Mexico
G2402	D1	Sd	III	Mexico
G2635	D1	S	III	Mexico
G2866	D1	S	III	Mexico
G2775	D1	Sb	III	Mexico
G2778	D1	M	III	Mexico
G10982	D1	Sd	III	Mexico
G10971	D1	Sd	III	Mexico
G11010	D1	Sb	III	Mexico
G19941	D1	S	III	Mexico
SXB418	Check	-	III	Breeding line
SER16	Check	-	III	Breeding line
SEA15	Check	-	III	Breeding line
SER109	Check	-	III	Breeding line
DOR390	Check	-	III	Breeding line
VAX3	Check	-	III	Breeding line
BAT93	Check	-	III	Breeding line
BAT477	Check	-	III	Breeding line
Masaai Red	Check	-	III	Breeding line
Pinto Villa	Check	-	III	Breeding line
NCB280	Check	-	III	Breeding line
Tio Canela 75	Check	-	III	Breeding line
Maharagi Soja	Check	-	III	Breeding line

D1- Durango 1; D2 - Durango 2; M1 - Mesoamerica 1; M2 - Mesoamerica 2; G - Guatemala; S - Sanilac; Sb - Sanilac Brazil; Sd - Sanilac Durango; T - Tender green; H - Huevo de huanchaco; M – Middle America; M1 – Middle America and Inca hybrid; B – phaseolin type unique to genotypes originating from Colombia; - represents unknown phaseolin type

3.3.3 Growth habit definitions

According to Singh (1995), growth habits vary from determinate bush to indeterminate climbing in common bean germplasm. Type I genotypes form a determinate inflorescence at the end of stems and branches and have a lower number of nodes. Types II and III have indeterminate growth with stem and branches ending in a vegetative guide. Type II genotypes are erect and have little guide development. Type III genotypes have a more prostate growth, many branches and show moderate climbing ability if given support. Type IV genotypes are indeterminate with excessively long stems and branches making them weak. Plants in this group have a strong climbing ability.

3.3.4 Methodologies for field experiments

3.3.4.1 Design of experiments

At both sites, two treatments, irrigation and rainfed, were applied to quantify the effects of the intensity and duration of terminal drought on crop growth and seed yield. At CIAT-Palmira, the two treatments were next to each other in one field. However, at Harare Research Station, the two treatments were in separate fields due to small sizes of the fields. The rainfed treatment represented the terminal drought experienced in common bean. Separate experiments of 9x9 lattices for Andean and 11x11 lattices for Mesoamerican genotypes were planted in each treatment. Genotypes were planted in two row plots, replicated three times in each treatment.

3.3.4.1.1 CIAT-Palmira, Colombia

The plot sizes were 2.4 m long with a row-to-row distance of 0.6 m and plant-to-plant spacing of 0.075 m. The two treatments were established with three early irrigations of 35 mm each at -1, 15 and 34 days from/after planting. The irrigated treatment received three additional gravity irrigations of 35 mm of water at 45, 55 and 72 days after planting. Liquid sprays of urea, boron and zinc were done at the second, third and fourth week after planting in both treatments. The liquid spray was composed of 1 kg urea ha^{-1}, 300 g boron ha^{-1}, 300 g zinc ha^{-1} and 200 l water ha^{-1}.

3.3.4.1.2 Harare Research Station, Zimbabwe

Plot sizes of 2.0 m long with a row-to-row distance of 0.6 m and plant-to-plant spacing of 0.1 m were established at Harare Research Station. Trial establishment was achieved by planting using natural rainfall for the two treatments which was followed by early sprinkler irrigations of 30 mm each at 10 and 20 days after planting. Plots representing the irrigated treatment received four supplementary sprinkler irrigations of 30 mm of water at 30, 42, 55 and 70 days after planting. Drought stressed plots also received supplementary sprinkler irrigation of 30 mm of water at 51 days after planting. A basal dress of compound D fertiliser (N P K: 14% 7% 7%) was applied at a rate of 300 kg ha^{-1} in both treatments a day before planting. A top dress of 80 kg ha^{-1} ammonium nitrate fertiliser was applied in both treatments at 21 days after planting. Sprays of copper oxychloride and dimethoate were done at the third, fourth and fifth week after planting as a measure against bacterial diseases and aphids in both treatments.

3.3.4.2 Data collection

Crop development was monitored by recording days to flowering and maturity. A number of morphological shoot traits were measured at mid-pod filling stage in order to determine variation of traits under irrigated and drought treatments. In addition, physiological traits were measured at CIAT-Palmira. Yield and yield components were determined at harvest time at both locations.

3.3.4.2.1 Morphological shoot traits determined at mid-pod filling stage

Morphological shoot traits were measured through destructive sampling at mid-pod filling growth stage. A row length of 0.5 m for each plot was selected for destructive sampling. The number of plants sampled was recorded and stems were cut at the soil surface. Plants were separated into leaves (without petioles), stems and reproductive structures (pods and flowers). Separated leaves, pods and stems were placed in well labelled paper bags. Dry biomass of plant parts was determined by oven drying the samples at 60^{o}C for 48 hours. After drying of samples, the dry weight of each sample was recorded.

3.3.4.2.2 Physiological traits

Quantum yield (QY): QY was measured by a non-destructive, hand-held QY meter (Fluorpen FP100, Photon Systems Instruments, Brno, Czech Republic) which measures photosystem II quantum yield. Fluorpen FP100 is a fluorometer that allows quick and precise measurement of chlorophyll fluorescence parameters in plants in the laboratory, greenhouse or in the field. Fluorpen FP100 measures F_T (continuous fluorescence yield in non-actinic light). F_T is equivalent to F_0 if the leaf sample is dark-adapted. F_0 is the yield of fluorescence in the absence of photosynthetic light and is the minimal fluorescence. Another fluorescence parameter measured is F_M and represents the maximum fluorescence when a highest intensity flash of light is applied on leaves. FV measures variable fluorescence and is calculated as F_M-F_0 and QY (Photosystem II quantum yield) is equivalent to F_V/F_M in dark-adapted samples and to $F_{V'}/F_{M'}$ in light-adapted samples. The QY value was measured on a fully expanded young leaf of one plant on each replication in both treatments.

Canopy temperature: An infrared thermometer (Telatemp model AG-42D, Telatemp, Fullerton, CA, USA) was held at 50 cm from the canopy surface in a 45^o angle in order to measure the canopy temperature and the difference in temperature between the leaf canopy and the surrounding air temperature.

3.3.4.3 Yield and yield components determination

The plants remaining after morphological traits determination were harvested for yield and yield components determination. Five plants were selected for determination of grain yield, 100-seed size, number of pods per plant and number of empty pods per plant. Hundred-seed weight is a measure of seed size.

3.3.4.4 Drought intensity index, percentage reduction and drought susceptibility index

The drought intensity index (DII), percentage reduction (PR) and drought susceptibility index (DSI) due to drought stress were calculated for the Andean and Mesoamerican trials at CIAT-Palmira and Harare Research Station according to Fischer and Maurer

(1978). DII is used to compare the drought stress between two or more experiments. DII values below 0.49 indicate moderate drought and those exceeding 0.7 indicate severe drought. It is calculated as:

DII = (1-Xs/Xi)

Xs is the grand mean yield of all genotypes grown under drought stress

Xi is the grand mean yield of all genotypes grown under optimum conditions.

PR = [1-(Xs/Xi) x 100]

DSI = PR/DII

3.3.4.5 Geometric mean

GM is used to calculate average performance of genotypes between irrigated and rainfed treatments in one location. GM = √ (Ys x Yi) where Ys is yield under the stressed treatment and Yi is yield under the irrigated treatment.

3.3.4.6 Soil moisture measurements

The watermark irrometer was used to measure water in the soil. The watermark sensor (granular matrix sensor) is an indirect, calibrated method of measuring soil water. It uses an electrical resistance type sensor, read by datalogging equipment which converts the electrical resistance reading to a calibrated reading of kilo Pascal's (kPa) of soil water tension (http://irrigatedw.irrometer.com/sensors.html#wm). These were installed at three different sites in each replication at 0-5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-60 cm and 60-80 cm soil depths. Soil water tension readings were recorded every day from planting to harvesting, at 0900 hrs.

3.3.4.7 Data analysis

The phenotypic data were initially analysed separately for each treatment in each location in a one way analysis of variance (ANOVA). Phenotypic data were also analysed across the two treatments in each location to compare performance between treatments. All data analysis was done using Agrobase Generation II software (Agronomix Software Inc., 2005) and Genstat Edition version 14. The data was not analysed combined across the two locations (Harare Research Station and CIAT-Palmira) since they represent different

mega environments, and are therefore not really comparable. The aim of the study was rather to determine the reaction of genotypes to drought stress. Pearson correlation coefficients (r) and regression analysis between grain yield and shoot biomass, days to maturity, seed size and physiological traits measured were calculated for each trial in Agronomix Software Inc. (2005) software. Broad sense heritability for each measured trait under irrigated and rainfed treatments was also determined in Agronomix Software Inc. (2005). Correlations between treatments at each location were determined using Genstat Edition version 14 and were based on grain yield.

3.4 Results

3.4.1 Weather conditions during the crop growing period

The maximum monthly mean temperatures recorded over the growing period ranged between 24.9-26.4˚C at Harare Research Station and 30.01-33.7˚C at CIAT-Palmira. The drought stress imposed on the trials at CIAT-Palmira was accompanied by heat stress since common bean thrive under temperatures ranging from 20-26˚C. The cool weather conditions experienced at Harare Research Station encouraged disease outbreaks that affected both Andean and Mesoamerican trials. There were some traces of common bacterial blight (CBB) (*Xanthomonas campestris phaseoli* (Smith) Dowson) and rust (*Uromyces appendiculatus* (Pers.) Unger) in most genotypes under rainfed conditions in both Andean and Mesoamerican trials (Appendices 1 and 2). Angular leaf spot (ALS) (*Phaeoisariopsis griseola* (Sacc.) Ferraris) was more pronounced under the irrigated treatment in Mesoamerican trials. CBB scores varied from 1.00-3.67 and 1.67-5.00 in Mesoamerican trials under rainfed and irrigated treatments respectively (Appendix 1). Variation for rust scores ranged from 1.00-7.33 and 1.00-3.67 under rainfed and irrigated treatments for Mesoamerican trials respectively. Meanwhile, rust scores varied from 1.00-6.67 under the rainfed treatment in Andean trials (Appendix 2). On the other hand, CCB scores ranged between 1.00 and 5.00 in Andean trials under the rainfed treatment.

3.4.2 Analysis of variance for Mesoamerican genotypes evaluated at CIAT-Palmira and Harare Research Station

The combined ANOVA across treatments showed that the effects of genotypes (G) and treatments (T) were highly significant ($P<0.001$) for grain yield, 100-seed weight, number of pods per plant, days to flowering and maturity at both locations (Tables 3.5 and 3.7). In addition to these traits, the expression of dry pod biomass, dry stem biomass, total dry biomass and leaf temperature were also significantly influenced by genotypes and treatments at CIAT-Palmira (Table 3.6). Genotypes accounted for the largest percentage of the variation observed for grain yield, 100-seed weight, pod length, days to flowering and maturity, dry pod and leaf biomass at both locations. Treatment effects made the largest contribution (38.7%) to variation in canopy temperature depression at CIAT-Palmira. GxT interaction also influenced the expression of grain yield at both locations and canopy temperature depression, leaf temperature and total dry biomass at CIAT-Palmira. At Harare Research Station, dry pod biomass was also affected by GxT interaction (Table 3.8). Variation accounted by treatment was below 20% for most traits measured at CIAT-Palmira except canopy temperature depression and total dry biomass. The mean correlation coefficient between treatments at CIAT-Palmira was 57% indicating a close relationship between them (data not shown). At Harare Research Station, treatments accounted for 23.9% of the total variation observed in grain yield and the highest amount in dry stem biomass (56%).

Table 3.5 Combined analysis of variance for agronomic data measured from Mesoamerican trials evaluated at CIAT-Palmira

Grain yield						100-seed weight					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	1102744	551372		0.36	Rep	2	55.54	27.77		0.40
Gen (G)	120	186775877	1556466	<0.001	60.41	Gen (G)	120	41619.7	346.83	<0.001	77.26
Trt (T)	1	29661708	29661708	<0.001	9.59	Trt (T)	1	316.16	316.16	<0.001	0.59
GxT	120	23156682	192972	0.013	7.49	GxT	120	2510.65	20.92	0.311	4.66
Error	482	68481397	142078		22.15	Error	482	9416.34	19.58		17.48
Total	725	309178408				Total	725	53867.4			
Days to flowering						**Days to maturity**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	6.118	3.059		0.06	Rep	2	6.11	3.06		
Gen (G)	120	10147.9	84.566	<0.001	92.10	Gen (G)	120	23446	195.38	<0.001	0.02
Trt (T)	1	28.562	28.562	<0.001	0.26	Trt (T)	1	2435.86	2435.86	<0.001	66.68
GxT	120	196.438	1.637	0.066	1.78	GxT	120	1959.87	16.33	0.308	6.93
Error	482	639.882	1.328		5.81	Error	482	7340.24	15.26		5.57
Total	725	110118.9				Total	725	35164.1			20.87
Number of pods per plant						**Pod length**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	35.35	17.675		0.41	Rep	2	0.8945	0.4472		0.08
Gen (G)	120	2826.07	23.551	<0.001	33.12	Gen (G)	120	717.611	5.9801	<0.001	61.19
Trt (T)	1	524.705	524.705	<0.001	6.15	Trt (T)	1	11.899	11.899	<0.001	1.01
GxT	120	890.068	7.417	0.876	10.43	GxT	120	95.721	0.7977	0.254	8.16
Error	482	4256.28	8.83		49.88	Error	482	350.462	0.7286		29.88
Total	725	8532.47				Total	725	1172.772			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment, %explained – percentage variation explained from sum of squares; F pr – F probability

Table 3.6 Combined analysis of variance for plant biomass measured from Mesoamerican trials evaluated at CIAT-Palmira

Dry leaf biomass						Dry stem biomass					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	6.917	3.459		0.35	Rep	2	57.337	28.669		1.44
Gen (G)	120	1032.916	8.608	<0.001	51.82	Gen (G)	120	1601.12	13.343	<0.001	40.32
Trt (T)	1	1.813	1.813	0.276	0.09	Trt (T)	1	782.336	782.336	<0.001	19.70
GxT	120	217.799	1.815	0.102	10.93	GxT	120	302.59	2.522	0.517	7.62
Error	482	733.769	1.522		36.81	Error	482	1227.87	2.547		30.92
Total	725	1993.214				Total	725	3971.26			
Dry pod biomass						**Total dry biomass**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	98.00	49.00		0.45	Rep	2	205.27	102.64		0.59
Gen (G)	120	11086.8	92.39	<0.001	51.10	Gen (G)	120	9163.97	76.37	<0.001	26.19
Trt (T)	1	1939.42	1939.42	<0.001	8.94	Trt (T)	1	13156.22	13156.22	<0.001	37.60
GxT	120	1852.37	15.44	0.229	8.54	GxT	120	3341.07	27.84	0.003	9.55
Error	482	6717.99	13.94		30.97	Error	482	9126.13	18.93		26.08
Total	725	21694.5				Total	725	34992.66			
Leaf temperature						**Canopy temperature depression**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	138.123	69.061		4.87	Rep	2	872.05	436.025		17.39
Gen (G)	120	580.203	4.835	<0.001	20.47	Gen (G)	120	418.856	3.49	0.031	8.35
Trt (T)	1	49.822	49.822	<0.001	1.76	Trt (T)	1	1939.88	1939.88	<0.001	38.69
GxT	120	554.024	4.617	0.003	19.55	GxT	120	483.989	4.033	0.002	9.65
Error	482	1512.17	3.144		53.36	Error	482	1298.98	2.695		25.91
Total	725	2833.8				Total	725	5013.75			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

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Table 3.7 Combined analysis of variance for agronomic data measured from Mesoamerican trials evaluated at Harare Research Station

Grain yield						100-seed weight					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	3992591	1996295		2.78	Rep	2	40.68	20.34		0.22
Gen (G)	120	58016881	483474	<0.001	40.35	Gen (G)	120	6140.16	51.17	<0.001	33.45
Trt (T)	1	34309112	34309112	<0.001	23.86	Trt (T)	1	6103.34	6103.34	<0.001	33.25
GxT	120	17464648	145539	0.036	12.15	GxT	120	1326.83	11.06	0.199	7.23
Error	482	30010376	62262.19		20.87	Error	482	4742.65	9.84		25.84
Total	725	143793608				Total	725	18353.66			
Days to flowering						**Days to maturity**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	2.142	1.071		0.02	Rep	2	444.74	222.37		0.61
Gen (G)	120	9628.94	80.241	<0.001	75.38	Gen (G)	120	44027.15	366.89	<0.001	60.34
Trt (T)	1	102.68	102.68	<0.001	0.80	Trt (T)	1	8098.46	8098.46	<0.001	11.10
GxT	120	601.54	5.013	0.522	4.71	GxT	120	4404.78	37.01	0.458	6.04
Error	482	2440.53	5.074		19.10	Error	482	17315.68	36.61		23.73
Total	725	12774.49				Total	725	72960.97			
Number of pods per plant						**Pod length**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	383.51	191.76		3.44	Rep	2	11.225	5.612		0.54
Gen (G)	120	5858.85	48.84	<0.001	52.53	Gen (G)	120	1268.805	10.573	0.01	61.27
Trt (T)	1	756.81	756.81	<0.001	6.79	Trt (T)	1	38.512	38.512	<0.001	1.86
GxT	120	1176.89	9.81	0.925	10.55	GxT	120	318.874	2.657	0.468	15.40
Error	482	2987.49	6.20		26.78	Error	482	436.573	0.906		21.08
Total	725	11153.8				Total	725	2070.999			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

Table 3.8 Combined analysis of variance for plant biomass measured from Mesoamerican trials evaluated at Harare Research Station

Dry leaf biomass						Dry stem biomass					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**% explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**% explained**
Rep	2	293.08	146.54		3.49	Rep	2	41.22	20.61		0.46
Gen (G)	120	5152.92	42.94	<0.001	61.34	Gen (G)	120	2329.77	19.41	<0.001	25.81
Trt (T)	1	0.11	0.11	0.919	0.00	Trt (T)	1	5054.49	5054.49	0.048	56.00
GxT	120	905.39	7.54	0.989	10.78	GxT	120	932.94	7.77	0.976	10.34
Error	482	2049.40	4.25		24.40	Error	482	668.18	1.39		7.40
Total	725	8400.90				Total	725	9026.60			
Dry pod biomass						**Total dry biomass**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**% explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**% explained**
Rep	2	3.03	1.52		0.02	Rep	2	1875.83	937.91		3.97
Gen (G)	120	7635.62	63.63	<0.001	51.41	Gen (G)	120	11912.25	99.27	<0.001	25.24
Trt (T)	1	7.75	7.75	0.408	0.05	Trt (T)	1	11.16	11.16	0.657	0.02
GxT	120	1823.09	15.19	0.013	12.28	GxT	120	6169.84	51.42	0.732	13.07
Error	482	5381.63	11.17		36.24	Error	482	27233.51	56.50		57.69
Total	725	14851.12				Total	725	47202.58			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

3.4.3 Analysis of variance for Andean genotypes evaluated at CIAT-Palmira and Harare Research Station

Yield, yield components and phenology traits are usually most affected by drought stress and were therefore first to be investigated in data analysis. Genotype and treatment effects were significant (P<0.001) for grain yield, days to maturity and 100-seed weight at CIAT-Palmira and Harare Research Station when data were subjected to combined ANOVA (Tables 3.9 and 3.11). Expression of these three traits was also affected by GxT interaction at both locations. In addition, dry leaf, stem and pod biomass were also significantly affected by GxT interaction at CIAT-Palmira. Treatment main effects accounted for less than 6% of the variation observed in most traits measured except dry stem (12.55%) and pod (27.80%) biomass as well as total dry biomass (31.01%) at CIAT-Palmira (Table 3.10). The irrigated and rainfed treatments showed a high correlation at CIAT-Palmira for Andean trials ($r=0.74^{***}$, data not shown) and might explain why treatments contributed less to the variation observed. In contrast, correlations between treatments were significant but low at Harare Research Station ($r=0.21^{***}$, data not shown) and treatments made higher contributions to the variation observed on grain 100-seed weight (68.8%), dry stem biomass (52.0%), yield (40.3%), dry pod biomass (35.2%), number of pods per plant (31.9%), pod length (21.3%), dry leaf biomass (20.1%) and days to maturity (12.3%) (Table 3.12). At Harare Research Station, 100-seed weight (68.8%), followed by dry stem biomass (52.0%) and grain yield (40.3%) were highly affected by treatments.

For physiological traits measured at CIAT-Palmira, treatments had a highly significant effect (P<0.001) on canopy temperature depression, photosynthetic efficiency and significant for leaf temperature (P=0.004) (Table 3.10). Contribution of treatments to the total variation observed was highest for photosynthetic efficiency (64.0%) and less than 10% for canopy temperature depression and leaf temperature. At Harare Research Station, 100-seed weight (68.8%), followed by dry stem biomass (52.0%) and grain yield (40.3%) were significantly affected by treatments.

Table 3.9 Combined analysis of variance for agronomic data measured from Andean trials evaluated at CIAT-Palmira

Grain yield						100-seed weight					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	428760	214380		0.23	Rep	2	316.11	158.06		0.33
Gen (G)	80	147072245	1838403	<0.001	77.93	Gen (G)	80	71383.20	892.29	<0.001	74.61
Trt (T)	1	7375270	7375270	<0.001	3.91	Trt (T)	1	5007.77	5007.77	<0.001	5.23
GxT	80	11361766	142022	<0.001	6.02	GxT	80	6098.78	76.23	<0.001	6.37
Error	322	22477589	69806		11.91	Error	322	12870.70	39.97		13.45
Total	485	188715630				Total	485	95676.60			
Days to flowering						**Days to maturity**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	14.13	7.06		0.08	Rep	2	200.94	100.47		0.16
Gen (G)	80	15934.60	199.18	<0.001	92.63	Gen (G)	80	81779.30	1022.24	<0.001	63.75
Trt (T)	1	5.35	5.35	0.187	0.03	Trt (T)	1	2225.51	2225.51	<0.001	1.73
GxT	80	263.82	3.30	0.322	1.53	GxT	80	13199.80	165.00	<0.001	10.29
Error	322	985.21	3.06		5.73	Error	322	30866.40	95.86		24.06
Total	485	17203.1				Total	485	128272.00			
Number of pods per plant						**Pod length**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	6.64	3.33		0.11	Rep	2	4.40	2.20		0.14
Gen (G)	80	4340.23	54.25	<0.001	70.31	Gen (G)	80	2272.87	28.41	<0.001	74.01
Trt (T)	1	91.26	91.26	<0.001	1.48	Trt (T)	1	68.83	68.83	<0.001	2.24
GxT	80	341.68	4.27	0.516	5.53	GxT	80	156.63	1.96	0.265	5.10
Error	322	1393.49	4.33		22.57	Error	322	568.42	1.77		18.51
Total	485	6173.3				Total	485	3071.16			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

Table 3.10 Combined analysis of variance for plant biomass and temperatures measured from Andean trials evaluated at CIAT-Palmira

Dry leaf biomass						Dry stem biomass					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	38.07	19.04		4.10	Rep	2	126.29	63.13		7.66
Gen (G)	80	428.86	5.36	<0.001	46.22	Gen (G)	80	594.96	7.44	<0.001	36.10
Trt (T)	1	9.28	9.28	0.002	1.00	Trt (T)	1	206.77	206.77	<0.001	12.55
GxT	80	135.06	1.688	<0.001	14.55	GxT	80	232.54	2.91	<0.001	14.11
Error	322	316.66	0.98		34.13	Error	322	487.43	1.51		29.58
Total	485	927.94				Total	485	1647.97			
Dry pod biomass						**Total dry biomass**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	6.25	3.13		0.06	Rep	2	222.03	111.02		1.63
Gen (G)	80	4508.22	56.35	<0.001	43.66	Gen (G)	80	3178.75	39.73	<0.001	23.39
Trt (T)	1	2871.25	2871.25	<0.001	27.80	Trt (T)	1	4215.42	4215.42	<0.001	31.01
GxT	80	951.94	11.90	<0.001	9.22	GxT	80	1434.89	17.94	0.077	10.56
Error	322	1989.03	6.18		19.26	Error	322	4541.81	14.11		33.41
Total	485	10326.7				Total	485	13592.92			
Leaf temperature						**Canopy temperature depression**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	55.64	27.82		2.99	Rep	2	8.76	4.38		0.50
Gen (G)	80	242.12	3.03	0.934	13.02	Gen (G)	80	250.16	3.13	0.683	14.14
Trt (T)	1	34.40	34.40	0.004	1.85	Trt (T)	1	149.16	149.16	<0.001	8.43
GxT	80	236.42	3.00	0.949	12.71	GxT	80	257.46	3.22	0.624	14.56
Error	322	1291.12	4.01		69.43	Error	322	1103.33	3.43		62.37
Total	485	1859.69				Total	485	1768.87			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

Table 3.11 Combined analysis of variance for agronomic data measured from Andean trials evaluated at Harare Research Station

Grain yield						100-seed weight					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	218864	109432		0.20	Rep	2	36.41	18.21		0.11
Gen (G)	80	31512964	393912.1	<0.001	29.51	Gen (G)	80	3040.45	38.01	<0.001	9.07
Trt (T)	1	43019393	43019393	<0.001	40.28	Trt (T)	1	23064	23064	<0.001	68.83
GxT	80	10758530	134482	0.030	10.07	GxT	80	2555	31.94	<0.001	7.63
Error	322	21291425	66122.44		19.94	Error	322	4811.59	14.94		14.36
Total	485	106801176				Total	485	33507.45			
Days to flowering						**Days to maturity**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	9.20	4.60		0.14	Rep	2	6.922	3.46		0.02
Gen (G)	80	5992.39	74.91	<0.001	89.19	Gen (G)	80	26788	334.85	<0.001	74.81
Trt (T)	1	1.00	1.00	0.437	0.01	Trt (T)	1	4385.54	4385.54	<0.001	12.25
GxT	80	186.34	2.33	0.019	2.77	GxT	80	2983.43	37.77	<0.001	8.33
Error	322	529.47	1.64		7.88	Error	322	2702.70			7.55
Total	485	6718.39				Total	485	35808.50			
Number of pods per plant						**Pod length**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	34.29	17.14		1.23	Rep	2	4.96	2.47		0.19
Gen (G)	80	1435.71	17.95	<0.001	51.60	Gen (G)	80	1187.76	14.85	<0.001	45.09
Trt (T)	1	888.77	888.77	0.036	31.94	Trt (T)	1	562.05	562.05	0.007	21.34
GxT	80	403.91	5.05	0.228	14.52	GxT	80	493.45	6.17	0.576	18.73
Error	322	19.76	0.061		0.71	Error	322	385.87	1.20		14.65
Total	485	2782.44				Total	485	2634.09			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

Table 3.12 Combined analysis of variance for plant biomass measured from Andean trials evaluated at Harare Research Station

Dry leaf biomass						Dry stem biomass					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	1.99	1.00		0.76	Rep	2	4.84	2.42		2.07
Gen (G)	80	104.60	1.31	<0.001	40.16	Gen (G)	80	67.15	0.84	<0.001	28.75
Trt (T)	1	52.29	52.29	<0.001	20.08	Trt (T)	1	121.56	121.56	0.002	52.04
GxT	80	39.36	0.49	0.100	15.11	GxT	80	36.45	0.46	0.132	15.61
Error	322	62.72	0.19		24.08	Error	322	3.56	0.01		1.52
Total	485	260.44				Total	485	233.56			
Dry pod biomass						**Total dry biomass**					
Source	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**	**Source**	**D.f.**	**S.S.**	**M.S.**	**F pr.**	**%explained**
Rep	2	1.70	0.85		0.35	Rep	2	23.20	11.60		1.81
Gen (G)	80	261.46	3.27	<0.001	53.85	Gen (G)	80	326.60	4.08	<0.001	25.42
Trt (T)	1	170.83	170.83	0.002	35.19	Trt (T)	1	106.50	106.50	0.088	8.29
GxT	80	46.53	0.58	0.288	9.58	GxT	80	212.75	2.66	0.143	16.56
Error	322	4.98	0.02		1.03	Error	322	615.90	1.91		47.93
Total	485	485.50				Total	485	1284.94			

D.f. – degrees of freedom; S.S. – sum of squares; M.S. – mean squares; Gen – genotype; Trt – treatment; %explained – percentage variation explained from sum of squares; F pr – F probability

3.4.4 Intensity of drought applied at different locations

Drought stress was higher at Harare Research Station in both Andean and Mesoamerican trials than at CIAT-Palmira (Table 3.13). Grain yield reductions of more than 40% were recorded at Harare Research Station in Andean and Mesoamerican trials. A high disease pressure from angular leaf spot, common bacterial blight and rust experienced at this location might have amplified yield losses under the drought treatment. Low mean rank correlation coefficients (Andean $r=0.2104^{***}$ and $r=0.3210^{***}$ for Mesoamerican trials, data not shown) between treatments at Harare Research Station also showed wide differences between treatments at this location.

Table 3.13 Drought intensity index (DII) due to drought stress calculated for Andean and Mesoamerican trials at CIAT-Palmira and Harare Research Station

Location	CIAT-Palmira	Harare Research Station
Trial	**DII**	**DII**
Andean	0.22	0.41
Mesoamerican	0.23	0.51

DII – drought intensity index

3.4.5 Performance of Mesoamerican and Andean genotypes under drought stress

Under the rainfed treatment, grain yield for experimental lines varied from 64.50 kg ha^{-1} to 2 338.30 kg ha^{-1} at CIAT-Palmira and 88.00 kg ha^{-1} to 960.00 kg ha^{-1} at Harare Research Station for the Mesoamerican trials (Appendixes 3 and 4). At CIAT-Palmira, grain yield from Mesoamerican check genotypes varied from 870.00 kg ha^{-1} to 2 770.90 ka ha^{-1} under the rainfed treatment. Meanwhile, grain yield for experimental lines ranged from 246.67 kg ha^{-1} to 2 723.40 kg ha^{-1} at CIAT-Palmira and 232.00 kg ha^{-1} to 1 872.00 kg ha^{-1} at Harare Research Station under irrigation. Grain yield for Mesoamerican check genotypes ranged from 803.20 kg ha^{-1} to 2 524.70 kg ha^{-1} at CIAT-Palmira and 448.00 kg ha^{-1} to 1 624.00 kg ha^{-1} at Harare Research Station under irrigated treatments. Check genotypes, BAT477 and DOR390 as well as landrace G11721 ranked in the top 15 at both locations. Grain yield ranged from 0.00 kg ha^{-1} to 1 809.30 kg ha^{-1} under rainfed and 0.00 kg ha^{-1} to 2 158.10 kg ha^{-1} under irrigated conditions at CIAT-Palmira for Andean

experimental lines (Appendix 5). At CIAT-Palmira, the yield performance of check genotypes ranged from 595.97 kg ha^{-1} to 1 672.40 kg ha^{-1} under rainfed treatment and 839.27 kg ha^{-1} to 2 075.50 kg ha^{-1} under irrigated treatment. At Harare Research Station, grain yield for experimental lines varied from 12.33 kg ha^{-1} to 1 184 kg ha^{-1} under the rainfed treatment and 272.00 kg ha^{-1} to 1520.00 kg ha^{-1} under the irrigated treatment (Appendix 6). Yield performance of check genotypes varied between 344.00 kg ha^{-1} to 824.00 kg ha^{-1} under rainfed treatment and 696.00 kg ha^{-1} to 1 264.00 kg ha^{-1} under irrigated treatment at Harare Research Station. Among the Andean genotypes, G19860, G12529 and G19833 (all race Peru genotypes) failed to produce any seed at CIAT-Palmira and had low yield at Harare Research Station showing the poor adaptation of Peru genotypes to the testing environments due to heat under lower elevation.

3.4.5.1 Mesoamerican trials

The largest reductions in yield due to drought stress was in race Mesoamerica sub-race 1 at CIAT-Palmira (27%) and Harare Research Station (57%) (Tables 3.14 and 3.15). Race Mesoamerica 1 also had DSI values larger than 1 at both locations. In contrast, genotypes from checks and race Durango sub-race 1 genotypes showed comparatively lower seed yield reductions at both locations. At CIAT-Palmira, Mesoamerica sub-race 1 and race Guatemala genotypes were less affected by drought stress for 100-seed weight and days to maturity respectively. Meanwhile, 100-seed weight were less affected in checks and Mesoamerica sub-race 2 genotypes and days to maturity were less affected in Durango sub-race 1 genotypes at Harare Research Station. Genotypes of race Mesoamerica sub-race 2 exhibited the largest reduction in 100-seed weight and days to maturity at CIAT-Palmira whereas races Guatemala and Durango-Jalisco sub-race 2 had the largest reduction in 100-seed weight and days to maturity at Harare Research Station. Drought stress accelerated maturity and reduced 100-seed weight of genotypes within each group at both locations. Reductions in days to maturity under the rainfed treatment ranged from 3-6% and 5-8% at CIAT-Palmira and Harare Research Station, respectively. Hundred seed weight was reduced by 2-7% and 18-27% under the rainfed treatment at CIAT-Palmira and Harare Research Station respectively.

Broad sense heritabilities for the measured traits were higher under irrigated than rainfed treatments at both locations for grain yield, days to maturity and total biomass (Tables 3.14 and 3.15). At Harare Research Station the other measured traits had higher heritabilities under irrigated than rainfed treatments except for pod biomass at mid-pod fill. At both locations, broad sense heritabilities were highest for days to flowering and lowest for numbers of pods per plant under both irrigated and rainfed treatments. Leaf biomass at mid-pod fill also had low heritability at Harare Research Station under both irrigated and rainfed treatments. At CIAT-Palmira, 100-seed weight had high heritabilities under both treatments.

Table 3.14 Performance of genotypes based on race classification in Mesoamerican trials at CIAT-Palmira

Race	Treatm	Traits												
		Yield	**PR**	**DSI**	**P100**	**PR**	**DM**	**PR**	**PP**	**PL**	**LB**	**SB**	**PB**	**TB**	**DF**
Checks	Irr	2212.49			27.87		61.92		11.16	9.67	4.94	8.04	15.28	14.98	33.95
(13)	Rain	1952.49	12.00	0.51	26.10	6.00	58.92	5.00	9.56	9.49	5.01	6.21	12.09	23.31	33.46
D1	Irr	1760.85			36.63		60.92		15.84	8.45	4.50	7.83	14.47	14.46	30.29
(17)	Rain	1479.79	16.00	0.69	35.28	4.00	57.09	6.00	12.60	8.63	4.36	5.73	11.17	21.25	30.06
D2	Irr	1641.72			24.90		64.13		17.00	8.70	5.51	8.39	11.93	12.63	35.15
(20)	Rain	1248.82	24.00	1.04	23.49	6.00	60.03	6.00	13.46	8.37	5.04	6.13	8.13	19.29	34.48
M1	Irr	1895.21			22.54		62.73		13.57	9.61	5.67	8.67	11.65	11.22	35.79
(28)	Rain	968.03	27.00	1.19	22.06	2.00	59.51	5.00	9.45	9.32	5.74	6.59	8.27	20.60	35.57
M2	Irr	1757.06			23.38		63.37		13.91	9.38	5.27	8.22	11.35	10.96	35.59
(33)	Rain	1301.92	26.00	1.13	21.76	7.00	59.60	6.00	10.96	8.91	5.23	6.17	8.22	19.61	35.23
G	Irr	1299.49			24.61		66.50		19.03	8.30	5.66	9.06	8.69	8.41	34.97
(10)	Rain	968.03	26.00	1.11	23.46	5.00	64.78	3.00	19.19	7.97	5.52	7.01	6.33	18.86	34.30
Grand	Irr	1781.61			25.88		63.11		10.83	9.13	5.29	8.35	12.16	12.01	34.59
mean	Rain	1377.32			24.51		59.26		9.14	8.86	5.19	6.27	8.89	20.35	34.19
h^2 (%)	Irr	70.31			86.64		78.32		37.37	75.99	65.74	68.40	71.54	70.35	94.72
h^2 (%)	Rain	62.31			89.84		70.21		53.16	78.72	73.89	70.49	75.89	54.99	95.86
LSDIrr		547.01			8.08		4.31		5.15	1.45	1.40	1.67	4.34	4.89	1.97
LSDRain		607.73			6.12		9.58		4.15	1.60	1.46	2.13	4.16	5.36	1.73
LSD*		408.79			5.05		5.24		3.30	1.01	1.40	1.81	4.24	4.94	1.30

Treatm – treatment; Irr – irrigated treatment; Rain – rainfed treatment; PR – percentage reduction; DSI – drought sensitivity index; P100 – 100-seed weight; DM – days to maturity; PP – number of pods per plant; PL – pod length; LB – dry leaf biomass at mid pod filling stage; SB – dry stem biomass at mid pod filling stage; PB – dry pod biomass at mid pod filling stage; TB – total shoot biomass at mid pod filling stage; DF – days to flowering; LSD Irr – least significant difference for the irrigated treatment; LSDRain – least significant difference for the rainfed treatment; LSD* - least significant difference separating means between treatments; numbers in brackets () represent the number of genotypes constituting a race; h^2 – broad sense heritability; D1 – Durango 1; D2 – Durango 2; M1 – Mesoamerica 1; M2 – Mesoamerica 2; G – Guatemala

Table 3.15 Performance of genotypes based on race classification in Mesoamerican trials at Harare Research Station

Race	Treatm	Traits												
		Yield	**PR**	**DSI**	**P100**	**PR**	**DM**	**PR**	**PP**	**PL**	**LB**	**SB**	**PB**	**TB**	**DF**
Checks	Irr	808.00			12.62		92.69		9.23	7.82	7.67	8.08	4.05	19.80	38.13
(13)	Rain	476.31	41.00	0.80	10.33	18.00	85.87	7.00	8.02	7.82	8.77	8.69	6.26	23.72	37.56
D1	Irr	836.71			17.69		84.98		8.39	7.67	7.37	8.86	8.35	24.59	34.41
(17)	Rain	460.24	45.00	0.88	13.74	22.00	81.04	5.00	6.90	7.06	8.06	8.18	7.41	23.71	33.94
D2	Irr	828.80			12.02		93.65		10.08	7.65	8.32	8.55	4.13	21.07	37.77
(20)	Rain	366.90	56.00	1.09	9.37	22.00	86.42	8.00	7.42	7.48	7.80	7.82	4.57	19.98	37.43
M1	Irr	851.71			11.40		93.27		10.31	8.14	8.19	7.75	2.87	18.81	39.95
(28)	Rain	364.57	57.00	1.12	8.52	25.00	87.37	6.00	7.67	7.54	7.71	7.37	3.48	18.82	38.58
M2	Irr	853.09			11.44		95.49		10.11	7.59	7.99	7.79	3.37	19.05	39.17
(33)	Rain	459.23	46.00	0.91	9.14	20.00	88.57	7.00	8.61	7.13	8.08	7.37	3.63	19.07	38.25
G	Irr	969.60			14.07		96.07		11.10	7.40	7.87	9.33	5.00	22.20	37.37
(10)	Rain	423.20	56.00	1.10	10.27	27.00	90.03	6.00	8.63	6.63	7.50	8.23	3.30	19.03	37.07
Grand	Irr	851.24			13.67		92.95		9.90	7.75	7.96	8.22	4.29	20.45	38.19
mean	Rain	421.06			9.79		86.71		7.89	7.31	7.97	7.77	4.53	20.31	37.42
h^2 (%)	Irr	61.66			73.60		71.98		32.94	65.23	14.51	69.21	66.78	62.35	91.87
h^2 (%)	Rain	47.92			64.31		62.12		29.93	49.47	13.93	51.20	74.72	43.94	86.72
LSD Irr		653.27			4.47		13.00		6.23	2.74	5.09	4.86	5.36	11.13	2.83
LSDRain		385.41			5.12		9.54		4.69	2.44	5.29	5.16	5.25	12.20	4.60
LSD		378.29			3.39		8.04		3.89	1.83	3.66	3.54	3.74	8.24	2.69

Treatm – treatment; Irr – irrigated treatment; Rain – rainfed treatment; PR – percentage reduction; DSI – drought sensitivity index; P100 – 100-seed weight; DM – days to maturity; PP – number of pods per plant; PL – pod length; LB – dry leaf biomass at mid pod filling stage; SB – dry stem biomass at mid pod filling stage; PB – dry pod biomass at mid pod filling stage; TB – total shoot biomass at mid pod filling stage; DF – days to flowering; LSD Irr – least significant difference for the irrigated treatment; LSDRain – least significant difference for the rainfed treatment; LSD - least significant difference separating means between treatments; numbers in brackets () represent the number of genotypes constituting a race; h^2 – broad sense heritability; D1 – Durango 1; D2 – Durango 2; M1 – Mesoamerica 1; M2 – Mesoamerica 2; G – Guatemala

At Harare Research Station, races Durango sub-race 2, Guatemala, Mesoamerica sub-races 1 had significantly lower seed yield under rainfed than irrigated conditions. Yield reductions were highest in Mesoamerica sub-races 1 and 2 as well as race Guatemala under rainfed compared to irrigated conditions at CIAT-Palmira. The advanced line check genotypes as a group had significantly higher seed yield compared to landraces from the Durango sub-race 2, Guatemala, Mesoamerica sub-races 1 and 2 under the rainfed treatment at CIAT-Palmira. At Harare Research Station, the check genotypes also had the highest seed yield compared to all races and sub-races under the rainfed treatment.

Race Durango sub-race 1 had the largest 100-seed weight under irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station. The other four races and checks generally had small seeds at both locations.

3.4.5.2 Andean trials

Drought stress significantly reduced seed yield for race Nueva Granada sub-race 1 genotypes at CIAT-Palmira (Table 3.16). On the other hand, significant yield reduction due to drought stress was observed for race Peru at Harare Research Station (Table 3.17). Seed yield was significantly higher for check genotypes compared to races Nueva Granada 2 and Peru under the rainfed treatment at CIAT-Palmira. Race Nueva Granada 1 also had significantly higher seed yield than race Peru genotypes under the rainfed treatment at CIAT-Palmira. Race Peru had the lowest yield at both locations, possibly because of their limited adaptation to different environments since they are normally cultivated in high altitude cool areas (Singh *et al.* 1991). Race Nueva Granada 2 and race Peru both contained genotypes that were susceptible to drought conditions, while race Nueva Granada sub-race 1 had some early genotypes with good dry-down that were tolerant of drought conditions. At Harare Research Station, where the intensity of drought was more intense, race Peru had the highest DSI and PR values observed in all the traits.

In terms of component traits, race Peru had the highest percentage reduction in days to maturity at CIAT-Palmira. Contrary, percentage reduction in days to maturity and 100-seed weight for this race was low at Harare Research Station where the temperatures

Table 3.16 Performance of genotypes based on race classification in Andean trials at CIAT-Palmira

Race	Treatm	Traits												
		Yield	**PR**	**DSI**	**P100**	**PR**	**DM**	**PR**	**PP**	**PL**	**LB**	**SB**	**PB**	**TB**	**DF**
Checks	Irr	1486.85			44.18		63.62		8.63	9.44	3.60	5.46	10.28	19.29	33.24
(7)	Rain	1265.05	15.00	0.68	40.26	9.00	60.43	5.00	7.35	9.05	4.01	4.25	4.57	12.76	33.33
NG1	Irr	1434.92			44.84		62.53		8.45	9.67	3.04	5.12	10.21	18.43	32.80
(27)	Rain	1053.88	27.00	1.21	36.30	19.00	58.90	6.00	7.54	9.03	3.38	4.07	4.02	11.46	32.83
NG2	Irr	971.57			35.35		67.72		6.73	8.82	3.53	5.60	7.36	16.49	35.88
(30)	Rain	821.19	15.00	0.70	30.12	15.00	65.57	3.00	6.14	8.22	4.04	4.40	2.47	10.81	35.70
Peru	Irr	612.95			28.86		60.12		4.14	7.82	4.34	5.88	3.71	14.00	41.18
(17)	Rain	466.36	24.00	1.09	27.44	5.00	67.48	12.00	3.00	8.11	4.05	3.96	1.53	9.49	40.41
Grand	Irr	1096.67			37.71		64.03		6.86	8.95	3.54	5.49	7.79	16.86	35.74
mean	Rain	850.29			31.29		59.75		6.04	8.19	3.82	4.18	2.97	10.92	35.53
h^2 (%)	Irr	64.01			93.55		97.86		86.18	92.87	81.36	76.97	79.78	51.48	97.00
h^2 (%)	Rain	61.60			87.79		64.55		82.74	80.35	55.14	57.74	88.58	53.28	94.41
LSD Irr		387.46			9.14		3.96		3.20	1.70	1.43	1.95	5.24	7.04	2.23
LSDRain		426.86			10.77		21.91		3.60	2.59	1.73	2.01	1.95	4.71	3.32
LSD*		287.15			7.04		8.08		2.40	1.54	1.12	1.39	2.78	4.22	1.99

Treatm – treatment; Irr – irrigated treatment; Rain – rainfed treatment; PR – percentage reduction; DSI – drought sensitivity index; P100 – 100-seed weight; DM – days to maturity; PP – number of pods per plant; PL – pod length; LB – dry leaf biomass at mid pod filling stage; SB – dry stem biomass at mid pod filling stage; PB – dry pod biomass at mid pod filling stage; TB – total shoot biomass at mid pod filling stage; DF – days to flowering; LSD Irr – least significant difference for the irrigated treatment; LSDRain – least significant difference for the rainfed treatment; LSD* - least significant difference separating means between treatments; numbers in brackets () represent the number of genotypes constituting a race; h^2 – broad sense heritability; NG1 – Nueva Granada 1; NG2 – Nueva Granada 2

Table 3.17 Performance of genotypes based on race classification in Andean trials at Harare Research Station

Race	Treatm	Traits												
		Yield	**PR**	**DSI**	**P100**	**PR**	**DM**	**PR**	**PP**	**PL**	**LB**	**SB**	**PB**	**TB**	**DF**
Checks	Irr	925.71			34.62		91.24		6.91	8.76	4.05	4.09	3.19	11.38	36.00
(7)	Rain	618.29	33.00	0.88	19.00	45.00	85.48	6.00	7.67	9.00	4.08	3.92	3.76	11.86	36.05
NG1	Irr	911.41			31.78		84.20		7.20	8.82	3.87	4.20	3.46	11.32	35.91
(27)	Rain	553.89	39.00	0.96	18.19	43.00	82.83	2.00	6.53	8.19	3.64	4.02	3.80	11.57	35.85
NG2	Irr	874.67			32.33		92.61		7.10	9.03	4.04	4.02	3.03	10.80	37.18
(30)	Rain	550.44	37.00	0.90	18.54	43.00	87.24	6.00	6.68	8.54	3.74	3.85	3.02	10.93	37.10
Peru	Irr	792.94			32.12		96.55		7.00	9.92	4.23	4.14	2.65	10.88	38.88
(17)	Rain	365.02	54.00	1.32	19.29	40.00	93.90	3.00	6.57	9.29	4.00	3.97	2.74	10.90	39.53
Grand	Irr	873.58			32.40		90.51		7.10	9.12	4.02	4.11	3.11	11.04	37.01
mean	Rain	518.54			18.62		87.02		6.69	8.62	3.79	3.94	3.29	11.22	37.10
h^2 (%)	Irr	62.63			84.60		95.14		67.05	57.80	46.65	61.85	65.61	45.00	93.83
h^2 (%)	Rain	45.27			75.16		90.58		52.17	37.70	45.88	42.75	75.13	42.16	95.01
LSD Irr		608.29			8.10		17.70		3.27	3.14	1.04	0.96	1.25	2.31	1.98
LSDRain		361.45			3.41		5.09		3.50	3.41	0.98	1.02	1.36	2.55	2.16
LSD*		352.44			4.38		9.17		2.39	2.31	0.71	0.70	0.92	1.71	1.46

Treatm – treatment; Irr – irrigated treatment; Rain – rainfed treatment; PR – percentage reduction; DSI – drought sensitivity index; P100 – 100-seed weight; DM – days to maturity; PP – number of pods per plant; PL – pod length; LB – dry leaf biomass at mid pod filling stage; SB – dry stem biomass at mid pod filling stage; PB – dry pod biomass at mid pod filling stage; TB – total shoot biomass at mid pod filling stage; DF – days to flowering; LSD Irr – least significant difference for the irrigated treatment; LSDRain – least significant difference for the rainfed treatment; LSD* - least significant difference separating means between treatments; numbers in brackets () represent the number of genotypes constituting a race; h^2 – broad sense heritability; NG1 – Nueva Granada 1; NG2 – Nueva Granada 2

were decreasing as the season progressed. Race Peru is more adaptable to high altitude cool areas in equatorial latitudes (Singh *et al.* 1991). Lower temperatures may have reduced the metabolic activity of plants, resulting in a longer duration of phenological stages (Lambers *et al.* 2000). At both locations, Nueva Granada sub-race 1, especially type I growth habit beans, reached physiological maturity earlier than other races or sub-races explaining why the race Nueva Granada was reported as the earliest Andean race with Peru taking longer to mature (Singh *et al.* 1991).

Drought stress significantly reduced 100-seed weight for all genotypes in the reference collection at Harare Research Station and race Nueva Granada 1 at CIAT-Palmira. The highest seed reductions were observed in race Nueva Granada 1 and check genotypes at CIAT-Palmira and Harare Research Station respectively. Furthermore, check genotypes and Nueva Granada sub-race 1 accessions had a significantly higher number of pods per plant under drought stress than race Peru at CIAT-Palmira. Stem biomass was significantly reduced by drought stress in race Peru at CIAT-Palmira. In addition, pod biomass and total shoot biomass were significantly reduced in all genotypes (except pod biomass for race Peru) at CIAT-Palmira.

Most traits measured, except total biomass and dry pod biomass at mid-pod fill (CIAT-Palmira) and pod biomass at mid-pod fill and days to flowering at Harare Research Station, had higher heritabilities under irrigated than rainfed treatments at both locations (Tables 3.16 and 3.17). Days to flowering had heritabilities above 80% under both treatments at both locations. At both locations, broad sense heritabilities were lowest for total biomass at mid-pod fill under both irrigated and rainfed treatments.

3.4.6 Selection of genotypes based on geometric mean and drought sensitivity index

The group of drought tolerant genotypes was characterised by mean DSI values of less than 0.33. These genotypes appeared to be stable under both rainfed and irrigated treatments at CIAT-Palmira and Harare Research Station. In the Mesoamerican trials, on the one hand, the following genotypes were found to have DSI values lower than 0.33;

G2402 (0.19) and G2866 (0.16) (sub-race D1), G12778 (0.02) and G4637 (0.01) (sub-race M1) and G11721 (0.14) and G4280 (0.12) (sub-race M2) at CIAT-Palmira (Appendix 3). The GM yields of all these genotypes had seed yields above 1 500 kg ha^{-1} except G4637 at CIAT-Palmira. On the other hand, SXB418 (0.14) (check/breeding line), G18440 (0.05) (sub-race D1), G12796 (0.05) and G22044 (0.15) (sub-race D2), G2137 (0.07) (sub-race M1) and G18157 (0.22), G7761 (0.23) and G803 (0.13) (sub-race M2) had DSI values lower than 0.33 at Harare Research Station (Appendix 4). Where drought was more severe, G18440 and G2137 had geometric mean yields larger 700 kg ha^{-1} at Harare Research Station.

In Andean trials, G11982 (0.20) (sub-race Nueva Granada 1) had DSI value lower than 0.33 and GM yield above 1 200 kg ha^{-1} at CIAT-Palmira (Appendix 5). At the same site, G16346 (0.28) and G11727 (0.22) had DSI values lower than 0.33 but had poor GM values (273.56 and 243.99 kg ha^{-1}) respectively. Meanwhile, GM yields for G4534 (0.06) and G4906 (0.10) (all sub-race Nueva Granada 1) and G11585 (0.29), G5034 (0.03), G13910 (0.21) and G9335 (0.29) (all sub-race Nueva Granada 2) were larger than 600 kg ha^{-1} and these genotypes had DSI values lower than 0.33 at Harare Research Station (Appendix 6).

3.4.7 Correlations among traits in different treatments at CIAT-Palmira and Harare Research Station

3.4.7.1 Mesoamerican trials at CIAT-Palmira

In the Mesoamerican trials under drought stress at CIAT-Palmira, the number of pods per plant, pod length, dry pod and total biomass accumulated at mid pod filling stage had larger than 40% correlations with seed yield (Table 3.18). Meanwhile, total biomass and pod biomass accumulated at mid pod filling stage had correlations with seed yield under the irrigated treatment of larger than 50%. Days to flowering and maturity were significantly and negatively correlated with seed yield, 100-seed weight and dry pod biomass at mid pod-filling stage under both treatments at CIAT-Palmira. Meanwhile, the correlations between days to flowering and maturity to dry stem and leaf biomass at mid

Table 3.18 Correlations among agronomic traits measured at CIAT-Palmira in the Mesoamerican trials. Top diagonal (bold) represents the rainfed treatment and the bottom diagonal, the irrigated treatment

	DF	DM	PP	PL	P100	Yield	SB	LB	PB	TB
DF	**1**	**0.57*****	**-0.19*****	**-0.08**	**-0.63*****	**-0.36*****	**0.40*****	**0.47*****	**-0.45*****	**-0.13***
DM	0.72***	1	**-0.11***	**-0.02**	**-0.26*****	**-0.32*****	**0.43*****	**0.43*****	**-0.40*****	**-0.09**
PP	-0.07	-0.16**	1	**0.34*****	**0.11***	**0.45*****	**-0.16****	**-0.17****	**0.34*****	**0.20*****
PL	-0.002	-0.23***	0.21***	1	**0.18****	**0.47*****	**-0.04**	**-0.02**	**0.39*****	**0.32*****
P100	-0.57***	-0.34***	0.04	0.01	1	**0.32*****	**-0.22*****	**-0.30*****	**0.39*****	**0.19*****
Yield	-0.23***	-0.36***	0.31***	0.38***	0.20***	1	**-0.09**	**-0.18*****	**0.66*****	**0.50*****
SB	0.48***	0.53***	-0.09	-0.14**	-0.18**	-0.16**	1	**0.79*****	**-0.06**	**0.52*****
LB	0.48***	0.50***	-0.11*	-0.08	-0.21***	-0.18**	0.79***	1	**-0.22*****	**0.36*****
PB	-0.40***	-0.38***	0.28***	0.26***	0.32***	0.53***	-0.01	-0.07	1	**0.81*****
TB	-0.40***	-0.36***	0.26***	0.24***	0.32***	0.51***	-0.02	-0.08	0.99***	1

DF – days to flowering; DM – days to maturity; PP - number of pods per plant; PL – pod length at maturity; P100 – 100-seed weight; SB – dry stem biomass at mid pod filling stage; LB – dry leaf biomass at mid pod filling stage; PB – dry pod biomass at mid pod filling stage; TB – total shoot biomass at mid pod filling stage; $^{*}P\leq0.05$; $^{**}P\leq0.01$; $^{***}P\leq0.001$

pod-filling were positive and significant under both treatments at CIAT-Palmira. Under both treatments, the highest correlations between traits were observed for dry pod biomass and total biomass which were significantly larger than 80%. In addition, dry stem and leaf biomass were the second most highly correlated traits.

3.4.7.2 Mesoamerican trials at Harare Research Station

In the Mesoamerican trials at Harare Research Station, number of pods per plant was highly correlated with seed yield followed by 100-seed weight under rainfed treatment (Table 3.19). Again, the number of pods per plant had the highest correlation with seed yield under irrigated treatment at the same location. Dry leaf, stem and total biomass were also significantly correlated to seed yield under both treatments at Harare Research Station. In addition to these shoot traits; pod length at maturity was significantly correlated to seed yield under drought stress. Like at CIAT-Palmira, days to maturity was significantly correlated to seed yield, 100-seed weight and dry pod biomass at mid pod filling stage under both treatments at Harare Research Station. Days to flowering and maturity had high negative correlations with dry pod biomass at mid pod filling stage under both treatments. Significantly highest correlations were observed between dry stem biomass and total biomass followed by dry leaf biomass and total biomass under both treatments at Harare Research Station.

Table 3.19 Correlations among agronomic traits measured at Harare Research Station in the Mesoamerican trials. Top diagonal (bold) represents the rainfed treatment and the bottom diagonal, the irrigated treatment

	DF	DM	PP	PL	P100	Yield	SB	LB	PB	TB
DF	1	**0.67*****	**0.14****	**0.12***	**-0.20*****	**-0.09**	**0.09**	**0.19*****	**-0.51*****	**-0.17****
DM	0.55***	1	**0.25*****	**0.11***	**-0.03***	**-0.20*****	**0.24*****	**0.31*****	**-0.48*****	**-0.03**
PP	0.32***	0.35***	1	**0.05**	**0.10**	**0.64*****	**0.13***	**0.15****	**0.004**	**0.11***
PL	0.02	0.10	0.12*	1	**0.15****	**0.18*****	**0.09**	**0.13***	**-0.04**	**0.07**
P100	-0.29***	-0.13*	0.004	0.19***	1	**0.48*****	**0.20*****	**0.17****	**0.28*****	**0.30*****
Yield	0.27***	0.36***	0.67***	0.20***	0.32***	1	**0.25*****	**0.25*****	**0.10**	**0.25*****
SB	0.07	0.13*	0.24***	-0.001	0.18**	0.32***	1	**0.71*****	**0.11***	**0.77*****
LB	0.30***	0.21***	0.22***	0.06	0.08	0.31***	0.64***	1	**0.06**	**0.75*****
PB	-0.51***	-0.47***	-0.17**	-0.12*	0.26***	-0.14**	0.13*	-0.06	1	**0.62*****
TB	-0.13*	-0.11*	0.11*	-0.04	0.26***	0.20***	0.81***	0.69***	0.59***	1

DF=days to flowering, DM = days to maturity, PP = number of pods per plant, PL = pod length at maturity, P100 = 100-seed weight, SB = dry stem biomass at mid pod filling stage, LB = dry leaf biomass at mid pod filling stage, PB = dry pod biomass at mid pod filling stage, TB = total shoot biomass at mid pod filling stage, $^{*}P\leq0.05$, $^{**}P\leq0.01$, $^{***}P\leq0.001$

3.4.7.3 Andean trials at CIAT-Palmira

For the Andean trials at CIAT-Palmira, the highest positive correlations (>50%) were detected between seed yield and 100-seed weight, dry pod biomass at mid pod filling stage, number of pods per plant and pod length at maturity under both irrigated and rainfed treatments at CIAT-Palmira (Table 3.20). Days to maturity were significantly positively correlated with pod length at maturity, 100-seed weight and dry stem biomass at mid pod filling stage under both treatments. Dry stem and leaf biomass highest correlated traits under both irrigated and rainfed treatments (up to r=0.83). Yield component traits, number of pods per plant and 100-seed weight had highly significant correlation under both irrigated and rainfed treatments. In addition, number of pods per plant was also highly correlated with dry pod biomass at mid pod filling stage under both irrigated and rainfed treatments. Highly significant and negative correlations were detected between days to flowering and number of pods per plant, pod length at maturity, 100-seed weight, yield and dry pod biomass at mid pod filling stage under irrigated and rainfed treatments at CIAT-Palmira.

3.4.7.4 Andean trials at Harare Research Station

For the Andean trials at the Harare Research Station, the number of pods per plant and dry pod biomass had significant and positive correlations with seed yield under the rainfed treatment (Table 3.21). Significant negative correlations were observed for days to flowering and maturity with seed yield under drought stress. Under the irrigated treatment, 100-seed weight, numbers of pods per plant and pod length at maturity were also correlated with seed yield. Highly significant correlations ($r > 0.20$) were observed between yield and dry stem biomass, dry leaf biomass and total dry biomass measured at mid pod filling stage under the irrigated treatment at Harare Research Station. Phenology traits, days to flowering and maturity were highly correlated (r=0.82; r=0.77) under rainfed and irrigated treatments respectively. Negative and highly significant correlations between dry pod biomass and days to flowering as well as days to maturity were detected under both irrigated and rainfed treatments. Negative and significant correlations were also detected between yield and days to flowering and maturity under the rainfed treatment.

Table 3.20 Correlations among agronomic traits measured at CIAT-Palmira in the Andean trials. Top diagonal (bold) represents the rainfed treatment and the bottom diagonal, the irrigated treatment

	DF	DM	PP	PL	P100	Yield	SB	LB	PB	TB
DF	1	**-0.08**	**-0.61*****	**-0.56*****	**-0.66*****	**-0.69*****	**0.10**	**0.30*****	**-0.67*****	**-0.30*****
DM	-0.24***	1	**0.08**	**0.60*****	**0.32*****	**0.004**	**0.13***	**0.12**	**-0.14***	**0.01**
PP	-0.70***	0.03	1	**0.47*****	**0.48*****	**0.66*****	**-0.05**	**-0.21****	**0.55*****	**0.27*****
PL	-0.69***	0.42***	0.53***	1	**0.67*****	**0.51*****	**0.06**	**-0.08**	**0.41*****	**0.28*****
P100	-0.71***	0.17**	0.50***	0.68***	1	**0.72*****	**-0.01**	**-0.12**	**0.58*****	**0.35*****
Yield	-0.76***	-0.10	0.72***	0.57***	0.73***	1	**-0.11**	**-0.21****	**0.77*****	**0.40*****
SB	0.37***	0.29***	-0.36***	-0.25***	-0.28***	-0.43***	1	**0.83*****	**-0.05**	**0.74*****
LB	0.45***	0.25***	-0.46***	-0.31***	-0.40***	-0.53***	0.83***	1	**-0.16***	**0.65*****
PB	-0.66***	-0.07	0.55***	0.39***	0.60***	0.71***	-0.20**	-0.31***	1	**0.61*****
TB	-0.37***	0.11	0.28***	0.20**	0.36***	0.38***	0.40***	0.28***	0.28***	1

DF=days to flowering, DM = days to maturity, PP = number of pods per plant, PL = pod length at maturity, P100 = 100-seed weight, SB = dry stem biomass at mid pod filling stage, LB = dry leaf biomass at mid pod filling stage, PB = dry pod biomass at mid pod filling stage, TB = total shoot biomass at mid pod filling stage, $^{*}P\leq0.05$, $^{**}P\leq0.01$, $^{***}P\leq0.001$

Table 3.21 Correlations among agronomic traits measured at Harare Research Station in the Andean trials. Top diagonal (bold) represents rainfed treatment and the bottom diagonal, irrigated treatment

	DF	DM	PP	PL	P100	Yield	SB	LB	PB	TB
DF	1	**0.82*****	**0.09**	**0.02**	**0.02**	**-0.29*****	**0.21****	**0.38*****	**-0.59*****	**-0.10**
DM	0.77***	1	**0.25****	**0.12**	**0.12**	**-0.16***	**0.24*****	**0.43*****	**-0.58*****	**-0.06**
PP	0.31***	0.28***	1	**0.04**	**0.04**	**0.25*****	**0.08**	**0.11**	**-0.04**	**0.07**
PL	0.21**	0.24***	0.05	1	**0.91*****	**0.12**	**0.13***	**0.09**	**-0.08**	**0.07**
P100	-0.05	-0.006	0.07	0.29***	1	**0.12***	**0.12***	**0.09**	**-0.08**	**0.07**
Yield	0.17**	0.18**	0.50***	0.24***	0.55***	1	**0.10**	**-0.04**	**0.18****	**0.12**
SB	0.14*	0.13*	0.17**	0.08	0.22***	0.33***	1	**0.64*****	**0.15***	**0.77*****
LB	0.30***	0.27***	0.20**	0.11	0.09	0.29***	0.57***	1	**-0.09**	**0.65*****
PB	-0.55***	-0.60***	-0.13*	-0.21**	0.08	-0.08	0.15*	-0.08	1	**0.62*****
TB	-0.14*	-0.18**	0.09	-0.05	0.18**	0.23***	0.78***	0.65***	0.63***	1

DF=days to flowering, DM = days to maturity, PP = number of pods per plant, PL = pod length at maturity, P100 = 100-seed weight, SB = dry stem biomass at mid pod filling stage, PB = dry pod biomass at mid pod filling stage, TB = total shoot biomass at mid pod filling stage, LB = dry leaf biomass at mid pod filling stage, *P≤0.05, **P≤0.01, ***P≤0.001

3.4.8 Regression analysis

A stepwise multiple linear regression analysis was conducted to estimate the effects of 100-seed weight, days to flowering and maturity, leaf biomass, pod biomass, pod length, number of pods per plant and stem biomass on grain yield for each treatment at CIAT-Palmira and Harare Research Station for the Andean and Mesoamerican trials. In addition to these traits, leaf temperature and canopy temperature depression were also included in the analysis at CIAT-Palmira in both Andean and Mesoamerican trials. The two traits were not measured at Harare Research Station due to unavailability of the equipment. Regression sums of squares were highly significant ($P \leq 0.001$) for both Andean and Mesoamerican trials under irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station (data not shown).

The regression model, on the one hand explained 37.5% and 52.6% of variation observed in grain yield in the Mesoamerican genotypes under irrigated and rainfed treatments at CIAT-Palmira respectively (data not shown). On the other hand, it accounted for 58.4% and 65.5% of the variation observed on grain yield in Mesoamerican trials under irrigated and rainfed treatments at Harare Research Station respectively (data not shown).

In Andean trials, more than 70% of the variation observed for grain yield under irrigated and rainfed treatments at CIAT-Palmira was explained by the regression model (data not shown), but could only account for 27.8% and 54.5% of the variation in grain yield under rainfed and irrigated treatments at Harare Research Station respectively (data not shown).

The number of pods per plant made highly significant ($P \leq 0.001$) contributions to grain yield of genotypes in both Mesoamerican and Andean trials under both irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station (Tables 3.22 and 3.23). In Mesoamerican trials, the number of pods per plant made the highest contribution to grain yield under rainfed treatments at CIAT-Palmira and Harare Research Station (Table 3.22). Furthermore, the number of pods per plant made the highest contribution to grain yield under irrigated treatment at Harare Research Station. Positive and highly significant contributions to grain yield were detected for 100-seed weight at Harare Research Station

Table 3.22 Estimated contributions of evaluated traits to grain yield and their significance as determined by stepwise regression analysis in Mesoamerican trials at CIAT-Palmira and Harare Research Station

	CIAT-Palmira		Harare Research Station	
	Contribution to variation (%)		Contribution to variation (%)	
Trait	**Irrigated treatment**	**Rainfed treatment**	**Irrigated treatment**	**Rainfed treatment**
Number of pods per plant	20.57***	38.44***	43.57***	46.28***
100-seed weight	ns	Ns	42.77***	25.93***
Total shoot biomass at mid pod filling stage	ns	Ns	4.68*	2.26***
Days to maturity	-17.92**	-10.73*	-5.08*	-3.89*
Pod length at maturity	17.40***	13.60***	Ns	ns
Dry pod biomass at mid pod filling stage	24.25***	21.20***	Ns	ns
Days to flowering	11.50*	Ns	Ns	ns
Canopy temperature depression	4.3*	9.5*	-	-
Leaf temperature	2.7***	Ns	-	-

*P≤0.05; **P≤0.01; ***P≤0.001; ns – not significant, - not measured

Table 3.23 Estimated contributions of evaluated traits to grain yield and their significance as determined by step wise regression analysis in Andean trials at CIAT-Palmira and Harare Research Station

	CIAT-Palmira		Harare Research Station	
	Contribution to variation (%)		Contribution to variation (%)	
Trait	**Irrigated treatment**	**Rainfed treatment**	**Irrigated treatment**	**Rainfed treatment**
Number of pods per plant	48.98***	38.23***	40.96***	31.40***
100-seed weight	12.88***	17.22***	32.54***	14.12***
Days to maturity	9.55***	3.81*	Ns	ns
Pod length at maturity	Ns	Ns	Ns	ns
Dry pod biomass at mid pod filling stage	15.48***	16.90***	Ns	ns
Dry stem biomass at mid pod filling stage	Ns	Ns	Ns	33.30*
Days to flowering	11.87***	Ns	Ns	11.35***

*P≤0.05; **P≤0.01; ***P≤0.001; ns – not significant

under both irrigated and rainfed treatments. The contributions of 100-seed weight towards grain yield were second in magnitude after the number of pods per plant at Harare Research Station for both treatments. Pod length at maturity and dry pod biomass at mid pod filling stage were also highly significant in yield determination at CIAT-Palmira under both irrigated and rainfed treatments. Canopy temperature depression was also significant in determining the yield of Mesoamerican genotypes at CIAT-Palmira under both treatments. Leaf temperature made significant contributions towards yield under the irrigated treatment at CIAT-Palmira. At Harare Research Station, the total shoot weight at mid-pod filling stage made significant and highly significant contributions towards yield in Mesoamerican trials under irrigated and rainfed treatments respectively.

For the Andean trials, the number of pods per plant made the highest contribution to variation in grain yield under irrigated treatments at CIAT-Palmira (48.98%) and Harare Research Station (40.96%) (Table 3.23). One hundred seed weight also had highly significant and positive effects on grain yield under both irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station. At CIAT-Palmira, dry pod biomass accumulated at mid pod filling stage was also important in determining grain yield in Andean genotypes subjected to drought stress. Dry pod biomass at mid pod filling stage (16.90%) made the third highest contributions to grain yield variation at CIAT-Palmira under the rainfed treatment after the number of pods per plant and 100-seed weight in descending order. At Harare Research Station, the grain yield variation under the rainfed treatment was mainly influenced by dry stem biomass at mid pod filling stage (33.30%) followed by the number of pods per plant, 100-seed weight and days to flowering in descending order.

3.5 Discussion

The success of plant breeding programmes depends on genetic variation that exists within cultivated crop species. Genotypes in the reference collection of common bean responded to drought in several ways. In general, drought reduced grain yield, the number of pods per plant, 100-seed weight, pod biomass, stem biomass, total shoot biomass and days to

maturity at both locations. Similar effects of drought stress on grain yield, yield components, shoot biomass and plant phenology were previously observed in common bean (Ramírez-Vallejo and Kelly 1998; Szilagyi 2003; Rosales-Serna *et al.* 2004; Emam *et al.* 2010).

Drought tolerance has been defined in terms of the ability to produce grain yield in common bean despite drought conditions (Subbarao *et al.* 1995; Ramírez-Vallejo and Kelly 1998; Blair *et al.* 2012) and as such grain yield offers the most practical way to screen and select drought tolerant common bean genotypes (White and Singh 1991; Terán and Singh 2002). However, grain yield is influenced by a number of external variables. The combined ANOVA for grain yield at CIAT-Palmira and Harare Research Station indicated that treatments, genotypes and GxT interaction were significant in affecting the yield of genotypes in both Andean and Mesoamerican trials. Grain yield was the only trait affected by GxT interaction across the two treatments in Andean and Mesoamerican trials.

GxE interaction has often posed major problems in variety selection in the sense that high yielding genotypes in one environment sometimes perform below expectations in another (Casquero *et al.* 2006). Contributions of GxE interaction have been estimated between 17% and 27% in legume crops (Kumar *et al.* 2011). In the current study, ranking of genotypes changed across treatments and locations. It is common for multi-location yield trials to encompass a mixture of crossover and non-crossover types of GxE interactions.

Apart from the water levels, diseases also influenced the results to some extent, particularly angular leaf spot, common bacterial blight and rust under drought stress at Harare Research Station. At CIAT-Palmira, the fungus *Sclerotium rolfsii* Sacc., caused grain yield losses under the irrigated treatment in both Andean and Mesoamerican trials. Ramírez-Vallejo and Kelly (1998) also reported interactions between drought and diseases in reducing grain yield. Diseases that attack susceptible genotypes mask the expression of the desired drought tolerance traits such as grain yield and shoot biomass, hence complicating the efforts of breeders to identify superior genotypes under drought

stress. Premature leaf loss, reduced vigour and death of susceptible plants due to diseases results in reduced shoot biomass and poor plant stand and hence affect the interpretation of results (Mayek-Pérez *et al.* 2002). Since common bean production environments are varied in nature and are exposed to different abiotic and biotic stresses that co-occur together with drought, Beebe *et al.* (2008) suggested breeding for multiple constraint resistance as the best strategy for developing drought resistant genotypes in common bean.

Drought intensity index (DII) levels of between 0.22 and 0.71 have been reported in common bean (Ramírez-Vallejo and Kelly 1998). The drought stress levels at Harare Research Station (DII=0.5344, Andean trials; DII=0.3992, Mesoamerican trials) were comparable to previous studies on common bean under rainfed conditions (DII=0.49, Schneider *et al.* 1997, DII=0.48, Rosales-Serna *et al.* 2004, DII= 0.44 and 0.48, Urrea *et al.* 2007; Frahm *et al.* 2004) while stress levels in CIAT-Palmira (DII=0.2268, Andean; DII=0.2247, Mesoamerican) were lower, though similar, between the two genepool trials run parallel to each other in one big field. Harare Research Station has small fields which could only accommodate one trial of this magnitude. Consequently the Andean and Mesoamerican trials were planted in two different fields at Harare Research Station resulting in varying stress levels and disease pressure. Therefore the drought stress at Harare Research Station was fairly severe while at CIAT-Palmira it was moderate to low. The reduction is caused by a decrease in photo assimilates and water that goes into seeds during the seed filling stage (Muñoz-Perea *et al.* 2006). The amount of reduction in yield under drought can also be due to soil types and other abiotic or biotic stresses (Asfaw *et al.* 2012; Blair *et al.* 2012).

The duration and intensity of drought stress in common bean determines the level of grain yield reduction (Porch *et al.* 2009). In general, grain yield was reduced by 22% and 53% at CIAT-Palmira and Harare Research Station respectively in the Andean trials. Grain yield reductions for Mesoamerican trials were 23% and 40% at CIAT-Palmira and Harare Research Station respectively. The differences in the stress levels between locations showed that it is difficult to apply similar levels of drought stress across

locations and control other stress factors to the same level. This makes breeding for drought tolerance more complex since it is difficult to homogenise testing sites

The mean grain yields obtained at Harare Research Station for Andean and Mesoamerican trials under irrigated and terminal drought were in the same range as reported in other drought experiments conducted with landraces and partially improved lines in common bean (Frahm *et al.* 2004; Urrea *et al.* 2007; Porch *et al.* 2009; Blair *et al.* 2012). Grain yield under terminal drought for both Andean and Mesoamerican material was higher at CIAT-Palmira, probably because of the lower level of drought stress applied and higher soil fertility at this site. However, grain yields for both Andean and Mesoamerican trials under the irrigated treatment at CIAT-Palmira were comparable to other high yielding bean producing environments (Urrea *et al.* 2007).

Despite the presence of GxT interaction, the moderate to high estimates for heritability for grain yield and other traits in both Andean and Mesoamerican trials showed that the genotypic variance component made a larger contribution than the environmental effect in relation to the phenotypic variance component. However the presence of cross-over type GxT interaction showed that selection of suitable varieties under drought stress alone is not adequate since this could result in reduced yield under optimum environments (Rosielle and Hamblin 1981). Therefore, in common bean as in other crops, the GM has frequently been used in selecting for drought tolerant genotypes (Schneider *et al.* 1997).

Based on the GM combined with DSI data, the selected genotypes for the Mesoamerican genepool would be BAT477, G11721, G4017 and DOR390 as well as the Andeans SAB645, PVA1111, G5142, SEQ1003, SEQ1027 and G17076. Mean yields for these genotypes were above 800 kg ha^{-1} across treatments at both locations. If G11721, G4017, G5142 and G17076 were found to be acceptable for other traits and for seed type, recommendations could be made for their release and wider production. These genotypes could also serve as parents in crossing programmes targeting drought tolerance. The other genotypes are already widely used in many breeding programmes and are released in

Ethiopia (SEQ1003), Kenya (SEQ1027) and advanced stages of release in Zimbabwe (SEQ1003).

Replicated multi-location trials across multiple sites (more than the two used in this study) could be used with a smaller set of elite germplasm to decide on breeding parents or varietal releases as is done for various crop improvement programmes. Significant improvements in grain yield under both water stressed and non-stressed environments could be anticipated by using these genotypes in breeding programmes for drought tolerance. However, for effective utilisation of genotypes identified in the current study, breeding programmes need to test these genotypes under their local conditions before initiating crossing programmes.

A significant finding was that the geographical origins of the genotypes played a role in contributing to drought tolerance. In the current study, race Durango sub-race 1 was least affected by drought stress at both locations and in addition most of the top 20 genotypes across treatments at both locations were of Durango or Mesoamerica race origins with type II and III growth habits. Terán and Singh (2002) also found race Durango genotypes to be drought tolerant. Brick and Grafton (1999) found genotypes from race Durango to be more drought tolerant than any other races in common bean. Race Durango from the semi-arid and arid northern highlands in Mexico has a long history of adaptation in drought prone environments. White *et al.* (1994) recognised germplasm from race Mesoamerica as sources of yield genes for both stressed and non-stressed environments of Central America. Some Andean genotypes with high biomass at pod-fill and that were medium in maturity were also drought tolerant. The Andean gene pool has been poorly studied for drought tolerance genes, hence the importance of developing a reference collection for both gene pools (Blair *et al.* 2009). However, the high performance of some race Nueva Granada sub-race 1 genotypes under drought stress may have been due to selection of these genotypes to tropical and subtropical conditions of dry and high temperatures at drier locations or lower altitudes.

Some genotypes from both the Andean and the Mesoamerican gene pools are sensitive to long days and as such could not be cultivated in high latitude areas (White and Laing 1989). Breeding programmes and farmers in these areas might not find some of the promising genotypes identified in the current study useful. However, a backcross breeding scheme could be useful to introduce drought tolerance genes into varieties adapted to high latitude environments. It is evident from the genotypes identified above that both Andean and Mesoamerican landraces could be used together in multiple crosses to generate progenies with different drought tolerance mechanisms.

Andean and Mesoamerican genotypes with high geometric means for grain yield identified in the current study could be used to study different components and the genetics of drought tolerance in common bean as was done by Asfaw *et al.* (2012) and Blair *et al.* (2012).

Among the components that are important for drought tolerance, avoiding reductions in 100-seed weight and number of pods per plant are critical. Various authors have found that grain yield reduction due to drought stress has been strongly associated with the number of pods per plant (Szilagyi 2003) as well as 100-seed weight and pod length (Singh 1995, Schneider *et al.* 1997; Rosales-Serna *et al.* 2004; Singh 2007). Drought during anthesis was shown by Mwanamwenge *et al.* (1999) and Habibi (2011) to cause up to a 47% reduction in the total number of flowers in common bean. Consequently, the total number of pods is negatively affected and the reduction has been reported in the range of between 21% to 65% depending on intensity and duration of the drought stress (Terán and Singh 2002; Singh *et al.* 2001). The regression analysis carried out in this study found, that the number of pods per plant made highly significant contributions to grain yield under both irrigated and rainfed treatments. In addition, pod length made the highest contribution to yield in Mesoamerican genotypes subjected to drought stress at CIAT-Palmira.

Previous studies on common bean suggested that the decrease in the number of flowers and pods per plant were due to limited vegetative growth of branches located in the lower

nodes of the main stem (Board and Harville 1998). In the current study, dry leaf and stem biomass were significantly reduced in some Andean and Mesoamerica genotypes under drought stress at both locations. Shading of older leaves is a common phenomenon for common bean under drought or nutrient stress. Barrios *et al.* (2005) demonstrated small and newly formed leaves had limited capacity as a source of photosynthates to support many flowers and pods. In the current study, common bean under drought stress aborted flowers and pods to maintain a few which could be supported by the new leaves.

In most legume crops, marketability and ability to attract high prices is determined by seed weight, colour and shape. A reduced plant canopy or biomass at mid pod filling stage has been shown to also have a negative effect on seed filling (Asfaw *et al.* 2012). The ability of leaves and stems to serve as sources of photosynthates is reduced. In the current study, 100-seed weight was reduced in some genotypes under the rainfed treatment. Seed development and filling are both affected by drought and many seeds shrivel during seed production (Isik *et al.* 2005). In some grain legumes such as soybean, pods abort due to the low ovule fertility resulting from a decrease in the hexose to sucrose ratio after anthesis. This negatively affects both seed quality and yield produced under drought stress. Once genes contributing to high yield, high shoot biomass, number of pods per plant and seed set are tagged, the associated markers can be used in MAS breeding programmes.

Drought escape is desirable and has proven to be useful in legume crops. Over the last few decades, breeding programmes in both cereals and legumes worldwide have been breeding for earliness as a way of minimising crop losses to terminal drought stress. In this study, days to flowering were not affected by drought stress in the majority of Andean and Mesoamerican genotypes at both locations. Previous drought experiments in common bean also showed that days to flowering were not affected by drought (Ramírez-Vallejo and Kelly 1998; Lizzana *et al.* 2006). However, a reduction in number of days to maturity was observed for some Andean and Mesoamerican genotypes under the rainfed treatment at both locations in the current study. Terán and Singh (2002) found a 3% decrease in the number of days to maturity between irrigated and rainfed treatments in

Palmira in Mesoamerican genotypes. Singh (2007) also reported a reduction of up to 4 days in race Durango. Negative correlations between days to maturity and seed yield in Andean and Mesoamerican trials at both locations indicated that genotypes with lower days to maturity under drought stress reached the highest yields. Both Beebe *et al.* (2008) and Blair *et al.* (2012) found that late maturing genotypes in an advanced breeding line trial and a QTL population suffered some decreases in performance under terminal drought stress. Nleya *et al.* (2001) cited early maturity as one of the components of terminal drought avoidance in common bean. Drought accelerates the maturity as a mechanism of resistance to drought that involves escaping the drought period.

Matching of crop phenology and rainfall patterns is essential for improving adaptation of common bean in water stressed environments (Ludlow and Muchow 1990; Rosales-Serna *et al.* 2004). Passioura (1977) also suggested the manipulation of phenology of a crop to fit its environment in terms of water management as a key to drought tolerance. Some Durango genotypes that showed early maturity exhibited higher seed yields under drought conditions. This observation was supported by the negative and significant relationship observed between yield and days to maturity under rainfed treatments at both locations for the Mesoamerican trials.

Stem, leaf and pod biomasses were reduced under drought stress at both locations through restrictions in stem and pod expansion as well as decreased leaf area and accelerated leaf senescence. Inhibition of expansion of leaves and stems reduces the surface area for transpiration and has been used by plants as an adaptive mechanism to drought stress. Similar variability for shoot biomass has also been reported among common bean cultivars grown under moderate to severe drought stress (Rosales-Serna *et al.* 2004; Emam *et al.* 2010) indicating the feasibility of manipulating this trait through classical breeding techniques. Shenkut and Brick (2003) and Rosales-Serna *et al.* (2004) proposed the use of plant biomass as an indirect selection criterion for drought tolerance since it has moderate to high heritability and exhibits low GxE interaction.

The Andean and Mesoamerican genotypes with high GM for grain yield across treatments at each location in this study had high total biomass at mid-pod filling stage under terminal drought. A high shoot biomass accumulation prior to flowering has been effective in supporting yield under drought conditions (Plaut *et al.* 2004; Blum 2005). A high shoot biomass translates to a big canopy which helps in reducing surface soil evaporation, thus increasing the amount of moisture available for transpiration (Sarker *et al.* 2005).

Most of race Durango genotypes have small leaves and short lower internodes that provide good ground cover. In the current study, some genotypes from race Durango were early maturing and were indeterminate growth habit III and sprawl across the row. These characteristics help reduce evapo-transpiration and conserve soil moisture. Soil moisture remains for plant use thereby facilitating normal plant metabolic processes (Singh 2007). These genotypes may provide the foundation for the development of genotypes with wide adaptability to drought, but agronomic considerations are important as well as GxT interactions with irrigated conditions.

This indicated that apart from genetic and physiological mechanisms, morphological characteristics can act to minimise water loss at least in some Mesoamerican genotypes such as the Durango accessions. However, for the Andean genotypes in the reference collection of common bean, the role of plant architecture may be different with an advantage of type I over type II beans. Therefore, it remains to be seen if indeterminate plant architecture might be useful in improving drought tolerance in all common beans. Ghassemi-Golezani and Mardfar (2008) also realised the importance of morphological characters in the adaptation of plants to stress environments.

Although quantitative in nature, total biomass was less influenced by GxT than other yield component traits and might be a useful trait for drought tolerance. The identification of specific morphological and physiological traits that improve adaptation to terminal drought will lead to improvements in drought tolerance (Subbarao *et al.* 1995). Despite its potential use in drought tolerance, in the current study total shoot biomass was

measured by destructive sampling which is labour intensive and time consuming for the evaluation of a large number of genotypes. Rapid and non-destructive surrogate traits to shoot biomass need to be identified for quick evaluations of a large number of genotypes and wider use in breeding programmes.

In both Andean and Mesoamerican trials, advanced lines or check genotypes had highest seed yield values under irrigated and rainfed treatments at both locations. Improvement towards tolerance to water stressed environments may have caused check genotypes to perform well under both treatments. This shows the possibility that breeding programmes have the capacity to develop high yielding genotypes under varying drought conditions in the world once tolerant parents are identified. Some of the easy to phenotype and relatively inexpensive physiological, morphological, phenological and yield component traits identified in the current study could speed the selection process of drought tolerant genotypes as was done in Bourgault and Smith (2010).

3.6 Conclusions

Traits conferring dehydration avoidance and tolerance were expressed by genotypes in the reference collection of common bean and an integrated physiological, phenological, genetic and morphological approach is needed to utilise such traits in breeding programmes. Apparently, the best drought tolerant genotype should combine the high yield and architecture of the Mesoamerican race and the drought tolerance from Durango race. Race Nueva Granada could also serve as a good source of drought tolerance in Andean beans.

3.7 References

Agronomix Software, Inc. 2005. AGROBASE Generation II User's Manual. Version II, Revised Edition. www.agronomix.com

Asfaw A, Blair MW, Struick P. 2012. Multi-environment quantitative trait locus analyses for photosynthate acquisition, accumulation and remobilization traits in a common bean. G3: Genetics, Genomics and Genomes 2:579-595.

Barrios A, Hoogenboom G, Nesmith DS. 2005. Drought stress and distribution of vegetative and reproductive traits of a bean cultivar. Brazilian Journal of Agricultural Sciences 62:18-22.

Beebe SE, Rao IM, Cajiao C, Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favourable environments. Crop Science 48:582-592.

Blair MW, Díaz JM, Hidalgo R, Díaz LM, Duque MC. 2007. Microsatellite characterisation of Andean races of common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 116:29-43.

Blair MW, Díaz LM, Buendía HF, Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 119:955-972.

Blair MW, Galeano CH, Tovar E, Muñoz-Torres MC, Velasco A, Beebe SE, Rao IM. 2012. Development of a Mesoamerican intra-genepool genetic map for QTL detection in a drought tolerant x susceptible common bean (*Phaseolus vulgaris* L.) cross. Molecular Breeding 29:71-88.

Blum A. 2005. Drought resistance, water use efficiency and yield potential – are they compatible, dissonant or mutually exclusive? Australian Journal of Agricultural Research 56:1159-1168.

Board JE, Harville BG. 1998. Late planted soybean yield response to reproductive source/sink stress. Crop Science 38:119-128.

Bourgault M, Smith DL. 2010. Comparative study of common bean (*Phaseolus vulgaris* L.) and mungbean (*Vigna radiate* (L.) Wilczek) response to seven watering regimes in a controlled environment. Crop and Pasture Science 61:918-928.

Brick M, Grafton KF. 1999. Improvement of medium-seeded race Durango cultivars. In: Singh SP (Ed.) Common Bean Improvement in the Twenty-first Century. Kluwer Academic Publishers. Netherlands, pp. 56-84.

Casquero PA, Lema M, Santalla M, de Ron AM. 2006. Performance of common bean (*Phaseolus vulgaris* L.) landraces from Spain in the Atlantic and Mediterranean environment. Genetics Resources and Crop Evolution 53:1021-1032.

CIAT. 2008. Annual Report. Outcome line SBA-1. Improved beans for the developing world. pp. 39-65.

Emam Y, Shekoofa A, Salehi F, Jalali AH. 2010. Water stress effects on two common bean cultivars with contrasting growth habits. American-Eurasian Journal of Agriculture and Environmental Science 9:495-499.

Fischer RA, Maurer R. 1978. Drought resistance in spring wheat cultivars. III. Yield association with morpho-physiological traits. Australian Journal of Agricultural Research 30:1001-1020.

Frahm MA, Rosas JC, Mayek-Perez N, Lopez-Salinas E, Acosta-Gallegos JA, Kelly JD. 2004. Breeding beans for resistance to terminal drought in lowland tropics. Euphytica 136:223-232.

GenStat for Windows 14th Edition. VSN International, Hemel, Hempstead, UK. GenStat.co.uk.

Ghassemi-Golezani K, Mardfar RA. 2008. Effects of limited irrigation on growth and grain yield of common bean. Journal of Plant Sciences 3:230-235.

Graham PH, Vance CP. 2003. Legumes: Importance and constraints to greater use. Plant Physiology 131:872-877.

Habibi G. 2011. Influence of drought on yield and yield components in white bean. World Academy of Science, Engineering and Technology 79:244-253.

IPGRI. 2000. Core collections of plant genetic resources, IPGRI. Rome. Italy.

Isik M, Önceler Z, Cakir S, Altay F. 2005. Effect of different irrigation regimes on the yield and yield components of dry bean (*Phaseolus vulgaris*). Acta Agronomy Hungary 52:381-382.

Khan HR, Link W, Hocking TJ, Stoddard FL. 2007. Evaluation of physiological traits for improving drought tolerance in faba bean (*Vicia faba* L.). Plant Soil 292:205-217.

Kumar J, Choudhary AK, Solanki RK, Pratap A. 2011. Towards marker-assisted selection in pulses: a review. Plant Breeding 130:297-313.

Lambers H, Chapin FS, Pons TL. 2000. Growth and carbon allocation. In: Singh (Eds.) Plant Physiological Ecology. Springer-Verlag, New York. pp. 236-256.

Lizzana C, Wentworth M, Martinez JP, Villegas D, Meneses R, Murche EH, Pastenes C, Lercari B, Vernieri P, Harton P, Pinto M. 2006. Differential adaptation of two varieties of common bean to abiotic stress. Journal of Experimental Botany 57: 685-697.

Liu FL, Anderson MW, Jenson CR.2003. Loss of pod set caused by drought stress is associated with water stress and ABA content of reproductive structures in soybean. Functional Plant Biology 30:271-280.

Mayek-Pérez N, Garcia-Espinosa R, López-Castañeda C, Acosta-Gallegos J, Simpson J. 2002. Water relations, histo-pathology and growth of common bean (*Phaseolus vulgaris* L.) during pathogenesis of *Macrophomina phaseolina* under drought stress. Physiological and Molecular Plant Pathology 60:185-195.

Muñoz-Perea CG, Terán H, Allen RG, Wright JL, Westermann DT, Singh SP. 2006. Selection for drought resistance in dry bean landraces and cultivars. Crop Science 46:2111-2120.

Mwanamwenge J, Loss SP, Siddique KHM, Cocks PS. 1999. Effect of water stress during floral initiation, flowering and podding on the growth and yield of faba bean (*Vicia faba* L). European Journal of Agronomy 11:1-11.

Nleya TM, Slinkard AE, Vandernberg A. 2001. Differential performance of pinto bean under varying levels of soil moisture. Canadian Journal of Plant Science 81:233-239.

Passioura J. 1977. Grain yield, harvest index and water use of wheat. Journal of the Australian Instute of Agricultural Science 43:117-120.

Plaut Z, Butow BJ, Blumenthal CS, Wrigley CW. 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. Field Crops Research 86:185-198.

Porch TG, Ramirez VH, Santana D, Harmsen EW. 2009. Evaluation of Common bean for drought tolerance in Juana Diaz, Puerto Rico. Agronomy and Crop Science 195:328-334.

Ramírez-Vallejo P, Kelly JD. 1998. Traits related to drought stress resistance in common bean. Euphytica 99:127-136.

Rosales-Serna R, Kohashi-Shibata J, Acosta-Gallegos JA, Trejo-López C, Ortiz-Cereceres J, Kelly JD. 2004. Biomass distribution, maturity acceleration and yield in drought-stressed common bean cultivars. Field Crops Research 85:203-211.

Rosielle AA, Hamblin J. 1981. Theoretical aspects of selection for yield in stress and non – stress environments. Crop Science 21:943-946.

Sarker A, Erskine W, Singh M. 2005. Variation in shoot and root characteristics and their association with drought tolerance in lentil landraces. Genetic Resources and Crop Evolution 52:89-97.

Schneider KA, Rosales-Serna R, Ibarra-Perez F, Cazares-Enríquez B, Acosta-Gallegos JA, Ramírez-Vallejo P, Wassimi N, Kelly JD. 1997. Improving common bean performance under drought stress. Crop Science 37:43-50.

Shenkut AA, Brick MA.2003. Traits associated with dry edible bean (Phaseolus vulgaris L.) productivity under diverse moisture environments. Euphytica 133:339-347.

Singh SP. 1995. Selection for water-stress tolerance in interracial populations of common bean. Crop Science 35:118-124.

Singh SP. 2007. Drought resistance in race Durango dry bean landraces and cultivars. Agronomy Journal 99:1219-1225.

Singh SP, Gepts P, Debouck D. 1991. Races of common bean (*Phaseolus vulgaris*, Fabaceae). Economic Botany 45:379-396.

Singh SP, Terán H, Gutiérrez JA. 2001. Registration of SEA5 and SEA13 drought tolerant dry bean germplasm. Crop Science 41:276-277.

Subbarao GV, Johansen C, Slinkard AE, Nageswara Rao RC, Saxena NP, Chauhan YS. 1995. Strategies for improving drought resistance in grain legumes. Critical Review in Plant Science 14:469-523.

Szilagyi L. 2003. Influence of drought on seed yield components in common bean. Bulgarian Journal of Plant Physiology, special issue: 320-330.

Terán H, Singh SP. 2002. Comparison of sources and lines selected for drought resistance in common bean. Crop Science 42:64-70.

Urrea CA, Yonts CD, Lyon D. 2007. Breeding for drought tolerance in dry beans. http://www.panhandle.unl.edu.

White JW, Laing DR.1989. Photoperiod response of flowering in diverse genotypes of common bean (*Phaseolus vulgaris*). Field Crops Research 22:113-128.

White JW, Ochoa R, Ibarra P. 1994. Inheritance of seed yield, maturity and seed weight of common bean (*Phaseolus vulgaris*) under semi-arid rainfed conditions. Journal of Agricultural Science 122:265-273.

White JW, Singh SP. 1991. Breeding for adaptation to drought. In: van Schoonhoven A, Voysest O (Eds.) Common Beans, Research for Crop Improvement. CAB International CIAT, Colombia. pp. 501-560.

Wortmann C, Kirkby R, Eledu C, Allen D. 1998. Atlas of common bean production in Africa. CIAT publication no. 297. Cali Colombia.

Chapter 4

Phenotyping for drought adaptive root traits under greenhouse conditions

4.1 Abstract

Drought affects common bean productivity in 60% of bean producing areas in the world. The objectives of this study were to determine the role of deep rooting and other root properties in improving yield under drought stress in common bean landraces and to determine phenotypic differences among elite common bean genotypes for root development under water stress. Experiments were conducted in a greenhouse at CIAT headquarters, Palmira, Colombia in 2009 and 2010 using the soil cylinder system. A randomised complete block design with three replicates was used in each trial. Well watered and water stressed treatments were applied in each trial. A total of 33 Andean landraces and three Mesoamerican checks were evaluated for objective one. The Andean landraces and Mesoamerican checks were part of the reference collection of common bean. A total of 40 elite Andean and Mesoamerican genotypes, mostly used as parents targeting different traits in many breeding programmes, were evaluated for objective two. Root, leaf, stem, pod and physiological traits were measured in both trials. Genotypes had different responses to water stress in both trials. Some genotypes had faster root growth rate, longer root length, volume and biomass under water stressed than well watered conditions in both trials. Leaf, stem and pod traits as well as stomatal conductance were reduced in many genotypes under water stress in both trials. On the contrary, the total root biomass and mean root diameter were not significantly different between the two treatments. In conclusion, deep rooting alone may not be adequate for drought tolerance in common bean. Variability of root traits was expressed either as adaptive or constitutive traits depending on genotype and development of shoot traits was reduced under water stress.

4.2 Introduction

Plant adaptability and productivity depend on the environment's ability to supply resources required for plant metabolic and physiological needs (Ho *et al.* 2005). Roots dictate how plants acquire essential underground resources for growth. Roots provide the mechanical support of the plant and absorb water as well as nutrients required for plant growth and function (Gregory 2006). In legume crops, roots have an additional function of providing sites for nodulation and nitrogen fixation. Crop productivity under abiotic constraints can be enhanced by improved root traits responsible for water scavenging and improved nutrient acquisition (Clark *et al.* 2011). However, root development, morphology and architecture are affected by soil physical, chemical and biological properties, plant genotypes and the climate (Sponchiado *et al.* 1989; Clark *et al.* 2011).

Soil water supply is one of the major factors affecting root development (Pritchard 1994). Roots are the first tissue to experience a reduction in soil moisture, initiating morphological and metabolic changes before observable signs of water deficit on leaves and other plant parts are noticed. A study by Pritchard (1994) showed that roots experiencing water stress increase their extension growth. Root growth is influenced by an increase of ABA production in roots (Pritchard 1994). During this process, roots become a stronger sink than any other plant part and the transport of assimilates to the roots is enhanced at the expense of a reduced growth of leaves (Saab *et al.* 1990).

Deep roots have the ability to extract residual moisture available in deeper soil layers in arid and semi-arid environments and contribute to high crop yields under these environments (Blum 1988). Deep rooting and other root characteristics have been demonstrated to play a major role in drought avoidance in many crops. A study by Sponchiado *et al.* (1989) showed a significant correlation of deep rooting with shoot growth and seed yield in common bean. BAT477, a CIAT bred line, has a high yield under water stressed conditions due to its deep rooting ability (Rao 2001). Modifications of root systems through breeding and selection of beneficial root traits can offer a cost effective way of improving common bean productivity under drought stress (de Dorlodot *et al.* 2007). Common bean breeders have also used some elite genotypes for biotic and

abiotic tolerance improvement. However, root traits of these genotypes are unknown. Yet root characteristics offer part of the solution to drought and low soil fertility problems.

The objectives of this study were to:

- Determine the role of deep rooting, root length and biomass distribution and mean root diameter in improving yield under water stressed conditions in selected Andean and Mesoamerican genotypes from the reference collection.
- Determine phenotypic differences among elite common bean genotypes, commonly used as parents in breeding programmes, for root development under water stress induced by progressive soil drying.

4.3 Materials and methods

4.3.1 Materials

Two greenhouse studies were conducted at CIAT headquarters in Palmira in 2009 and 2010 using the soil cylinder system (Butare *et al*. 2011). Trial 1 (2009) involved evaluation of a sub-set of Andean landraces in the reference collection. A total of 36 genotypes were evaluated (Table 4.1). Genotypes selected represented all three races of Andean beans with the exception of race Chile which is not adapted to water stress conditions. Most genotypes were included in this trial based on their high yield under field trials at CIAT-Palmira in 2009 and G19833 was used because of its historical use in genetic studies. Seven Andean and three Mesoamerican checks were included (Table 4.1). The Mesoamerican checks were included in this study because of their known root and physiological characters.

Trial 2 (2010) consisted of 40 mixed elite Andean and Mesoamerican genotypes (Table 4.2). The composition of genotypes included released varieties in southern Africa and elite genotypes commonly used in breeding programmes for genetic improvement targeting such stresses as: drought, low P and common bacterial blight.

Table 4.1 **Andean genotypes, principal characteristics and country of origin evaluated for morphological root traits under greenhouse conditions at CIAT-Palmira**

Genotype	Race	Seed size	Phaseolin type	Growth habit	Country of origin
G14253	NG2	L	T	I	Peru
G11512	NG2	L	T	I	Ecuador
G6873	NG2	L	T	I	Brazil
AND1005	NG2	L	T	II	Colombia
G18264	NG2	L	T	III	Dominican Republic
G4644	NG2	L	T	I	Colombia
G11585	NG2	L	T	I	Peru
G17076	NG2	L	T	I	Ecuador
G5708	NG2	L	T	I	Colombia
G5034	NG2	L	T	I	Brazil
G21210	NG1	L	T	I	Colombia
G1688	NG1	L	T	II	Brazil
G5625	NG1	L	T	I	Mexico
G4534	NG1	L	CA	I	Colombia
G16115	NG1	L	T	I	Peru
G4001	NG1	L	T	II	Costa Rica
G22247	NG1	L	T	II	Dominican Republic
G18255	NG1	L	T	II	Cuba
G6639	NG1	L	TM	I	Haiti
G17070	NG1	L	T	I	Ecuador
PVA773	P	L	T	I	Colombia
G2686	P	L	T	I	Peru
G4721	P	L	H	II	Peru
G22147	P	L	T	I	Peru
DRK47	P	L	T	I	Colombia
G19833	P	L	H	III	Peru
SEQ1027	Andean	L	-	I	Breeding line
CAL96	Andean	L	-	I	Breeding line
SEQ1003	Andean	L	-	I	Breeding line
SAB645	Andean	L	-	I	Breeding line
CAL143	Andean	L	-	I	Breeding line
SAB258	Andean	L	-	I	Breeding line
AFR619	Andean	L	-	I	Breeding line
G21212	M	S	-	III	Breeding line
DOR364	M	S	-	III	Breeding line
BAT477	M	S	-	III	Breeding line

NG1 – Nueva Granada 1; NG2 – Nueva Granada 2; P – Peru; M – Mesoamerican; S – small; M – medium; L – large; T – Tender green; CA – Contender and Ayacucho hybrid; TM – Tender green and Middle America hybrid; H – Huevo de huanchaco; - represents unknown phaseolin type.

Table 4.2 Elite varieties and production merits evaluated for morphological root traits under greenhouse conditions at CIAT-Palmira

Genotype	Origin	Growth habit	Seed size	Merits
AFR298	A	I	L	Released in Colombia, drought tolerant and widely used in breeding programmes in Africa
AND277	A	I	M	Angular leaf spot tolerance
CAL96	A	I	L	Released in Uganda, angular leaf spot tolerance and widely used in breeding programmes in East and Central Africa
BRB191	A	I	L	Has the *bc3* gene for common bean mosaic virus
CAL143	A	I	M	Released in Malawi and has tolerance to angular leaf spot and low fertile soils
DAB147	A	I	M	Drought tolerance
DAB62	A	I	L	Drought tolerance
DRK149	A	I	L	Drought tolerance
DRK156	A	I	L	Drought tolerance
G19833	A	III	L	Low phosphorus tolerance
G19839	A	III	L	Low phosphorus tolerance
G4523	A	I	M	Released in Colombia, good drought tolerance
KATB1	A	I	S	Drought tolerance
KATB9	A	I	S	Drought tolerance
Natal Sugar	A	II	M	Drought susceptible but widely distributed in southern Africa
PAN127	A	II	M	Drought susceptible. Released in South Africa and registered in some SADC countries
RAA21	A	II	S	Drought tolerance
Red Canadian Wonder	A	I	L	Drought tolerant through earliness and widely distributed in Africa
SAB259	A	I	M	Drought tolerance
SAB686	A	I	M	Drought tolerance
SAB712	A	I	M	Drought tolerance
SEQ1003	A	II	L	Drought tolerance
SEQ1006	A	I	L	Drought tolerance
SEQ1027	A	I	L	Drought tolerance
SEQ1036	A	II	L	Drought tolerance
SUG131	A	I	L	Good market class and released variety in Zimbabwe, Malawi and Ethiopia. Susceptible to drought
VAX6	M	II	S	Common bacterial blight resistance and wide breeding use

Table 4.2 continued

Genotype	Origin	Growth habit	Seed size	Merits
VAX3	M	II	S	Common bacterial blight resistance and wide breeding use
VAX1	M	II	S	Common bacterial blight resistance and wide breeding use
BAT477	M	III	S	Resistant to drought and low soil phosphorus
SER8	M	II	S	Drought tolerance
SER22	M	II	S	Drought tolerance
SER16	M	II	S	Drought tolerance and released in Rwanda, Nicaragua and widely tested in Profiijol
SEQ11	M	II	S	Drought tolerance
SEC16	M	II	S	Drought tolerance
SEA5	M	II	S	Drought tolerance
SEA15	M	II	S	Drought tolerance
Pinto Villa	M	II	S	Drought tolerance
G2333	M	IV	S	Anthracnose and low soil phosphorus tolerance
DOR364	M	II	S	Released in Central America. Tolerant to bean golden mosaic virus and low soil phosphorus.

A – Andean; M – Mesoamerican; S – Small; M – Medium; L – large

4.3.2 Methods

Soil of the Andisol classification was collected from Darien, Colombia, ground and sieved before mixing it with river sand in a 2:1 ratio at CIAT-Palmira. The soil-sand mixture was fertilised with an adequate level of nutrients (kg ha^{-1}: 80 N, 50 P, 100 K, 101 Ca, 29.4 Mg, 20 S, 2 Zn, 2 Cu, 0.1 B and 0.1 Mo) using different sources of nutrients shown in Table 4.3 and mixed thoroughly with a mixer (Butare *et al.* 2011).

A total of 4.25 kg of the soil-sand-fertiliser mixture was added to reach a depth of 75 cm in transparent plastic cylinders which were 80 cm deep with a 7.5 cm diameter. The process of filling up the cylinders involved weighing and placing 500 g of soil-sand-fertiliser mixture in the cylinders and adding 100 ml of deionised water. When the deionised water had infiltrated through the soil-sand-fertiliser mixture another 500 g of soil-sand-fertiliser mixture was added. The whole process was repeated until the 75 cm mark of the transparent plastic cylinders was reached. Cylinders were then inserted into

PVC tubes and placed in the greenhouse and maintained at 80% field capacity until planting.

Table 4.3 Source and level of nutrients applied to the soil used for the root studies

Source	Nutrient	Content of nutrient by source (%)	Nutrient level (kg ha^{-1})
Urea	N	46.0	80.0
Triple super phosphate	P	20.0	50.0
	Ca	14.0	35.0
KCl	K	52.0	100.0
Dolomitic lime	Ca	22.0	66.0
	Mg	9.8	29.4
Elemental sulfur	S	86.0	20.0
$ZnCl_2$	Zn	47.0	2.0
$CuCl_2\,2H_2O$	Cu	37.1	2.0
H_3BO_3	B	17.4	0.1
$Na_2\,MoO_4\,2H_2O$	Mo	39.4	0.1

Field capacity was determined by watering the cylinder and allowing the water to drain from the cylinder and then weighed to register the amount of soil moisture in the cylinder. Seeds were sterilised by soaking them in 5% calcium hypochlorite for 5 minutes and germinated on germinating paper. Seedlings with uniform small roots were transplanted into the cylinders after 48 hours. Only one seedling was planted at the centre of each cylinder at a depth of about 5 cm.

4.3.2.1 Experimental design

A randomised complete block design with three replications was used in each trial. Two levels of water [well watered (WW) and water stress (WS) induced by progressive soil drying)] were employed in each trial. Cylinders for WW and WS treatments were randomised together in each replication.

4.3.2.2 Trial management

Cylinders in both treatments were weighed every second day to monitor water loss and the initial 80% field capacity of the cylinders in both treatments was maintained until day ten after transplanting. Water was withheld in the WS treatment ten days after transplanting while cylinders in the WW treatment received water every second day to maintain the initial 80% field capacity. This was achieved by weighing each cylinder at two day intervals and applying the required water to the top of the cylinder. Weighing cylinders in both treatments continued until harvesting to monitor the moisture content in the soil.

4.3.2.3 Traits measured

Phenotypic traits measured were classified into two groups, namely morphological (shoot and root) and physiological. Shoot morphological traits included green leaf biomass (GLB), dead leaf biomass (DLB), stem biomass (SB), pod biomass (PB) and leaf area (LA). The root morphological traits included total visual rooting depth (VRD) measured at different days after planting (DAP), total root length (TRL), total root length with diameter 0-0.5 mm ($TRL_{0.5mm}$), total root length with diameter 0.5-1 mm (TRL_{1mm}), mean root diameter (MRD), total root biomass (TRB) and root volume (RV). Physiological traits included chlorophyll content (SCMR, SPAD chlorophyll meter reading), leaf stomatal conductance (SCOND) and photosynthetic efficiency (PE).

4.3.2.3.1 Visual rooting depth

In both trials, VRD was determined at 10, 17, 24, 31, 40 and 45 DAP. A ruler was used to measure the root depths.

4.3.2.3.2 Leaf chlorophyll content

SCMR was measured using a non-destructive, hand-held chlorophyll meter (SPAD-502 Chlorophyll Meter, Minolta Camera Co., Ltd., Tokyo, Japan). The SPAD value was measured on a fully expanded young leaf of one plant of each replication in both treatments. SPAD-502 measures the chlorophyll content available in the leaf using the blue (400-500 nm) and red (600-700 nm) solar radiation absorbance peaks. Only the

absorbance in the red and near-infrared wavelengths is registered by SPAD-502 and is used to determine the amount of chlorophyll available in the leaf. The SPAD-502 readings range between 0 and 80 nmol cm^{-2}.

4.3.2.3.3 Stomatal conductance

SCOND was measured using a portable leaf porometer (Decagon Devices INC) as mmol m^{-2} s^{-1} and is a measure of stomatal conductance for water vapour. This instrument measures the water vapour flux from the leaf surface to the atmosphere. A fixed diffusion path is clamped to the surface of the leaf and the vapour flux is determined from the vapour pressure gradient in the diffusion path and the known vapour conductance through the fixed path. Stomatal conductance was measured on a fully expanded young leaf on three different plants within each replication in both treatments.

4.3.2.3.4 Other measurements

Trials for both the WS and WW treatments were harvested 45 days after transplanting. Harvesting involved separating the leaves, pods and stems (Butare *et al.* 2011). Stems were cut at the soil surface. Separated leaves, pods and stems were placed in well labelled paper bags and leaves were scanned in the laboratory for LA analysis using a LI-3100 Area Meter (LI-COR Biosciences, Lincoln, NE USA) and the dry biomass of plant parts was determined by oven drying samples at 60^{o}C for 48 hours. The plastic cylinders were cut into at the following depths; 0-5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-60 cm and 60-75 cm to determine root length, biomass and volume for each profile. Roots at each depth level were separated from soil by washing with water and placed in well labelled plastic packets. Root length, diameter and density were measured with an image analysis system (WinRHIZO V. 2003b, Regent Instruments Inc, Quebec, Canada). Root weight was determined after roots were dried in an oven at 60^{o}C for 48 hours.

4.3.3 Statistical analysis

The phenotypic data collected were initially analysed separately for each treatment and then combined for the two treatments. Pearson correlation coefficients (r) between traits evaluated under both treatments were calculated. All analyses were done using Agrobase Generation II software (Agronomix Software Inc. 2005).

4.4 Results for the sub-set of Andean landraces

As the genotypes were too many to discuss them all in detail, only genotypes which had the most significant differences in TRL between the WW and WS treatments were selected for discussion purposes. A total of 20 Andean genotypes were selected based on this criterion for both the sub-sets for Andean landraces and mixed elite Andean and Mesoamerican trials. Genotypes were distributed as follows; checks (9), sub races NG1 (5), Peru (4) and NG2 (2) according to race designation in the sub-set of Andean landraces.

4.4.1 Visual rooting depth

VRD was significantly different between water levels at 17, 24, 31, 40 and 45 DAP (Table 4.4). Under the WS treatment, root growth of some genotypes was hastened, where lines: DRK47, G2686, SEQ1003, G19833, G4001, AFR619 and G5625 had significantly deeper roots than under WW treatment from 24 to 45 DAP.

4.4.2 Total root length and its distribution among different soil depths

Results of the analysis of variance for TRL, $TRL_{0.5mm}$ and TRL_{1mm} are given in Table 4.5 (all 36 entries included in analysis). The proportions of the total sum of squares for genotypes and treatments contributing to variation were below 6% for TRL, $TRL_{0.5mm}$ and TRL_{1mm}. The combined ANOVA showed that TRL, $TRL_{0.5mm}$ and TRL_{1mm} were significantly affected by soil depth main effects, which explained more than 45% of the total variation of each trait.

Table 4.4 **Visual root depth (cm) measured at different days after planting for the Andean reference collection sub-set under greenhouse well watered and water stressed treatments**

Trait	VRD at 10 DAP		VRD at 17 DAP		VRD at 24 DAP		VRD at 31 DAP		VRD at 40 DAP		VRD at 45 DAP	
Environment	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
Genotype												
DOR364	13.70	17.43	21.13	28.40	30.63	33.70	38.57	39.87	44.87	42.43	50.53	48.73
SAB258	14.00	14.13	24.33	27.13	35.23	45.57	46.37	56.27	51.13	62.90	59.07	70.43
DRK47	14.10	17.33	18.23	27.00	22.47	47.27	27.77	55.87	33.53	64.40	39.90	69.27
G2686	17.53	20.57	27.10	33.70	34.47	50.97	40.87	64.80	43.23	67.03	46.80	70.67
G11512	14.67	11.63	26.10	19.97	35.57	30.20	48.53	44.10	54.20	52.13	61.50	61.33
SEQ1003	19.80	17.90	28.70	28.83	34.80	43.93	39.37	55.83	42.30	60.17	46.77	66.00
SEQ1027	19.60	18.90	28.33	26.67	36.50	41.33	46.80	55.73	54.63	61.63	59.53	70.80
BAT477	18.27	14.47	26.13	26.80	38.07	38.00	50.77	47.97	59.07	59.00	70.60	64.87
G19833	16.57	17.97	25.47	29.67	37.37	43.93	44.80	59.87	52.17	70.67	54.63	72.80
SAB645	19.30	21.23	34.27	32.00	42.27	40.30	49.70	55.33	56.37	62.10	61.07	66.60
G4001	16.80	18.27	25.47	28.07	35.27	42.77	45.63	58.27	48.43	69.47	54.00	75.00
G4534	19.10	14.53	27.43	25.57	36.13	41.93	43.47	47.87	48.23	55.30	58.20	58.73
G4721	17.33	16.93	27.43	27.33	37.60	52.00	48.03	54.90	57.13	64.63	64.87	67.33
G18255	22.13	16.97	32.57	26.47	41.93	41.13	48.77	48.57	57.10	54.60	58.23	58.60

Table 4.4 continued

Trait	VRD at 10DAP		VRD at 17 DAP		VRD at 24 DAP		VRD at 31 DAP		VRD at 40 DAP		VRD at 45 DAP	
Environm	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
Genotype												
AFR619	17.93	18.10	29.30	32.73	39.50	46.30	48.27	59.27	51.17	65.90	55.87	71.37
G5625	16.37	23.30	27.40	38.00	39.37	50.97	43.40	61.97	48.47	71.23	52.60	73.77
CAL96	15.97	16.83	27.83	28.93	42.90	42.10	51.67	51.83	56.03	59.67	69.50	64.40
Trial mean	16.92	16.61	25.99	27.44	35.74	40.74	44.97	52.31	50.72	59.44	56.61	64.73
LSD	5.43	6.81	8.08	9.13	9.97	14.67	16.03	18.64	20.86	18.29	23.15	16.50
MS	14.63	27.61	31.71	45.96	50.85	74.85	101.93	123.61	124.93	150.21	169.67	135.75
Error	11.11	17.50	24.60	31.42	37.45	81.12	96.96	131.07	164.08	126.08	202.14	102.72
MS^+	VRD at 10DAP		VRD at 17 DAP		VRD at 24DAP		VRD at 31 DAP		VRD at 40 DAP		VRD at 45 DAP	
Wl MS	5.05		114.26*		1348.50***		2906.93***		4102.94***		3563.22***	
G MS	27.92*		44.85*		65.46		105.34		139.33		146.07	
G x Wl	14.32		32.82		60.23		120.21		135.81		159.35	
LSD	5.43		6.04		8.79		12.19		13.75		14.09	

*P≤0.05; **P≤0.01; *** P≤0.001; VRD – visual root depth; DAP – days after planting; WW – well watered; WS – water stressed; lsd – least significant difference; G – genotype; T – treatment; LSD – least significant difference; m.s. – mean square; Wl – water level; MS^+ - mean squares between treatments

Table 4.5 Analysis of variance for root traits data derived from the reference collection genotypes under greenhouse conditions at CIAT-Palmira, 2009

Trait: Total root length					**Trait: Root length with diameter 0-0.5 mm**				
Source	**D.f.**	**s.s.**	**m.s.**	**% explained**	**Source**	**D.f.**	**s.s.**	**m.s.**	**% explained**
Genotype (G)	35	1555.03	44.00***	3.88	Genotype (G)	35	988.95	28.26***	3.65
Treatment (T)	1	361.06	361.06***	0.9	Treatment (T)	1	89.33	89.33***	0.33
Soil depth (S)	5	23025.6	4605.12***	57.41	Soil depth (S)	5	15724.58	3144.92***	58.07
GxT	35	1004.82	28.71***	2.51	GxT	35	670.39	19.15***	2.48
GxS	175	1779.14	10.17	4.44	GxS	175	1240.14	7.09	4.58
TxS	5	843.53	168.71***	2.1	TxS	5	464.62	92.92***	1.72
GxTxS	175	2011.47	11.49	5.02	GxTxS	175	1341.42	7.67	4.95
Error	856	9364.28	10.94	23.35	Error	856	6461.06	7.55	23.86
Total	1289	40106.9			Total	1289	27078.95		
Trait: Root length with_diameter 0.5-1 mm					**Trait: Root volume**				
Genotype (G)	35	58.69	1.68***	4.8	Genotype (G)	35	33.16	0.95***	5.76
Treatment (T)	1	64.27	64.27***	5.22	Treatment (T)	1	28.57	29.57***	4.96
Soil depth (S)	5	602.93	120.59***	49.05	Soil depth (S)	5	277.17	55.43***	48.16
GxT	35	32.7	0.93***	2.66	GxT	35	16.55	0.47***	2.88
GxS	175	62.75	0.36	5.15	GxS	175	28.9	0.17	5.07
TxS	5	44.71	8.94***	3.64	TxS	5	20.01	4.00***	3.48
GxTxS	175	67.59	0.39	5.5	GxTxS	175	29.71	0.17	5.16
Error	856	290.06	0.34	23.6	Error	856	138.3	0.16	24.03
Total	1289	1229.22			Total	1289	575.55		
Trait: Mean root diameter					**Trait: Total root biomass**				
Genotype (G)	35	0.923	0.027***	4.25	Genotype (G)	35	0.3445	0.0098***	5.38
Treatment (T)	1	0.176	0.176***	0.8	Treatment (T)	1	0.0949	0.0949***	1.48
Soil depth (S)	5	4.02	0.804***	18.37	Soil depth (S)	5	4.0329	0.8066***	62.99
GxT	35	0.711	0.020**	3.25	GxT	35	0.1499	0.0043***	2.34
GxS	175	2.493	0.014	11.39	GxS	175	0.2467	0.0014	3.85
TxS	5	0.292	0.058***	1.33	TxS	5	0.0871	0.0174***	1.36
GxTxS	175	3.065	0.018***	14.01	GxTxS	175	0.2335	0.0013	3.65
Error	856	10.195	0.012	46.59	Error	856	1.1757	0.0014	18.36
Total	1289	21.88			Total	1289	6.4022		

***P≤0.001; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares

ANOVAs for root length traits revealed a highly significant effect of genotype and treatment interaction. DRK47, G5034, SEQ1003, G2686 and G5625 exhibited significantly higher TRL under WS than WW treatments (Table 4.6). In contrast, the remaining 15 genotypes had significantly longer TRL under WW than WS. DRK47, G5034 and G5625 had also higher $TRL_{0.5mm}$ under WS than WW (Table 4.7). TRL_{1mm} was not significantly different between treatments in a number of genotypes including DRK47 and G5625 (Table 4.8). No genotype portrayed higher TRL_{1mm} under WS than WW while most genotypes had significantly higher TRL_{1mm} under WW than WS treatments.

The results of the ANOVA in Table 4.5 showed highly significant treatment x soil depth interactions for TRL, $TRL_{0.5mm}$ and TRL_{1mm}. Table 4.9 showed trial means for root length traits measured at different soil depths under WS and WW treatments. The WS treatment had significantly higher trial means for TRL and $TRL_{0.5mm}$ than WW at the 40-60 cm soil profile level.

Figure 4.1 presents trial means for the root length traits to elucidate the interaction that existed between treatments and soil depths. A crossover type of interaction existed for TRL and $TRL_{0.5mm}$. TRL and $TRL_{0.5mm}$ were higher under WW than WS at the first four soil depth levels. However, the two root length traits were higher under WS than WW at the last two soil depth levels. TRL_{1mm} ranked higher under WW than WS on the first five soil depth levels.

Table 4.6 **Genotypic means for 20 genotypes for total root length (cm) in the Andean reference collection under greenhouse conditions at CIAT-Palmira, 2009**

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	11.31	7.51	6.92	9.24	5.43	2.08	7.08
	WW	8.52	11.64	17.31	15.81	4.92	0.64	9.81
BAT477	WS	13.21	8.17	9.05	9.81	7.05	0.50	7.96
	WW	13.25	10.93	14.44	16.25	10.18	2.20	11.21
CAL96	WS	12.26	7.22	8.15	12.07	3.35	1.76	7.47
	WW	16.51	11.96	16.24	17.20	4.40	0.56	11.15
DOR364	WS	10.41	7.19	8.10	5.86	1.51	0.00	5.51
	WW	14.49	10.05	13.58	6.90	3.01	1.32	8.23
DRK47	WS	16.49	11.00	12.21	17.45	6.68	2.99	**11.14**
	WW	17.25	8.55	12.18	6.77	0.48	0.00	**7.54**
G11512	WS	17.50	9.58	8.85	7.26	3.33	0.44	7.83
	WW	12.39	9.07	14.45	17.49	6.49	1.17	10.18
G18255	WS	9.80	7.54	6.65	4.84	3.07	0.46	5.40
	WW	8.92	11.98	11.78	13.17	4.87	1.00	8.62
G19833	WS	15.23	10.33	8.09	8.82	7.62	2.05	8.69
	WW	15.73	9.97	14.45	17.96	4.25	0.18	10.42
G21210	WS	9.47	9.77	12.09	9.75	4.35	0.52	7.66
	WW	10.03	9.85	14.53	17.68	4.41	1.75	9.71
G21212	WS	9.08	8.82	10.08	7.77	1.59	0.03	6.23
	WW	16.93	9.80	15.37	17.34	5.40	1.04	10.98
G2686	WS	11.21	5.70	6.67	6.12	5.50	2.32	6.25
	WW	7.65	8.66	9.38	7.73	1.26	0.04	5.78
G4001	WS	10.26	9.96	9.47	9.80	5.36	1.58	7.74
	WW	17.17	16.85	15.97	14.11	4.23	0.58	11.49

Table 4.6 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	11.72	6.25	9.68	8.82	1.95	0.18	6.43
	WW	9.16	6.87	11.49	14.39	2.56	0.11	7.43
G4721	WS	15.80	9.40	10.29	11.65	5.85	2.86	9.31
	WW	16.08	12.41	18.88	23.16	6.21	0.69	12.91
G5034	WS	13.14	8.97	11.04	10.96	4.65	0.16	8.15
	WW	14.08	7.76	9.17	6.07	1.95	0.16	6.53
G5625	**WS**	**12.22**	**9.91**	**11.27**	**10.52**	**6.38**	**1.23**	**8.59**
	WW	**9.84**	**6.68**	**7.84**	**8.08**	**2.75**	**0.93**	**6.02**
SAB258	WS	8.99	5.89	7.14	7.56	5.06	1.16	5.97
	WW	13.28	7.58	11.47	8.92	2.79	0.00	7.34
SAB645	WS	10.83	9.64	12.74	11.58	3.83	1.41	8.34
	WW	13.46	11.13	12.69	14.70	3.00	0.23	9.20
SEQ1003	WS	9.85	11.21	8.77	10.61	5.54	1.86	7.97
	WW	10.05	8.18	13.71	13.13	0.71	0.00	7.63
SEQ1027	WS	11.86	10.32	10.01	9.08	5.70	1.78	8.13
	WW	13.91	12.47	9.83	11.86	3.83	1.23	8.85
LSD between treatments								**0.36**
LSD among soil depth levels								**0.63**

WW – well watered; WS – water stressed; LSD – least significance difference

Table 4.7 **Genotypic means for 20 genotypes for $TRL_{0.5mm}$ (cm) in the Andean reference collection under greenhouse conditions at CIAT-Palmira, 2009**

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	9.99	6.47	5.59	7.47	4.55	1.89	5.99
	WW	7.11	10.28	13.71	11.56	3.80	0.48	7.82
BAT477	WS	11.87	7.27	7.59	8.08	5.74	0.40	6.82
	WW	11.74	9.50	11.92	12.60	7.36	1.43	9.09
CAL96	WS	10.60	6.25	6.92	10.28	2.89	1.53	6.41
	WW	13.79	9.72	12.73	13.31	3.13	0.29	8.83
DOR364	WS	9.19	6.30	6.84	5.05	1.26	0.00	4.77
	WW	12.91	9.03	11.61	5.86	2.58	1.06	7.18
DRK47	WS	14.69	9.64	10.10	13.77	5.43	2.40	**9.34**
	WW	14.72	7.09	9.24	5.15	0.25	0.00	**6.08**
G11512	WS	15.54	8.28	7.18	5.84	2.78	0.35	6.66
	WW	10.53	7.54	11.71	13.66	5.02	0.86	8.22
G18255	WS	8.61	6.33	5.41	3.85	2.67	0.43	4.55
	WW	7.09	9.92	8.82	9.65	3.84	0.79	6.69
G19833	WS	13.46	8.66	6.46	6.95	6.20	1.57	7.22
	WW	13.18	8.00	10.84	13.25	2.91	0.09	8.05
G21210	WS	7.73	8.27	9.55	7.44	3.68	0.43	6.19
	WW	8.31	7.90	10.42	13.32	3.43	1.38	7.46
G21212	WS	8.16	7.64	8.38	6.48	1.33	0.02	5.33
	WW	14.61	8.26	12.50	13.58	4.13	0.67	8.96
G2686	WS	10.11	5.05	5.96	5.36	4.99	2.02	5.58
	WW	6.74	7.82	8.07	6.75	1.12	0.03	5.09
G4001	WS	8.92	8.40	7.17	7.32	4.28	1.38	6.24
	WW	14.87	14.11	11.89	10.26	3.24	0.40	9.13

Table 4.7 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	10.22	5.22	7.69	7.01	1.71	0.16	5.34
	WW	7.58	5.75	9.14	11.10	1.93	0.04	5.92
G4721	WS	14.14	7.98	8.53	9.49	4.90	2.26	7.88
	WW	13.78	10.36	14.09	17.22	4.29	0.52	10.04
G5034	WS	11.99	8.10	9.61	9.13	3.97	0.10	7.15
	WW	12.40	6.42	7.14	4.79	1.54	0.11	5.40
G5625	**WS**	**10.81**	**8.79**	**9.31**	**8.18**	**5.36**	**1.04**	**7.25**
	WW	**7.95**	**5.25**	**6.15**	**5.71**	**1.92**	**0.60**	**4.60**
SAB258	WS	8.00	4.87	5.44	5.41	3.97	0.98	4.78
	WW	11.23	6.25	8.88	6.65	2.24	0.00	5.88
SAB645	WS	9.70	8.61	10.70	8.92	3.14	1.19	7.05
	WW	11.25	9.25	9.88	11.36	2.46	0.17	7.40
SEQ1003	WS	8.60	9.49	6.87	8.22	4.30	1.48	6.49
	WW	8.15	6.51	10.54	9.57	0.49	0.00	5.88
SEQ1027	WS	10.24	8.49	7.59	6.80	4.48	1.41	6.50
	WW	11.90	10.36	7.23	8.97	2.97	0.85	7.05
LSD between treatments								**0.30**
LSD among soil depth levels								**0.52**

WW – well watered; WS – water stressed; LSD – least significant difference; $TRL_{0.5mm}$ – total root length with diameter between 0-0.5 mm

Table 4.8 Genotypic means for 20 genotypes for TRL_{1mm} (cm) in the Andean reference collection under greenhouse conditions at CIAT-Palmira, 2009

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	1.06	0.87	1.11	1.47	0.74	0.16	0.90
	WW	1.11	1.20	3.07	3.50	0.94	0.13	1.66
BAT477	WS	1.11	0.74	1.26	1.44	1.19	0.09	0.97
	WW	1.20	1.20	2.19	3.22	2.50	0.61	1.82
CAL96	WS	1.44	0.84	1.04	1.47	0.38	0.17	0.89
	WW	2.25	1.90	2.72	2.91	1.06	0.22	1.84
DOR364	WS	1.08	0.82	1.19	0.76	0.24	0.00	0.68
	WW	1.38	0.92	1.84	0.97	0.42	0.20	0.96
DRK47	WS	1.47	1.21	1.76	2.86	0.99	0.46	**1.46**
	WW	1.95	1.22	2.41	1.34	0.16	0.00	**1.18**
G11512	WS	1.69	1.09	1.42	1.20	0.49	0.07	0.99
	WW	1.49	1.28	2.42	3.25	1.23	0.26	1.66
G18255	WS	1.02	1.03	1.12	0.88	0.37	0.02	0.74
	WW	1.52	1.82	2.48	2.90	0.89	0.19	1.63
G19833	WS	1.49	1.37	1.17	1.22	1.03	0.37	1.11
	WW	2.02	1.61	2.98	3.68	0.99	0.07	1.89
G21210	WS	1.53	1.21	2.06	1.93	0.60	0.08	1.23
	WW	1.36	1.63	3.27	3.48	0.76	0.30	1.80
G21212	WS	0.81	1.07	1.50	1.10	0.24	0.01	0.79
	WW	2.02	1.38	2.59	3.35	1.00	0.33	1.78
G2686	WS	0.94	0.57	0.66	0.67	0.45	0.25	0.59
	WW	0.77	0.76	1.22	0.94	0.13	0.01	0.64
G4001	WS	1.11	1.32	1.81	1.86	0.89	0.14	1.19
	WW	1.85	2.25	3.44	3.10	0.79	0.17	1.93

Table 4.8 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	1.29	0.82	1.61	1.58	0.22	0.02	0.92
	WW	1.24	0.92	1.86	2.68	0.57	0.05	1.22
G4721	WS	1.42	1.21	1.45	1.51	0.75	0.51	1.14
	WW	1.87	1.73	3.80	4.60	1.29	0.11	2.23
G5034	WS	0.97	0.74	1.19	1.54	0.59	0.05	0.85
	WW	1.46	1.18	1.71	1.11	0.35	0.04	0.98
G5625	**WS**	**1.17**	**0.97**	**1.58**	**1.89**	**0.83**	**0.17**	**1.10**
	WW	**1.44**	**1.16**	**1.38**	**1.95**	**0.61**	**0.24**	**1.13**
SAB258	WS	0.85	0.89	1.44	1.83	0.84	0.16	1.00
	WW	1.78	1.18	2.28	1.98	0.44	0.00	1.28
SAB645	WS	0.92	0.90	1.76	2.19	0.63	0.19	1.10
	WW	1.87	1.64	2.38	2.78	0.48	0.05	1.53
SEQ1003	WS	1.03	1.44	1.50	1.89	1.01	0.34	1.20
	WW	1.48	1.33	2.65	3.11	0.19	0.00	1.46
SEQ1027	WS	1.37	1.54	1.95	1.81	1.00	0.28	1.33
	WW	1.63	1.91	2.25	2.44	0.63	0.28	1.52
LSD between treatments								**0.06**
LSD among soil depth levels								**0.11**

WW – well watered; WS – water stressed; LSD – least significant difference; TRL_{1mm} – total root length with diameter between 0.5-1 mm

Table 4.9 **Trial means for TRL, $TRL_{0.5mm}$ and TRL_{1mm} (cm) measured at different soil depths under well watered and water stressed treatments**

Trait	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	LSD
TRL	WS	11.80^{a}	8.92^{a}	9.50^{a}	9.57^{a}	4.61^{b}	1.08^{a}	0.89
	WW	12.81^{b}	9.80^{a}	12.66^{b}	12.58^{b}	3.48^{a}	0.50^{a}	
$TRL_{0.5mm}$	WS	10.40^{a}	7.63^{a}	7.65^{a}	7.58^{a}	3.82^{b}	0.90^{a}	0.74
	WW	10.82^{a}	8.07^{a}	9.78^{b}	9.50^{b}	2.61^{a}	0.35^{a}	
TRL_{1mm}	WS	1.19^{a}	1.10^{a}	1.53^{a}	1.61^{a}	0.66^{a}	0.15^{a}	0.16
	WW	1.63^{b}	1.49^{b}	2.42^{b}	2.55^{b}	0.71^{a}	0.12^{a}	

LSD - least significant difference between treatments, means followed by the same letter are not significantly different at P≤0.05 between treatments

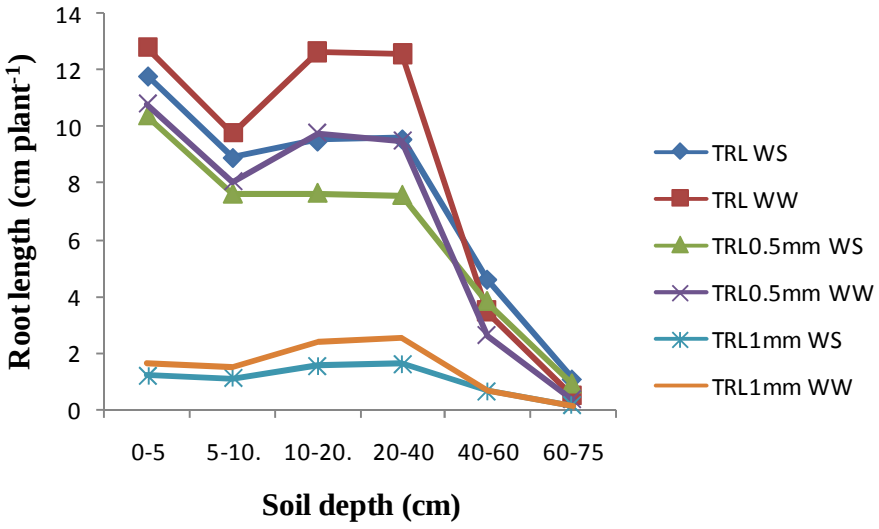


Figure 4.1 Interactions between treatments and soil depths for TRL, $TRL_{0.5mm}$ and TRL_{1mm}. TRL – total root length; $TRL_{0.5mm}$ – total root length with diameter between 0-0.5 mm; TRL_{1mm} – total root length with diameter between 0.5-1 mm.

4.4.3 Total root biomass and its distribution among different soil depths

Results of the combined ANOVA for total root biomass are given in Table 4.5. Genotypes (G), treatments (T), soil depth (S), GxT interaction and TxS interactions were highly significant for total root biomass. Soil depth main effects accounted for the highest phenotypic variation observed (62.99%).

Table 4.10 shows the genotypic means for TRB under different soil depth levels. Treatments significantly affected TRB accrued in the WW and WS conditions. DRK47 had significantly higher TRB under WS than WW. On the other hand, AFR619, CAL96, G21512, G18255, G21212, G4001 and G4721 had significantly higher TRB under WW than WS treatment.

Total root biomass among different soil depths

ANOVA for TRB data showed a highly significant treatment and soil depth interaction. The trial means for TRB among different soil depths showed differences between the two treatments (Table 4.11).

4.4.4 Mean root diameter and its distribution among different soil depths

Genotype (G), treatment (T), soil depth (S), GxT, TxS, GxTxS interactions significantly affected MRD (Table 4.5). Of these components, soil depth and GxTxS contributed 18.37% and 14.01% to the total sum of squares observed for MRD. The genotypic means for MRD under WS and WW treatments are given in Table 4.12. Particularly genotypes BAT477 and CAL96 had significantly higher MRD under WW than WS. The majority of the genotypes did not show any significant differences for MRD between treatments.

Table 4.10 **Total root biomass (g) for 20 genotypes for total root length in the reference collection under greenhouse conditions at CIAT-Palmira, 2009**

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	0.16	0.08	0.08	0.09	0.04	0.02	0.08
	WW	0.16	0.12	0.21	0.18	0.04	0.01	0.12
BAT477	WS	0.16	0.09	0.10	0.10	0.06	0.00	0.09
	WW	0.19	0.14	0.17	0.18	0.11	0.03	0.14
CAL96	WS	0.18	0.08	0.08	0.11	0.03	0.01	0.08
	WW	0.21	0.13	0.19	0.17	0.05	0.01	0.13
DOR364	WS	0.13	0.07	0.08	0.04	0.01	0.00	0.05
	WW	0.17	0.11	0.13	0.05	0.02	0.01	0.08
DRK47	WS	0.23	0.11	0.14	0.18	0.06	0.03	**0.13**
	WW	0.24	0.10	0.15	0.07	0.01	0.00	**0.09**
G11512	WS	0.18	0.09	0.08	0.06	0.02	0.00	0.07
	WW	0.18	0.12	0.16	0.19	0.07	0.01	0.12
G18255	WS	0.15	0.09	0.08	0.05	0.02	0.00	0.07
	WW	0.17	0.14	0.15	0.15	0.04	0.01	0.11
G19833	WS	0.20	0.12	0.11	0.11	0.07	0.02	0.11
	WW	0.22	0.13	0.18	0.21	0.05	0.00	0.13
G21210	WS	0.16	0.12	0.15	0.11	0.04	0.00	0.10
	WW	0.16	0.13	0.20	0.19	0.04	0.02	0.12
G21212	WS	0.10	0.09	0.10	0.07	0.01	0.00	0.06
	WW	0.21	0.12	0.16	0.17	0.05	0.01	0.12
G2686	WS	0.11	0.05	0.06	0.05	0.03	0.02	0.05
	WW	0.09	0.08	0.08	0.05	0.01	0.00	0.05
G4001	WS	0.14	0.12	0.13	0.12	0.05	0.01	0.10
	WW	0.25	0.19	0.20	0.15	0.04	0.01	0.14

Table 4.10 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	0.15	0.07	0.11	0.08	0.02	0.00	0.07
	WW	0.15	0.09	0.14	0.15	0.03	0.00	0.09
G4721	WS	0.20	0.12	0.13	0.14	0.06	0.03	0.11
	WW	0.22	0.15	0.26	0.26	0.07	0.01	0.16
G5034	WS	0.16	0.10	0.13	0.17	0.04	0.00	0.10
	WW	0.18	0.10	0.12	0.06	0.02	0.00	0.08
G5625	**WS**	**0.18**	**0.10**	**0.13**	**0.13**	**0.05**	**0.01**	**0.10**
	WW	**0.17**	**0.09**	**0.10**	**0.10**	**0.02**	**0.01**	**0.08**
SAB258	WS	0.13	0.07	0.09	0.10	0.05	0.01	0.08
	WW	0.12	0.08	0.11	0.09	0.02	0.00	0.07
SAB645	WS	0.16	0.11	0.14	0.14	0.03	0.01	0.10
	WW	0.22	0.14	0.17	0.17	0.03	0.00	0.12
SEQ1003	WS	0.16	0.14	0.13	0.14	0.06	0.02	0.11
	WW	0.18	0.13	0.19	0.16	0.01	0.00	0.11
SEQ1027	WS	0.17	0.13	0.14	0.11	0.05	0.02	0.10
	WW	0.19	0.15	0.14	0.14	0.04	0.02	0.11
LSD between treatments								**0.01**
LSD among soil depth levels								**0.01**

WW – well watered; WS – water stressed; LSD – least significant difference; LSD – least significant difference

Table 4.11 Trial means for total root biomass (g) among different soil depths under well watered and water stressed treatments

Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	LSD
WS	0.158[a]	0.099[a]	0.114[a]	0.105[a]	0.041[a]	0.009[a]	0.01
WW	0.181[b]	0.118[b]	0.154[b]	0.135[b]	0.036[a]	0.006[a]	

LSD - least significant difference between treatments, means followed by the same letter are not significantly different at P≤0.05

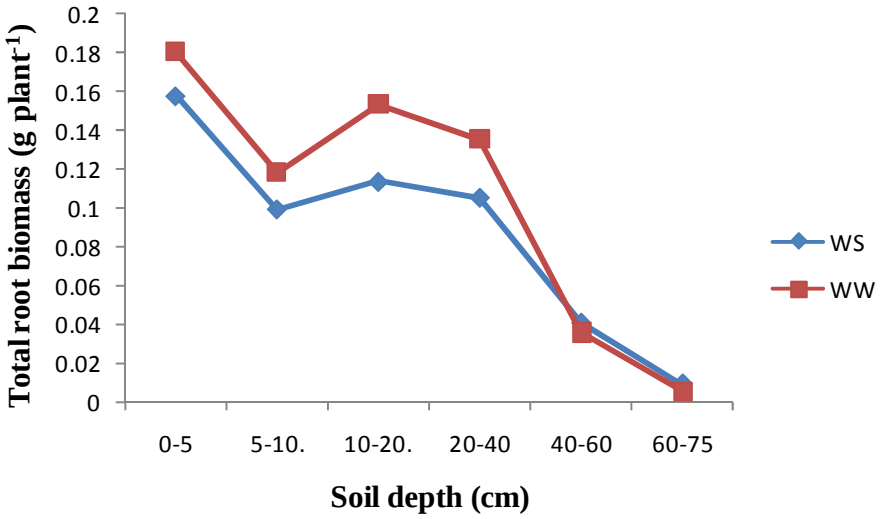


Figure 4.2 Interactions between treatments and soil depths for total root biomass along different soil depth levels. WS – water stressed; WW – well watered.

Table 4.12 Mean root diameter (mm) for 20 genotypes for total root length in the reference collection under greenhouse conditions at CIAT-Palmira, 2009

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	0.31	0.33	0.36	0.37	0.34	0.35	0.34
	WW	0.37	0.32	0.39	0.43	0.55	0.14	0.37
BAT477	WS	0.30	0.32	0.35	0.35	0.34	0.25	0.32
	WW	0.33	0.35	0.37	0.40	0.42	0.64	0.42
CAL96	WS	0.33	0.32	0.33	0.33	0.31	0.11	0.29
	WW	0.36	0.37	0.40	0.41	0.42	0.60	0.43
DOR364	WS	0.31	0.31	0.33	0.32	0.25	0.00	0.25
	WW	0.30	0.30	0.34	0.34	0.11	0.13	0.26
DRK47	WS	0.31	0.32	0.36	0.39	0.35	0.42	**0.36**
	WW	0.34	0.36	0.39	0.28	0.44	0.00	**0.30**
G11512	WS	0.30	0.34	0.36	0.35	0.23	0.32	0.32
	WW	0.36	0.38	0.37	0.39	0.40	0.35	0.38
G18255	WS	0.31	0.35	0.35	0.36	0.32	0.09	0.30
	WW	0.41	0.36	0.41	0.42	0.25	0.26	0.35
G19833	WS	0.31	0.35	0.40	0.41	0.37	0.41	0.38
	WW	0.36	0.38	0.42	0.43	0.32	0.22	0.35
G21210	WS	0.35	0.34	0.38	0.40	0.34	0.11	0.32
	WW	0.36	0.38	0.44	0.43	0.41	0.30	0.39
G21212	WS	0.29	0.31	0.34	0.34	0.33	0.13	0.29
	WW	0.34	0.35	0.39	0.39	0.41	0.28	0.36
G2686	WS	0.29	0.32	0.31	0.31	0.29	0.21	0.29
	WW	0.33	0.31	0.34	0.32	0.19	0.12	0.27
G4001	WS	0.32	0.35	0.40	0.41	0.37	0.34	0.36
	WW	0.33	0.36	0.42	0.45	0.50	0.14	0.37

Table 4.12 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	0.32	0.35	0.38	0.36	0.32	0.10	0.30
	WW	0.37	0.35	0.38	0.40	0.35	0.23	0.35
G4721	WS	0.31	0.34	0.35	0.36	0.34	0.25	0.32
	WW	0.36	0.36	0.43	0.43	0.49	0.33	0.40
G5034	WS	0.28	0.29	0.32	0.34	0.32	0.43	0.33
	WW	0.32	0.37	0.40	0.37	0.23	0.28	0.33
G5625	**WS**	**0.30**	**0.30**	**0.36**	**0.39**	**0.34**	**0.33**	**0.34**
	WW	**0.40**	**0.39**	**0.39**	**0.43**	**0.32**	**0.16**	**0.35**
SAB258	WS	0.30	0.34	0.40	0.41	0.38	0.36	0.36
	WW	0.34	0.35	0.39	0.40	0.37	0.00	0.31
SAB645	WS	0.30	0.31	0.35	0.38	0.35	0.22	0.32
	WW	0.34	0.35	0.39	0.40	0.34	0.26	0.35
SEQ1003	WS	0.31	0.35	0.40	0.39	0.37	0.23	0.34
	WW	0.40	0.40	0.41	0.43	0.55	0.00	0.37
SEQ1027	WS	0.32	0.36	0.41	0.41	0.38	0.47	0.39
	WW	0.35	0.37	0.43	0.43	0.27	0.31	0.36
LSD between treatments								**0.01**
LSD among soil depth levels								**0.02**

WW – well watered; WS – water stressed; LSD – least significant difference

A crossover type interaction occurred for TRB between treatments. The WW treatment had significantly higher TRB than WS on the first four soil depth levels. Figure 4.2 shows a visual presentation of the treatment and soil depth interaction where trial mean rankings changed at the 40-60 cm and 60-75 cm in favour of the WS treatment.

MRD was significantly higher under the WW compared to the WS treatment at the 0-5, 20-40 and 40-60 cm depth levels (Table 4.13). On the other hand, MRD was significantly higher under WS treatment than WW at the 60-75 cm soil depth level.

Table 4.13 Trial means for mean root diameter (mm) among different soil depths under well watered and water stressed treatments

Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	LSD
WS	0.31[a]	0.34[a]	0.37[a]	0.37[a]	0.34[a]	0.24[b]	0.03
WW	0.36[b]	0.37[a]	0.40[a]	0.41[b]	0.38[b]	0.20[a]	

LSD – least significant difference between treatments, means followed by the same letter are not significantly different at $P \leq 0.05$ between treatments

A highly significant treatment and soil depth interaction existed for MRD. Figure 4.3 shows a crossover type of interaction between treatments. The WW treatment had a higher ranking for MRD on the first five soil depth levels compared to the WS treatment. MRD was ranked higher at the 60-75cm depth level for the WS than WW.

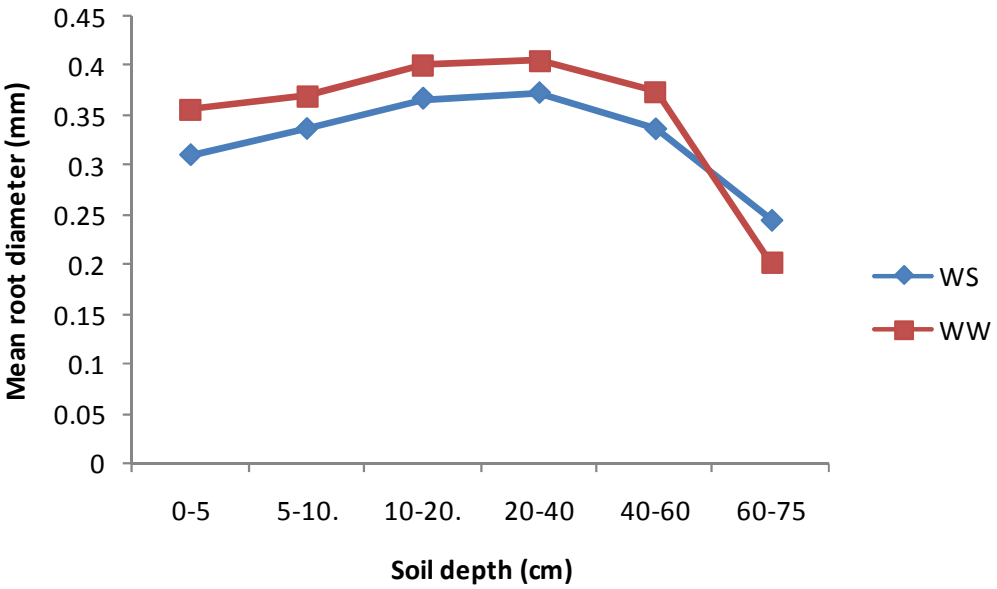


Figure 4.3 Interactions between treatments and soil depths for mean root diameter along different soil depth levels. WS – water stressed; WW – well watered.

4.4.5 Root volume among the different soil depths

Genotype, treatment, soil depth, GxT and TxS contributed significantly to the total variation observed in root volume (Table 4.5). Soil depth main effects accounted for almost half of the total variation (48.16%). Genotypic means for root volume were significantly different between treatments (Table 4.14). Root volume was significantly higher under WW than WS conditions in the following genotypes: AFR619, BAT477, CAL96, G11512, G18255, G19833, G21210, G21212, G4001 and G4721. The remaining genotypes portrayed no significant differences for root volume between treatments.

The trial means for RV showed that the WW treatment caused significantly higher RV in the first four soil depth levels than the WS treatment (Table 4.15). A crossover interaction occurred for RV between treatments at the 60-75 cm soil depth level when the WS treatment had a higher ranking for RV.

4.4.6 Leaf, stem and pod traits

4.4.6.1 Leaf area

The ANOVA for leaf area data showed that treatment main effects were highly significant and accounted for 44.40% of the total variation observed (Table 4.16). Genotype and GxT interaction were also highly significant.

Leaf area was significantly different among genotypes under WW and WS conditions (Table 4.17). Most genotypes except DRK47 had significantly lower leaf area under WS than WW.

Table 4.14 Root volume (cm^3) for 20 genotypes in the Andean reference collection under greenhouse conditions at CIAT-Palmira, 2009

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AFR619	WS	0.90	0.66	0.69	0.97	0.47	0.14	0.64
	WW	0.89	0.94	2.09	2.29	0.58	0.09	1.15
BAT477	WS	0.93	0.64	0.83	0.99	0.66	0.05	0.68
	WW	1.11	1.02	1.57	2.01	1.40	0.42	1.26
CAL96	WS	0.99	0.60	0.72	1.07	0.28	0.16	0.64
	WW	1.69	1.31	2.03	2.25	0.61	0.13	1.34
DOR364	WS	0.79	0.56	0.70	0.46	0.14	0.00	0.44
	WW	1.05	0.73	1.24	0.62	0.25	0.16	0.68
DRK47	WS	1.22	0.90	1.23	2.05	0.68	0.33	**1.07**
	WW	1.68	0.87	1.65	0.86	0.13	0.00	**0.87**
G11512	WS	1.29	0.80	0.88	0.71	0.30	0.04	0.67
	WW	1.21	0.93	1.57	2.11	0.78	0.17	1.13
G18255	WS	0.74	0.71	0.66	0.48	0.24	0.03	0.47
	WW	1.04	1.27	1.60	1.89	0.54	0.11	1.07
G19833	WS	1.15	1.01	0.95	1.13	0.82	0.27	0.89
	WW	1.59	1.14	1.99	2.67	0.78	0.06	1.37
G21210	WS	0.93	0.94	1.42	1.22	0.40	0.05	0.83
	WW	1.03	1.14	2.18	2.51	0.53	0.23	1.27
G21212	WS	0.61	0.68	0.93	0.72	0.15	0.00	0.51
	WW	1.50	0.95	1.77	2.09	0.73	0.16	1.20
G2686	WS	0.75	0.47	0.50	0.46	0.35	0.19	0.45
	WW	0.64	0.67	0.85	0.66	0.09	0.00	0.49
G4001	WS	0.82	0.94	1.21	1.30	0.57	0.14	0.83
	WW	1.52	1.82	2.28	2.09	0.53	0.08	1.39

Table 4.14 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
G4534	WS	0.94	0.59	1.09	0.90	0.14	0.01	0.61
	WW	0.97	0.68	1.33	1.83	0.29	0.04	0.86
G4721	WS	1.15	0.84	0.98	1.23	0.53	0.30	0.84
	WW	1.53	1.26	2.67	3.36	1.12	0.14	1.68
G5034	WS	0.81	0.60	0.87	1.00	0.37	0.02	0.61
	WW	1.11	0.83	1.16	0.69	0.21	0.02	0.67
G5625	**WS**	**0.88**	**0.73**	**1.16**	**1.23**	**0.57**	**0.11**	**0.78**
	WW	**1.15**	**0.79**	**0.92**	**1.21**	**0.41**	**0.17**	**0.78**
SAB258	WS	0.62	0.54	0.87	0.99	0.58	0.13	0.62
	WW	1.22	0.73	1.35	1.09	0.31	0.00	0.78
SAB645	WS	0.75	0.72	1.18	1.41	0.34	0.12	0.75
	WW	1.25	1.12	1.53	1.83	0.29	0.03	1.01
SEQ1003	WS	0.76	1.06	1.08	1.36	0.69	0.20	0.86
	WW	1.16	1.01	1.81	1.87	0.10	0.00	0.99
SEQ1027	WS	0.98	1.07	1.32	1.19	0.64	0.21	0.90
	WW	1.30	1.29	1.39	1.61	0.48	0.21	1.05
LSD between treatments								**0.04**
LSD among soil depth levels								**0.08**

WW – well watered; WS – water stressed; LSD – least significant difference

Table 4.15 Trial means for root volume (cm^3) among different soil depths under well watered and water stressed treatments

Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	LSD
WS	0.898[a]	0.795[a]	1.019[a]	1.077[a]	0.439[a]	0.105[a]	0.04
WW	1.247[b]	1.043[b]	1.612[b]	1.684[b]	0.454[a]	0.079[a]	

LSD - least significant difference between treatments, means followed by the same letter are not significantly different at P≤0.05 between treatments

Table 4.16 Analysis of variance for leaf area data for the reference collection evaluated under well watered and water stressed treatments in the greenhouse at CIAT-Palmira, 2009

Source	D.f.	s.s.	m.s.	% variation explained	LSD
Genotype (G)	35	712417.00	20355.00***	20.99	79.12
Treatment (T)	1	1507107.00	1507107.00***	44.40	18.65
G x T	35	457358.00	13067.00***	13.47	111.90
Error	142	682470.00	4806.00	20.10	
Total	215	3394622.00			

***P≤0.001; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; LSD – least significant difference

Table 4.17 Leaf area (cm^2), dry leaf-, stem- and pod biomass (g) production of 20 genotypes for total root volume in the Andean reference collection under greenhouse conditions at CIAT-Palmira, 2009

Trait	**Leaf area**		**Dry green leaf biomass**		**Dry pod biomass**		**Dry stem biomass**	
Genotype	WW	WS	WW	WS	WW	WS	WW	WS
AFR619	414.60	153.80	1.35	0.55	0.73	0.24	1.40	0.59
BAT477	508.90	206.30	2.25	0.82	0.16	0.03	1.18	0.48
CAL96	321.10	182.00	1.16	0.69	0.95	0.28	0.96	0.55
DOR364	487.80	146.20	1.62	0.46	0.14	0.03	0.95	0.42
DRK47	198.30	240.30	0.72	0.83	0.86	0.63	0.71	0.64
G11512	417.50	130.30	1.33	0.37	0.35	0.26	1.05	0.34
G18255	268.70	138.30	0.91	0.41	2.41	0.38	0.91	0.39
G19833	518.00	238.50	1.49	0.75	0.01	0.01	1.07	0.47
G21210	400.20	210.80	1.08	0.64	0.93	0.39	0.64	0.52
G21212	439.40	110.10	1.33	0.33	0.66	0.55	0.91	0.26
G2686	221.20	156.40	0.83	0.55	1.56	0.85	0.69	0.57
G4001	517.50	170.50	1.58	0.57	0.53	0.16	1.18	0.50
G4534	319.70	180.40	1.15	0.56	2.69	0.58	0.93	0.40
G4721	614.00	310.60	1.91	1.17	0.06	0.02	1.37	0.70
G5034	287.80	208.40	0.98	0.66	0.86	0.50	0.68	0.43
G5625	257.50	154.00	0.86	0.51	1.48	0.56	0.69	0.45
SAB258	216.50	124.60	0.84	0.49	1.46	0.40	0.59	0.42
SAB645	334.40	133.90	1.06	0.44	3.08	0.40	1.12	0.53
SEQ1003	332.10	148.70	1.08	0.52	1.11	0.63	0.95	0.49
SEQ1027	461.20	223.50	1.45	0.79	0.19	0.12	1.15	0.55
Grand mean	345.90	178.80	1.13	0.59	1.09	0.40	0.89	0.47
LSD	18.65		0.07		0.12		0.05	

LSD – least significant difference between treatments

4.4.6.2 Green leaf biomass

Genotypes, treatments and GxT interactions were significant for GLB (Table 4.18). Treatment main effects contributed 39.63% to the total sum of squares. GxT interaction was significant and accounted for 11.40% of the variation observed. The majority of the genotypes produced significantly higher green leaf biomass under WW than WS (Table 4.17). DRK47 had higher GLB under WS than WW conditions.

Table 4.18 Analysis of variance for green leaf biomass data for the Andean reference collection evaluated under well watered and water stressed treatments in the greenhouse at CIAT-Palmira, 2009

Source	D.f.	s.s.	m.s.	% variation explained	LSD
Genotype (G)	35	9.14	0.26***	22.79	0.30
Treatment (T)	1	15.89	15.89***	39.63	0.07
GxT	35	4.57	0.13**	11.40	0.43
Error	142	9.90	0.07	24.69	
Total	215	40.10			

***P≤0.001; **P≤0.001; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; D.f. – degrees of freedom; LSD – least significance difference

4.4.6.3 Stem biomass

Genotype and treatment effects were significant for SB and accounted for 18.98% and 45.51% of the total variation observed (Table 4.19). All genotypes had significantly higher stem biomass under WW than WS conditions. Genotypes were significantly different for stem biomass production under WW and WS.

Table 4.19 Analysis of variance for stem biomass data for the Andean reference collection evaluated under well watered and water stress treatments in the greenhouse at CIAT-Palmira, 2009

Source	D.f.	s.s.	m.s.	% explained	LSD
Genotype (G)	35	3.96	0.11***	18.98	0.22
Treatment (T)	1	9.50	9.50***	45.51	0.05
GxT	35	1.86	0.05	8.90	0.32
Error	142	5.41	0.04	25.92	
Total	215	20.87			

***P≤0.001; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; LSD – least significance difference

4.4.6.4 Pod biomass

The percentage sum of squares due to genotype, treatment and GxT interaction were 37.16%, 21.27% and 16.90% respectively, indicating that genotype was the predominant source of variation (Table 4.20).

Table 4.20 Analysis of variance for pod biomass data for the Andean reference collection evaluated under well watered and water stressed treatments in the greenhouse at CIAT-Palmira, 2009

Source	D.f.	s.s.	m.s.	% variation explained	LSD
Genotype (G)	35	44.42	1.27***	37.16	0.51
Treatment (T)	1	25.43	25.43***	21.27	0.12
GxT	35	20.21	0.58***	16.90	0.72
Error	142	28.51	0.20	23.85	
Total	215	119.55			

***P≤0.001; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; LSD – least significance difference

The treatments caused highly significant differences for pod biomass (Table 4.20). SAB258, G2686, SAB645, G4534, G21210, G5625 and CAL96 had significantly higher pod biomass under WW than WS conditions (Table 4.17).

4.4.6.5 Chlorophyll content at 10 and 17 days after water stress application

Highly significant differences were observed among genotypes and between treatments for SCMR at 10 and 17 days after water stress application (Table 4.21). Genotype made the biggest contribution to the total variation for SCMR at 10 and 17 days after water stress. GxT interaction was significant for SCMR at 10 ($P \leq 0.05$) and 17 days ($P \leq 0.001$) after water stress application.

G2686 had significantly higher SCMR under WS than WW at 10 days after water stress application (Table 4.22). SAB258, DRK47 and G2686 had significantly higher SCMR under WS than WW at 17 days after water stress application.

4.4.6.6 Stomatal conductance at 17 and 26 days after stress application

SCOND was significantly different among genotypes during the two days when measurements were done (Table 4.21). Treatment values were also significantly different for SCOND at 17 and 26 days after stress. Water stress caused a decrease in SCOND on both, 17 and 26 days after stress application. Most genotypes had significantly higher SCOND under WW than WS at 26 days after application of stress (Table 4.22).

Table 4.21 Analysis of variance for chlorophyll content and stomatal conductance data for the Andean reference collection evaluated under well watered and water stressed treatments in the greenhouse at CIAT-Palmira, 2009

Trait	Source	D.f.	s.s.	m.s.	%variation explained	LSD
SCMR1	Genotype (G)	35	2087.58	59.65***	43.07	3.95
	Treatment (T)	1	185.13	185.13***	3.82	0.93
	GxT	35	640.33	18.30*	13.21	5.59
	Error	142	1689.77	11.98	34.86	
	Total	215	4847.50			
SCMR2	Genotype (G)	35	2363.23	67.52***	42.32	3.97
	Treatment (T)	1	307.25	307.25***	5.50	0.94
	GxT	35	941.26	26.89***	16.86	5.61
	Error	142	1704.68	12.09	30.53	
	Total	215	5583.90			
SCOND1	Genotype (G)	35	263802.00	7537.00*	16.68	80.02
	Treatment (T)	1	392576.00	392576.00***	24.83	18.86
	GxT	35	161896.00	4626.00	10.24	113.17
	Error	142	698047.00	4916.00	44.14	
	Total	215	1581365.00			
SCOND2	Genotype (G)	35	575650.00	16447.00***	15.43	91.57
	Treatment (T)	1	1873824.00	1873824.00**	50.24	21.58
	GxT	35	360227.00	10292.00*	9.66	129.50
	Error	142	914131.00	6438.00	24.51	
	Total	215	3729560.00			

***P≤0.001; *P≤0.05; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; SCMR1 and 2 – chlorophyll content measured at 10 and 17 days after water stress respectively; SCOND1 and 2 – stomatal conductance measured at 17 and 26 days after water stress respectively; LSD – least significance difference

Table 4.22 Mean performance of Andean genotypes for chlorophyll content (nmol cm^{-2}), stomatal conductance (mmol m^{-2} s^{-1}) and photosynthetic efficiency under well watered and water stressed greenhouse conditions at CIAT-Palmira

	SCMR at 10 days		SCMR at 17 days		SCOND at 17 days		SCOND at 26 days		PE at 25 days	
Genotype	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
AFR619	35.53	32.57	37.23	32.50	210.80	185.70	315.30	233.80	0.43	0.48
BAT477	34.27	36.07	39.20	39.23	219.10	192.20	482.00	149.90	0.50	0.49
CAL96	39.57	36.67	42.30	38.10	161.50	166.20	363.00	116.20	0.44	0.45
DOR364	33.70	32.20	32.37	30.63	260.20	160.40	171.80	135.60	0.52	0.47
DRK47	34.70	36.53	34.40	39.03	214.10	113.50	284.60	176.90	0.46	0.49
G11512	32.30	34.17	36.83	36.97	252.70	191.30	384.80	152.00	0.52	0.45
G18255	38.03	32.00	38.20	31.60	286.30	95.80	322.50	111.80	0.42	0.41
G19833	28.90	28.93	30.73	29.33	208.60	145.50	305.50	139.20	0.45	0.55
G21210	33.57	32.33	33.27	33.90	196.90	143.80	292.60	84.50	0.45	0.44
G21212	34.37	34.20	36.83	32.03	250.70	202.10	358.30	216.60	0.48	0.48
G2686	37.77	41.87	41.50	45.93	276.10	241.20	391.00	108.30	0.51	0.48
G4001	32.80	31.33	34.83	29.20	329.10	136.10	241.50	208.90	0.47	0.49
G4534	30.63	23.93	34.03	25.00	266.70	82.30	380.50	79.50	0.45	0.37
G4721	29.93	31.07	32.40	36.03	215.40	109.50	281.90	85.20	0.42	0.54
G5034	34.20	33.83	33.47	33.83	237.10	143.70	285.30	67.10	0.41	0.45
G5625	34.40	36.13	36.47	35.83	270.50	139.80	423.10	159.10	0.44	0.44
SAB258	35.83	37.47	34.97	39.86	244.00	151.70	338.30	240.50	0.51	0.39
SAB645	35.53	33.53	32.40	31.43	175.50	117.40	309.10	158.80	0.44	0.45
SEQ1003	35.57	33.27	39.17	37.60	162.10	133.30	397.40	152.30	0.49	0.48
SEQ1027	36.43	26.97	38.73	30.43	195.90	145.50	230.80	114.80	0.42	0.48
Mean	34.70	32.85	36.11	33.72	226.70	141.50	326.10	139.80	0.45	0.47
LSD	0.93		0.94		18.86		21.58		0.02	

SCMR – chlorophyll content; SCOND - stomatal conductance; PE – photosynthetic efficiency; LSD – least significance difference

4.4.7 Correlation coefficients among the root and shoot traits measured under well watered and water stressed treatments in 2009

Highly significant positive correlations existed between root length and green leaf biomass as well as stem biomass under both WW and WS conditions (Table 4.23). Total root biomass was positively correlated with green leaf biomass and stem biomass under both treatments. The correlations of total root biomass to both green leaf biomass and stem biomass were highly significant under WW and WS treatments. Highly significant positive correlations were observed between green leaf biomass and stem biomass under both treatments. SCOND at 17 and 26 days after water stress were highly significantly correlated to each other under both treatments. PE and SCMR2 had significant positive correlations to each under WW and WS treatments.

Under WS treatment, SCOND2 was significantly correlated to both SCMR1 and SCMR2. In addition, PE and SCMR1 were significantly correlated to each other under WS treatment. SCMR1 and SCOND2 were significantly correlated to each other under WS treatment.

Table 4.23 Correlation coefficients among root and shoot traits measured under well watered and water stressed treatments in 2009

TRT	Trait	TRL	TRB	MRD	GLB	DLB	SB	PB	PE	SCMR1	SCMR2	SCOND1
WW	TRB	0.92										
WS		0.90										
WW	MRD	0.09	0.28*									
WS		0.10	0.26*									
WW	GLB	0.70**	0.68***	0.07								
WS		0.62***	0.63***	0.01								
WW	DLB	-0.08	-0.04	0.01	-0.18							
WS		-0.12	-0.17	-0.14	-0.04**							
WW	SB	0.69***	0.73***	0.17	0.76***	0.03						
WS		0.62***	0.62***	-0.05	0.72***	-0.09						
WW	PB	-0.11	-0.08	-0.13	-0.21*	0.08	-0.01					
WS		0.09	0.09	-0.17	-0.04	0.03	0.14					
WW	PE	-0.04	-0.07	-0.05	0.11	0.13	-0.05	-0.15				
WS		0.06	0.10	-0.04	0.14	0.03	0.08	-0.27*				
WW	SCMR1	-0.02	-0.12	-0.24*	0.07	-0.06	0.00	-0.12	0.14			
WS		-0.15	-0.23*	-0.13	-0.14	0.10	-0.08	-0.24*	0.25*			
WW	SCMR2	0.01	0.01	0.12	0.12	0.01	0.02	0.11	0.31*	0.27*		
WS		-0.12	-0.12	0.13	-0.22*	0.13	-0.17	-0.17	0.21*	0.19		
WW	SCOND1	0.05	0.04	0.83	-0.01	0.02	0.04	0.15	0.15	-0.12	0.12	
WS		0.13	0.05	-0.15	0.05	0.03	0.11	-0.07	0.09	-0.10	0.07	
WW	SCOND2	0.12	0.11	0.03	0.09	0.06	0.17	0.02	0.06	-0.04	0.24*	0.57***
WS		0.09	0.02	-0.10	0.14	-0.11	0.14	-0.01	0.21	0.26*	0.35**	0.83***

TRT – treatment; WW – well watered; WS – water stressed; TRL – total root length (cm plant^{-1}); TRB – dry root biomass (g); MRD – mean root diameter (mm); GLB – dry green leaf biomass (g); DLB – dry dead leaf biomass (g); SB – dry stem biomass (g); PB – dry pod biomass (g); PE – photosynthetic efficiency; SCMR1 – chlorophyll content at 10 days after water stress; SCMR2 – chlorophyll content at 17 days after water stress; SCOND1 – stomatal conductance at 17 days after water stress; SCOND2 – stomatal conductance at 26 days after water stress; *P≤0.05; **P≤0.01; *** P≤0.001

Table 4.24 Visual rooting depth (cm) measured at different days after planting for elite genotypes under greenhouse well watered and water stressed treatments

Trait	VRD at 10DAP		VRD at 17 DAP		VRD at 24DAP		VRD at 31 DAP		VRD at 40 DAP		VRD at 45 DAP	
Environment	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
Genotype												
SEQ1006	13.40	14.17	22.50	24.93	25.67	32.00	28.33	41.33	29.67	56.00	29.67	59.00
CAL143	18.43	16.37	23.27	22.70	26.33	25.67	28.33	34.33	31.00	44.00	31.67	48.00
G4523	18.60	15.33	24.17	22.23	26.00	29.00	28.00	38.67	32.00	51.67	33.33	56.00
AND277	13.40	13.77	23.53	21.03	27.00	23.67	30.67	28.67	32.67	36.67	33.00	41.00
PAN127	14.43	15.80	18.77	21.63	22.00	28.00	23.67	39.33	26.67	51.33	26.67	54.67
SEA5	18.33	20.50	23.37	28.80	24.67	36.00	26.00	50.00	28.33	63.00	29.67	66.67
BAT477	15.27	15.87	21.97	22.40	25.33	26.00	28.00	31.00	29.00	37.00	29.33	40.00
SAB686	16.27	17.93	23.17	25.03	25.67	29.33	28.00	40.00	29.67	46.67	30.33	52.67
CAL96	11.23	17.17	20.60	23.50	24.67	27.67	27.00	33.00	29.67	39.67	30.67	40.67
P Villa	12.07	17.33	19.37	22.23	22.33	28.00	24.33	32.67	27.00	47.33	27.67	51.00
VAX1	17.03	12.77	22.67	17.83	24.33	20.67	26.67	27.33	33.33	41.00	37.00	41.00
DRK149	10.17	16.37	18.07	22.10	20.67	29.00	22.33	38.33	23.67	43.00	24.67	45.33
DRK156	9.50	8.47	17.33	15.57	21.33	21.33	28.33	29.33	28.67	39.33	29.33	41.00
VAX3	12.50	14.20	14.73	18.57	16.00	24.33	16.00	31.00	17.67	39.33	19.33	44.33

Table 4.24 continued:

Trait	**VRD at 10DAP**		VRD at 17 DAP		**VRD at 24DAP**		**VRD at 31 DAP**		**VRD at 40 DAP**		**VRD at 45 DAP**	
Environment	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**
Genotype												
G19833	16.40	13.40	20.13	17.60	22.33	24.67	25.67	36.00	28.33	47.33	29.00	50.00
SEQ1027	16.97	14.00	19.63	21.23	22.00	24.67	28.00	36.00	30.67	41.33	30.67	42.00
DAB147	15.63	15.47	21.90	23.17	24.00	30.33	24.67	35.33	27.67	41.33	29.33	42.67
SEA15	13.17	14.10	19.97	21.80	21.67	26.00	24.00	34.67	26.00	42.33	26.33	47.67
RCW	18.10	17.70	21.03	22.33	22.33	27.67	23.33	31.67	25.67	38.33	27.33	40.33
Trial mean	14.43	14.71	20.03	21.48	22.69	26.75	24.91	34.25	27.02	43.60	27.68	46.25
LSD	6.41	6.49	6.26	7.46	7.47	8.68	8.75	12.27	9.01	16.44	9.17	17.10
MS	21.23	20.20	21.87	31.63	29.10	51.55*	38.87	105.35*	46.94	234.88**	49.98*	259.50**
Error	15.57	15.93	14.85	21.07	21.12	28.53	28.99	57.00	30.71	102.27	31.85	110.70
MS^{+}	VRD at 10DAP		VRD at 17 DAP		VRD at 24DAP		VRD at 31 DAP		VRD at 40 DAP		VRD at 45 DAP	
Wl MS	4.82		127.17**		988.2***		52.36***		16500.42***		20683.27***	
G MS	20.07		22.95		34.7		74.46**		135.78**		141.93**	
G x Wl	21.35		30.55*		45.96**		69.76*		146.03**		167.56**	
LSD	4.53		4.83		5.68		7.48		9.3		9.63	

*P≤0.05; **P≤0.01; *** P≤0.001; VRD – visual root depth; DAP – days after planting; WW – well watered; WS – water stressed; LSD – least significance difference; m.s. – mean square; Wl – water level, MS+ - mean square between treatments; P villa – Pinto villa; RCW – Red Canadian Wonder

4.5 Results for the mixed elite Andean and Mesoamerican genotypes

4.5.1 Visual rooting depth

Genotypes were only significantly different for VRD under WS at 24, 31 and 40 DAP (Table 4.24). Genotypes also showed significant differences for VRD at 45 DAP under both WW and WS treatments. SEA5 had significantly higher VRD than BAT477 under WS at 24, 31, 40 and 45 DAP. Water levels caused significant differences for VRD at 17, 24, 31, 40 and 45 DAP. More than half of the genotypes had significantly higher VRD under WS than WW at 24, 31, 40 and 45 DAP.

Trial means for VRD increased under the WS treatment with number of days of stress. WS treatment had significantly higher VRD than the WW treatment at 31, 40 and 45 DAP. The genotype x water level interaction was significant at 17, 24, 31, 40 and 45 DAP.

4.5.2 Root traits

Genotype, treatment, soil depth, GxS interaction and TxS interaction were highly significantly different ($P \leq 0.001$) for all root traits measured (Table 4.25). GxT interaction was also highly significant ($P \leq 0.001$) for root volume, mean root diameter, total root length and root length with 0-0.5 mm and 0.5-1 mm diameter.

4.5.2.1 Total root length and its distribution among different soil depths

Treatments were highly significant for total root length. WS restricted root growth at the 0-5 cm, 5-10 cm and 10-20 cm soil depth level. All genotypes presented in Table 4.26 had significantly longer roots under WW than WS at these soil depth levels.

Table 4.27 summarises TRL distribution along soil depth levels. Under both WS and WW, TRL was significantly higher under the 0-5 cm soil depth level than any other soil depth level. There were significant differences between WS and WW at 20-40 cm profile level. Genotypes did not grow roots beyond the 20-40 cm soil depth level under the WW treatment. TxS interaction was also highly significant for TRL. Figure 4.4 shows the graphical representation of the TxS interaction. TRL ranked higher under WW than WS

in the first three soil depth levels and the WS treatment had a higher TRL ranking in the last three soil depth levels. No genotype had significantly higher TRL_{1mm} and $TRL_{0.5mm}$ under WS than WW among the elite genotypes (Tables 4.28 and 4.29).

Table 4.25 Analysis of variance for root length data derived from elite genotypes under greenhouse conditions at CIAT-Palmira, 2010

D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$

Table 4.26 Genotypic means for 20 genotypes that had significant differences for total root length (cm plant^{-1}) in elite genotypes under greenhouse conditions at CIAT-Palmira, 2010

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	20.02	10.54	10.14	5.26	0.09	0.00	46.05
	WW	25.23	15.17	14.20	4.20	0.00	0.00	58.80
BAT477	WS	22.11	9.35	7.85	3.36	0.09	0.00	42.76
	WW	30.57	14.07	12.08	1.19	0.00	0.00	57.91
CAL143	WS	23.58	10.17	8.96	4.45	0.10	0.00	47.26
	WW	28.48	13.16	13.45	2.01	0.00	0.00	57.10
CAL96	WS	18.45	7.62	7.99	5.53	0.00	0.00	39.59
	WW	37.99	12.99	9.56	0.55	0.00	0.00	61.09
DAB147	WS	16.92	7.61	6.89	2.95	0.06	0.00	34.43
	WW	19.12	10.97	11.68	1.19	0.00	0.00	42.96
DRK149	WS	11.97	9.28	7.82	8.70	0.06	0.00	37.83
	WW	23.16	12.36	8.69	0.26	0.00	0.00	44.47
DRK156	WS	17.20	6.88	6.41	6.47	0.48	0.00	37.44
	WW	23.56	9.92	10.34	3.00	0.00	0.00	46.82
G19833	WS	15.38	8.33	7.19	3.88	1.24	0.37	36.39
	WW	26.39	13.82	14.04	3.29	0.00	0.00	57.54
G4523	WS	23.04	10.32	6.91	5.58	0.73	0.06	46.64
	WW	26.50	11.60	14.59	3.64	0.00	0.00	56.33
PAN127	WS	17.00	7.96	9.68	7.06	2.80	0.57	45.07
	WW	38.11	15.14	10.36	1.37	0.00	0.00	64.98
Pinto Villa	WS	19.93	8.99	8.03	2.52	0.10	0.00	39.57
	WW	29.73	13.23	9.03	0.42	0.00	0.00	52.41
RCW	WS	16.46	6.29	5.61	2.98	0.11	0.00	31.45
	WW	24.17	10.58	9.24	0.59	0.00	0.00	44.58

Table 4.26 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	15.63	7.05	9.79	8.40	1.05	0.06	41.98
	WW	28.40	11.12	13.22	1.70	0.00	0.00	54.44
SEA15	WS	13.98	7.91	7.86	4.51	0.15	0.00	34.41
	WW	19.09	12.16	9.44	0.54	0.00	0.00	41.23
SEA5	WS	16.04	8.46	7.82	9.34	2.59	0.59	44.84
	WW	22.08	13.26	13.02	2.68	0.00	0.00	51.04
SEQ1006	WS	18.99	9.48	11.01	10.69	2.68	0.19	53.04
	WW	31.24	14.63	14.38	2.33	0.00	0.00	62.58
SEQ1027	WS	12.49	8.89	7.82	5.25	0.05	0.00	34.50
	WW	23.96	11.37	12.96	1.52	0.00	0.00	49.81
SER16	WS	15.67	5.90	6.74	3.99	0.74	0.00	33.04
	WW	21.89	10.55	7.90	0.90	0.00	0.00	41.24
VAX1	WS	18.69	9.99	7.18	3.39	0.00	0.00	39.25
	WW	27.83	12.18	10.02	2.99	0.00	0.00	53.02
VAX3	WS	17.27	7.88	7.48	3.97	0.23	0.00	36.83
	WW	29.40	11.40	2.77	0.00	0.00	0.00	43.57
LSD between treatments								**5.06**
LSD among soil profile levels								**0.51**

WW – well watered; WS – water stressed; LSD – least significance difference; RCW – Red Canadian Wonder

Table 4.27 Total root length (cm plant^{-1}) distribution along soil depth levels

	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	LSD
WS	17.43^{c}	8.18^{b}	7.90^{b}	5.27^{b}	0.63^{ab}	0.11^{a}	5.06
WW	25.58^{c}	11.60^{b}	9.81^{b}	1.47^{a}	0.00^{a}	0.00^{a}	

LSD presented separate means between treatments; means followed by the same letter are not significantly different at P≤0.05

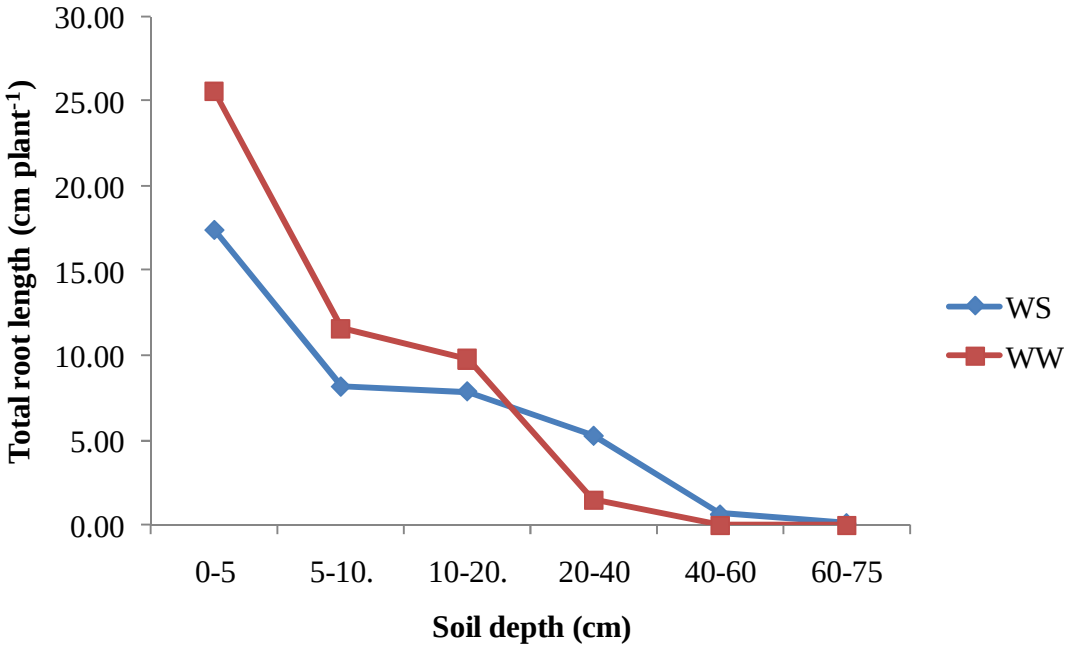


Figure 4.4 **Interaction between treatments and soil depths for total root length along different soil depth levels. WS – water stressed; WW – well watered.**

Table 4.28 Genotypic means for 20 genotypes for TRL_{1mm} (cm) in elite genotypes under greenhouse conditions at CIAT-Palmira, 2010

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	2.00	1.44	1.40	1.04	0.24	0.22	6.34
	WW	2.32	1.36	1.96	0.99	0.43	0.41	7.47
BAT477	WS	1.58	0.95	0.97	0.48	0.13	0.17	4.28
	WW	2.20	1.55	1.69	0.36	0.60	0.28	6.68
CAL143	WS	2.33	1.37	1.22	0.77	0.18	0.18	6.05
	WW	3.52	2.09	2.25	0.50	0.86	0.84	10.06
CAL96	WS	1.84	1.02	1.01	0.75	0.13	0.05	4.80
	WW	3.26	1.53	1.32	0.14	0.54	0.37	7.16
DAB147	WS	1.61	1.12	1.04	0.44	0.03	0.15	4.39
	WW	1.93	1.29	1.57	0.27	0.25	0.06	5.37
DRK149	WS	1.06	1.12	1.20	1.32	0.00	0.06	4.76
	WW	1.97	1.40	1.32	0.29	0.08	0.01	5.07
DRK156	WS	1.56	1.04	1.28	1.41	0.54	0.17	6.00
	WW	1.92	1.26	1.99	0.94	0.75	0.37	7.23
G19833	WS	1.45	0.98	1.07	0.59	0.17	0.23	4.49
	WW	3.02	1.73	2.23	1.03	1.15	1.21	10.37
G4523	WS	1.61	1.22	1.09	1.20	0.24	0.03	5.39
	WW	2.15	1.29	2.20	0.89	0.59	0.39	7.51
PAN127	WS	1.52	0.99	1.60	1.41	0.82	0.26	6.60
	WW	3.82	2.04	1.90	1.27	1.70	1.14	11.87
Pinto Villa	WS	1.38	0.78	0.80	0.24	0.02	0.35	3.57
	WW	2.03	1.08	1.11	0.15	0.32	0.06	4.75
RCW	WS	1.41	0.89	0.90	0.39	0.12	0.25	3.96
	WW	2.31	1.39	1.65	0.20	0.62	0.23	6.40

Table 4.28 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	1.50	0.88	1.56	1.54	0.41	0.06	5.95
	WW	2.86	1.62	2.30	0.49	0.87	0.40	8.54
SEA15	WS	1.45	1.28	1.30	0.74	0.06	0.03	4.86
	WW	1.80	1.79	1.74	0.10	0.22	0.13	5.78
SEA5	WS	1.66	1.26	1.43	1.72	0.35	0.15	6.57
	WW	2.44	1.71	2.46	0.48	0.61	0.40	8.10
SEQ1006	WS	2.26	1.84	2.59	2.67	0.77	0.08	10.21
	WW	3.09	2.38	2.90	0.59	0.67	0.02	9.65
SEQ1027	WS	1.29	1.19	1.23	0.80	0.16	0.06	4.73
	WW	2.31	1.51	2.00	0.38	0.59	0.36	7.15
SER16	WS	1.28	0.76	0.95	0.42	0.05	0.30	3.76
	WW	1.69	1.01	0.81	0.26	0.14	0.22	4.13
VAX1	WS	1.62	1.23	0.98	0.52	0.07	0.12	4.54
	WW	2.56	1.28	1.17	0.41	0.33	0.16	5.91
VAX3	WS	1.46	1.02	0.93	0.51	0.03	0.20	4.15
	WW	2.15	0.96	0.44	0.41	0.15	0.40	4.51
LSD between treatments								0.90
LSD among soil profile levels								0.09

WW – well watered; WS – water stressed; LSD – least significant difference; TRL_{1mm} – total root length with diameter between 0.5-1 mm; RCW – Red Canadian Wonder

Table 4.29 Genotypic means for 20 genotypes for $TRL_{0.5mm}$ (cm) in elite genotypes under greenhouse conditions at CIAT-Palmira, 2010

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	17.73	8.88	8.37	4.06	0.55	1.78	41.37
	WW	22.58	13.66	11.86	3.00	3.59	4.83	59.52
BAT477	WS	20.30	8.33	6.76	2.84	0.65	1.63	40.51
	WW	28.07	12.40	10.28	1.53	4.18	5.20	61.66
CAL143	WS	20.93	8.58	7.53	3.54	0.64	2.11	43.33
	WW	24.52	10.80	10.75	1.45	2.40	3.87	53.79
CAL96	WS	16.34	6.40	6.67	4.62	1.34	0.98	36.35
	WW	34.09	11.18	7.81	0.33	6.24	5.78	65.43
DAB147	WS	15.08	6.34	5.59	2.45	0.09	0.26	29.81
	WW	17.00	9.52	9.74	0.89	1.86	1.69	40.70
DRK149	WS	10.70	8.01	6.31	7.18	0.06	0.29	32.55
	WW	20.86	10.73	7.00	1.01	1.82	2.18	43.60
DRK156	WS	15.34	5.62	4.82	4.82	1.40	0.26	32.26
	WW	21.26	8.47	8.04	3.51	4.09	2.97	48.34
G19833	WS	13.74	7.10	5.92	3.17	1.73	1.39	33.05
	WW	22.95	11.80	11.38	3.52	6.67	6.35	62.67
G4523	WS	21.09	8.92	5.63	4.14	0.59	0.10	40.47
	WW	23.96	10.11	11.90	2.55	2.79	2.11	53.42
PAN127	WS	15.22	6.79	7.76	5.45	3.39	1.18	39.79
	WW	33.80	12.91	8.22	2.53	8.97	6.77	73.20
Pinto Villa	WS	18.35	8.13	7.14	2.26	0.04	1.04	36.96
	WW	27.41	12.04	7.83	0.60	3.06	4.09	55.03
RCW	WS	14.82	5.22	4.49	2.52	0.72	0.59	28.36
	WW	21.53	9.00	7.31	0.79	3.64	2.36	44.63

Table 4.29 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	13.92	6.04	7.87	6.62	2.45	0.01	36.91
	WW	25.08	9.21	10.52	1.14	5.37	2.90	54.22
SEA15	WS	12.25	6.34	6.18	3.58	0.28	0.41	29.04
	WW	17.01	10.18	7.42	0.44	1.95	1.28	38.28
SEA5	WS	14.14	7.05	6.18	7.33	2.20	0.85	37.75
	WW	19.30	11.41	10.32	2.15	4.32	2.97	50.47
SEQ1006	WS	16.21	7.05	7.68	7.45	3.26	0.33	41.98
	WW	27.59	11.85	10.84	1.67	6.65	3.73	62.33
SEQ1027	WS	10.98	7.44	6.22	4.23	0.51	0.26	29.64
	WW	21.24	9.60	10.62	1.05	3.95	3.19	49.65
SER16	WS	14.20	5.06	5.68	3.50	0.80	0.30	29.54
	WW	19.98	9.46	7.01	1.20	3.10	2.04	42.79
VAX1	WS	16.85	8.64	6.09	2.83	1.44	1.07	36.92
	WW	24.93	10.78	8.75	2.56	4.64	4.19	55.85
VAX3	WS	15.59	6.71	6.40	3.41	0.42	0.35	32.88
	WW	26.97	10.26	2.29	0.16	2.37	2.36	44.51
LSD between treatments								5.28
LSD among soil profile levels								0.53

WW - well watered; WS - water stressed; LSD – least significant difference; $TRL_{0.5mm}$ – total root length with diameter between 0-0.5 mm; Red Canadian Wonder

Table 4.30 Total root biomass (g) for 20 genotypes that had significant differences for TRB in elite genotypes under greenhouse conditions at CIAT-Palmira

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	0.21	0.11	0.11	0.05	0.00	0.00	0.48
	WW	0.24	0.13	0.14	0.05	0.00	0.00	0.55
BAT477	WS	0.19	0.08	0.07	0.03	0.00	0.00	0.37
	WW	0.26	0.14	0.11	0.01	0.00	0.00	0.52
CAL143	WS	0.23	0.10	0.09	0.04	0.00	0.00	0.45
	WW	0.28	0.14	0.14	0.02	0.00	0.00	0.58
CAL96	WS	0.18	0.07	0.08	0.05	0.00	0.00	0.38
	WW	0.33	0.12	0.09	0.01	0.00	0.00	0.55
DAB147	WS	0.17	0.08	0.07	0.03	0.00	0.00	0.34
	WW	0.17	0.11	0.12	0.01	0.00	0.00	0.41
DRK149	WS	0.13	0.09	0.09	0.07	0.00	0.00	0.38
	WW	0.21	0.12	0.08	0.00	0.00	0.00	0.41
DRK156	WS	0.20	0.07	0.07	0.07	0.01	0.00	0.41
	WW	0.24	0.11	0.11	0.03	0.00	0.00	0.49
G19833	WS	0.15	0.08	0.07	0.04	0.01	0.00	0.34
	WW	0.28	0.14	0.15	0.03	0.00	0.00	0.60
G4523	WS	0.18	0.09	0.07	0.06	0.01	0.00	0.40
	WW	0.22	0.10	0.15	0.05	0.00	0.00	0.51
PAN127	WS	0.18	0.08	0.10	0.08	0.03	0.01	0.47
	WW	0.31	0.12	0.09	0.01	0.00	0.00	0.53
Pinto Villa	WS	0.15	0.07	0.06	0.02	0.00	0.00	0.30
	WW	0.21	0.16	0.07	0.01	0.00	0.00	0.44
RCW	WS	0.15	0.07	0.06	0.02	0.00	0.00	0.31
	WW	0.22	0.11	0.10	0.01	0.00	0.00	0.43

Table 4.30 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	0.15	0.07	0.11	0.09	0.01	0.00	0.43
	WW	0.25	0.11	0.16	0.07	0.00	0.00	0.58
SEA15	WS	0.16	0.09	0.08	0.04	0.00	0.00	0.37
	WW	0.17	0.12	0.10	0.00	0.00	0.00	0.39
SEA5	WS	0.18	0.10	0.10	0.09	0.02	0.01	0.49
	WW	0.24	0.14	0.14	0.02	0.00	0.00	0.54
SEQ1006	WS	0.24	0.13	0.15	0.13	0.02	0.00	0.68
	WW	0.34	0.17	0.19	0.03	0.00	0.00	0.73
SEQ1027	WS	0.14	0.08	0.08	0.05	0.00	0.00	0.35
	WW	0.25	0.12	0.13	0.02	0.00	0.00	0.51
SER16	WS	0.14	0.06	0.05	0.03	0.01	0.00	0.29
	WW	0.19	0.10	0.06	0.01	0.00	0.00	0.36
VAX1	WS	0.15	0.09	0.06	0.03	0.00	0.00	0.32
	WW	0.24	0.11	0.08	0.02	0.00	0.00	0.45
VAX3	WS	0.16	0.07	0.06	0.03	0.00	0.00	0.31
	WW	0.23	0.09	0.02	0.00	0.00	0.00	0.35
LSD between treatments								**0.05**
LSD among soil profile levels								**0.01**

WW – well watered; WS – water stressed; LSD – least significant difference; Red Canadian Wonder

Table 4.31 Mean root diameter (mm) for 20 genotypes that had significant differences for total root length in elite genotypes under greenhouse conditions at CIAT-Palmira, 2010

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	0.30	0.34	0.35	0.37	0.55	0.40	2.31
	WW	0.29	0.30	0.35	0.42	0.55	0.40	2.31
BAT477	WS	0.28	0.31	0.32	0.33	0.29	0.32	1.85
	WW	0.29	0.33	0.34	0.37	0.31	0.35	1.99
CAL143	WS	0.31	0.35	0.34	0.36	0.41	0.37	2.14
	WW	0.32	0.36	0.38	0.42	0.44	0.40	2.32
CAL96	WS	0.30	0.34	0.34	0.33	0.36	0.35	2.02
	WW	0.30	0.34	0.38	0.58	0.43	0.42	2.45
DAB147	WS	0.30	0.34	0.35	0.32	0.37	0.35	2.03
	WW	0.30	0.33	0.36	0.40	0.39	0.38	2.16
DRK149	WS	0.30	0.32	0.36	0.34	0.30	0.34	1.96
	WW	0.29	0.32	0.38	0.39	0.31	0.36	2.05
DRK156	WS	0.30	0.36	0.39	0.40	0.44	0.40	2.29
	WW	0.30	0.35	0.39	0.41	0.44	0.40	2.29
G19833	WS	0.30	0.33	0.34	0.42	0.48	0.33	2.20
	WW	0.32	0.35	0.38	0.48	0.51	0.37	2.41
G4523	WS	0.28	0.32	0.35	0.39	0.37	0.41	2.12
	WW	0.29	0.33	0.36	0.45	0.39	0.44	2.26
PAN127	WS	0.30	0.33	0.36	0.38	0.43	0.36	2.16
	WW	0.32	0.36	0.39	0.44	0.47	0.39	2.37
Pinto Villa	WS	0.27	0.30	0.30	0.29	0.33	0.32	1.81
	WW	0.28	0.29	0.32	0.35	0.35	0.34	1.93
RCW	WS	0.29	0.34	0.37	0.32	0.29	0.34	1.95
	WW	0.30	0.33	0.37	0.38	0.31	0.36	2.05

Table 4.31 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	0.30	0.32	0.37	0.36	0.33	0.39	2.07
	WW	0.31	0.36	0.38	0.42	0.36	0.42	2.25
SEA15	WS	0.32	0.38	0.38	0.37	0.38	0.38	2.21
	WW	0.32	0.35	0.39	0.38	0.38	0.38	2.20
SEA5	WS	0.31	0.35	0.36	0.37	0.34	0.31	2.04
	WW	0.32	0.34	0.39	0.40	0.35	0.32	2.12
SEQ1006	WS	0.34	0.42	0.44	0.43	0.37	0.43	2.43
	WW	0.31	0.37	0.42	0.48	0.35	0.42	2.35
SEQ1027	WS	0.31	0.34	0.37	0.37	0.46	0.39	2.24
	WW	0.30	0.35	0.38	0.53	0.50	0.43	2.49
SER16	WS	0.29	0.32	0.33	0.30	0.30	0.33	1.87
	WW	0.29	0.30	0.31	0.35	0.30	0.33	1.88
VAX1	WS	0.29	0.33	0.32	0.33	0.35	0.34	1.96
	WW	0.30	0.32	0.32	0.33	0.35	0.34	1.96
VAX3	WS	0.30	0.33	0.32	0.31	0.33	0.33	1.92
	WW	0.29	0.31	0.35	0.37	0.34	0.35	2.01
LSD between treatments								**0.06**
LSD among soil profile levels								**0.01**

WW – well watered; WS – water stressed; LSD – least significant difference; RCW – Red Canadian Wonder

Table 4.32 Root volume (cm^3) for 20 genotypes that had significant differences for total root length in elite genotypes under greenhouse conditions at CIAT-Palmira

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
AND277	WS	1.45	0.94	0.98	0.59	0.14	0.14	4.22
	WW	1.69	1.08	1.38	0.62	0.35	0.35	5.47
BAT477	WS	1.38	0.67	0.62	0.27	0.09	0.07	3.10
	WW	2.02	1.17	1.09	0.20	0.48	0.31	5.27
CAL143	WS	1.74	0.98	0.82	0.46	0.11	0.15	4.26
	WW	2.35	1.37	1.55	0.27	0.50	0.53	6.57
CAL96	WS	1.32	0.68	0.73	0.49	0.08	0.02	3.32
	WW	2.74	1.17	1.07	0.12	0.55	0.46	6.11
DAB147	WS	1.21	0.71	0.69	0.26	0.00	0.10	2.97
	WW	1.38	0.97	1.18	0.16	0.21	0.10	4.00
DRK149	WS	0.83	0.74	0.79	0.81	0.00	0.04	3.21
	WW	1.54	1.04	0.97	0.16	0.14	0.09	3.94
DRK156	WS	1.25	0.71	0.80	0.86	0.29	0.11	4.02
	WW	1.70	0.95	1.26	0.58	0.51	0.32	5.32
G19833	WS	1.10	0.75	0.67	0.36	0.17	0.17	3.22
	WW	2.11	1.30	1.58	0.57	0.84	0.84	7.24
G4523	WS	1.47	0.85	0.65	0.68	0.09	0.01	3.75
	WW	1.80	0.96	1.52	0.56	0.40	0.32	5.56
PAN127	WS	1.19	0.68	0.98	0.77	0.47	0.13	4.22
	WW	3.02	1.47	1.22	0.59	1.15	0.80	8.25
Pinto Villa	WS	1.19	0.63	0.56	0.17	0.01	0.16	2.72
	WW	1.81	0.90	0.73	0.09	0.26	0.08	3.87
RCW	WS	1.06	0.57	0.58	0.25	0.09	0.16	2.71
	WW	1.74	0.94	1.04	0.12	0.44	0.18	4.46

Table 4.32 continued

Genotype	Treatment	0-5 cm	5-10 cm	10-20 cm	20-40 cm	40-60 cm	60-75 cm	Grand mean
SAB686	WS	1.11	0.57	1.02	0.91	0.23	0.03	3.87
	WW	2.18	1.11	1.49	0.26	0.59	0.33	5.96
SEA15	WS	1.11	0.91	0.91	0.48	0.03	0.01	3.45
	WW	1.48	1.20	1.11	0.06	0.14	0.12	4.11
SEA5	WS	1.19	0.80	0.83	1.04	0.23	0.10	4.19
	WW	1.80	1.20	1.50	0.29	0.46	0.34	5.59
SEQ1006	WS	1.73	1.36	1.73	1.53	0.42	0.05	6.82
	WW	2.44	1.61	1.97	0.34	0.42	0.05	6.83
SEQ1027	WS	0.95	0.83	0.83	0.55	0.10	0.02	3.28
	WW	1.75	1.10	1.44	0.26	0.45	0.32	5.32
SER16	WS	1.02	0.49	0.56	0.29	0.04	0.20	2.60
	WW	1.40	0.76	0.58	0.15	0.17	0.07	3.13
VAX1	WS	1.27	0.83	0.60	0.29	0.03	0.07	3.09
	WW	2.00	0.98	0.83	0.26	0.29	0.20	4.56
VAX3	WS	1.22	0.69	0.62	0.30	0.01	0.11	2.95
	WW	1.90	0.84	0.26	0.22	0.01	0.12	3.35
LSD between treatments								**0.61**
LSD among soil profile levels								**0.06**

WW – well watered; WS – water stressed; LSD – least significant difference; RCW – Red Canadian Wonder

4.5.2.2 Total root biomass and its distribution among different soil depths

Significant differences for TRB were observed between genotypes under WS and WW treatments (Table 4.25). SEQ1006 had significantly higher TRB than BAT477 under both WW and WS treatments. Treatment effects were highly significant and WS restricted the amount of TRB accrued by the genotypes (Table 4.30).

4.5.2.3 Mean root diameter and its variation among different soil depths

Most genotypes had thicker roots under WW than WS treatments (Table 4.31).

4.5.2.4 Root volume and its distribution among different soil depths

Most genotypes had significantly higher root volume under WW than WS conditions except SEQ1006 and VAX3 (Table 4.32).

4.5.3 Shoot traits

Genotypes and treatment effects were highly significant for leaf area, dry leaf, stem and pod biomass measured (Table 4.33). GxT interaction influenced dry stem biomass accrued by genotypes. WS affected shoot traits significantly. Leaf area for all genotypes was severely reduced under the WS treatment (Table 4.34). Meanwhile, the majority of genotypes had reduced green leaf and stem biomass under WS. In addition, half of the genotypes had significantly higher pod biomass under the WW than WS treatments. Water stress restricted stem and leaf growth and promoted leaf abscission in some genotypes. SEQ1006, G19839 and CAL96 had significantly higher dead leaf biomass under WS than WW.

Table 4.33 Combined analysis of variance for leaf area, dry leaf-, stem- and pod biomass measured for the elite genotypes in 2010

Trait: Leaf area					**Trait: Leaf biomass**				
Source of variation	**D.f.**	**s.s.**	**m.s.**	**Fpr.**	**Source of variation**	**D.f.**	**s.s.**	**m.s.**	**Fpr.**
Replication	2	8787	4394		Replication	2	0.22863	0.11431	
Genotype (G)	39	565098	14490	<.001	Genotype (G)	39	11.2499	0.28846	<.001
Treatment (T)	1	1213593	1213593	<.001	Treatment (T)	1	20.9778	20.9778	<.001
GxT interaction	39	158897	4074	0.373	GxT interaction	39	4.32146	0.11081	0.094
Error	158	601158	3805		Error	158	12.8297	0.0812	
Total	239	2547534			Total	239	49.6075		
Trait: Pod biomass					**Trait: Stem biomass**				
Source of variation	**D.f.**	**s.s.**	**m.s.**	**Fpr.**	**Source of variation**	**D.f.**	**s.s.**	**m.s.**	**Fpr.**
Replication	2	0.3515	0.1757		Replication	2	0.0779	0.03895	
Genotype (G)	39	21.3354	0.5471	<.001	Genotype (G)	39	5.01973	0.12871	<.001
Treatment (T)	1	8.3068	8.3068	<.001	Treatment (T)	1	5.70108	5.70108	<.001
GxT interaction	39	4.5007	0.1154	0.354	GxT interaction	39	1.5568	0.03992	0.041
Error	158	16.8065	0.1064		Error	158	4.18424	0.02648	
Total	239	51.3008			Total	239	16.5398		

D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; F pr. – F probability

Table 4.34 Leaf area (cm^2), dry leaf-, stem- and pod biomass (g) produced by 20 elite genotypes evaluated under well watered and water stressed treatments in the greenhouse at CIAT-Palmira, 2010

	Leaf area		Dry leaf biomass		Dry pod biomass		Dry stem biomass		Dead leaf biomass	
Genotype	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**
AND277	157.60	317.20	0.54	1.14	0.11	0.46	0.36	0.66	0.25	0.10
BAT477	171.60	391.90	0.56	1.86	0.01	0.03	0.46	0.92	0.18	0.13
CAL143	141.50	279.50	0.56	1.08	0.35	1.05	0.34	0.62	0.33	0.20
CAL96	129.10	252.20	0.47	0.97	0.23	0.85	0.42	0.87	0.30	0.06
DAB147	86.80	222.10	0.32	0.72	0.36	1.01	0.28	0.48	0.35	0.34
DRK149	144.10	213.80	0.56	0.88	0.59	0.93	0.45	0.69	0.15	0.07
DRK156	152.00	300.40	0.53	1.10	0.15	0.66	0.42	0.79	0.17	0.08
G19833	184.50	408.20	0.55	1.27	0.01	0.02	0.38	0.90	0.48	0.35
G4523	136.80	409.50	0.43	1.26	0.36	0.58	0.43	1.04	0.19	0.11
PAN127	198.40	279.70	0.69	1.15	0.19	0.21	0.51	0.71	0.13	0.06
P Villa	115.60	229.30	0.55	0.75	0.46	1.29	0.37	0.62	0.11	0.06
RCW	124.30	202.50	0.45	0.75	0.63	1.11	0.32	0.51	0.15	0.17
SAB686	122.10	261.60	0.49	1.20	0.40	0.87	0.40	0.65	0.12	0.03
SEA15	179.20	309.40	0.59	1.37	0.62	1.21	0.42	0.79	0.19	0.11
SEA5	131.50	290.80	0.59	1.71	0.50	0.44	0.20	0.54	0.21	0.12
SEQ1006	180.30	338.10	0.59	1.27	0.34	0.80	0.59	1.01	0.42	0.31
SEQ1027	126.10	352.80	0.43	1.26	0.10	0.25	0.37	0.92	0.28	0.11
SER16	110.80	221.00	0.38	0.83	0.77	1.03	0.38	0.52	0.20	0.19
VAX1	62.90	265.50	0.23	1.06	0.03	0.50	0.37	0.85	0.32	0.15
VAX3	172.50	320.00	0.53	1.42	0.06	0.03	0.36	0.56	0.07	0.06
Grand mean	135.69	277.92	0.49	1.08	0.3	0.67	0.41	0.72	0.26	0.17
LSD	15.73		0.07		0.08		0.04		0.04	

LSD – least significant difference between genotypic means of the two treatments; WW – well watered; WS – water stressed; P Villa – Pinto Villa; RCW – Red Canadian Wonder

4.5.4 Physiological traits

While the differences among the treatments (WS and WW) were significantly different for all traits that were measured, those among genotypes were only significant for SCMR measured at 34 and 43 DAP (Table 4.35). Most genotypes except DRK149 and SAB686 had significantly higher SCMR under WS than WW at 43 DAP (Table 4.36). At 34 DAP; SAB686 was the only genotype with higher SCMR for WW than WS. CAL96, DAB147 and SEA5 had no significant differences for SCMR between WS and WW at 34 DAP. All genotypes had significantly higher SCOND under WW than WS.

Table 4.35 Combined analysis of variance for physiological traits measured for the elite genotypes evaluated under greenhouse conditions at CIAT-Palmira, 2010

Trait: SCMR at 43 days after planting					**Trait: SCMR at 34 days after planting**				
Source of variation	**D.f.**	**s.s.**	**m.s.**	**Fpr.**	**Source of variation**	**D.f.**	**s.s.**	**m.s.**	**Fpr.**
Replication	2	108.21	54.11		Replication	2	42.3	21.15	
Genotype (G)	39	3815.28	97.83	<.001	Genotype (G)	39	2247	57.62	<.001
Treatment (T)	1	1692.83	1692.83	<.001	Treatment (T)	1	1113.27	1113.27	<.001
GxT interaction	39	867.49	22.24	0.361	GxT interaction	39	931.71	23.89	0.036
Error	158	3254.05	20.6		Error	158	2467.62	15.62	
Total	239	9737.86			Total	239	6801.9		
Trait: SCOND at 34 days after planting									
Source of variation	**D.f.**	**s.s.**	**m.s.**	**Fpr.**					
Replication	2	75175	37588						
Genotype (G)	39	313775	8046	0.227					
Treatment (T)	1	1278887	1278887	<.001					
GxT interaction	39	203133	5209	0.829					
Error	158	1068110	6760						
Total	239	2939081							

SCMR – chlorophyll content; SCOND – stomatal conductance; D.f. – degrees of freedom; s.s. – sum of squares; m.s. – mean squares; F pr. – F probability

Table 4.36 Mean performance of genotypes for chlorophyll content (nmol cm^{-2}) and stomatal conductance (mmol m^{-2} s^{-1}) under greenhouse conditions at CIAT-Palmira, 2010

	SCMR at 43 DAP		SCMR at 34 DAP		SCOND at 34DAP	
Genotype	**WS**	**WW**	**WS**	**WW**	**WS**	**WW**
AND277	36.10	32.53	38.63	34.27	131.40	317.00
BAT477	45.83	31.93	42.77	34.17	145.90	244.70
CAL143	35.67	32.57	36.87	32.80	103.80	309.60
CAL96	43.03	35.63	34.53	33.83	100.70	214.70
DAB147	38.00	30.20	32.77	33.17	168.60	352.50
DRK149	43.93	43.60	42.10	38.60	140.30	328.30
DRK156	44.70	36.07	43.97	35.83	165.80	264.50
G19833	30.13	27.23	30.63	27.27	170.90	233.30
G4523	35.63	30.70	34.27	30.03	144.10	262.50
PAN127	36.40	33.37	37.47	34.63	193.80	335.30
P Villa	42.20	39.23	39.83	37.40	79.70	160.60
RCW	43.33	36.63	42.47	34.40	173.80	343.20
SAB686	35.47	35.33	34.53	38.27	154.10	295.50
SEA15	41.17	38.50	39.57	32.87	101.60	256.40
SEA5	45.07	43.77	39.67	40.53	130.90	273.60
SEQ1006	36.97	32.87	37.27	35.03	103.90	160.20
SEQ1027	35.83	29.43	36.10	30.43	79.60	332.60
SER16	40.70	36.53	39.87	33.37	108.70	306.30
VAX1	41.17	37.00	38.10	32.63	115.30	293.50
VAX3	39.37	30.17	37.03	35.10	122.90	321.30
Grand mean	39.68	34.67	37.89	33.59	136.79	282.78
LSD	1.16		1.01		20.96	

SCMR – chlorophyll content; SCOND – stomatal conductance; Lsd – least significant difference between treatments; WW – well watered; WS – water stressed; P Villa – Pinto Villa; RCW – Red Canadian Wonder

4.5.5 Correlation coefficients among root and shoot traits measured under well watered and water stressed treatments in 2010

Table 4.37 shows the correlations among the measured traits under WW and WS conditions. Significant positive correlations existed between root length and green leaf biomass as well as stem biomass under both irrigated and water stressed treatment. Stem biomass and green leaf biomass also had significant correlations with root biomass under both irrigated and water stressed treatments.

Highly significant positive correlations existed between GLB and SB under WW and WS. SCMR1 and SCMR2 were also highly significantly correlated under WW and WS treatments. TRB and MRD were highly significantly correlated under both treatments. The correlations between SCMR1 and SCMR2 as well as TRB and MRD were positive. PB and SCMR2 had significant and positive correlation between each other under WW and WS treatments. PB and SCMR1 were significantly correlated to each other under WS treatment.

Table 4.37 Correlation coefficients among root and shoot traits measured under well watered and water stressed treatments

TRT	Trait	TRL	TRB	MRD	GLB	DLB	SB	PB	SCMR1
WW	TRB	0.89							
WS		0.88							
WW	MRD	0.38*	0.51***						
WS		0.30*	0.56***						
WW	GLB	0.55***	0.51***	0.20*					
WS		0.49***	0.41***	0.02					
WW	DLB	-0.09	-0.01	0.18*	-0.25*				
WS		0.07	0.19*	0.36***	-0.42***				
WW	SB	0.59**	0.66***	0.34**	0.59***	-0.07			
WS		0.60***	0.62***	0.24*	0.58***	-0.06			
WW	PB	0.13	0.22*	0.08	-0.15	0.00	0.03		
WS		-0.06	-0.75	-0.10	-0.07	-0.05	-0.13		
WW	SCMR1	0.31**	0.22*	0.26*	0.21*	-0.13	0.06	0.17	
WS		-0.11	-0.15	-0.27*	0.16	-0.30*	0.12	0.26*	
WW	SCMR2	0.08	0.05	0.25*	0.06	-0.10	0.02	0.32**	0.61***
WS		-0.16	-0.21*	-0.33**	0.08	-0.20*	-0.08	0.37***	0.60***

TRT – treatment; WW – well watered; WS – water stressed; TRL – total root length (cm plant^{-1}); TRB – dry root biomass (g); MRD - mean root diameter (mm); GLB – dry green leaf biomass (g); DLB – dry dead leaf biomass (g), SB – dry stem biomass (g); PB – dry pod biomass (g); PE – photosynthetic efficiency; SCMR1 – chlorophyll content at 10 days after water stress; *P≤0.05; **P≤0.01; *** P≤0.001

4.6 Discussion

Roots are the first plant organs to sense depletion of water in the soil. Significant differences between water levels for visual rooting depth were noticed from the 7th day after the stress induction in both trials. Most genotypes under WS occupied deep soil layers faster than under WW conditions. The faster root growth rate in these genotypes was induced by depleted water resources. As the duration of WS progressed, more genotypes had significantly higher visual rooting depth under the WS than WW treatment. Pritchard (1994) had earlier on made observations that roots have a tendency of growing away from dry soil pockets to wetter soil pockets. The total root length was evidently higher for some genotypes at the 40-60 cm and 60-75 cm soil profile levels under the WS treatment than the WW condition in both trials. Root growth was influenced by the underground environment (Price *et al.* 2002) and WS caused root extension (Pritchard 1994). Under WS, plant roots need to pursue the receding moisture in the soil. Apart from water capture, deep roots are also capable of extracting mobile nutrients such as nitrates (Ho *et al.* 2004; 2005). However, it is important to note that some genotypes in both trials did not differ significantly for VRD and TRL between water levels at all soil profile levels. In these genotypes root growth was not triggered by the receding water front in the soil. Nicotra *et al.* (2010) argued that the adaptive responses to the drying soil environment are genotype specific and do not apply to all genotypes within a species.

Top soil drying is a common phenomenon under drought conditions and has a deleterious effect on fine roots residing close to the soil surface. In both trials, the WW had higher grand TRL and $TRL_{0.5mm}$ compared to WS and could be attributed to the higher mortality of fine roots under WS than WW. Lynch and Brown (2001) argued that shading of fine roots allows the main roots to occupy great soil volumes at a low metabolic cost.

Some genotypes had higher root volume and biomass under WS than WW conditions, especially at deeper soil layers in both trials and these data support the idea that deep rooting is an adaptive trait. Sponchiado *et al.* (1989), Pritchard (1994) and Ho *et al.* (2005) reported similar findings in common bean. The elasticity in deep rooting (adaptive and constitutive) found among genotypes in both trials could be used to improve plant productivity under different production environments. Beebe *et al.* (2008) also found that there existed diversity in common bean for

aluminium tolerance and tolerance to low phosphorus availability in soil. The presence of some Andean genotypes in both trials with better or comparable root attributes to the check, BAT477, makes prospects of improving Andean beans feasible without embarking on advanced backcrossing schemes. G19833 had deeper and thicker roots which facilitated better acquisition and transport of water. DRK47, G5625, PAN127 and SUG131 had deeper roots than BAT477 and the other root traits were comparable to BAT477 under WS. These genotypes could be used to improve drought tolerance in Andean beans. Previous work indicates that crosses involving Mesoamerican and Andean genotypes often produce poor progenies and in some crosses resulted in F_1 lethality (Singh 1995). These gene pools are separated by reproductive isolation (Koinange and Gepts 1992). Drought tolerance mapping populations for genetic studies could be created within the Andean sub-group without searching for deep rooting from Mesoamerican genotypes.

Referring to grain yield data shown in Chapter 3, some genotypes in the reference collection such as BAT477, G5625 and DRK47 had deep roots under WS in the greenhouse and high yields under WS field conditions at both CIAT-Palmira and Harare Research Station. However, there was another group of genotypes with root lengths not significantly different from DRK47, G5625 and BAT477 that had poor yields under WS field conditions at both locations. In these genotypes, deep rooting appears only to be important for plant survival and biomass production and does not result in a high seed yield under WS. G19833 had long roots under water stress but yielded below 400 kg ha^{-1} under WS field conditions at CIAT-Palmira and Harare Research Station. Under WS, G19833 had the ability to capture water from deep soil layers and maintained a high leaf conductance as well as a high shoot biomass to the same extent as under irrigated conditions. The captured water was, however, not translated into higher grain yield. In contrast G1688, G21212, SAB258 and G18255 had significantly lower TRL across soil depths than G19833 and G4721 under WS but had grain yields larger than 1000 kg ha^{-1} under WS field conditions. G21212 and G1688 maintained their normal leaf conductance even under stress conditions. These two genotypes maintained photosynthetic efficiency using the small amount of water drawn from the soil. It is important to note that some genotypes with deeper roots had faster root growth under WS and have the potential of depleting water resources well before maturity. If no additional rain is received in between the stress periods, grain filling can be affected and consequently grain yield could be reduced. This could be the case with G4721.

Deep rooting is desirable for extracting water from deep soil layers and allows plants to sustain photosynthesis and other metabolic processes. High, positive and significant correlations existed between total root length and root biomass with green leaf biomass and stem biomass. The ability of plants to convert the limited water resources into grain yield requires other mechanisms in plant shoots. Control of water loss through transpiration and improved WUE could aid in achieving high yield by deep rooting of common bean genotypes grown under WS. Ceccarelli *et al.* (1991) noted that it is the interaction among traits that determine the overall crop response to drought stress rather than the expression of any specific trait by itself. In common bean, drought tolerance could be achieved through combining deep rooting with WUE and other physiological traits involved in water saving mechanisms.

Under WS, leaf expansion was restricted and stem elongation and pod development were reduced, resulting in significantly lower stem, pod and green leaf biomass accumulated by most genotypes in both trials. These results are in agreement with previous work by Specht *et al.* (2001), Farooq *et al.* (2008) and Wu *et al.* (2008). It is also important to note that while significant changes were happening at the shoot structures, genotypes were not significantly different for the mean root diameter and total root biomass between the two water levels. Blum (2005) found that root biomass or root diameter rarely changes due to differences in water levels, however, it is the shoot structures that are reduced in size. This resulted in a significantly higher root:shoot biomass under WS than WW treatments. In both trials, some genotypes had significantly higher root:shoot biomass ratio under WS compared to WW conditions. The increase in root:shoot ratio has been demonstrated in common bean under WS by Sponchiado *et al.* (1989). Dewar (1993) noted that plants respond to changes in resource supply by allocating carbon to the organ involved in capturing the limited resource. Underground resource acquisition is enhanced at the expense of carbon gain through photosynthesis. The plant shoot biomass is jeopardised, hence limiting plant growth under water stress.

Thick roots as observed in G19833 at deep soil profile levels facilitated water movement. A large root diameter has larger hydraulic conductance which facilitates more efficient water transport (Passioura 1988). This genotype had higher stomatal conductance and high leaf biomass under

WS greenhouse and field conditions (Chapter 3). Experiences with other crops such as rice demonstrated that deep rooting genotypes under greenhouse conditions also have deep roots under field conditions (Price *et al.* 2002). The low yielding ability of this genotype under WS environments could be attributed to a huge investment of carbon in a deep and thick root system, decreasing the proportion of carbon allocated to the shoots.

Most genotypes in the reference collection closed their stomata as the duration of WS increased. Significant differences were also observed on trial means for SCOND between the two treatments. Stomatal closure is one way of minimising water loss under water stress conditions. Studies by Pimentel *et al.* (1999) and Lizzana *et al.* (2006) also showed that tolerant common bean genotypes tended to close their stomata as the intensity of drought increased. BAT477, G21212, SEQ1027 and SEQ1003 were among genotypes that had significantly lower stomatal conductance under WS than the WW treatment when the duration of WS intensified.

In the current study, soil depth main effects had significantly higher contributions to the variation observed among genotypes for the different traits in both trials. This could have arisen due to the fact that most genotypes did not grow beyond 40-60 cm under WW and WS treatments and there were huge differences between the last two soil depth levels and the top three depth levels. In addition, the level of variability found in the reference collection (trial 1) compared to elite genotypes (trial 2) supported the idea that landraces harbour a lot of genetic diversity. Elite genotypes have been subjected to decades of selection under irrigation and fertiliser conditions and could have lost useful deep rooting traits under drought conditions. DRK47 and G5625 showed an adaptive response towards WS in trial 1 and no genotype in trial 2 had this mechanism of dealing with drought.

4.7 Conclusions

In both trials, genotypes under WS obeyed the Le Chatelier's principle that says 'when subjected to a perturbation a system tends to respond in such a way to minimise the effect of the perturbation'. Leaf area, dry leaf, stem and pod biomass were all reduced under water stress as a way of minimising water loss through transpiration. To capture the dwindling water resources, some genotypes responded by growing long roots at a much faster rate than under optimum

conditions. Deep rooting is essential for plant survival under WS conditions but may not be adequate for drought tolerance in common bean. A combination of deep rooting with other shoot traits that minimise water loss or efficiently utilise the captured water into seed yield can improve drought tolerance in common bean. The identification of DRK47, G5625 and PAN127 in this current study as deep rooted genotypes will enhance chances of drought tolerance improvement in Andean beans without using Mesoamerican genotypes in crossing schemes or genetic studies.

4.8 References

Agronomix Software, Inc. 2005. AGROBASE Generation II User's Manual. Version II, Revised Edition. www.agronomix.com

Beebe SE, Rao IM, Cajiao C, Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. Crop Science 48: 582-592.

Blum A. 1988. Plant Breeding for Stress Environments. Boca Raton, USA, CRC Press. pp. 45-52.

Blum A. 2005. Drought resistance, water use efficiency and yield potential - are they compatible, dissonant or mutually exclusive? Australian Journal of Agricultural Research 56:1159-1168.

Butare L, Rao IM, Lepoivre P, Polania J, Cajiao C, Cuasquer JB, Beebe S. 2011. New sources of resistance in *Phaseolus* species to individual and combined aluminium toxicity and progressive soil drying stresses. Euphytica 181:385-404.

Ceccarelli S, Acevedo E, Grando S. 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits and architecture of genotypes. Euphytica 56:169-185.

Clark RT, MacCurdy RB, Jung JK, Shaff JE, McCouch SR, Aneshansley J, Kochian LV. 2011. Three-dimensional root phenotyping with a novel imaging and software platform. Plant Physiology 156:455-465.

de Dorlodot S, Forster B, Pages L, Prince A, Tuberosa R, Draye X. 2007. Root system architecture: opportunities and constraints for genetic improvement of crops. Trends in Plant Science 12:474-481.

Dewar RC. 1993. A root-shoot partitioning model based on carbon-nitrogen water interactions and Munch phloem flow. Functional Ecology 7:356-368.

Farooq M, Basra SMA, Wahid A, Cheema ZA, Cheema MA, Khaliq A. 2008. Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). Crop Science 194:325-333.

Gregory P. 2006. Plant Roots. Growth, Activity and Interaction with Soils. Blackwell Publishing Ltd., Oxford, UK. pp. 126-129.

Ho MD, McCannon BC, Lynch JP. 2004. Optimization modelling of plant root architecture for water and phosphorus acquisition. Journal of Theoretical Biology 226:331-340.

Ho MD, Rosas JC, Brown KM, Lynch JP. 2005. Root architectural tradeoffs for water and phosphorous acquisition. Functional Plant Biology 32:737-748.

Koinange EMK, Gepts P. 1992. Hybrid weakness in wild *Phaseolus vulgaris* L. Journal of Heredity 83:135-139.

Lizzana C, Wentworth M, Martinez JP, Villegas D, Meneses R, Murche EH, Pastenes C, Lercari B, Vernieri P, Harton P, Pinto M. 2006. Differential adaptation of two varieties of common bean to abiotic stress. Journal of Experimental Botany 57:685-697.

Lynch JP, Brown KM. 2001. Topsoil foraging: an architectural adaptation of plants to low phosphorus availability. Plant and Soil 237:225-237.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F. 2010. Plant phenotypic plasticity in a changing climate. Trends in Plant Science 15:684-692.

Passioura JB. 1988. Water transport in and to roots. Annual Review of Plant Physiology and Plant Molecular Biology 39:245-265.

Pimentel C, Herbert G, da Silva JV. 1999. Effects of drought on oxygen evolution and stomatal conductance of beans at the pollination stage. Environmental and Experimental Botany 42:155-162.

Price AH, Cairns JE, Horton P, Jones HG, Griffiths H. 2002. Linking drought resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to intergrate stomatal and mesophyll responses. Journal of Experimental Botany 53:989-1004.

Pritchard J. 1994. The control of cell expansion in roots. New Phytology 127:3-27.

Rao IM. 2001. Role of physiology in improving crop adaptation to abiotic stresses in tropics. The case of common bean and tropical forages. In: Pessaraki M (Ed.) Handbook of Plant and Crop Physiology, Marcel Dekker, New York, USA. pp. 583-613.

Saab IN, Sharp RR, Pritchard J, Veetberg GS. 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. Plant Physiology 93:1329-1336.

Singh SP. 1995. Selection of water stress tolerance in interracial populations of common bean. Crop Science 35:118-124.

Specht JE, Chase K, Macrander M, Graef GL, Chung J, Markwell JP, Germann M, Orf JH, Lark KG. 2001. Soybean response to water. A QTL analysis of drought tolerance. Crop Science 41:493-509.

Sponchiado BN, White JW, Castillo JA, Jones PG. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Experimental Agriculture 25:249-257.

Wu QS, Xia RX, Zou YN. 2008. Improved soil structure and citrus growth after inoculation with three arbuscular mycorrhizal fungi under drought stress. European Journal of Soil Biology 44:122-128.

Chapter 5

Genetic diversity and population structure of a reference collection of common bean

5.1 Abstract

Molecular markers are now the preferred choice in studying diversity in crop germplasm. The main objective of this study was to determine genetic diversity and population structure in a reference collection of common bean. Genomic DNA was extracted from 201 genotypes and a total of 86 fluorescently labelled microsatellites were used in PCR amplifications. These microsatellites detected 847 alleles with an average of 9.85 alleles per locus. The average observed heterozygosity was 0.066, indicating inbreeding in common bean. F-statistics, analysis of molecular variance, principal coordinate analysis, neighbour joining and STRUCTURE results confirmed the existence of the Andean and Mesoamerican gene pools with races Durango, Mesoamerica 1, Mesoamerica 2, Andean breeding lines and landraces in the reference collection. Gene pools and races contributed significantly to the observed variation. STRUCTURE bar plot results indicated admixed genotypes within each race. Races within gene pools were closely related to each other. Race Mesoamerica 1 was closely related to both races Mesoamerica 2 and Durango. Gene diversity was 0.609 in the entire reference collection. Race Mesoamerica 2 was more diverse than any other race. In conclusion, landraces contained significantly higher levels of genetic diversity than advanced breeding lines and it should be possible to initiate inter-racial crosses within each gene pool. Microsatellites were robust in defining the relationship between race Mesoamerica 1 and races Durango and Mesoamerica 2.

5.2 Introduction

Improvement of economically and nutritionally important agricultural traits depends on the availability of genetic variation of traits in plant germplasm collections. Landraces provide the much needed genetic diversity required in plant improvement programmes (Laurentin 2008). A narrow genetic base has been reported in commercially cultivated common bean due to a bottleneck and the founder effect that has occurred during domestication of the crop (Blair *et al.* 2006). Common bean breeding programmes should thus consider mining the genetic variability available in landraces (Beebe *et al.* 1997a).

The reference collection of common bean was assembled with the aim to study the genetic diversity that exists in common bean for drought tolerance and promote better utilisation of germplasm in breeding programmes. The information generated could lead to identification of pre-breeding lines that could help in designing of crosses that maximise diversity and also forms the basis of association genetic studies (Blair *et al.* 2009; Cabral *et al.* 2011). Association mapping facilitates the molecular characterisation of functional loci (Yu and Buckler 2006). The discovery of functional loci facilitates marker-assisted breeding in the improvement of complex traits such as drought tolerance (Yu and Buckler 2006). The correct exploitation and utilisation of genetic diversity present in landraces would ultimately lead to increased crop productivity in unfavourable environments (Laurentin 2008).

Previous studies in common bean have contributed by grouping germplasm into two distinct classes according to gene pools, namely Andean and Mesoamerican (Singh *et al.* 1991a; b; c; Beebe *et al.* 2000). In each of their studies, Singh *et al.* (1991a; b; c) and Beebe *et al.* (2000) identified further variation within each gene pool. Further subdivisions within gene pools were termed ‘races’. The Andean gene pool has races Nueva Granada, Peru and Chile whilst the Mesoamerican gene pool has races Durango, Mesoamerica 1, Mesoamerica 2 and Guatemala. Each race has distinct agronomical, physiological, biochemical and molecular characters that differ from other races (Singh *et al.* 1991a; b; c). Race designation and differentiation have been successful, particularly for races Durango and Mesoamerica, in the Mesoamerican gene pool, using molecular markers (Beebe *et al.* 2000; Díaz and Blair 2006; Blair *et al.* 2007). However, further research is needed to classify race Guatemala and other races in the Andean gene pool

(Blair *et al.* 2007). Differentiation of genotypes into races represents the genetic diversity looked for in plant breeding programmes. Moreover, a precise population structure is one key requirement for identification of molecular markers correlated with desirable drought tolerance traits in the reference collection of common bean (Abdurakhmonov and Abdukarimov 2008) and permits the exploitation of inter-racial crosses in common bean improvement programmes (Miklas *et al.* 2006). Molecular markers assess genetic diversity at DNA level and are not influenced by the environment as would be the case for morphological or protein assays (Cabral *et al.* 2011). Microsatellite markers are useful in studying population structure in common bean because they detect high levels of polymorphism and offer a better resolution in diversity studies (Díaz and Blair 2006; Blair *et al.* 2007; 2009).

The objectives of this study were to:

- Estimate the genetic diversity in a reference collection of common bean
- Determine the population structure that affects association mapping analysis and help planning of crosses in future common bean breeding programmes.
- Establish genetic relationships between gene pools and among races in a reference collection of common bean.

5.3 Materials and methods

5.3.1 Plant materials

A total of 201 genotypes were evaluated in this study and consisted of 121 Mesoamerican (Chapter 3, Table 3.4) and 80 Andean genotypes (Chapter 3, Table 3.3). However, two of the Andean genotypes presented in Table 3.3, G1938 and G22247, were omitted in this study because of poor DNA quality. Instead G1939 was added to the Andean genotypes listed in Table 3.3 to give a total of 80 genotypes. The G-genotypes (Chapter 3, Tables 3.3 and 3.4) were supplied by the CIAT gene bank while the check genotypes came from the CIAT bean breeding programme. The control genotypes for the molecular diversity study included Tio Canela 75, DOR364 and Pinto Villa for Mesoamerican and G19833 and G4494 for Andean genotypes. These control genotypes had been characterised in previous diversity studies (Blair *et al.* 2006). The 201 genotypes had been evaluated for drought tolerance under terminal drought stress conditions in the field and the majority of genotypes were determinate or indeterminate type I

and type II according to the CIAT growth scale. Genotypes used in this study represented the broadest possible diversity which could be evaluated under terminal drought conditions (Beebe *et al.* 1997b).

5.3.2 Genomic DNA extraction

For each genotype, 10 seeds were randomly selected from the original genebank accessions (Díaz and Blair 2006; Blair *et al.* 2007; 2009). Seed was scarified to ensure uniform germination in the laboratory and pre-germinated in the darkness on germination paper. The first trifoliate leaves were harvested from the eight day old seedlings of each genotype and mixed prior to grinding in liquid nitrogen. The bulked tissue was used for DNA extraction following procedures described by Afanador *et al.* (1993). DNA was resuspended with Tris (hydroxymethyl) aminomethane-ethylenediaminetetraacetic (EDTA) (TE) buffer and its quality was evaluated on 0.8% (w/v) agarose gels. This was followed by quantification of DNA with Hoescht H 33258 dye on a Hoefer DyNA Quant^{TM} 200 fluorometer (Hoefer Biotechnology, San Francisco, CA, USA). DNA was diluted to 10 ng ml^{-1} for the diversity and other molecular characterisation studies.

5.3.3 Microsatellite amplifications

Microsatellite amplifications used a fluorescent marker kit developed by Blair *et al.* (2009). The kit included a total of four colour marker panels. A total of 86 individual microsatellites were used in this study and are presented in Appendix 7. Microsatellite markers were selected based on their high PIC as determined by Blair *et al.* (2006) and even distribution over the entire genome of common bean based on data of Blair *et al.* (2003) (Appendix 7). The forward primers of each microsatellite were 5′-end labelled with one of FAM, NED, PET or VIC fluorescent labels (Appendix 7) while reverse primers were unlabelled during PCR amplification. PCR amplifications were conducted in 96-well plates using a PTC-100 MJ Research thermal cycler (Global Medical Instrumentation, California, USA) with conditions described in Blair *et al.* (2006). A PCR volume of 12 µl containing a cocktail of the following reagents: 50 ng genomic DNA, 0.16 µM of each primer (forward and reverse), 10 mM Tris-HCl (pH 7.2), 50 mM KCl, 1.5-2.5 mM $MgCl_2$ depending on primer (Appendix 7), 0.2 nM of each deoxyribonucleotide triphosphate (dNTP) and 1.0 U of *Taq* DNA polymerase was used for PCR amplifications. The

amplifications were run under the following cycling conditions: an initial hot start for 3 min at 95^{o}C, 28 cycles of 40 sec at 95^{o}C, 40 sec at the specific annealing temperature for each primer (Appendix 7) and 1 min at 72^{o}C, with final extension at 72^{o}C for 1 hr.

The quality of the amplification products were confirmed by resolving 3 µl of each of the PCR products on a 2% (w/v) agarose gel at 100 V for 30 min. After the quality of the PCR reaction was confirmed, a total of 2 µl from each of the four fluorescent PCR products, corresponding to the appropriate markers, were mixed into multiplex panels. Each panel contained a FAM, NED, PET and VIC fluorescent labelled PCR product. The mixture was diluted 1:1 with distilled water and 0.5 µl of the solution was prepared in 9 µl of formamide with 0.06 µl of Genescan LIZ500 size standard and 0.44 µl of distilled water. The mixture was sent to Cornell University Biotechnology Resource Centre and was run on an ABI PRISM 3730 fragment analysis system (Applied Biosystems) for allele size determination.

5.3.4 Data analysis

5.3.4.1 Allele size determination

Estimates of allele sizes in bp were done in GeneMapper v.3.7 software (Applied Biosystems) using the second order least squares size calling and the expected repeat size methods. The GeneMapper v.3.7 software was further used to run electropherograms as a quality test to ensure that clear peaks were found for the expected marker sizes. Visual electropherograms ensured that the proper selection of multiplex markers had been done and stutter peaks were not called during estimation of allele sizes. AlleloBin (http://www.icrisat.org/gt-bt/biometrics.htm) was used to assign a whole integer allele value to raw allele size calls. The software uses the least square minimisation algorithm of Idury and Cardon (1997) which transforms fragment sizes based on migration into a binned value with sizes in bp.

5.3.4.2 Genetic structure in the reference collection

Principal coordinate analysis (PCoA) is used to reveal population structure (Reeves and Richards 2009). This ordination technique has the ability to reduce large data sets into two or three dimensions that represent population structure with subgroups forming distinct clusters. To determine the genetic structure in the reference collection PCoA was carried out on the binned

allele data with the interactive matrix language (IML) module of the software Statistical Analysis Systems v.9.1.3 (SAS Institute 1996).

The tree-based neighbour joining (NJ) cluster analysis method was carried out on the binned allele data using the software DARwin 5.0 (Perrier *et al.* 2003) to visualise the genetic relationships among genotypes in the reference collection. Pairwise genetic distances were calculated using the Dice dissimilarity coefficient (Laurentin 2008) using the binned allele data.

5.3.4.3 Quantification of genetic diversity in the reference collection

Standard genetic diversity parameters which included number of alleles per locus, total number of alleles in the entire population and within subpopulations, allele frequency, observed heterozygosity (H_o), gene diversity (H_e) and PIC were determined using the software Power-Marker v. 3.25 (Liu and Muse 2005).

5.3.4.3.1 Analysis of molecular variance and Wright statistics

The partitioning of genetic diversity between and within gene pools was achieved through analysis of molecular variance (AMOVA) (Excoffier *et al.* 1992) and was determined using ARLEQUIN v. 3.11 (Excoffier 2007). AMOVA is a method used to estimate population differentiation directly from molecular data (Excoffier *et al.* 1992). In AMOVA, molecular data is treated as a Boolean vector $\mathbf{p}_i$, consisting of a 1xn matrix of ones and zeros. Zero and one indicates absence or presence of a marker, respectively. Euclidean distances between pairs of vectors are established by subtracting the Boolean vector of one haplotype from another ($\mathbf{p}_j$-$\mathbf{p}_k$). The Euclidean distances are then squared for all pair wise arrangements of Boolean vectors and arranged into a matrix. The matrix is partitioned into sub-matrices corresponding to subdivisions within the population. Sums of squares obtained from the diagonals in the matrix and sub-matrices are analysed in a nested ANOVA framework. The main difference between a nested ANOVA and simple ANOVA is in data arrangement. In a nested ANOVA data are arranged hierarchically and mean squares are computed for groupings at all levels of the hierarchy. The test for significance for individual variance components was done using 10 000 permutations. The variance components can be used in the calculation of phi-statistics (Φ) which summarise the degree of differentiation between population divisions and are similar to F-statistics

(Excoffier *et al.* 1992). For AMOVA, genotypes were initially grouped into two broad gene pools (Andean and Mesoamerican) and later subdivided into smaller groups within each gene pool according to previous race classification. The Andean gene pool had two groups, namely Andean landraces and Andean breeding lines while races Mesoamerica 1, Durango and Mesoamerica 2 were the main subgroups in the Mesoamerican gene pool.

Wright's F-statistics (Wright 1951) were determined using ARLEQUIN v. 3.11 (Excoffier 2007). The confidence intervals of F_{ST} were generated by bootstrapping over loci using 1 000 replicates. Both AMOVA and F-statistics are based on the hypothesis that isolation should lead to differentiation between and within gene pools (Laurentin 2008). Differentiation represents the genetic structures found in populations. F-statistics estimate the difference between the observed mean heterozygosity among the subdivisions in a population and potential heterozygosity if all members of the population mixed freely and non-assortatively (Hartl and Clark 1997). Differentiation is based on three hierarchical levels of a population; F_{IS} and F_{IT} which are both measures of inbreeding in subgroups and the entire group, respectively. The third level of F-statistics, F_{ST} measures the identity of individuals within subgroups compared to other individuals in other subgroups (Laurentin 2008). F_{ST} values range between zero for no differentiation between the overall population and its subpopulations and one for complete differentiation. F_{ST} of one is unlikely to be achieved practically even in highly differentiated populations (Hartl and Clark 1997). To determine the F-statistics, the mean heterozygosity at each locus must be determined. The relationship among these three F-statistics was presented by Wright (1951) as:

$(1 - F_{IT}) = (1 - F_{IS})\ (1 - F_{ST})$

F-statistics components are computed as follows:

$F_{IT} = 1 - (H_I / H_T)$

$F_{ST} = 1 - (H_S / H_T)$

$F_{IS} = 1 - (H_I / H_S)$

Where H_I is the observed heterozygosity averaged across all loci, H_T the average expected heterozygosity in the entire group and H_S the average expected heterozygosity at subgroup level (Wright 1951).

5.3.4.4 Population structure in the reference collection

The Bayesian clustering method of the software programme STRUCTURE 2.23 (Pritchard *et al.* 2000) was used to investigate population structure in the reference collection of common bean. STRUCTURE determines a Q matrix of population relatedness and finds the number of subpopulations (K) that fits the data. The assignment of individuals to subpopulations is automatic under the STUCTURE model but K values need to be determined. The K values were estimated using the *ad hoc* statistic ΔK (Evanno *et al.* 2005). A value of ΔK was calculated for each K and results from simulations with the highest likelihood within each number of different K simulations were chosen to assign genotypes to populations (Evanno *et al.* 2005). Independent STRUCTURE simulations amounting to 10 were performed for each K using the admixture model, correlated allele frequencies, a running length of 20 000 burn-in and 40 000 Markov chain Monte Carlo (MCMC) repetitions. The admixture model assumes that historically populations diverged from a single ancestral population and differences in allele frequencies are a result of genetic drift that has occurred since their divergence (Pritchard *et al.* 2000). MCMC estimate a posterior distribution of individuals' origins. Results of STRUCTURE were visualised with the software DISTRUCT (Rosenberg 2002).

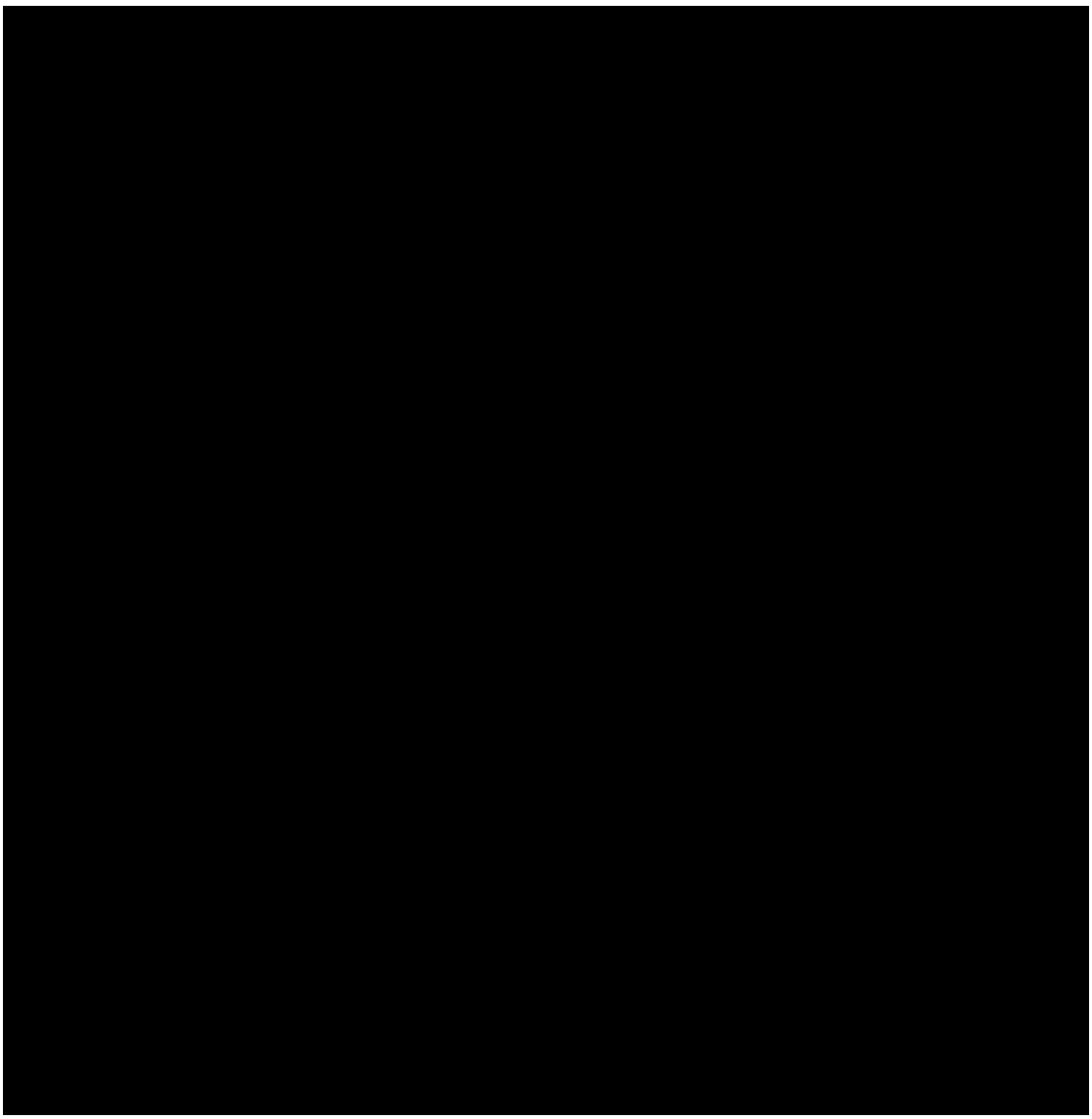
5.4 Results

5.4.1 Level of polymorphism and heterozygosity

The microsatellite markers used in this study amplified a total number of 847 alleles with an average of 9.85 alleles per locus (Table 5.1). All microsatellite markers were polymorphic identifying between 2 and 50 alleles per locus. Markers PV-at001 (0.967), BM137 (0.944), BM53 (0.928), BM200 (0.928) and BM187 (0.928) had the highest PIC and identified a total of 201 alleles in the population. PV-at001 (50) identified the highest number of alleles per locus followed by BM187 (42) and BM200 (41), respectively. Microsatellite markers that identified the lowest number of alleles per locus (2) included BM149, GATs54, BMd12, BMd45, BMd53 and BM68.

The lowest PIC's were observed for BMd51 (0.015), BM199 (0.100) and PV-cct001 (0.101), in ascending order, even though these markers detected three or more alleles each. PV-at001 and BM137 are perfect microsatellites with a high number of repeats and BM53 and BM187 are compound microsatellites with a higher combined number of repetitions compared to markers with lowest PICs (Appendix 7). Observed heterozygosity was detected in some markers and varied between 0.00 and 0.348 with an average of 0.066 across all markers. Higher than normal heterozygosity was detected in BMd42 (0.348) followed by BM167 (0.332) and BMd15 (0.282) in descending order. Multi-banding might have resulted in above than normal observed heterozygosity in BMd42, BM167 and BMd15. The majority of markers had observed heterozygosity lower than 0.10 and BMd46, PV-ag003, BM199, BM211, BMd10 and BMc161 had 0.00 values for the observed heterozygosity.

Table 5.1 Genetic diversity values for 86 microsatellite markers evaluated across the 201 genotypes of common bean in the reference collection



H_o – observed heterozygosity; PIC – polymorphic information content

The mean gene diversity in the reference collection was 0.609 (Table 5.1). Markers that presented the highest gene diversity (higher than 0.9) were PV-at001 (0.968), BM137 (0.947), BM187 (0.932), BM53 (0.932), BM200 (0.932), BMy08 (0.914), BM143 (0.910) and GATs91 (0.900) and some of these markers detected a large number of alleles and high PIC values. The lowest gene diversity (less than 0.3) was found in BMd18 (0.138), BMd51 (0.015), BMd56

(0.237), PV-cct001 (0.104), BM199 (0.104), BMd12 (0.252), BM67 (0.189), BM213 (0.272) and BMd44 (0.119) and corresponded to low PIC values and number of alleles.

The highest average number of alleles was detected in the Andean landrace subpopulation (6.221) followed by landraces from race Mesoamerica 2 (5.814) and race Mesoamerica 1 (4.360) of the Mesoamerican gene pool (Table 5.2). The Andean breeding lines (2.802) had the lowest number of alleles detected as could be expected given that only seven lines were evaluated. Among the Mesoamerican subpopulations the lowest number of alleles was detected in race Durango (3.395). The genetic diversity was 0.609 for the entire population and was similar to the entire core collection evaluated by Blair *et al.* (2009). Race Mesoamerica 2 (0.438) had the highest genetic diversity. The Andean landrace subpopulation (0.411) was second and race Durango (0.397) had the lowest level of gene diversity. The observed average heterozygosity in the entire population was 0.066 which was low and reflected the self-pollinating nature of common bean. No heterozygosity was detected among the Andean breeding lines. Heterozygosity was higher in Mesoamerican subpopulations than Andean subpopulations. Race Mesoamerica 2 (0.071) had the highest heterozygosity among the Mesoamerican subpopulations.

Table 5.2 Genetic diversity among the different subpopulations in the reference collection of common bean

	No.of alleles	**Gene diversity**	**Heterozygosity**	**PIC**
Andean gene pool				
Landraces	6.221	0.411	0.050	0.388
Breeding lines	2.802	0.403	0.000	0.368
Mesoamerican gene pool				
Mesoamerica 1	4.36	0.405	0.067	0.366
Mesoamerica 2	5.814	0.438	0.071	0.405
Durango	3.395	0.397	0.063	0.354
Average for all genotypes	**9.849**	**0.609**	**0.066**	**0.561**

PIC: Polymorphic information content

5.4.2 Genetic differentiation in the reference collection of common bean

AMOVAs were conducted to determine variation explained by gene pools and races in a reference collection of common bean (Table 5.3). The total variation explained by differences between the two gene pools was 44.23%. Variation between races within the two gene pools accounted for 41.4% of the total variation in the reference collection of common bean. A high percentage of variation (49.4%) could be attributed to variation among individuals within races. A smaller variation (9.21%) was explained by genetic variation within individual genotypes. In summary, most of the variation was between individuals within a genepool but most of the explained variation was either between genepools or between races.

Table 5.3 Molecular analysis of variance for genetic differentiation of the genotypes in the reference collection

D.f. – degrees of freedom

Genetic differentiation analysis confirmed that a genetic divergence existed between Andean and Mesoamerican subpopulations (F_{ST}=0.41) of the reference collection (Table 5.4). The highest degree of genetic variation existed between Andean breeding lines and race Durango (F_{ST}=0.515). Meanwhile, less than 25% of the genetic variation existed between Andean subpopulations. Low differentiation existed between Mesoamerican populations including Mesoamerica 1, Mesoamerica 2 or Durango races respectively. Race Durango was closer to Mesoamerica 1 (F_{ST}=0.133) than Mesoamerica 2 (F_{ST}=0.177). All in all, heterozygosity was below 20% for the entire population of the reference collection of common bean (F_{IT}=0.91) and the five subpopulations identified (F_{IS}=0.84).

Table 5.4 Genetic differentiation based on F_{ST} values for the races identified among the 201 genotypes of the reference collection

	Andean gene pool		Mesoamerican gene pool		
	Landraces	Breeding lines	Mesoamerica 1	Mesoamerica 2	Durango
Andean gene pool					
Landraces	-				
Breeding lines	0.221	-			
Mesoamerican gene pool					
Mesoamerica 1	0.498	0.509	-		
Mesoamerica 2	0.488	0.489	0.126	-	
Durango	0.508	0.515	0.133	0.177	-

F_{IS} - 0.84, F_{ST} - 0.41, F_{IT} - 0.91

5.4.3 Genetic structure of the reference collection using the ordination technique

The control genotypes occupied different positions in the PCoA (Figures 5.1A; B) and helped to designate genotypes to specific subpopulations. Figure 5.1A is a plot of coordinate 1 against coordinate 2. The first coordinate separated genotypes into two distinct clusters and based on the characteristics of the control genotypes represented the Andean and Mesoamerican gene pools (Figure 5.1A). The Andean gene pool was represented by two control genotypes, G19833 (G) and G4494 (C) and landraces (green) as well as breeding lines (yellow) (Figure 5.1A). Figure 5.1A shows the spread of the Mesoamerican control genotypes Tio Canela 75 (TC), Pinto Villa (PV) and DOR364 (D), as well as Mesoamerica 1 (pink), Mesoamerica 2 (red) and Durango (blue) races that constituted the Mesoamerican gene pool. In the genepool separation, coordinate 1 explained 71.3% of the genetic variation in the reference collection.

Genotypes were further separated into subclusters within each gene pool based on coordinate 2 (Figure 5.1A). The Andean gene pool had two clusters, namely landraces (green) and breeding lines (yellow). The breeding lines were included because they were used as check varieties in field experiments. The Mesoamerican gene pool divided into three clusters, Mesoamerica 1 (pink), Mesoamerica 2 (red) and Durango (blue) representing known races in this gene pool (Figure 5.1A). Mesoamerica 1 clustered between the Durango and Mesoamerica 2 races (Figure 5.1A). PCo2 accounted for 7.97% of the variation in the reference collection.

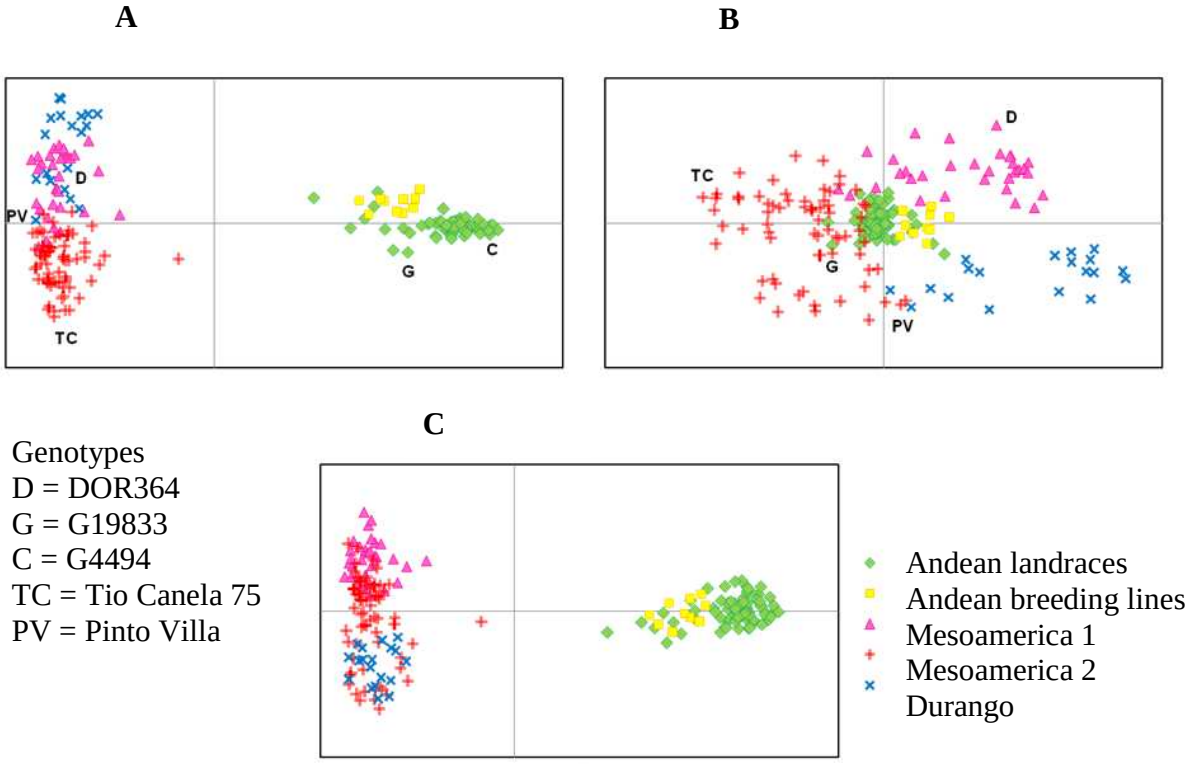


Figure 5.1 **Principal coordinate analysis based on the analysis of 201 genotypes in a reference collection of common bean. A: PCoA plot of principal coordinate (PCo)1 on the x-axis and PCo2 on y-axis. B: PCoA plot of PCo2 on x-axis and PCo3 on the y-axis. C: PCo1 on x-axis and PCo3 on the y-axis. Position of control genotypes for each subpopulation are shown in A and B.**

Figure 5.1B was drawn as a plot of coordinate 2 (x-axis) against coordinate 3 (y-axis). In this graph, genotypes were separated in four different clusters for Mesoamerican genotypes. Coordinate 3 separated races Durango and Mesoamerica 1 into two different clusters. The majority of the Andean landraces were clustered at the middle of the plane. Coordinate 3 contributed 6.09% to the variation. Subdivisions into gene pools and races in each gene pool were confirmed by plotting coordinate 1 against 3 (Figure 5.1C). All in all, PCoA explained 85.4% of the genetic variation in the reference collection of common bean. This satisfied rules of ordination techniques, where axes are considered until 70% to 90% of the total variation has been explained (Jolliffe 1986). A PCoA within each gene pool revealed two clusters within the Andean gene pool (Figure 5.2A).

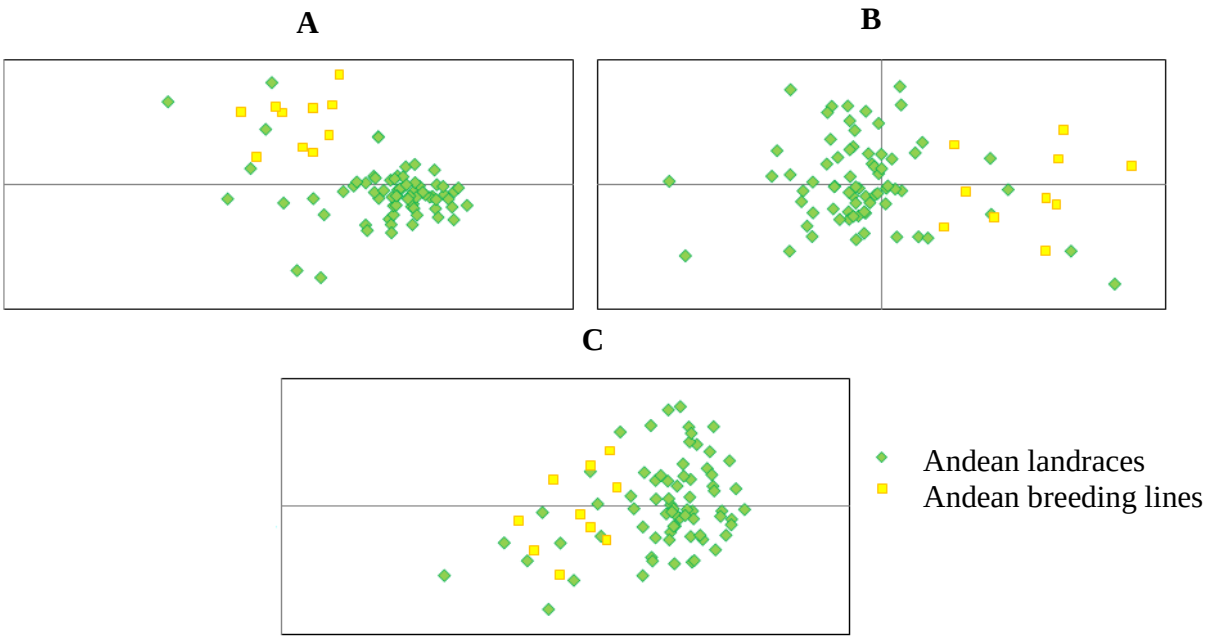


Figure 5.2 **Principal coordinate analysis based on the analysis of 81 Andean genotypes in a reference collection of common bean. A: PCoA plot of PCo1 on the x-axis and PCo2 on y-axis. B: PCoA plot of PCo2 on x-axis and PCo3 on the y-axis. C: PCo1 on x-axis and PCo3 on the y-axis.**

Coordinate 2 separated landraces from the small cluster containing the breeding lines. Some landraces clustered closely and/or within the breeding lines. Within the Mesoamerican gene pool, Coordinate 2 placed race Mesoamerica 2 between races Durango and Mesoamerica 1 (Figure 5.3A). A plot of PCo2 (x-axis) against PCo3 (y-axis) confirmed the presence of three subdivisions in Mesoamerican gene pool.

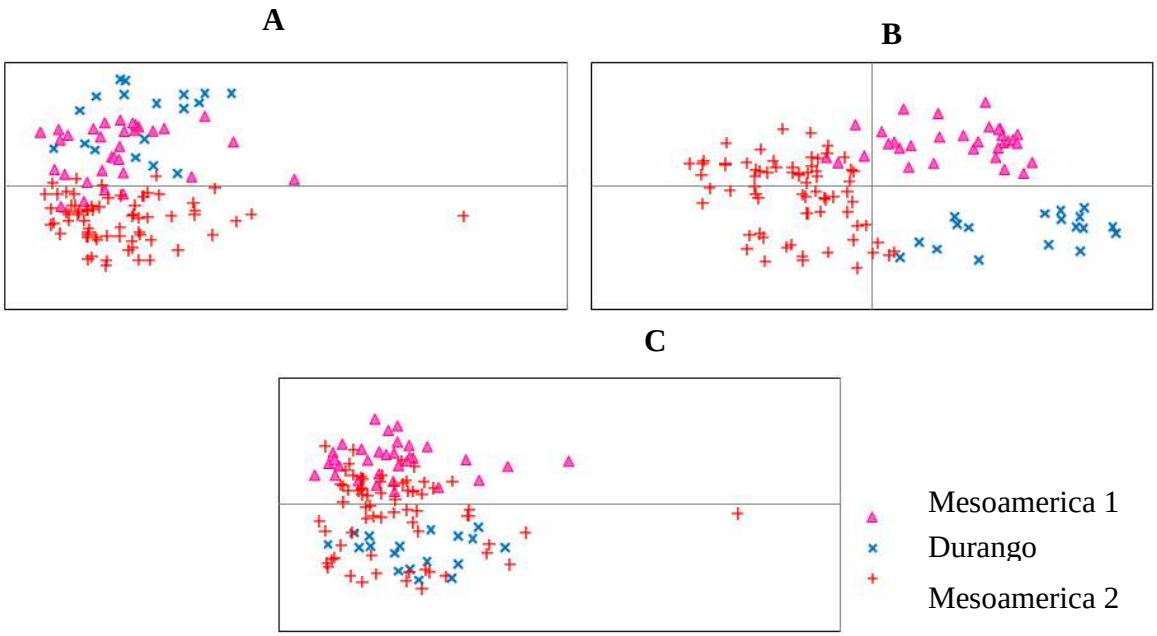


Figure 5.3 **Principal coordinate analysis based on the analysis of 120 Mesoamerican genotypes in a reference collection of common bean. A: PCoA plot of PCo1 on the x-axis and PCo2 on y-axis. B: PCoA plot of PCo2 on x-axis and PCo3 on the y-axis. C: PCo1 on x-axis and PCo3 on the y-axis.**

5.4.4 Population structure

Genotypes constituting the reference collection were classified into two gene pools (Andean and Mesoamerican), based on previous genetic diversity studies (Blair *et al.* 2009). The K-values recommended by Evanno *et al.* (2005) for identification of the best fitting number of populations within a sample, was highest at K=2 (Figure 5.4).

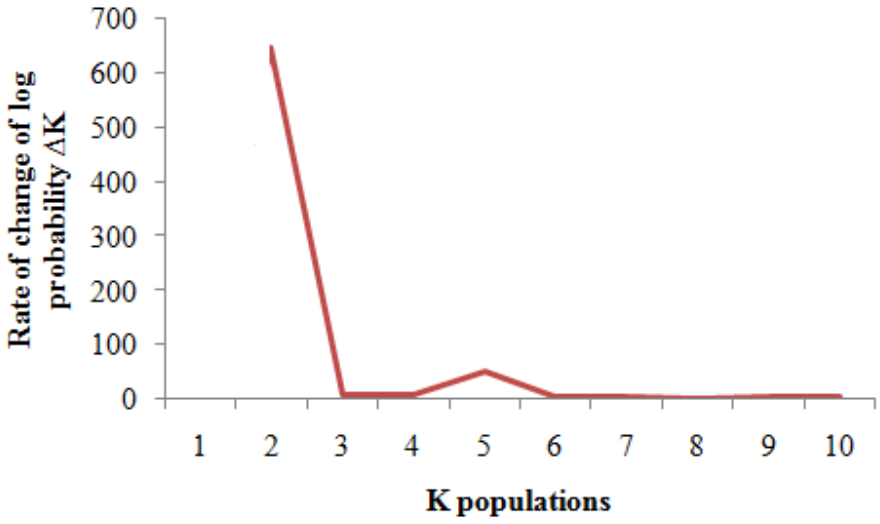


Figure 5.4 Evanno's *ad hoc* ΔK statistic against possible values for K.

The population subdivision as determined by STRUCTURE at K=2 showed significant Andean and Mesoamerican differentiation. The two subpopulations confirmed the previous clustering of genotypes into two gene pools (Figure 5.5).

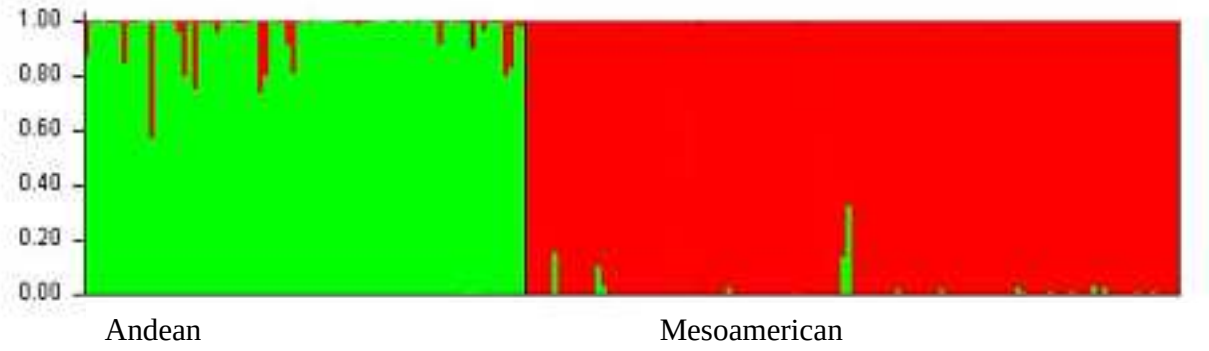


Figure 5.5 STRUCTURE bar plot of membership coefficients (y-axis) for all 201 genotypes in a reference collection of common bean (x-axis) classified according to preset K=2. The cluster names are indicated below the figure and are identified as Andean and Mesoamerican gene pools of cultivated common bean. Population 1 (Andean) is indicated in green and population 2 (Mesoamerican) in red.

Of the 80 previously defined Andean genotypes, all of them were assigned to population 1 (green) and had a genetic composition of 0.86 Andean alleles on average membership coefficient for that genepool (Table 5.5). The 121 Mesoamerican genotypes were clearly assigned to population 2 (red) (Figure 5.5) with average membership coefficients of 0.72 (Table 5.5). Cross assignment of membership coefficients were on average 0.14 and 0.27 from Mesoamerican to Andean and Andean to Mesoamerican respectively. This could also indicate shared ancestry and alleles that were not genepool associated.

Table 5.5 Mean proportion of estimated ancestry in each of K=2 inferred clusters for the reference collection of common bean

Gene pool	Inferred cluster		Number of individuals
	Population 1	**Population 2**	
Andean	0.86	0.14	80
Mesoamerican	0.27	0.73	121

To infer the existence of further subdivisions in the reference collection, additional STRUCTURE simulations were performed at higher preset K values. Using the test for ΔK, K=5 was the second best fit for number of populations in the reference collection and was next most significant after the K value for the reference collection. The standard deviations of likelihoods were smallest at K=5 (data not shown) and results for K=5 are given in Figure 5.6.

At K=5, the Andean genepool was subdivided into two different populations namely Andean landraces (green) and Andean breeding lines (yellow). All of the Andean landraces had a genetic composition of 50% or higher representative of population 1 (green). In addition, the Andean breeding lines had a genetic composition of 65% or higher representative of population 2 (yellow). Mesoamerican genotypes were subdivided into three basic populations (Figure 5.6) represented by races Mesoamerica 1 (pink), Durango (blue) and Mesoamerica 2 (red). All of the Mesoamerica 1 and Durango genotypes had a genetic composition of 50% or higher

representative of population 3 and population 4 (blue) respectively. Mesoamerica 2 genotypes were slightly more admixed having around 40% or higher representation of population 5 (red).

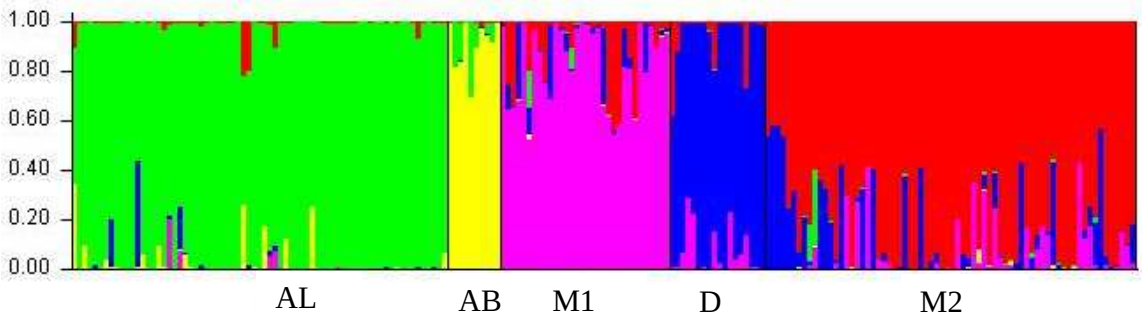


Figure 5.6 An estimated population structure at K=5 for the reference collection of common bean. Population 1 is indicated in green, population 2 in yellow, population 3 in pink, population 4 in blue and population 5 in red. AL represents the Andean landraces; AB represents the Andean breeding lines; M1 represents Mesoamerica 1 genotypes; D represents Durango genotypes and M2 represents Mesoamerica 2 genotypes.

The mean proportion of estimated ancestry in each inferred cluster is presented in Table 5.6. The highest genetic contribution to a single population was race Mesoamerica 2 with a 94.4% genetic contribution from the corresponding population. On the other hand, race Durango had the smallest genetic contribution to a single population, with 81.2% genetic contribution from population 4. Race Durango and the Andean landraces had the highest genetic contribution to other populations, making genetic contributions of 11.4% and 10.7% to population 3 and population 4 respectively.

Table 5.6 Mean proportion of estimated ancestry in each of the K=5 inferred clusters for the reference collection

Sub-population	Population 1	Population 2	Population 3	Population 4	Population 5
Andean gene pool					
Landraces	**0.827**	0.002	0.056	0.107	0.001
Breeding lines	0.002	**0.909**	0.002	0.003	0.085
Mesoamerican gene pool					
Mesoamerica 1	0.073	0.001	**0.869**	0.056	0.001
Durango	0.063	0.002	0.114	**0.812**	0.009
Mesoamerica 2	0.007	0.024	0.014	0.011	**0.944**

5.4.5 Neighbour joining analysis

The relationships among genotypes used in the current study were visualised by a NJ tree based on data from all 86 microsatellite markers (Figure 5.7). The tree showed high genetic variability in the reference collection with a clear grouping of genotypes into Andean and Mesoamerican gene pools as identified by STRUCTURE at K=2 (Figure 5.5), AMOVA (Table 5.3) and PCoA (Figure 5.1). Genotypes subdivided further into clusters within each gene pool and confirmed population structure results for K=5. The Andean gene pool consisted of two main clusters, namely landraces and breeding lines. The breeding lines were clustered tightly together and close to some Andean landraces. The Andean landraces clustered into five subclusters, **A1**, **A2, A3, A4** and **A5** (Figure 5.7). Some Andean landraces, for example G19842, G23829 and G19833 clustered separately. AFR619, a breeding line for Africa and G16345 clustered closely together in a separate group. The Andean landraces and breeding lines clustered into two clear groupings with no genotypes from other races (Figure 5.7).

The Mesoamerican gene pool constituted a separate subpopulation containing three major clusters (Figure 5.7). The three clusters obtained with NJ analysis also corresponded with population structure and PCoA results. The three major clusters represented Mesoamerica 1 (pink), Durango (blue) and Mesoamerica 2 (red). High levels of genetic variability were present in the Mesoamerica 2 cluster and genotypes could be further subdivided into three subclusters, **M2A**, **M2B** and **M2C** (Figure 5.7). The NJ also confirmed the F_{ST} results indicating high levels of genetic diversity in the Mesoamerican 2 subpopulation.

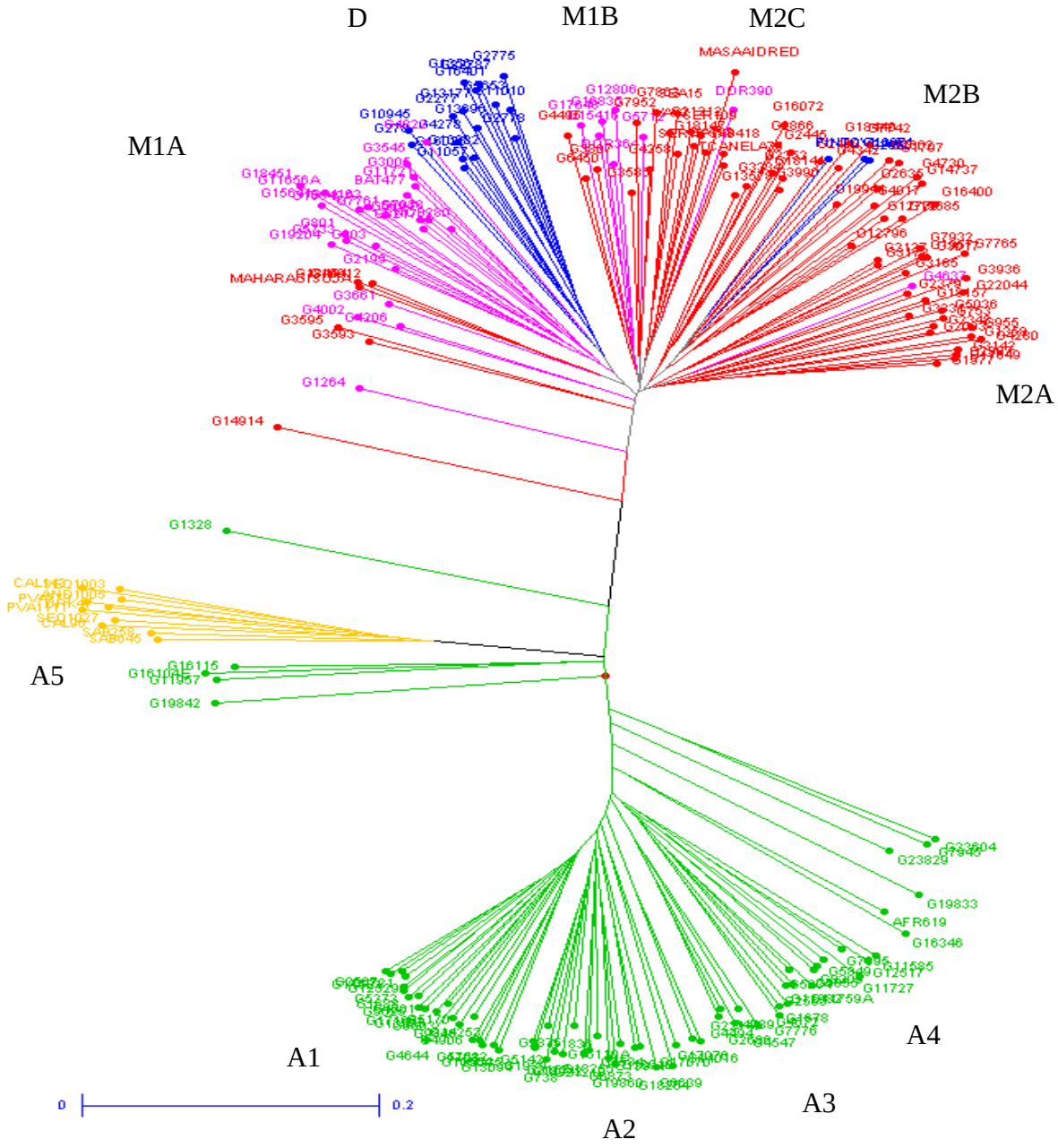


Figure 5.7 **A neighbour joining tree constructed for 201 genotypes in the reference collection of common bean determined using data from 86 microsatellite markers using Dice similarity coefficient in DARwin software. Colour coding is as follows: Andean landraces (green), Andean breeding lines (yellow), Mesoamerica 1 (pink), Durango (blue) and Mesoamerica 2 (red).**

Mesoamerica 1 was also divided into two clusters, **M1A** and **M1B**. **M1B** clustered separately from the Durango and Mesoamerica 1A subclusters and shared a close relationship with Mesoamerica 2 (cluster **M2C**). The F_{ST} results indicated this close relationship between Mesoamerica 1 and Mesoamerica 2. Mesoamerica 1, cluster **M1A** clustered closely with the Durango cluster (Figure 5.7) which also confirmed the F_{ST} results. Population structure results showed admixtures in subclusters of the Mesoamerican gene pool and this was confirmed by the NJ tree. One of the Mesoamerica 2 clusters (**M2B**) contained three Durango genotypes, while subcluster **M2A** contained two Mesoamerica 1 genotypes, DOR390 and G4637. Pinto Villa clustered in subcluster **M2C** rather than directly in the Durango group, perhaps because of its mixed pedigree as an improved variety.

5.5 Discussion

5.5.1 Level of polymorphism and heterozygosity

The current study detected about half the levels of allelic variation in the reference collection compared to that detected in Blair *et al.* (2009) but only slightly lower genetic diversity than the core collection study. Blair *et al.* (2009), analysing genetic diversity in 604 genotypes (304 Mesoamerican and 300 Andean genotypes) using 36 microsatellites detected an average of 18.86 alleles per locus compared to 9.85 alleles per locus identified in the current study. One obvious reason for the differences observed in the genetic diversity between the two studies would be associated to the sample size analysed. The 201 genotypes used in the current study were selected from the 604 genotypes used by Blair *et al.* (2009) based on their adaptation to semi-arid environments. Consequently, the reference collection was devoid of race Chile (Andean) and had few representatives from races Peru (Andean) and Guatemala (Mesoamerican) compared to Blair *et al.* (2009).

In addition, differences between the studies could be due to the selection and number of markers used for evaluation of the core *versus* the reference collection. The current study used an additional 50 microsatellites to those used in Blair *et al.* (2009). A total of 475 alleles were detected in the same group of genotypes constituting the reference collection in Blair *et al.* (2009) compared to 847 alleles detected in the current study. Saturation of the genome with many markers increases the likelihood of detecting more alleles even for a smaller number of

individuals. On the other hand, rare alleles were less likely to occur when outlier individuals from the core collection were removed to constitute the reference collection. Another finding from the current study was that the additional 50 microsatellites used were less polymorphic than the first set of 36 microsatellites used by Blair *et al.* (2009) and only detected 372 additional alleles for the reference collection of common bean.

Marker PV-at001 detected the highest number of alleles in the current study, similar to the study of Blair *et al.* (2009). Observed heterozygosity (0.066) of the entire reference collection was higher in the current study compared to values (0.038 and 0.049) previously reported for common bean (Díaz and Blair 2006; Blair *et al.* 2007; 2009). This is perhaps due to the inclusion of less-well studied microsatellites that had multiple banding patterns interpreted as observed heterozygosity. Care must be taken in which microsatellites to use in future studies, although in the current study all banding patterns were informative for the diversity analysis for the reference collection.

The higher levels of observed heterozygosity in the reference collection used in the current study could have arisen due to random sampling of heterogeneous seed from the gene bank or heterozygous individuals. Landraces by nature contain heterogeneous individuals (Blair *et al.* 2009). Results indicated that the Andean breeding lines were pure lines, with observed heterozygosity values of 0.00 and these lines were obtained from the CIAT bean breeding programme. The average observed heterozygosity (0.066) for the five subpopulations identified was higher for Mesoamerica 2 than Durango, Mesoamerica 1 and Andean landraces in that order.

The low level of observed heterozygosity values represented the inbreeding reproductive nature of common bean (Perseguini *et al.* 2011). Information on the nature of reproduction of a crop is useful in certified seed production programmes where isolation distances between different varieties are important and informs breeders on how to generate new variation in such kind of crop species. The Mesoamerica 2 subpopulation was genetically the most diverse of all tested subpopulations and the other subpopulations displayed more or less equivalent genetic diversity. The genetic diversity observed in the subpopulations of Andean landraces, Andean breeding

lines, Mesoamerica 2 and Durango corresponded to earlier results obtained in common bean (Blair *et al.* 2006; 2007; Díaz and Blair 2006; Chiorato *et al.* 2007).

5.5.2 Genetic differentiation in the reference collection

F_{ST} statistics indicated high and significant differentiation in the reference collection (F_{ST}=0.41). The high level of genetic divergence between the Andean and Mesoamerican gene pools could be a result of genetic drift and lack or limited gene flow between the gene pools (Zizumbo-Villarreal *et al.* 2005). Gene flow between common bean genotypes happens at an extremely low rate due to the high inbreeding of common bean as a crop (Debouck *et al.* 1993; Beebe *et al.* 1997b). In addition, dwarf F_1 lethals have been reported in some inter-gene pool crosses, showing a degree of reproductive incompatibility between the gene pools (Bitocchi *et al.* 2012). PCoA also supported the genetic divergence between Andean and Mesoamerican gene pools and further revealed the existence of races within gene pools. A similar pattern of genetic differentiation in common bean was observed by other researchers (Beebe *et al.* 2000; Blair *et al.* 2009; Cabral *et al.* 2011; Perseguini *et al.* 2011). A genetically structured population is expected in common bean after two parallel domestication events in two geographical regions in the American continent (Sauer 1993) that gave rise to the Andean and Mesoamerican gene pools.

5.5.3 Population structure in the reference collection

Results of STRUCTURE (K=2 analysis) along with the other diversity tests and F-statistics showed that genotypes in the reference collection of common bean belonged to the two major gene pools; Andean and Mesoamerican. These results are in agreement with previous studies conducted using common bean germplasm (Beebe *et al.* 2000; Blair *et al.* 2009; Perseguini *et al.* 2011). Grouping of genotypes into subclusters within each gene pool were observed using NJ analysis and population structure evaluation at the K=5. These subclusters were supported by PCoA of coordinate 2 versus coordinate 3.

The observed subclusters corresponded to the known races of common bean for the Mesoamerican genepool, namely Durango, Mesoamerica 1 and Mesoamerica 2. Results are consistent with previous race classification in the Mesoamerican gene pool (Díaz and Blair 2006; Blair *et al.* 2009). As distinct from other studies, all the Andean landraces grouped together when

evaluated for the distribution of genetic diversity for a large number of SSR loci giving a new picture of genetic diversity in the Andean genepool. This may be a reflection that all Andean landraces evaluated in the current study were all bush beans even though some of these genotypes were classified as race Peru by Blair *et al.* (2009). This race classification for Andean races agrees with the definitions by Singh *et al.* (1991c) and is useful when evaluating bush beans in the field.

In the current study, race Guatemala, identified as a fourth race within the Mesoamerican gene pool in previous studies (Beebe *et al.* 2000; Blair *et al.* 2009), was largely absent. Unlike Blair *et al.* (2009) who tested 61 genotypes of race Guatemala, only 10 genotypes represented race Guatemala in the current study. It could thus have been difficult for the statistical programmes used in data analysis to group them into a distinct subpopulation. NJ analysis indicated that the genotype G1328 (race Guatemala) was an intermediate between Andean and Mesoamerican gene pools and could possibly be a hybrid instead of a true representative of the race. In addition, other race Guatemala genotypes were similar to sub race Mesoamerica 2 genotypes indicating some shared ancestry.

F_{ST} statistics, PCoA and NJ analysis revealed the close relationships between races Mesoamerica 1, Durango and Mesoamerica 2 and their subclusters. Some genotypes from sub-races Mesoamerica 1 and 2 jointly formed subcluster **M1B** in the NJ tree that was closely related to the Mesoamerican 2 cluster and between the Durango and Mesoamerican 2 clusters. On the other hand, several Mesoamerican 1 genotypes (**M1A**) formed a cluster closely related to the race Durango cluster as well. Studies reported so far on genetic diversity of the core collection of common bean (Díaz and Blair 2006; Blair *et al.* 2009) are equally informative for revealing relationships based on similarities but the 86 SSR markers used in the current study were better able to discriminate closely related genotypes. The special relationships between some genotypes from the two Mesoamerica races and Durango versus Mesoamerica genotypes were able to be revealed which could not be distinguished using fewer SSR markers in previous studies. Some genotypes from Durango and Mesoamerica 1 shared the same countries of origin and these could have similar agronomic traits and marker alleles. It is thus possible that these genotypes only differ in a few major genes governing plant growth habits and seed colours. A preferable seed

colour and size vary from community to community for common bean. In terms of breeding, little genetic gains are expected when genetically similar genotypes are used together in hybridisation programmes. The 86 SSR markers evaluated in the current study showed a very high accuracy in providing information for grouping genotypes based on genetic similarity.

Population structure analysis at K=5 determined two subpopulations within the Andean gene pool namely Andean landraces and Andean breeding lines, supporting previous classification. Results for the Andean landraces are in contrast with previous findings of Blair *et al.* (2009) where there were four sub-races among the 300 Andean genotypes from the core collection namely Nueva Granada 1, Nueva Granada 2, Peru 1 and Peru 2. The differences in the number of genotypes evaluated (80 versus 300) in each study may partly explain the observed differences.

The assignment of Andean landraces to the same population in STRUCTURE analysis could be explained by factors that affect MCMC. Apart from the presence of multiple populations in a sample, the signal used by STRUCTURE to detect population structure is also sensitive to other factors such as non-random mating, null alleles, genotyping errors and genetic bottlenecks (Reeves and Richards 2009). A genetic bottleneck is likely to have caused the grouping of Andean landraces into one cluster. Andean genotypes appear to have a high allelic diversity compared to Mesoamerican lines but a major bottleneck prior to domestication was proposed for the Andean genepool (Gepts *et al.* 1986; Sonnante *et al.* 1994, Bitocchi *et al.* 2012). However, the bottlenecks experienced in common bean are a result of selection for domestication traits and local adaptation (Gepts 2004) and results from neutral microsatellite markers can detect higher levels of diversity for Andean beans (Blair *et al.* 2006).

The STRUCTURE bar plots indicated the presence of admixed genotypes in both gene pools and among all races but only in the Mesoamerican races in the NJ tree. For K=5, each race had a shared ancestry with other races estimated by the mean proportion of estimated ancestry and could be one reason of admixtures. Low levels of admixtures could also have been caused by either natural gene flow or deliberate crossing programmes by breeders (Debouck *et al.* 1993; Beebe *et al.* 1997b; Chiorato *et al.* 2007). The frequency of admixtures was high in the Mesoamerican gene pool and could possibly be explained by higher natural outcrossing of

landraces of this group. Race Mesoamerica is the most widely cultivated race of common bean in the world and many landraces are grown in mixtures (Singh *et al.* 1991a). One of the products of controlled gene flow is Pinto Villa, a hybrid between Andean and Durango genotypes (Miklas *et al.* 2006).

5.5.4 Application of population structure and neighbour joining results to common bean breeding programmes

The population structure of gene pools and sub-races identified in the reference collection of common bean is useful for future association analysis of traits found in bush beans. The importance of each race and gene pool has previously been explained in biotic resistance studies and all genotypes need to be conserved for future use in breeding programmes. Each race and gene pool was shown to have distinct resistance to particular pests and diseases (Geffroy *et al.* 1999; Kelly 2004). In addition, race Durango has been associated with drought tolerance in common bean (Miklas *et al.* 2006).

The NJ results indicated genetic distances between genotypes and the possibility of identifying divergent parents within each genepool for inter-racial crosses may be useful for combining ability studies for developing hybrids, should the technology arise. Hybrid vigour emanates from two divergent parents (Perseguini *et al.* 2011). The NJ results showed sufficient divergence between Andean breeding lines and some landraces which could be used to improve the Andean breeding lines. Races Mesoamerica 2 and Durango were distantly related in the current study and could possibly produce good progenies for drought tolerance. Inter-racial Durango x Andean or Durango x Mesoamerica crosses have been carried out in common bean breeding and useful progenies tolerant to drought and diseases have been produced (Singh 1999; Kelly 2004; Miklas *et al.* 2006). For drought tolerance, SEA5, a well-adapted line to drought conditions of Central America, was developed through a double cross between races Durango and Mesoamerica (Miklas *et al.* 2006). Some Mesoamerican genotypes have improved resistance to bean golden mosaic virus through introgressions with race Durango which is resistant to this virus (Singh 1999).

Despite a clear separation into gene pools there exists enough evidence in literature that suggests that inter-gene pool crosses in common bean yielded few useful progenies and in some genotypes resulted in F_1 lethality (Singh 1995). However, experienced breeding programmes with long-term objectives can utilise inter-gene pool crosses. As mentioned above, Pinto Villa is one good example of inter-gene pool crosses between race Durango and Andean germplasm (Miklas *et al.* 2006). Additional cycles of breeding calling for experience in breeding programmes will help refine inter-gene pool combinations and possibly result in more effective introgression of Mesoamerican genes into Andean germplasm, particularly for improving genetic adaptation to major abiotic stress factors such as drought or low phosphorus stress (Beebe *et al*. 2008).

5.6 Conclusions

The current study showed the robustness of microsatellites in defining the genetic structure of a reference collection of common bean. The level of polymorphism of markers, number of loci and extent of genome coverage by microsatellites is important in genetic diversity studies. An exciting result from this study was the detected relatedness between race Mesoamerica 1 and races Durango as well as Mesoamerica 2. Results of this study could serve as a guide for common bean breeders in selecting parents suitable for bean improvement programmes. In addition, based on the population structure identified by the microsatellite markers in this study, future work could look into association mapping for drought tolerance in the reference collection of common bean. The absence of admixtures in the Andean breeding lines and landraces indicated that less effort had been directed towards the improvement of Andean beans by breeding programmes but that the genepool as a whole can serve to find marker-trait associations. Finally, though few breeding lines were used in this study, indications are that landraces are more diverse than advanced breeding lines.

5.7 References

Abdurakhmonov IY, Abdukarimov A. 2008. Application of association mapping to understanding the genetic diversity of plant germplasm resources. International Journal of Plant Genomics. Article ID 574927:1-18.

Afanador L, Hadley S, Kelly JD. 1993. Adoption of a mini-prep DNA extraction method for RAPD marker analysis in common bean (*Phaseolus vulgaris* L.). Bean Improvement Cooperative 36:10-11.

Beebe SE, Rao IM, Cajiao C, Grajales M. 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. Crop Science 48:582-592.

Beebe S, Lynch J, Galwey N, Tohme J, Ochoa I. 1997a. A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica 95:325-336.

Beebe S, Skroch P, Tohme J, Duque MC, Pedraza F, Nienhuis J. 2000. Structure of genetic diversity among common bean landraces of Middle American origin based on correspondence analysis of RAPD. Crop Science 40:264-273.

Beebe S, Toro O, González A, Chacón M, Debouck DG. 1997b. Wild-weed-crop complexes of common bean (*Phaseolus vulgaris* L. Fabaceae) in the Andes of Peru and Colombia, and their implications for conservation and breeding. Genetic Resources and Crop Evolution 44:73-91.

Bitocchi E, Nanni L, Bellucci E, Rossi M, Giardini A, Spagnoletti Zeuli P, Logozzo G, Stougaard J, McClean P, Attene G, Papa R. 2012. Mesoamerican origin of the common bean (*Phaseolus vulgaris* L.) is revealed by sequence data. Proceedings of the National Academy of Sciences USA 109:24-33.

Blair MW, Díaz JM, Hidalgo R, Díaz LM, Duque MC. 2007. Microsatellite characterisation of Andean races of common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 116:29-43.

Blair MW, Díaz LM, Buendía HF, Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 119:955-972.

Blair MW, Giraldo MC, Buendía HF, Tovar E, Duque MC, Beebe S. 2006. Microsatellite marker diversity in common bean (*Phaseolus vulgaris* L). Theoretical and Applied Genetics 113:100-109.

Blair MW, Pedraza F, Buendia H, Gaitán-Solis E, Beebe S, Gepts P, Tohme J. 2003 Development of a genome-wide anchored microsatellite map for common bean (*Phaseolus vulgaris* L.) Theoretical and Applied Genetics 107:1362-1374.

Cabral PDS, Soares TCB, Lima ABP, de Miranda FD, Souza FB, Goncalves LSA. 2011. Genetic diversity in local and commercial dry bean (*Phaseolus vulgaris*) accessions based on microsatellite markers. Genetics and Molecular Research 10:140-149.

Chiorato AF, Carbonell SAM, Benchimol LL, Chiavegato MB, dos Santos Dias LA, Colombo CA. 2007. Genetic diversity in common bean accessions evaluated by means of morpho-agronomical and RAPD data. Scientia Agricola 64:256-262.

Debouck DG, Toro O, Paredes OM, Johnson WC, Gepts P. 1993. Genetic diversity and ecological distribution of *Phaseolus vulgaris* in northwestern South America. Economic Botany 47:408-423.

Díaz LM, Blair MW. 2006. Race structure within the Mesoamerican gene pool of common bean (*Phaseolus vulgaris* L.) as determined by microsatellite markers. Theoretical and Applied Genetics 114:143-154.

Evanno S, Regnaut S, Goudet J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611-2620.

Excoffier L. 2007. Arlequin ver 3.11. Computational and molecular population genetics lab CMPG. Zoological Institute, University of Berne. http://cmpg.unibe.ch/software/arlequin3/.

Excoffier L, Smouse PE, Quattro J. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. Genetics 131:479-491.

Geffroy V, Sicard D, de Oliveira J, Sévignac M, Cohen S, Gepts P, Neema C, Dron M. 1999. Identification of an ancestral resistance gene cluster involved in the co-evolution process between *Phaseolus vulgaris* and its fungal pathogen *Colletotrichum lindemuthianum*. Molecular Plant Microbe Interactions 12:774-784.

Gepts P. 2004. Crop domestication as a long-term selection experiment. In: Jannick J (Ed.) Plant Breeding Reviews. Long-term Selection: Crops, Animals and Bacteria, John Wiley and Sons, Inc. pp. 21-23.

Gepts P, Osborn T, Rashka K, Bliss F. 1986. Phaseolin-protein variability in wild forms and landraces of the common bean (*Phaseolus vulgaris* L.): Evidence for multiple centers of domestication. Economic Botany 40:451-468.

Hartl DL, Clark AG. 1997. Principles of population genetics. 3rd edition, Sunderland (MA): Sinauer Associates.

Idury RM, Cardon LR. 1997. A simple method of automated allele binning in microsatellite markers. Genome Research 11:1104-1109.

Jolliffe IT. 1986. Principal component analysis. New York: Springer. pp. 46-56.

Kelly DJ. 2004. Advances in common bean improvement: Some case histories with broader applications. Acta Horticulturae 637:99-122.

Laurentin H. 2008. Data analysis for molecular characterisation of plant genetic resources. Genetic Resources and Crop Evolution 8:58-71.

Liu K, Muse S. 2005. PowerMarker: integrated analysis environment for genetic marker data. Bioinformatics 21:2128-2129. http://www. PowerMarker.net.

Miklas PN, Kelly JD, Beebe SE, Blair MW. 2006. Common bean breeding for resistance against biotic and abiotic stresses: From classical to MAS breeding. Euphytica 147:105-131.

Perrier X, Flori A, Bonnot F. 2003. Data analysis methods. In: Genetic Diversity Of Cultivated Tropical Plants. Seguin B, Perrier X, Glaszmann JC (Eds.) Enfield Science Publishers, Montpellier. pp. 43-76.

Perseguini JMKC, Chioratto AF, Zucchi MI, Colombo CA, Carbonell SAM, Mondego JMC, Gazaffi R, Garcia AAF, de Campos T, de Souza AP, Rubiano LB. 2011. Genetic diversity in cultivated carioca common beans based on molecular marker analysis. Genetics and Molecular Biology 34:88-102.

Pritchard JK, Stephens M, Donnelly P. 2000. Influence of population structure using multilocus genotype data. Genetics 155:945-959.

Reeves PA, Richards CM. 2009. Accurate inference of subtle population structure (and other genetic discontinuities) using principal coordinates. PLoS ONE 4:4269-4270.

Rosenberg NA. 2002. DISTRUCT: a program for the graphical display of structure results. http://www.cmb.usc.edu/noahr/distruct.

SAS Institute. 1996. SAS/STAT Users guide 6.11. SAS Instutite, Cary.

Sauer JD. 1993. Historical geography of crop plants: A selected Roster. Boca Raton, USA, CRC Press.

Singh SP. 1995. Selection for water stress tolerance in interracial populations of common bean. Crop Science 35:118-124.

Singh SP. 1999. Integrated genetic improvement. In: Singh SP (Ed.) Common Bean Improvement in the Twenty First Century, Kluwer Dordrecht, The Netherlands. pp. 133-165.

Singh S, Gepts P, Debouck D. 1991a. Races of common bean (*Phaseolus vulgaris*, Fabaceae). Economic Botany 45:379-396.

Singh S, Gutierrez A, Molina A, Urrea C, Gepts P. 1991b. Genetic diversity in cultivated common bean. II. Marker-based analysis on morphological and agronomic traits. Crop Science 31:23-29.

Singh S, Nodari R, Gepts P. 1991c. Genetic mapping in cultivated common bean. I. Allozymes. Crop Science 31:19-23.

Sonnante G, Stockton T, Velásquez RO, Gepts P. 1994. Evolution of genetic diversity during the domestication of common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 89:629-635.

Wright S. 1951. The genetical structure of populations. Annals of Eugenics 15:323-354.

Yu J, Buckler ES. 2006. Genetic association mapping and genome organisation of maize. Current Opinion in Biotechnology 17:155-160.

Zizumbo-Villarreal D, Colunga-García Marin P, De la Cruz E, Payró Delgado-Valerio P, Gepts P. 2005. Landrace structure and evolutionary dynamics of wild-weedy domesticated complexes of common bean in a Mesoamerican region. Crop Science 45:1073-1083.

Chapter 6

Associations among SNPs and drought adaptive traits in a reference collection of common bean

6.1 Abstract

Searching for QTL for complex traits such as drought tolerance in natural populations is a valuable approach considering that landraces harbour sources of tolerance to both abiotic and biotic stresses. In the current study, SNPs were evaluated for genome wide association mapping due to their general availability. A total of 827 SNPs were evaluated using 186 Andean and Mesoamerican landraces by means of the Illumina GoldenGate Assay method. The SNP markers were validated in the Jalo 75 x BAT93 cross. The general linear model was used to estimate marker-trait associations for grain yield, days to flowering, days to maturity, number of pods per plant, total shoot biomass, 100-seed weight, leaf temperature and canopy temperature depression using TASSEL software. These phenotypic traits had significant correlations with grain yield under both irrigated and rainfed treatments in Chapter 3. The Q matrix to correct for population structure was generated from SSR analysis in a previous study. The association analysis yielded significant marker-trait associations for all traits studied. The level of significance for marker-trait associations varied from $P<0.01$ to $P<0.05$ in all traits studied. Days to flowering and 100-seed weight had more than 10 common markers under the rainfed treatments at CIAT-Palmira and Harare Research Station. Some SNP markers had significant associations with the phenotypic traits across the two treatments at both locations. Only three markers had significant associations with 100-seed weight and total shoot biomass across locations and treatments. Specifically, TOG896943-500 (linkage group 02) and TOG918200-347 (linkage group 05) had significant associations with 100-seed weight across locations and treatments. Meanwhile, TOG910860-634 (linkage group 06) was significantly associated with total shoot biomass at both locations across the irrigated and rainfed treatment. In conclusion, candidate gene analysis could be implemented in a reference collection of common bean using identified markers that overlap between treatments and locations.

6.2 Introduction

Drought tops the list of abiotic stresses that limit crop production and productivity in semi-arid and arid regions of the world. A number of agronomic practises ranging from water conservation, improved irrigation systems and improved soil fertility management are promoted to raise agricultural productivity in semi-arid regions. However, without drought adaptable crop varieties farmers in these regions often face food insecurity. Searching for genes and QTL that minimise the negative impacts of drought is one way of improving crop adaptation to drought stress. The importance of landraces as sources of genes for both biotic and abiotic stresses cannot be overemphasised. In some crops, genes and QTL have been tapped from wild relatives and landraces through genetic studies (Pswarayi *et al.* 2008).

Advances in science and statistical analysis have opened many avenues for genetic studies in plants. Linkage and association mapping as well as candidate gene analysis are the three most used approaches currently in genetic studies (Myles *et al.* 2009). Linkage mapping has been the traditional method and usually utilises two parents which show diversity for a single trait and are crossed to initiate a mapping population. Meanwhile, association mapping (AM) involves searching for marker-trait correlations in a diverse natural population. Therefore, AM can capture more variation than present in QTL mapping populations which only have two, or a few parents. The genetic resolution can furthermore be higher, sometimes down to gene level. More markers are necessary though, and usually bigger populations and extensive phenotyping are a requirement (Bradbury *et al.* 2007).

The genetic marker density per genome is an important consideration in association mapping to unmask functional alleles likely in LD with at least one of the genotyped markers. SNPs are the genetic marker of choice for association studies as they occur in abundance as differences of individual nucleotides between individuals. Their identification is done in a small set of samples and eventually applied to a larger set of samples (Myles *et al.* 2009). A total of five different methods have been used to detect SNPs in common bean. The cleaved amplified polymorphic sequences (CAPS) and derived cleaved amplified polymorphic sequences (dCAPS) are two popular techniques that have been used to convert expressed sequence tags (ESTs) based polymorphisms into SNPs (Hougaard *et al.* 2008). Gaitán-Solís *et al.* (2008) used the Luminex-

100 (http://www.luminexcorp.com) method to detect and validate SNPs in ten common bean genotypes (Galeano *et al.* 2009a). The CEL 1 mismatch digestion technique was used to analyse and map SNP-based, EST derived markers in common bean. In other studies, the single strand conformation polymorphism (SSCP) technology was employed to develop and map EST based SNP markers which led to the identification of 118 new marker loci in DOR364 x G19833 mapping population (Galeano *et al.* 2009b). Recently, an attempt was made to validate the predicted SNPs from the technologies mentioned above using 1 050-plex GoldenGate assay from Illumina (http://www.illumina.com). A total of 827 SNPs produced a working GoldenGate assay (Hyten *et al.* 2010) and were evaluated on the reference collection of common bean. The power to detect an association is a function of allele frequency where signals for functional variants at low frequency are difficult to detect due to low statistical significance

Due to the use of unstructurally related individuals in AM, it is important to consider the population structure (Q) among individuals in a population because false associations may be detected due to confounding effects of population admixture (Oraguzie *et al.* 2007). Genotypes constituting the reference collection were drawn from large collections, released varieties and breeding materials hence have a strong population structure. The knowledge of population structure (Q) of individuals in the population is a prerequisite in the general linear model (GLM) for association analysis. In the GLM, the Q matrix is integrated as covariate to correct for the effects of population substructure using the TASSEL software programme.

The objective of this study was to:

- Identify statistically significant genetic associations between a change in the DNA sequence and a change in traits associated with drought tolerance in a reference collection of common bean.

6.3 Materials and methods

6.3.1 Plant materials

Of the 202 genotypes constituting the reference collection, SNP evaluation was successful in 186 genotypes and were distributed as follows; 71 Andean genotypes (Table 3.3; Chapter 3) excluding G13094, G22247, G17168, G23829, G11512, G5849, PVA773, G4739, SAB258 and SAB645 and115 Mesoamerican genotypes (Table 3.4; Chapter 3) excluding Maharagi soya, G3331, G22787, G15416, G4495 and G1264. The excluded genotypes produced no results from the SNP evaluation process. Phenotypic data under the irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station was collected as described in sections 3.3.4.2.1, 3.3.4.2.2 and 3.3.4.3 of Chapter 3.

6.3.2 Genomic DNA extraction

Total genomic DNA was extracted as described in section 5.2.2. A total of 2 µl DNA of each genotype was sent to the University of California, Davies, USA where 827 SNPs were evaluated on each genotype using the Illumina GoldenGate R Assay procedure. SNPs for the common bean markers were discovered by Sanger resequencing and alignment comparisons of a total of 1,440 tentative orthologous gene (TOG) amplicons from Andean genotype (Jalo EEP558) and Mesoamerican genotype (BAT93) (Blair *et al.* 2013). The TOG markers were developed as part of a cross legume marker project using amplicons of BAT93 and Jalo EEP558. Polymorphisms were identified by sequence alignment of the two genotypes sequences. The target sequences were a set of primary single copy orthologous genes, whose orthology was inferred initially from legume EST data (transcriptomes of *Medicago truncatula*, *Lotus japonicus* and *Glycine max*) and subsequently based on conserved genome location in a multi-species comparative genetic analysis (Blair *et al.* 2013). The SNPs were selected based on the default design criteria found in software programme Assay Design Tool from Illumina and were converted to the 827 Illumina GoldenGate genotyping assay useful for common bean (Blair *et al* 2013). The TOG markers are individual gene based markers that were based on conserved legume sequences and therefore had a slightly lower average PIC values (Hyten *et al.* 2012). SNPs were distributed per each chromosome as follows b01 (79), b02 (92), b03 (77), b04 (22), b05 (40), b06 (78), b07 (85), b08 (84), b09 (76), b10 (27) and b11 (61). A total of 7 SNPs were unassigned.

6.3.3 SNP evaluation

A total of 827 SNPs which were predicted in Gaitán-Solís *et al.* (2008), Hougaard *et al.* (2008), Galeano *et al.* (2009a; b) and validated using 1 050-plex GoldenGate assay from Illumina (http://www.illumina.com) were evaluated on the reference collection of common bean. The GoldenGate assay procedure involved three steps namely sample preparation, cluster generation and sequencing.

6.3.3.1 Sample preparation

The TruSeq sample preparation kit was used to generate high quality libraries with insert sizes from 300-500 bp from the genomic DNA of the 202 genotypes. The sampling kit used was for high throughput studies and involved 96 dual indices adapters that were pre-loaded in a 96-well plate. The indices were added to sample genomic DNA using a free PCR procedure. The developed libraries were amenable to single-read, paired-end and multiplexed sequencing on all Illumina sequencing instruments. A total of 1 µg DNA was sheared by sonication. Library construction began with fragmented genomic DNA. The blunt-end DNA fragments were generated using a combination of fill-in reactions and exonuclease activity. An 'A'-base was then added to the blunt ends of each strand preparing them for ligation to the sequencing adapters. Each adapter contained a 'T'-base overhang at the 3′ end, providing a complementary overhang for ligating the adapter to the A-tailed fragmented DNA. Denaturation and amplification steps followed and the created libraries were pooled for sequencing.

6.3.3.2 Cluster generation

Cluster generation created hundreds of millions of clusters, each of which contained approximately 1 000 identical copies of a single template molecule. The cluster generation process was carried out in cBot, where the cDNA fragments that had been captured by complementary adapter oligonucleotides covalently bound to the surface of Illumina flow cells were amplified isothermally. Flow cells facilitate access of bound DNA to enzymes while ensuring high stability of surface-bound template and low non-specific binding of fluorescently labelled nucleotides. Attached DNA fragments were extended and bridge amplified to create hundreds of millions of clusters.

6.3.3.3 Sequencing

Illumina's BeadXpress Reader was used to analyse the bioassay using the VeraCode technology. The BeadXpress Reader drew up to eight samples at a time from the 96-well plate and loaded them onto the eight chambered transparent groove plate that formed the bottom of the systems fluidic cell. Through a unique combination of fluid flow, gravity and capillary force, the VeraCode microbead efficiently populated the groove plate and aligned closely within the grooves. Once the beads were aligned, the entire fluidic cell was actuated across the optical system and scanned for fluorescent intensity and code classification. During scanning, the BeadXpress Reader acquired fluorescence data and associated code data for each microbead, compiled a virtual representation of the 96-well plate and exported the data for downstream analysis with Illumina's VeraScan software. The BeadXpress Reader employed a dual colour laser detection system which identified the unique holographic code embedded in each VeraCode microbead and detected the signal intensity associated with each bead.

6.3.4 Data analysis

Data analysis was done in TASSEL software (www.maizegenetics.net/tassel). Data analysis involved loading and joining genotypic data, genetic map, Q matrix and phenotypic data in the software following procedures from the TASSEL user's guide (www.maizegenetics.net/tassel). Data for the genetic map (cM) were multiplied by 100 inorder to for it to resemble a physical map since the TASSEL programme does not understand the genetic map information (Appendix 22). Genotypic data was generated from the Illumina GoldenGate Assay and the genetic map was provided by the CIAT genetics laboratory. In association mapping there is need to account for false positives. Incorporating the outcome of population structure increases the power to detect true marker trait associations. The Q matrices were derived from STRUCTURE (Pritchard *et al.* 2000) using the 86 microsatellites in Chapter 5, section 5.3.4.4 and were entered into the TASSEL programme as covariates.

Phenotypic data were analysed in Agrobase Generation II software (Agronomix Software Inc. 2005) and entry means were calculated for each genotype under irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station (section 3.3.4.7; Chapter 3). Grain yield, total shoot biomass, 100-seed weight, number of pods per plant, days to maturity, days to flowering,

leaf temperature and canopy temperature depression were the phenotypic traits loaded into TASSEL software. These traits, excluding days to flowering, had significant correlations with grain yield under irrigated and rainfed conditions (Chapter 3). Q matrix was run for K upto 10 STRUCTURE simulations on the entire set of the reference collection (section 5.3.4.4; Chapter 5). The likelihood value of the STRUCTURE analysis showed that the most significant change was observed at K=2 which corresponded with the origin and breeding history of the populations, divided into Andean and Mesoamerican. This was considered the best possible partition as they showed a high consistency with the genotypes of a known gene pool origin. Population structure can lead to identification of loci that generate statistically significant but biologically invalid associations solely due to their tight correlation with population structure. Factors such as adaptation and domestication give rise to population structure in a population and were true for the reference collection of common bean.

Genotype data was filtered to remove monomorphic sites and SNP(s) with minor effects (www.maizegenetics.net/tassel). To overcome problems posed by population structure in AM studies, linear models with fixed effects for subpopulations have been used (Stich *et al.* 2008). The GLM was used to estimate the p-values, marker R^2 and estimated change in phenotype due to a SNP change from the filtered set of 700 polymorphisms. Marker R^2 measures the contribution of the marker to total sum of squares of a trait after accounting for all other effects in the model. Marker R^2 is more practical since it measures the contribution of loci where the marker resides to the total variation of the trait. The GLM performs association analysis using a least squares fixed effects linear model to test for marker-trait correlations. In the current study, the structured association analysis (Q method) implemented in TASSEL as GLM function was used to estimate marker-trait associations. The structured association controls false associations. Each trait by marker combination was tested following the model: Trait = Q + marker effect + residual.

The Bonferroni correction was also used to control Type I error rate. Type I error is a false positive, where significant associations are identified but are linked to population structure rather than the studied trait. Tests for significance were derived from permutations that generate p-values. The p-values are not dependent on the normal distribution of data. The p-values were

calculated from a two-sided Fisher's exact test. Marker R^2 was calculated as sum of squares of markers divided by total sum of squares.

6.4 Results

Of the 827 SNPs used in the assay, 768 SNPs were successful called in the 186 genotypes with less than 8% missing data points. A total of 700 and 68 SNPs were polymorphic and monomorphic in all genotypes respectively. The SNP markers provided coverage for every chromosome in the genome from 22 SNPs on linkage group b04 to 88 markers on linkage group b02 (Table 6.1). Variation for the minor allelic frequency (MAF) of the 700 SNPs ranged from 2 to 75. Of the 700 polymorphic SNPs, 620 had a MAF larger than 0.20.

Table 6.1 Summary of SNPs evaluated among the 202 reference collection genotypes

Linkage group	Number of SNPs	Allelic frequency	
		≤0.2	**>0.2**
b01	77	6	71
b02	88	14	74
b03	76	6	70
b04	22	2	20
b05	38	5	33
b06	77	9	68
b07	83	8	75
b08	79	17	62
b09	75	6	69
b10	25	3	22
b11	60	4	56
Total	700	80	620

6.4.1 Association mapping

The association analysis performed in this study identified significant marker-trait associations under irrigated and rainfed treatments for all traits evaluated at both locations. Some significant marker-trait associations were common between irrigated and rainfed treatments at each location and at times between locations for the rainfed treatment. The focus for the current study was to discover markers with potential value for use in MAS selection for drought tolerance in common bean.

6.4.1.1 Grain yield

A total of 15 and 76 markers were significantly associated with grain yield under irrigated and rainfed treatments at CIAT-Palmira respectively (Appendix 8). For these significant marker-grain yield associations, the significance levels ranged between 0.0011 (TOG895672-181 on linkage group 02) and 0.0048 (TOG901215-645 on linkage group 01) under the irrigated treatment while it varied from 0.0013 (on four SNPs located on linkage groups 03, 04, 05 and 10) to 0.0492 (TOG914901-92 on linkage group b11) under the rainfed treatment. Each linkage group had at least one marker significantly associated with grain yield under the rainfed treatment at CIAT-Palmira. A total of 10 markers (coloured red) were found to be significantly correlated with grain yield under both treatments at CIAT-Palmira.

At Harare Research Station, a total of 30 and 33 significant marker-grain yield associations were identified under rainfed and irrigated treatments respectively (Appendix 9). Linkage group 10 had no significant marker locus associated with grain yield under both treatments. Variation for significance levels ranged from 0.0032 (TOG896888-794 on linkage group b11) to 0.0483 (TOG906599-51 on linkage group b11) under the irrigated treatment and 0.0012 (TOG900006-352 on linkage group b07) to 0.047 (TOG901933-203 on linkage group b09) under the rainfed treatment. At Harare Research Station, four markers (coloured red) were significantly correlated with grain yield under both treatments.

A total of six significant marker-grain yield associations were common at both CIAT-Palmira and Harare Research Station under rainfed treatments (Table 6.2). These were located on linkage groups b03 (2), b05 (1), b07 (2) and b09 (1).

All SNP marker loci carried two genotypes (TT and AA). A minimum of 31% (TOG907013_1059) and maximum of 47% (TOG905371_69) of the 186 genotypes evaluated in the current study carried the TT genotype. The number of genotypes carrying the AA allele ranged between 47% (TOG905371_69) and 62% (TOG907013_1059). Markers TOG905371_69 and TOG905371_417, both on linkage group b03, were close to each other.

The largest differences in grain yield between the two alleles were observed for markers TOG898046_230 and TOG894794_142 at both locations. The allele TT was desirable for high yield under the rainfed environments. The GLM allele estimates provide effect estimates for each genotypic class (homozygous or heterozygous) for the markers associated with the trait. At CIAT-Palmira, a change in allele state from AA to TT caused a yield increase of 522.61 kg ha^{-1} and 442.20 kg ha^{-1} for TOG898046_230 and TOG894794_142 respectively. Grain yield differences were 160.48 kg ha^{-1} (TOG898046_230) and 150.55 kg ha^{-1} (TOG894794_142) for the change from the AA allele state to the TT state at Harare Research Station.

Table 6.2 Common associations between markers and grain yield obtained under rainfed treatments at CIAT-Palmira and Harare Research Station

		p values		marker_R2					Allele estimate	
Marker	linkage group	CIAT-Palmira	Harare	CIAT-Palmira	Harare	No. of observations	Marker position	Allele	CIAT-Palmira	Harare
TOG905371_69	3	0.0204	0.0271	0.0245	0.0264	87 87	1394442	TT AA	287.5940	104.9300
TOG905371_417	3	0.0219	0.0253	0.0247	0.0277	83 87	1394441	TT AA	301.3810	112.5440
TOG907013_1059	5	0.0424	0.0352	0.0193	0.0244	57 115	712783	TT AA	327.3020	125.1050
TOG898046_230	7	0.0024	0.0149	0.0420	0.0318	61 113	1207863	TT AA	522.6100	160.4760
TOG894794_142	7	0.0059	0.0109	0.0345	0.0352	60 114	351114	TT AA	442.2000	150.5540
TOG913042_381	9	0.0284	0.0211	0.0214	0.0283	68 107	169302	TT AA	245.6950	58.7940

6.4.1.2 Hundred seed weight

At CIAT-Palmira, 85 and 169 markers were significantly associated with 100-seed weight under irrigated and rainfed treatments, respectively (Appendix 10). Of these markers with 100 seed weight associations, 68 (coloured red) were common between the two treatments. Significance levels on the marker with 100-seed weight associations varied between 0.0000 and 0.0499 under the irrigated treatment and 0.0000 to 0.0494 under the rainfed treatment at CIAT-Palmira.

A total of 86 and 172 markers were significantly correlated with 100-seed weight under rainfed and irrigated treatments at Harare Research Station respectively (Appendix 11). Of these markers with 100-seed weight associations, 24 (coloured red) were common between the two treatments. At Harare Research Station, significance levels for marker with 100-seed weight correlations

varied between 0.0000 and 0.0493 under the irrigated treatment. On the other hand, variation for significance levels was in the region of 0.0000 to 0.0475 under the rainfed treatment at Harare Research Station. A total of 18 markers with 100-seed weight associations were common under rainfed treatments between CIAT-Palmira and Harare Research Station (Table 6.3).

Individual genotypes carrying the AA allele at locus positions 658347 (TOG908646_276), 658347 (TOG903088_74) and 16514 (TOG9000784_136) had higher 100-seed weights than those carrying the TT allele at both locations. Genotypes that carried the AA allele at these loci positions represented less than 24% of the whole population evaluated. A change in allele state (AA to TT) at loci positions 1904825 (TOG918275_1006) and 1904826 (TOG923111_969), both on linkage group b03, caused an increase in 100-seed weight at CIAT-Palmira (by almost 8.00 g) and Harare Research Station (by almost 2.00 g). Some of the significant markers on the same linkage groups were relatively close to each other and these included TOG 894060_416 and TOG907046_267 (b10), TOG896306_360 and TOG900450_243 (b06), TOG906318_220 and TOG894052_203 (b06), TOG918275_1006 and TOG923111_969 (b03) as well as TOG908646_276 and TOG903088_74 (b09).

Table 6.3 Common associations between markers and 100-seed weight obtained under rainfed treatments at CIAT-Palmira and Harare Research Station

		p-values		Marker R^2					Allelic estimate	
Marker	linkage group	CIAT-Palmira	Harare	CIAT-Palmira	Harare	No. of observations	Marker position	Allele	CIAT-Palmira	Harare
TOG928916_162	2	0.0023	0.0246	0.0377	0.0072	96 76	254832	TT AA	5.8793	1.3880
TOG896943_500	2	0.0043	0.0023	0.0325	0.013	70 102	1427030	TT AA	1.6764	0.7879
TOG896943_422	2	0.0413	0.0273	0.0311	0.0145	76 38	1491556	TT AA	7.4547	2.3508
TOG918275_1006	3	0.0012	0.0241	0.0444	0.0058	77 70	1904825	TT AA	8.0150	1.6432
TOG923111_969	3	0.0012	0.0241	0.0444	0.0058	77 70	1904826	TT AA	8.0150	1.6432
TOG896074_553	6	0.0045	0.0294	0.0339	0.0071	109 59	298879	TT AA	4.7606	1.1727
TOG896306_360	6	0.0072	0.0014	0.0300	0.0145	84 86	1376101	TT AA	5.5453	2.0717
TOG900450_243	6	0.0072	0.0014	0.0300	0.0145	84 86	1376105	TT AA	4.7204	0.9751
TOG906318_220	6	0.0212	0.0102	0.0217	0.0093	80 93	1134317	TT AA	4.7204	1.6714
TOG894052_203	6	0.0251	0.0098	0.0204	0.0097	79 94	1134315	TT AA	4.7400	1.7512
TOG896197_226	9	0.0019	0.0191	0.0399	0.0083	106 62	626582	TT AA	5.0569	1.2306
TOG908646_276	9	0.0042	0.0093	0.0333	0.0097	131 43	658347	TT AA	-5.2868	-1.5247
TOG895760_820	9	0.0046	0.0337	0.0366	0.0062	85 68	930447	TT AA	6.7087	1.5082
TOG903088_74	9	0.0081	0.0089	0.0284	0.0096	133 42	658346	TT AA	-5.0167	-1.5731
TOG894060_416	10	0.0062	0.0205	0.0302	0.0077	97 72	774886	TT AA	6.7087	1.2995
TOG900784_136	10	0.0085	0.0475	0.0291	0.0057	155 15	16514	TT AA	-5.9678	-1.4194
TOG907046_267	10	0.0182	0.0357	0.0233	0.0063	99 67	774887	TT AA	4.1493	1.1695
TOG917669_433	11	0.0165	0.0011	0.0232	0.0147	84 91	898224	TT AA	4.4407	1.9099

6.4.1.3 Days to flowering

A total of 59 and 108 significant marker with days to flowering associations were identified under irrigated and rainfed treatments at CIAT-Palmira respectively (Appendix 12). Of these markers with trait associations, 42 maker loci (coloured red) were correlated with days to flowering under both treatments at CIAT-Palmira.

At Harare Research Station, 60 and 55 significant associations were identified for this trait under irrigated and rainfed treatments respectively (Appendix 13). Of these markers, 34 were significantly associated with days to flowering under both treatments at Harare Research Station. Significance levels for marker with days to flowering associations varied between 0.0011 (TOG895245_245 on linkage group b08) and 0.0491 (TOG898284_346 on linkage group b08) under the irrigated treatment at CIAT-Palmira. On the other hand, significance levels varied from 0.0014 (TOG919227_1306 on linkage group b08) to 0.0493 (TOG895900_416 on linkage group b09) under irrigated conditions at Harare Research Station.

Variation for significance levels on marker with days to flowering associations ranged from 0.0012 to 0.0494 and 0.0012 to 0.0499 under the rainfed treatments at CIAT-Palmira and Harare Research Station respectively. A total of 12 markers were identified that were significantly correlated with days to flowering under rainfed treatments at both locations (Table 6.4). Individuals that carried the TT allele at marker loci TOG894818_243, TOG899382_247, TOG911121_130, TOG895163_666 and TOG900006_352 flowered earlier than individuals that carried the AA allele under rainfed conditions at both locations. Early flowering is a good trait in environments prone to terminal drought stress.

Table 6.4 Common associations between markers and days to flowering obtained under rainfed treatments at CIAT-Palmira and Harare Research Station

		p values		Marker R^2					Allelic estimate	
Marker	linkage group	Harare	CIAT-Palmira	Harare	CIA-Palmira	No. of observations	Marker position	Allele	Harare	CIAT-Palmira
TOG894818_243	1	0.0437	0.0032	0.0231	0.0482	146 16	1178516	TT AA	-1.9500	-3.5560
TOG899382_247	2	0.0040	0.0062	0.0436	0.3920	115 59	1280152	TT AA	-2.0474	-2.4518
TOG896361_260	2	0.0130	0.0353	0.0331	0.0236	93 80	348596	TT AA	1.8387	1.9613
TOG906764_376	2	0.0294	0.0063	0.0269	0.0417	106 60	80	AA TT	1.4903	2.3188
TOG906764_834	2	0.0294	0.0063	0.0269	0.0417	106 60	81	AA TT	1.4903	2.3188
TOG894196_495	3	0.0180	0.0361	0.0305	0.0238	101 70	1363672	TT AA	-2.5164	-2.8040
TOG911121_130	3	0.0230	0.0013	0.0278	0.0539	35 138	332824	TT AA	-2.0375	-3.5867
TOG895163_666	3	0.0346	0.0071	0.0237	0.0378	93 82	1456965	TT AA	-1.9109	-3.0442
TOG900268_798	6	0.0019	0.0081	0.0515	0.0371	85 88	1570761	TT AA	2.6222	2.8132
TOG900006_352	7	0.0074	0.0017	0.0376	0.0511	86 90	1176102	TT AA	-2.2334	-3.2600
TOG899729_237	8	0.0041	0.0067	0.0450	0.0400	100 69	2428698	TT AA	2.2073	2.6376
TOG894141_219	8	0.0413	0.0154	0.0230	0.0307	61 105	2292273	TT AA	3.0179	4.6195

6.4.1.4 Days to maturity

At CIAT-Palmira, a total of 28 markers under each treatment were significantly associated with days to maturity (Appendix 14). Of these, 12 markers (coloured red) were significantly correlated with days to maturity under both treatments. On the other hand, 28 and 70 markers associated with days to maturity were identified at Harare Research Station under irrigated and rainfed treatments respectively (Appendix 15). A total of 13 markers (coloured red) were commonly associated with days to maturity under both treatments at Harare Research Station. In addition, six markers were significantly correlated with days to maturity under rainfed treatments at both Harare Research Station and CIAT-Palmira (Table 6.5).

Table 6.5 Common associations between markers and days to maturity obtained under rainfed treatments at CIAT-Palmira and Harare Research Station

		p value		Marker R^2					Allelic estimate	
Marker	linkage group	CIAT-Palmira	Harare	CIAT-Palmira	Harare	No. of observations	Marker position	Allele	CIAT-Palmira	Harare
TOG894818_489	1	0.0095	0.0192	0.0451	0.0375	124 18	1178517	TT AA	-6.5896	-5.7051
TOG906969_104	2	0.0100	0.0472	0.0361	0.022	53 123	2212891	TT AA	5.99	4.5406
TOG906764_376	2	0.0122	0.0223	0.0368	0.0312	106 60	80	AA TT	4.2263	3.7488
TOG906764_834	2	0.0122	0.0223	0.0368	0.0312	106 60	81	AA TT	4.2263	3.7488
TOG897188_682	6	0.0013	0.0242	0.0563	0.0283	23 152	1674765	TT AA	7.5001	5.198
TOG901700_397	6	0.0412	0.0157	0.0243	0.035	102 55	1054653	TT AA	3.3199	4.3481

Early maturity is a desirable trait under terminal drought conditions in common bean. A change in allele state from AA to TT at marker locus TOG894818_489 caused a decrease in number of days taken to reach maturity at both locations. Days to maturity were reduced by 6.59 and 5.71 days at CIAT-Palmira and Harare Research Station respectively by this change in allele state. Some markers on linkage group b02 (TOG907664_376 and TOG906764_834) were relatively close to each other and possibly could be on one locus.

6.4.1.5 Total shoot biomass

A total of 48 and 87 markers were significantly associated with total shoot biomass under irrigated and rainfed treatments at CIAT-Palmira respectively (Appendix 16).

On the other hand, 62 and 86 markers were significantly correlated with this trait under irrigated and rainfed treatments at Harare Research Station (Appendix 17). At CIAT-Palmira, 14 marker-trait associations were common under both treatments while at Harare Research Station, 26 common marker-with-trait associations were identified. A total of 14 significant markers with traits associations were common under rainfed treatments at both CIAT-Palmira and Harare Research Station (Table 6.6).

Table 6.6 Common associations between markers and total shoot biomass obtained under rainfed treatments at CIAT-Palmira and Harare Research Station

		p value		Marker R^2					Allelic estimate	
Marker	linkage group	Harare	CIAT-Palmira	Harare	CIAT-Palmira	No. of observations	Marker position	Allele	CIAT-Palmira	Harare
TOG897362_457	6	0.0028	0.0076	0.0242	0.0338	164 11	1643502	TT AA	-2.2655	-4.1766
TOG897362_571	6	0.0030	0.0076	0.0240	0.0341	163 11	1643503	TT AA	-2.274	-4.1627
TOG895575_317	11	0.0049	0.0371	0.0217	0.0207	66 108	393328	AA TT	-1.2109	-2.7368
TOG914633_385	7	0.0059	0.0201	0.0347	0.0352	58 71	1923876	AA TT	1.1674	2.2584
TOG900222_165	11	0.0102	0.0371	0.0191	0.0207	99 70	551159	TT AA	1.4572	2.3213
TOG906530_971	8	0.0165	0.0144	0.0144	0.0298	100 68	1549852	TT AA	-1.3915	-1.9448
TOG908034_427	11	0.0203	0.0082	0.0150	0.0337	78 96	425114	AA TT	-1.5812	-2.3282
TOG925468_198	3	0.0299	0.0252	0.0132	0.0247	73 100	1615017	TT AA	-2.091	-3.3903
TOG894712_405	3	0.0327	0.0080	0.0125	0.0336	111 64	77215	TT AA	1.9472	2.6
TOG895163_666	3	0.0340	0.0014	0.0125	0.0488	93 82	1456965	TT AA	2.0827	2.3044
TOG910860_172	6	0.0343	0.0108	0.0125	0.0311	118 55	1166079	TT AA	-1.3644	-1.8864
TOG910860_634	6	0.0404	0.0094	0.0117	0.0325	117 55	1103074	TT AA	-1.3972	-1.8349
TOG900594_110	2	0.0460	0.0034	0.0103	0.0422	86 84	286573	TT AA	-1.9136	-1.8965
TOG895760_342	9	0.0482	0.0324	0.0109	0.0224	82 92	930446	TT AA	1.5408	2.3729

6.4.1.6 Number of pods per plant

The association analysis identified 48 and 62 significant marker with number of pods per plant associations under irrigated and rainfed treatments at CIAT-Palmira respectively (Appendix 18). At Harare Research Station 39 and 16 markers were significantly associated with this trait under irrigated and rainfed treatments respectively (Appendix 19). A total of 23 and eight markers with number of pods per plant correlations (coloured red) were common under both treatments at CIAT-Palmira and Harare Research Station respectively.

6.4.1.7 Canopy temperature depression

A total of 38 and 67 markers were significantly correlated with canopy temperature depression under rainfed and irrigated treatments at CIAT-Palmira respectively (Appendix 20). Of these significant marker with canopy temperature depression associations, four were common (coloured red) under both treatments. This trait was unstable between treatments at CIAT-Palmira.

6.4.1.8 Leaf temperature

At CIAT-Palmira, 12 and 18 markers were significantly correlated with leaf temperature under irrigated and rainfed treatments respectively (Appendix 21). There was no marker with trait overlaps between treatments for leaf temperature. There were no good markers for leaf temperature between treatments.

6.5 Discussion

The AM analysis carried out in the current study was the first in a reference collection of common bean to search for SNP markers correlated with different traits under drought stress conditions. The number of days to maturity, 100-seed weight, number of pods per plant and total shoot biomass were found to have significantly high correlations with grain yield under semi-arid environments (Téran and Singh 2002; Szilagyi 2003). Results from this study showed that genome wide association analysis identified markers which were significantly correlated with these individual traits constituting drought tolerance in common bean. It was an important achievement to identify some significant marker-trait associations for grain yield and these other traits responsible for high yield under semi-arid environments. The most reported results from AM so far have targeted candidate genes with known mutant phenotypes. AM has been found useful in identifying SNP markers that were associated with CBB resistance and were recommended to replace BC420 and SU91 markers that were previously used in MAS for CBB resistance (Shi *et al.* 2011).

The 45 common significant associations identified under rainfed treatments at both CIAT-Palmira and Harare Research Station could provide a list of candidate genes for further investigations. All the significant marker-trait associations accounted for relatively small

proportions of the phenotypic variance. The marker_R^2 values in the current study were similar or slightly lower than those calculated for marker-trait associations in Shi *et al.* (2011) for CBB candidate genes and Weber *et al.* (2008) for complex traits in teosinte. There are some possible reasons which might give an explanation for these small values. If the marker assayed is not the causative site but in LD with the causative site, the marker_ R^2 value will be an underestimate of the actual effect (Nielsen and Weir 1999). Secondly, most of the traits evaluated had low to moderate heritabilities such that the treatment variance had also a significant influence on the expression of the traits. Heat stress (CIAT-Palmira) and disease pressure (Harare Research Station) contributed to the phenotypic variance of both Andean and Mesoamerican genotypes. It is also possible that these associations were actually due to alleles of small effects. Marker_ R^2 could also be low in the current study possibly due to the complex nature of the studied traits. Lastly, the Bonferroni correction is conservative and has been reported to lead to power loss for detection if traits are correlated with one another. In the current study, most traits were correlated to each other and had high correlations with grain yield as discussed in Chapter 3.

Some markers were significantly associated with traits of interest between treatments at each location and across rainfed treatments at both locations. However, markers common between treatments and across rainfed treatments between locations were less than 40 for each trait. Rong *et al.* (2007) reported a few or non-overlapping sets of markers in different environments. There are several reasons why so few marker-trait associations were repeated between rainfed treatments at both locations. First, phenotyping was performed by different individuals at the different locations possibly leading to subtle differences in timing of measuring traits. Secondly, treatments used for phenotyping in the current study were significantly different from each other as identified from the correlation analysis for environments in Chapter 3. Differences in treatments caused large contributions to phenotypic variation among genotypes. In addition, landraces by nature are heterogeneous and it is possible that not exactly the same plants were evaluated across locations. All of these factors could have contributed to true positive associations not being detected in one environment or the other.

Overlaps in marker-trait associations over different drought environments are useful for marker-assisted breeding. The identified marker-trait associations in the current study could provide a

base for MAS of parents and segregating populations earmarked for the semi-arid environments. In terms of breeding for drought stressed environments, BAT477, SER22, SER16, SEA5, SEA15, SEQ1003, SEQ1027, CAL96 and CAL143 were parents in many breeding experiments. A quick confirmation on the value of the identified markers could be performed in RIL populations developed from the CAL96 x SEA5 cross or any advanced lines developed from these parents, for example the drought tolerant Andean bean lines (DAB). The RIL populations and advanced DAB lines have already been phenotyped under different drought conditions in Malawi, Rwanda, Ethiopia and Zimbabwe for a number of seasons. Phenotypic traits evaluated in these RIL populations and advanced DAB lines were similar to those in the current study.

Linkage group b02 has been previously reported to contain QTL for days to maturity, 100-seed weight and number of pods per plant in common bean (Chavarro and Blair 2010; Pérez-Vega *et al.* 2010; Blair *et al.* 2012). In addition, 100-seed weight was also found to be linked to linkage groups b03 and b11 in a wild x cultivated backcross and RIL populations by Blair *et al.* (2006). In the current study, there were some SNP markers which had significant associations with these traits on linkage groups b02, b03 and b11 which supported these findings and alluded to the importance of these linkage groups to the associated traits.

It is estimated that a total of three to four million SNPs exist in cultivated common bean based on the rate of 237 SNPs observed in 38.2 kbp of sequence in six diverse genotypes (Shi *et al.* 2011). Compared to the estimated number of SNPs existing in common bean, the number of SNPs used in the current study was extremely few and might not have favoured low frequency mutations and those with weak effects. In addition, the numbers of captured marker-trait associations were few for a genome wide scan due the small number of markers deployed. There were some huge gaps between some markers on each linkage group suggesting there is potential to increase the number of SNP markers in future genotyping exercises in a reference collection of common bean. The importance of marker density was demonstrated by Aranzana *et al.* (2005) in *Arabidopsis thaliana*. Aranzana *et al.* (2005) used too many markers around four loci and were removing some markers and checked the disappearance of the signal. They concluded that 6 000 SNP markers were sufficient for AM in *A. thaliana*. Genome wide AM should therefore have thousands of SNP markers for detection of all marker-trait associations.

SNPs evaluated in the current study were not discovered from within genepool crosses and might have missed some polymorphisms in the Mesoamerican genotypes and *vice versa*. Blair *et al.* (2009) noted that markers developed from an Andean background were more polymorphic in Andean genotypes than Mesoamerican ones.

Correction of population structure was achieved through the use of the Q matrices generated from a previous diversity study (Chapter 5). Correction of population structure reduced type I and II errors between molecular markers and traits of interest (Zhu *et al.* 2008). Already, common bean is a strongly structured species due to the domestication events which led to the evolution of two main gene pools, Andean and Mesoamerican. In addition, due to differences in production environments, further subdivisions were noted in each gene pool (Bitocchi *et al.* 2012).

6.6 Conclusions

The current study serves as an initial effort for genome wide AM for drought tolerance in common bean. The genotypes evaluated in the current study retained 60% of the genetic diversity of the core collection of common bean and was suitable for phenotyping for drought tolerance. Increased crop productivity under stressed environments relies on mining of the best alleles from diverse germplasm and incorporated in elite breeding material. Traditionally, genetic markers had been used for trait improvement through many breeding approaches such as MAS, marker-assisted breeding and QTL cloning. AM has the potential to provide numerous useful alleles to these marker assisted breeding programmes.

6.7 References

Agronomix Software, Inc. 2005. AGROBASE Generation II User's Manual. Version II, Revised Edition. www.agronomix.com.

Bitocchi E, Nanni L, Bellucci E, Rossi M, Giardini A, Spagnoletti Zeuli P, Logozzo G, Stougaard J, McClean P, Attene G, Papa R. 2012. Mesoamerican origin of the common bean (*Phaseolus vulgaris* L.) is revealed by sequence data. Proceedings of the National Academy of Sciences USA 109:24-33.

Blair MW, Giraldo MC, Buendia HF, Tovar E, Duque MC, Beebe SE. 2006. Microsatellite marker diversity in common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 113:100-109.

Blair MW, Díaz LM, Buendía HF, Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 119:955-972.

Blair M, Galeano C, Tovar E, Muñoz Torres M, Castrillón A, Beebe S, Rao I. 2012. Development of a Mesoamerican intra-genepool genetic map for quantitative trait loci detection in a drought tolerant × susceptible common bean (*Phaseolus vulgaris* L.) cross. Molecular Breeding 29:71-88.

Bradbury PJ, Zhang Z, Kroon DE, Casstevens TM, Ramdoss Y, Buckler ES. 2007. Genetics and population analysis. TASSEL: software for association mapping of complex traits in diverse samples. Bioinformatics 23:2633-2635.

Chavarro MC, Blair MW. 2010. QTL analysis and effect of the fin locus on tropical adaptation in an inter-gene pool common bean population. Tropical Plant Biology 3:204-218.

Gaitán-Solis E, Choi IY, Quigley C, Cregan P, Tohme J. 2008. SNP in common bean: Their discovery and genotyping using a multiplex detection system. The Plant Genome 1:125-134.

Galeano CH, Fernandez AC, Gomez M, Blair MW. 2009a. Single strand conformation polymorphism based SNP and Indel markers for genetic mapping and syteny analysis of common bean (*Phaseolus vulgaris* L). BioMedical Central Genomics 10:629-638.

Galeano CH, Gomez M, Rodriguez LM, Blair MW. 2009b. CEL 1 nuclease digestion for SNP discovery and marker development in common bean (*Phaseolus vulgaris* L). Crop Science 49:381-394.

Hougaard BK, Madsen LH, Sandal N, Moretzsohn MDC, Fredslund J, Schauser L, Nielsen AM, Rohde T, Sato S, Tabata S. 2008. Legume anchor markers link syntenic regions between *Phaseolus vulgaris*, *Lotus japonicus*, *Medicago truncatula* and *Arachis*. Genetics 179:2299-2312.

Hyten DL, Song Q, Fickus EW, Quigley CV, Lim JS, Choi IY, Hwang EY, Pastor-Corrales M, Cregan PB. 2010. High-throughput SNP discovery and assay development in common bean. Biomedical Central Genomics 11:475-488.

Myles S, Peiffer J, Brown PJ, Ersoz ES, Zhang Z, Costich DE, Buckler ES. 2009. Association mapping: Critical considerations shift from genotyping to experimental design. Plant Cell 21:2194-2202.

Nielsen DM, Weir BS. 1999. A classical setting for associations between markers and loci affecting quantitative traits. Genetics 74:271-277.

Oraguzie NC, Rikkerink EHA, Gardiner SE, de Silva HN. 2007. Association mapping in plants. Springer, Tokyo and New York. pp. 277.

Pérez-Vega E, Pañeda A, Rodríguez-Suárez C, Campa A, Giraldez R, Ferreira J. 2010. Mapping of QTLs for morpho-agronomic and seed quality traits in a RIL population of common bean (*Phaseolus vulgaris* L.). Theoretical and Applied Genetics 120:1367-1380.

Pritchard JK, Stephens M, Donnelly P. 2000. Influence of population structure using multilocus genotype data. Genetics 155:945-959.

Pswarayi A, van Eeuwijk FA, Ceccarelli S, Grando S, Comadran J, Russell JR, Pecchion N, Tondelli A, Akar T, Al-Yassin A, Benbelkacem A, Quabbou H, Thomas WT,

Romagosa I. 2008. Changes in allele frequencies in landraces, old and modern barley cultivars of marker loci close to QTL for grain yield under high and low input conditions. Euphytica 163:435-447.

Rong J, Feltus FA, Waghmare VN, Pierce GJ, Chee PW, Draye X, Saranga Y, Wright RJ, Wilkins TA, May OL, Smith CW, Gannaway JR, Wendel JF, Paterson AH. 2007. Meta-analysis of polyploid cotton QTL shows unequal contributions of subgenomes to a complex network of genes and gene clusters implicated in lint fiber development. Genetics 176:2577-2588.

Shi C, Navabi A, Yu K. 2011. Association mapping of common bacterial blight resistance QTL in Ontario bean breeding populations. BMC Plant Biology 11:52-65.

Stich B, Möhring J, Piepho HP, Heckenberger M, Buckler ES, Melchinger AE. 2008. Comparison of mixed-model approaches for association mapping. Genetics 178: 1745-1754.

Szilagyi L. 2003. Influence of drought on seed yield components in common bean. Bulgarian Journal of Plant Physiology, special issue, 320-330.

Terán H, Singh SP. 2002. Comparison of sources and lines selected for drought resistance in common bean. Crop Science 42:64-70.

Weber AL, Briggs WH, Rucker J, Baltazar BM, Sánchez-Gonzalez JJ, Feng P, Buckler ES,

Doebley J. 2008. The genetic architecture of complex traits in teosinte (*Zea may* ssp. parviglumis): New evidence from association mapping. Genetics 180:1221-1232.

Zhu C, Gore M, Buckler ES, Yu J. 2008. Status and prospects of association mapping in plants. The Plant Genome 1:5-20.

Chapter 7

General discussion, conclusions and recommendations

Production of common bean is predominantly rainfed in developing countries and 60% of cultivated beans suffer from water deficit at some stage during their growth. Sub-Saharan Africa is likely to face more frequent drought episodes due to the predicted climate changes. The development of drought adapted common bean varieties is a practical approach to minimise crop failure and improve food security in bean growing areas.

The current study identified several phenotypic traits that have the potential to improve drought tolerance in common bean and possibly other legume crops. These traits included total shoot biomass, number of pods per plant, 100-seed weight, grain yield, deep rooting, days to maturity, leaf temperature and canopy temperature depression. In addition, based on GM and DSI data, four Mesoamerican and six Andean genotypes were identified which have potential as parents for drought tolerance breeding, or could be recommended for wider production in drought prone areas. The existence of a strong geographical structure in common bean (Andean versus Mesoamerican) and within the Mesoamerican gene pool (races Durango and Mesoamerica) was defined by STRUCTURE and NJ analysis. This information will contribute toward the conservation and judicious use of genetic resources in common bean. Association mapping analysis allowed the identification of SNP markers significantly associated with 100-seed weight and total shoot biomass across locations and between treatments. This offers the possibility of searching candidate genes controlling these two traits in common bean. Once candidate genes are identified, markers can be developed for use in marker assisted breeding programmes. This demonstrated the merits of association mapping as a tool in genetic studies where complex traits can be reduced to individual components which can be used for selection.

High total shoot biomass potentially represents storage capacity of assimilates for grain filling. Some wheat varieties accumulate water soluble carbohydrates in stems which act as grain filling reserve, which help maintain grain yields under drought stress. This mechanism could also be present in common bean, as total shoot biomass was positively correlated with grain yield and

some highly yielding genotypes under drought stress had a high shoot biomass. Breeding for high shoot biomass could significantly improve grain yield under drought prone environments.

The existing relationships between Durango and Mesoamerican races were more clearly defined in NJ analysis in the current study than in previous studies in common bean. Previous molecular characterisation studies in common bean used a lower number of markers than in this study. Many markers which saturate the genome of a species produce more precise molecular data. SSR results indicated lower genetic diversity in the Andean gene pool compared to the Mesoamerican one. For those regions, including southern Africa, where drought occurs frequently and Andean beans are a priority, strategies need to be put in place to source drought tolerance genes from other types of common bean.

Genotypes from race Durango demonstrated better adaptation to water stressed environments than other races in common bean. Genes for drought tolerance and yield can be harnessed from races Durango and Mesoamerica respectively for improving drought tolerance in the Andean gene pool. This could be achieved through backcross breeding programmes. Future identification of candidate genes controlling total shoot biomass, number of pods per plant and 100-seed weight and the development of markers for these genes would shorten the backcross breeding schemes through accurate selection of progeny with the correct background and necessary QTL. In addition, initial field selections could be carried out even under normal or greenhouse conditions. However, this would require the necessary equipment and expertise in breeding programmes. Interracial crosses are possible within genotypes in the Mesoamerican gene pool of the reference collection between some high yielding Mesoamerica 2 genotypes and drought tolerant Durango genotypes to create high yielding drought tolerant genotypes.

Alternatively, a parallel scheme aimed at promoting the production and consumption of small seeded beans by farmers and consumers in regions where large seeded beans are priority would ensure direct utilisation of drought tolerant Mesoamerican genotypes. Initial steps would involve participatory evaluation of drought tolerant Mesoamerican genotypes in farmer's and researcher's fields to ensure that the agronomic merits of small seeded beans are captured by smallholder farmers and other stakeholders. Other measurements taken during this evaluation

exercise should include culinary and nutritional tests and should involve researchers, farmers, common bean industry, traders, nutritionists and farmer representatives.

Water uptake from deep soil layers is another important parameter for drought avoidance in crops. Some Mesoamerican genotypes under the rainfed treatment had cooler canopies, indicating that they were extracting water from the soil and maintaining transpiration. Greenhouse studies showed that deep rooting is an adaptive trait in some genotypes. In the current study, deep rooting or cooler canopies did not guarantee high grain yield under the rainfed treatment. Some genotypes with cooler canopies had the lowest yield observed at both locations. This suggested that while deep rooting is important for water extraction under water stress, other mechanisms at shoot level are equally important in utilising the water efficiently.

Leaf temperature, a surrogate trait for stomatal closure, varied among Mesoamerican genotypes under the rainfed treatment. Since some genotypes were extracting and controlling water movement to the atmosphere, WUE would be recommended for evaluation on a small group of genotypes that showed potential for drought tolerance. Economical screening of large numbers of breeding lines can be achieved through the use of leaf temperature, which can be followed by expensive, precision screening of small numbers of lines with WUE combined with detailed multi-environment field trials. With the predicted climate change and its effect on rainfall variability, efficient use of extracted water is one possible strategy for improving grain yield of common bean in semi-arid environments.

Grain yield was strongly influenced by environments and GxT interactions in both Andean and Mesoamerican genotypes. This makes it difficult to recommend tolerant genotypes for different environments. Already, smallholder farmers' fields are highly variable in terms of soil types, fertility and pH levels, date of planting, planting methods, weed, pest and disease control. Many smallholder farmers, who are the main growers of common bean, do not have the ability to homogenise their fields. The presence of other stresses is inevitable under natural environments and in the current study additional stress in form of diseases was present at especially Harare Research Station. This indicates that successes in drought tolerance breeding also rely on tolerance to other stress conditions that might co-occur with drought. The best strategy for

developing drought tolerant genotypes for smallholder farmers would be to combine drought tolerance with resistance to other stresses into a single genotype. A dimorphic root system that combines deep rooting and lateral roots in the top soil layers is helpful for water extraction at deep soil layers and nutrient absorption in the top soil. Smallholder farmers also have a role to play in reducing the negative impacts of drought on crop yields. They need to adopt good agronomic practises that improve soil nutrition, minimise soil heterogeneity and pest/disease outbreaks and water loss on their farms.

Measurements of some of the traits (e.g. shoot biomass at mid pod filling stage) that are correlated with high yield under drought were tedious and time consuming. A faster and easier way of measuring shoot biomass needs to be developed for wider use in developing countries and could contribute to better management of drought effects in these countries. However, measurement of grain yield remains the most practical and easiest method of selecting drought tolerant genotypes.

The growth habits of the entries made a contribution to their final yield under both irrigated and terminal drought conditions. Variation in growth habit is limited to bush determinate in most Andean genotypes and mean lower number of flowers and pods per plant than indeterminate Mesoamerican genotypes. Breeding should aim at improving plant architecture in Andean genotypes to enhance their yielding ability under both optimum and terminal drought conditions.

Measurement of deep rooting under field conditions is a difficult and tedious process. However, the positive correlations found between deep rooting and stem as well as green leaf biomass under the water stressed treatment in the greenhouse suggested that deep rooting could be estimated from aerial plant parts. Supply of water by deep roots ensures a high shoot biomass under drought conditions. Other supporting traits that indicate that plants are obtaining water under drought conditions are leaf temperature and canopy temperature depression. Leaf temperature is a marker for both low stomatal conductance and high transpiration efficiency.

The immediate use of field and molecular data would be to identify parents which could be used in interracial crosses within each gene pool. These crosses would aim at combining drought

tolerance with high yield within each gene pool. In the long term, association analysis can be expanded to searching for candidate genes using SNP markers correlated with grain yield, number of pods per plant, days to maturity, total shoot biomass and 100-seed weight. This would accelerate breeding for drought tolerance in common bean through use of marker-assisted breeding methods.

In conclusion, SSR markers used in the current study supported evidence to the existence of two major domesticated gene pools of common bean. Association mapping is an attractive approach to study complex traits such as drought tolerance in common bean. Estimation of positions and effects of QTL is important for MAS, marker-assisted recurrent selection and marker-assisted breeding. This has been accomplished through classical linkage mapping which is expensive, has poor resolution in detecting QTL and requires the generation of crosses for mapping. AM offers a quick way of identifying marker-trait association and reduces time for the development of markers which can be used in marker-assisted breeding programmes. Breeding programmes aiming to improve drought tolerance in common bean would be recommended to investigate the genetic variability in adaptive traits mentioned above and establish their relationship with grain yield under drought stress. The first trait to be recommended for investigation is deep rooting. If destructive measurements are necessary, total plant biomass is probably an appropriate alternative, though it is time consuming and requires appropriate equipment. Last but not least, selection of drought tolerant genotypes is difficult due to variability of drought episodes even within the same location in consecutive years.

Abstract

The aims of this study were to identify sources of drought tolerance in a common bean reference collection, to improve genetic and physiological understanding of drought tolerance in different gene pools of common bean, to establish the role of rooting characteristics in improving grain yield under drought conditions, to determine the genetic structure and diversity in the reference collection using SSR marker data, and to identify simply inherited markers in close proximity to genes affecting drought tolerance.

Field experiments were laid out as 11x11 Mesoamerican and 9x9 Andean lattices with three replicates under irrigated and rainfed treatments at CIAT-Palmira and Harare Research Station. Yield was significantly correlated with total shoot biomass at mid pod fill, 100-seed weight, number of pods per plant and days to maturity under both treatments at both locations. Based on geometric means and drought sensitivity indices, BAT477, G11721, G4017, DOR390 (Mesoamerican) and SAB645, PVA1111, SEQ1003, SEQ1027, G17076 and G5142 (Andean) genotypes had high and stable yields across treatments in both locations and could serve as sources of drought tolerance in common bean.

Two greenhouse experiments were conducted at CIAT-Palmira using the soil cylinder system, in a randomised complete block design with three replicates. Well watered and water stressed treatments were applied in each trial. In 2009 a total of 33 Andean landraces and three Mesoamerican checks were evaluated for deep rooting and other root properties. In 2010 phenotypic differences were determined between elite genotypes in root development under water stress. A total of 40 elite Andean and Mesoamerican genotypes commonly used as parents in many breeding programmes, were evaluated. Variability of root traits under water stress was expressed either as adaptive or constitutive traits depending on genotype. It was found that deep rooting alone may not be adequate for drought tolerance in common bean, as some deep rooted genotypes had poor yields under field conditions.

SSR and SNP markers were used for molecular characterisation of the reference collection to determine the population structure and identify statistically significant marker-trait associations

relevant for drought tolerance in the reference collection. The reference collection is strongly structured following the geographical origins of the genotypes. TOG896943-500, TOG918200-347 and TOG 910860-634 were significantly associated with 100-seed weight and total shoot biomass across locations and treatments. In conclusion, all findings in the current study need to be integrated to develop drought tolerant common bean varieties in future. Mapping studies should be extended to candidate gene analysis for the identified marker-trait associations.

Opsomming

Die doelwitte van hierdie studie was om bronne van droogtetoleransie in ‘n algemene droëboon verwysingsversameling te bepaal, om die genetiese en fisiologiese begrip van droogtetoleransie in verskillende geenpoele van droëbone te verbeter, om die rol van worteleienskappe in die verbetering van saadopbrengs onder droogtetoestande te bepaal, om die genetiese struktuur en diversiteit in die verwysingsversameling met die gebruik van SSR merkerdata te bepaal, en om eenvoudig oorgeërfde merkers te identifiseer wat naby aan gene lê wat droogtetoleransie bepaal.

Veldproewe is uitgelê as 11x11 Mesoamerikaanse and 9x9 Andiese vierkante met drie herhalings, onder besproeiings en droëlandtoestande by CIAT-Palmira en Harare Navorsingsstasie. Opbrengs was betekenisvol gekorreleer met totale bogrondse biomassa teen mid-peulvulstadium, 100-saadmassa, aantal peule per plant en dae tot volwassenheid onder beide behandelings by beide omgewings. Volgens geometriese gemiddeldes en droogtesensitiwiteitsindekse, het BAT477, G11721, G4017, DOR390 (Mesoamerikaans) en SAB645, PVA1111, SEQ1003, SEQ1027, G17076 en G5142 (Andiese) genotipes hoë en stabiele opbrengste oor die behandelings in beide omgewings getoon en kan dien as bronne van droogtetoleransie in droëbone.

Twee glashuisproewe is by CIAT-Palmira uitgevoer waar die grond silindersisteem in ‘n gerandomiseerde blokontwerp met drie herhalings gebruik is. Optimale en water gestremde behandelings is toegepas in beide proewe. In 2009 is ‘n totaal van 33 Andiese landrasse en drie Mesoamerikaanse standaarde vir diep wortelvermoë en ander worteleienskappe geëvalueer. In 2010 is fenotipiese verskille tussen elite genotipes vir wortelontwikkeling onder waterstremming bepaal. ‘n Totaal van 40 elite Andiese en Mesoamerikaanse genotipes wat algemeen as ouers gebruik word in teelprogramme, is geëvalueer. Variasie in worteleienskappe onder waterstremming is as aanpassingseienskappe of samestelling van eienskappe uitgedruk. Daar is gevind dat die vermoë om diep wortels te vorm nie alleen genoeg is om droogtetoleransie in droëbone te verseker nie omdat sommige genotipes wat diep wortels kon vorm, swak opbrengste onder veldtoestande gehad het.

SSR en SNP merkers is vir die molekulêre karakterisering van die verwysingsversameling gebruik om populasiestruktuur te bepaal en om statisties betekenisvolle merker-eienskap assosiasies relevant vir droogtetoleransie in die verwysingsversameling te bepaal. Die verwysingsversameling het ‘n baie duidelike struktuur volgens die geografiese oorsprong van die genotipes getoon. TOG896943-500, TOG918200-347 en TOG 910860-634 was betekenisvol met 100-saadmassa en totale bogrondse biomassa oor lokaliteite en behandelings geassosieer. Alle bevindings van hierdie studie moet geïntegreer word om in die toekoms droogtetolerante droëboonvariëteite te ontwikkel. Karteringsstudies moet uitgebrei word om kandidaat gene te analiseer en identifiseer vir merker-eienskap assosiasies.

Appendix 1 Intensity of diseases in Mesoamerican trials under irrigated and rainfed treatments at Harare Research Station

Environment	Rainfed treatment		Irrigated treatment		
Genotype	CBB	RUST	CBB	RUST	ALS
G4278	2.00	2.00	3.33	1.33	1.67
G7952	1.67	2.67	1.33	1.00	1.00
G11057	3.67	4.67	5.33	1.33	1.67
G12778	3.00	4.00	5.00	1.00	3.00
G12796	1.67	3.33	3.67	2.33	2.33
G12806	1.67	4.00	2.67	2.00	1.33
G13177	3.00	7.00	3.00	7.00	2.00
G13578	1.33	3.00	2.33	1.67	1.33
G13696	1.67	2.67	3.67	1.00	1.33
G14163	2.00	3.00	2.33	1.00	1.33
G15641	2.00	1.33	2.33	1.33	2.67
G15685	2.00	4.33	3.67	1.67	2.00
G16026	3.00	6.67	5.00	2.67	2.33
G16072	3.00	7.00	4.00	3.33	2.00
G16400	2.00	3.00	2.33	2.00	1.67
G16401	2.33	1.33	3.00	1.00	2.00
G16835	1.33	1.33	2.67	1.67	1.67
G16849A	3.67	1.33	4.67	1.00	1.33
G18141	1.00	1.67	2.67	1.00	1.67
G18147	1.67	1.67	2.67	1.67	1.33
G18157	2.67	4.00	2.67	1.33	1.33
G18451	2.67	1.00	3.33	1.00	1.67
G18454	2.33	1.33	3.33	1.00	1.33
G19012	2.00	3.00	3.33	3.33	1.67
G19204	1.67	1.67	3.00	1.33	1.67
G19941	4.33	8.00	2.33	3.67	2.67
G21212	2.00	1.33	3.33	1.33	1.67
G22787	1.33	2.00	3.00	2.00	2.00
BAT93	2.33	1.00	2.67	1.00	2.00
BAT477	1.00	1.00	2.33	1.00	1.33
DOR390	2.00	1.00	1.67	1.00	1.00
Maharagi soya	1.67	1.00	3.00	1.00	2.00
Masaai Red	2.33	2.00	2.33	1.00	1.67
NCB280	2.67	1.33	4.00	1.33	2.00
Pinto villa	2.67	1.33	3.67	1.00	1.67
SEA15	2.00	1.00	3.00	1.33	1.67
SER109	1.67	2.67	3.33	1.00	1.67
SER16	1.33	1.00	3.00	1.00	2.33
SXB418	2.00	1.00	3.67	1.00	1.67
Tio Canela 75	1.67	1.67	2.33	1.00	1.33
VAX3	1.67	2.00	2.67	1.00	1.00
Grand mean	1.97	2.22	2.81	1.40	1.65
LSD	1.06	0.93	1.03	0.87	0.83
CV%	23.34	26.20	22.80	24.00	21.00
m.s.	1.08***	6.64***	1.62***	1.81***	0.53***
Error	0.43	0.34	0.41	0.29	0.27

CBB – Common bacterial blight; ALS – Angular leaf spot; LSD – least significant difference; CV – coefficient of variation; m.s. – mean square; ***P<0.001

Appendix 2 Intensity of diseases in Andean trials under rainfed treatment at Harare Research Station

Environment	Drought treatment		
Trait	CBB	RUST	ALS
Genotype			
AND1005	2.33	1.67	2.00
DRK47	2.00	4.00	2.33
G738	3.33	2.00	2.00
G1678	2.33	3.33	2.33
G1688	5.00	3.67	5.00
G1836	2.33	3.67	2.33
G1939	2.33	5.00	2.33
G2563	2.33	6.00	2.33
G2567	2.33	3.00	2.33
G2686	1.67	3.00	1.67
G2875	2.67	4.00	2.67
G4001	3.67	4.00	3.67
G4547	2.33	2.00	1.00
G4644	3.33	3.33	3.00
G4721	2.00	1.00	1.67
G4739	2.00	1.67	1.33
G4906	2.67	3.33	3.33
G5034	2.67	5.00	3.67
G5142	4.00	4.33	3.33
G5170	2.67	5.00	2.00
G5273	3.33	4.00	2.00
G5708	3.33	2.00	2.67
G5849	3.33	6.67	2.67
G6639	2.67	5.00	2.00
G6873	3.33	3.33	2.33
G7776	2.67	2.33	2.00
G7895	3.00	5.33	2.33
G7945	3.33	6.33	2.67
G8209	1.67	1.33	1.00
G9603	2.33	1.67	1.33
G9846	2.00	2.33	2.00
G11512	3.00	3.00	3.00
G11521	2.33	3.67	1.33
G11564	2.67	2.00	2.00
G11585	2.33	3.33	2.33
G11727	2.00	1.33	2.33
G11759A	2.33	1.33	2.00
G4534	3.67	2.33	3.33
G11957	3.00	2.67	2.33
G11982	3.67	4.67	2.33
G12517	2.67	3.00	1.67
G13094	3.67	2.33	4.33
G14253	3.67	5.33	2.67
G16104E	1.67	4.00	1.67
G16115	2.67	3.33	2.67
G17070	2.67	3.67	2.67
G17168	1.67	1.00	1.67
G18255	3.67	5.00	3.67
G18264	2.67	4.00	2.67
G18942	2.33	4.00	2.33
G19833	1.33	1.00	1.33
G17076	2.67	2.67	2.67
G21210	4.33	3.33	4.33
G22147	3.00	3.67	3.00
G22247	2.00	4.33	2.00
G23604	1.00	2.00	1.00
G23829	2.00	3.00	2.00
PVA773	2.67	2.00	2.33
PVA1111	3.33	3.00	2.67
G4494	2.67	2.67	3.67
G4672	2.00	3.67	2.33
G9335	3.33	5.33	3.33
G9855	2.67	3.00	2.33
G12529	2.33	1.00	1.33
G13595	3.67	2.67	2.67
G13910	2.67	2.33	2.67
G13911	3.00	2.67	1.67
G14016	1.67	1.33	1.00
G16110A	2.00	2.33	2.00
G16346	3.33	3.67	3.33
G5625	1.67	1.00	1.00
G3157	1.67	1.00	1.67
G19842	1.67	1.67	1.67
G19860	1.00	1.00	1.00
AFR619	1.67	2.33	1.67
CAL143	3.00	3.33	2.33
CAL96	3.67	1.67	2.67
SAB258	3.67	5.00	2.67
SAB645	4.00	4.67	2.33
SEQ1003	3.33	2.67	2.67
SEQ1027	2.00	2.33	2.00
Grand mean	2.92	3.11	2.34
LSD	1.44	1.67	1.43
CV%	20.70	23.00	28.00
m.s.	1.87***	5.67***	1.92***
Error	0.80	1.09	0.79

CBB – Common bacterial blight; ALS – Angular leaf spot; LSD – least significant difference; CV – coefficient of variation; m.s. – mean square

Appendix 3 Performance of 121 Mesoamerican genotypes evaluated under irrigated and rainfed treatments at CIAT-Palmira, 2009.

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	Genotype	Irr	Dro	Irr	Dro	PR	Irr	Dro	GMY	DSI	PR	Irr	Dro	PR	Irr	Dro	Irr	Dro	Irr	Dro
check	SEA15	29.67	29.67	55.33	54.00	0.02	2524.70	2770.90	2644.94	-0.42	-0.10	38.33	32.73	0.15	11.27	9.47	8.40	2.93	10.67	10.33
check	SER16	31.67	31.00	57.33	54.67	0.05	2806.50	2486.90	2641.87	0.50	0.11	25.97	26.80	-0.03	14.87	10.53	4.63	2.33	9.00	8.33
check	NCB280	30.00	30.67	55.67	55.00	0.01	2631.20	2542.40	2586.42	0.15	0.03	31.77	30.43	0.04	11.07	9.33	5.50	5.17	10.00	9.33
check	SER109	31.33	31.33	59.00	55.00	0.07	2566.00	2355.80	2458.65	0.36	0.08	25.67	24.90	0.03	11.40	9.67	12.97	2.00	10.67	10.00
check	BAT477	35.67	35.00	63.00	59.67	0.05	2538.30	2177.90	2351.20	0.62	0.14	22.23	23.37	-0.05	10.07	8.40	4.10	9.13	10.00	10.67
check	SXB418	37.00	34.33	64.67	59.67	0.08	2468.60	2031.00	2239.14	0.77	0.18	54.33	28.77	0.47	8.93	9.93	1.87	14.23	11.33	11.33
check	DOR390	37.00	37.00	66.00	62.00	0.06	2598.60	1806.90	2166.89	1.32	0.30	20.03	21.03	-0.05	10.33	8.60	6.03	5.67	9.00	9.33
check	Tio Canela 75	35.00	34.67	65.00	61.67	0.05	2351.30	1907.70	2117.92	0.82	0.19	22.07	24.87	-0.13	10.80	11.00	3.80	4.07	9.33	9.33
check	Maharagi Soya	37.00	37.00	68.00	65.33	0.04	2354.50	1504.30	1881.99	1.57	0.36	22.23	21.40	0.04	9.33	8.33	4.77	8.50	9.00	9.33
check	Pinto Villa	27.33	26.33	51.33	52.00	-0.01	1587.40	1976.30	1771.21	-1.07	-0.24	33.27	33.60	-0.01	13.60	10.53	21.10	15.77	9.00	8.67
check	VAX3	35.00	34.67	65.33	60.00	0.08	1764.90	1710.60	1737.54	0.13	0.03	28.17	24.67	0.12	9.60	9.47	9.73	8.40	9.33	9.33
check	BAT93	36.33	36.33	65.33	60.67	0.07	1767.20	1244.60	1483.06	1.29	0.30	17.93	21.40	-0.19	15.67	11.53	5.57	13.87	10.33	9.33
check	Masaai Red	38.33	37.00	69.00	66.33	0.04	803.20	870.23	836.04	-0.36	-0.08	20.37	25.33	-0.24	8.13	7.47	29.90	10.67	8.00	8.00
Mean		**33.95**	**33.46**	**61.92**	**58.92**	**0.05**	**2212.49**	**1952.73**	**2070.53**	**0.51**	**0.12**	**27.87**	**26.10**	**0.06**	**11.16**	**9.56**	**9.11**	**7.90**	**9.67**	**9.49**
D1	G2379	33.67	33.00	61.33	57.33	0.07	2325.70	1737.80	2010.37	1.10	0.25	26.03	25.23	0.03	13.07	9.67	5.87	8.63	10.33	10.00
D1	G2402	27.00	26.00	53.00	52.67	0.01	2040.00	1951.70	1995.36	0.19	0.04	36.33	36.27	0.00	10.47	10.13	12.57	8.27	9.33	8.67
D1	G10982	26.00	26.33	52.00	51.33	0.01	1900.10	1955.50	1927.60	-0.13	-0.03	46.67	39.90	0.15	11.47	11.73	6.43	3.90	9.00	9.00
D1	G11010	32.00	31.67	65.33	59.00	0.10	1811.20	1840.20	1825.64	-0.07	-0.02	45.00	45.83	-0.02	12.67	10.13	6.30	7.90	8.33	9.00
D1	G2778	27.67	28.00	53.33	52.33	0.02	1605.50	2067.20	1821.78	-1.25	-0.29	32.13	32.50	-0.01	11.07	9.80	15.43	19.43	8.33	8.67
D1	G13696	27.33	26.00	59.00	51.33	0.13	1835.00	1585.80	1705.86	0.59	0.14	39.07	39.47	-0.01	12.33	11.33	12.07	11.63	6.67	7.00
D1	G18440	30.33	30.00	62.33	57.00	0.09	2071.30	1400.30	1703.07	1.41	0.32	37.07	41.83	-0.13	8.00	7.60	7.77	13.57	8.67	8.00
D1	G2635	33.67	33.33	67.67	61.00	0.10	1980.60	1424.30	1679.57	1.22	0.28	27.60	27.30	0.01	13.33	14.20	19.10	18.53	7.33	8.33
D1	G13177	26.00	27.00	58.00	56.00	0.03	1858.90	1493.90	1666.44	0.85	0.20	53.53	46.67	0.13	6.93	8.20	16.63	12.87	8.67	9.33
D1	G2866	32.00	31.00	65.33	58.00	0.11	1696.80	1635.20	1665.72	0.16	0.04	35.90	32.80	0.09	10.60	13.00	22.63	19.50	9.33	9.33
D1	G19941	27.00	26.67	51.33	52.33	-0.02	1807.90	1498.00	1645.67	0.75	0.17	35.77	33.70	0.06	10.73	9.73	14.97	13.20	9.33	8.67
D1	G10971	29.00	28.33	58.33	56.67	0.03	1757.80	1371.50	1552.68	0.96	0.22	43.23	47.03	-0.09	8.20	8.87	4.90	9.40	7.67	9.33
D1	G4342	32.33	32.67	64.33	57.67	0.10	1687.10	1378.50	1525.01	0.80	0.18	28.03	25.00	0.11	15.33	8.53	21.87	26.40	8.67	8.67
D1	G7602	30.33	29.67	63.33	56.33	0.11	1528.20	1321.70	1421.20	0.59	0.14	51.13	49.43	0.03	12.40	10.33	40.43	9.77	8.00	9.00
D1	G2775	27.33	27.00	56.33	54.83	0.03	1840.40	995.20	1353.35	2.00	0.46	36.23	37.67	-0.04	10.13	7.20	12.53	4.70	8.33	8.33
D1	G10945	37.00	37.00	70.00	68.33	0.02	1396.00	1133.20	1257.75	0.82	0.19	24.40	16.57	0.32	9.07	7.13	14.87	6.77	9.33	8.67
D1	G1797	36.33	37.33	74.67	68.33	0.08	791.90	366.50	538.73	2.34	0.54	24.53	22.50	0.08	6.40	5.33	34.90	19.73	6.33	6.67
Mean		**30.29**	**30.06**	**60.92**	**57.09**	**0.06**	**1760.85**	**1479.79**	**1605.64**	**0.69**	**0.16**	**36.63**	**35.28**	**0.04**	**10.72**	**9.58**	**15.84**	**12.60**	**8.45**	**8.63**
D2	G14914	34.00	33.67	61.00	57.33	0.06	2500.00	1989.90	2230.41	0.89	0.20	22.77	24.87	-0.09	11.67	11.87	14.77	6.00	9.67	10.00
D2	G11057	29.00	28.67	50.00	48.67	0.03	2337.70	2076.40	2203.18	0.49	0.11	36.90	34.37	0.07	9.07	8.20	20.23	4.67	10.33	9.67
D2	G4017	37.00	36.67	66.67	62.33	0.07	2340.30	1818.70	2063.08	0.97	0.22	28.87	29.07	-0.01	9.73	9.87	15.53	4.80	9.33	10.33
D2	G3807	36.67	36.67	67.33	61.33	0.09	2484.50	1549.70	1962.20	1.64	0.38	23.00	23.43	-0.02	12.87	10.47	11.57	8.67	9.33	9.33
D2	G4822	36.33	35.33	64.67	59.67	0.08	2195.70	1592.00	1869.64	1.20	0.27	26.37	22.83	0.13	11.13	6.73	13.97	8.43	10.00	9.67
D2	G278	35.67	34.00	65.33	59.00	0.10	1739.90	1775.30	1757.51	-0.09	-0.02	15.93	17.60	-0.10	11.53	13.20	27.50	1.80	7.33	7.33
D2	G16026	31.67	30.00	54.67	50.00	0.09	1623.20	1887.20	1750.23	-0.71	-0.16	29.27	24.50	0.16	12.27	11.67	20.43	15.30	9.00	9.67
D2	G13578	38.33	39.00	62.67	59.00	0.06	1822.80	1530.80	1670.43	0.70	0.16	19.97	19.07	0.05	13.13	9.47	11.50	6.57	9.67	8.67
D2	G12796	32.00	32.00	58.00	55.67	0.04	1759.50	1569.70	1661.89	0.47	0.11	22.93	20.60	0.10	11.87	12.80	11.13	5.90	9.33	9.00
D2	G4278	33.67	33.33	62.67	59.00	0.06	1489.00	1775.80	1626.09	-0.84	-0.19	19.43	18.07	0.07	11.53	15.53	24.23	21.70	7.33	8.00
D2	G15685	36.33	33.33	67.33	63.33	0.06	1711.20	1337.40	1512.80	0.95	0.22	27.43	26.47	0.03	9.40	11.40	13.53	8.20	8.67	9.00
D2	G19012	30.33	29.33	65.00	59.00	0.09	2029.50	1119.60	1507.39	1.95	0.45	60.40	49.33	0.18	8.13	7.53	17.33	10.13	8.00	8.33
D2	G3334	31.33	31.00	56.33	56.33	0.00	1858.70	1132.60	1450.92	1.70	0.39	20.67	21.00	-0.02	11.47	12.47	16.87	16.77	8.67	8.67
D2	G22044	33.00	30.67	67.67	62.00	0.08	2041.90	1003.90	1431.73	2.21	0.51	33.33	29.60	0.11	9.07	6.93	6.40	12.10	8.33	9.00
D2	G753	28.67	28.33	54.67	53.00	0.03	1728.90	976.00	1299.00	1.89	0.44	22.43	20.67	0.08	8.73	8.27	2.00	4.97	9.67	9.67
D2	G3331	41.33	36.67	64.00	57.33	0.10	1280.90	861.17	1050.27	1.42	0.33	19.67	16.30	0.17	13.67	9.13	15.40	28.00	8.67	8.00
D2	G3936	36.67	37.00	64.67	64.33	0.01	986.93	671.27	813.94	1.39	0.32	16.23	12.47	0.23	11.13	8.20	19.27	22.23	7.67	7.00
D2	G11656A	40.00	40.00	78.33	73.67	0.06	246.67	142.73	187.64	1.83	0.42	12.27	18.03	-0.47	3.13	8.20	21.03	17.10	6.00	5.00
D2	G7742	37.00	37.00	74.00	63.67	0.14	317.67	101.70	179.74	2.96	0.68	20.90	19.87	0.05	2.73	3.40	34.93	26.57	8.33	6.00
D2	G14737	44.00	47.00	77.67	76.00	0.02	339.43	64.50	147.96	3.52	0.81	19.20	21.65	-0.13	7.13	3.13	22.40	39.30	8.67	5.00
Mean		**35.15**	**34.48**	**64.13**	**60.03**	**0.06**	**1641.72**	**1248.82**	**1418.80**	**1.04**	**0.24**	**24.90**	**23.49**	**0.06**	**9.97**	**9.42**	**17.00**	**13.46**	**8.70**	**8.37**
G	G16072	30.00	29.33	51.67	51.00	0.01	1788.90	2338.30	2045.23	-1.34	-0.31	39.27	36.97	0.06	9.27	10.33	12.90	13.50	10.00	9.33
G	G1356	37.00	37.33	64.67	61.67	0.05	1919.40	1761.80	1838.91	0.36	0.08	19.83	20.30	-0.02	11.87	10.80	12.03	4.73	8.33	8.00
G	G2277	37.00	37.00	64.33	66.33	-0.03	1812.40	1312.50	1542.33	1.20	0.28	21.93	23.53	-0.07	10.27	10.00	9.50	4.77	8.00	7.33
G	G22787	29.67	29.67	70.33	63.67	0.09	1409.20	870.63	1107.65	1.66	0.38	34.23	27.77	0.19	11.27	10.00	29.00	20.00	7.67	7.67
G	G16401	32.67	32.00	69.33	68.00	0.02	1040.20	775.70	898.27	1.11	0.25	25.77	25.40	0.01	10.60	7.73	29.53	17.37	7.00	6.67
G	G4730	37.00	36.00	67.33	65.33	0.03	1315.80	578.23	872.26	2.44	0.56	18.97	17.57	0.07	9.07	8.07	3.07	13.63	8.33	8.00
G	G1328	36.67	36.67	70.33	71.00	-0.01	1131.80	546.23	786.27	2.25	0.52	17.63	15.67	0.11	10.53	7.93	16.43	16.07	8.00	8.00
G	G16400	36.33	35.67	69.33	65.33	0.06	959.53	618.40	770.31	1.55	0.36	20.13	18.27	0.09	11.00	10.13	39.10	41.83	8.33	8.33
G	G5653	36.67	35.33	69.00	67.50	0.02	863.77	432.73	611.37	2.17	0.50	25.37	24.67	0.03	12.00	8.40	18.50	35.87	10.33	9.33
G	G2660	36.67	34.00	68.67	68.00	0.01	753.90	445.80	579.73	1.78	0.41	23.00	24.47	-0.06	7.47	3.87	20.27	24.17	7.00	7.00
Mean		**34.97**	**34.30**	**66.50**	**64.78**	**0.03**	**1299.49**	**968.03**	**1105.23**	**1.11**	**0.26**	**24.61**	**23.46**	**0.05**	**10.34**	**8.73**	**19.03**	**19.19**	**8.30**	**7.97**

D1 – Durango 1; D2 – Durango 2; G – Guatemala; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index; PR – Percent reduction

Appendix 3 continued

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	**Genotype**	**Irr**	**Dro**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**GMY**	**DSI**	**PR**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**Irr**	**Dro**	**Irr**	**Dro**
M1	G15416	35.67	36.67	65.67	59.33	0.10	2553.60	1991.90	2255.33	0.96	0.22	21.20	21.70	-0.02	11.73	8.13	11.87	10.17	9.00	8.67
M1	DOR364	37.00	37.00	65.00	61.00	0.06	2545.90	1925.50	2214.08	1.06	0.24	25.73	22.13	0.14	10.13	8.47	7.10	7.07	10.33	10.00
M1	G2199	36.33	37.00	64.67	63.00	0.03	2218.80	2026.30	2120.37	0.38	0.09	18.33	20.03	-0.09	12.93	10.73	7.70	11.63	9.67	9.33
M1	G4002	37.00	37.00	68.00	60.33	0.11	2668.10	1607.40	2070.92	1.73	0.40	25.83	27.83	-0.08	13.93	7.87	13.13	9.00	9.67	9.67
M1	G4206	37.00	37.00	67.00	64.33	0.04	2345.00	1699.50	1996.33	1.20	0.28	20.27	18.43	0.09	9.73	12.20	16.33	1.83	9.67	10.00
M1	G18147	31.67	30.00	57.00	51.67	0.09	2554.00	1527.30	1975.03	1.75	0.40	24.53	22.70	0.07	12.80	7.80	7.73	1.90	10.00	8.67
M1	G4495	37.00	37.00	65.67	64.00	0.03	2381.00	1476.20	1874.79	1.65	0.38	23.23	22.30	0.04	8.73	8.33	5.93	1.40	9.67	9.67
M1	G21212	35.33	34.00	66.00	62.00	0.06	1503.30	2306.90	1862.25	-2.32	-0.53	19.63	23.93	-0.22	9.47	10.40	19.20	16.37	9.67	10.00
M1	G2352	36.33	35.33	63.67	58.33	0.08	2011.50	1668.60	1832.05	0.74	0.17	26.13	27.27	-0.04	11.13	8.73	7.97	5.00	10.33	10.00
M1	G12778	33.00	31.67	58.67	55.67	0.05	1811.20	1801.90	1806.54	0.02	0.01	31.43	27.20	0.13	10.87	14.13	13.20	5.80	9.67	9.67
M1	G2348	36.33	37.33	65.33	62.67	0.04	1966.10	1641.80	1796.65	0.72	0.16	23.57	24.00	-0.02	10.27	8.20	4.77	8.73	12.00	11.00
M1	G7932	30.67	30.00	50.00	47.33	0.05	2361.10	1321.30	1766.27	1.91	0.44	28.47	27.97	0.02	10.93	7.40	11.87	3.93	10.67	9.67
M1	G17648	30.00	29.33	51.33	49.00	0.05	2182.40	1284.70	1674.43	1.79	0.41	26.43	22.87	0.13	11.33	8.13	7.03	13.00	9.67	9.33
M1	G2997	32.00	30.00	53.00	51.67	0.03	1953.50	1425.20	1668.57	1.18	0.27	24.13	23.80	0.01	13.33	8.40	6.27	3.50	10.00	8.67
M1	G5694	37.00	37.00	64.33	61.00	0.05	2198.10	1241.80	1652.15	1.89	0.44	18.43	19.10	-0.04	16.07	9.07	16.77	9.50	9.33	9.33
M1	G5036	37.33	37.00	58.00	55.67	0.04	2100.90	1259.00	1626.36	1.74	0.40	20.00	19.07	0.05	8.47	10.87	10.87	3.53	7.00	8.67
M1	G2137	35.33	35.33	63.67	59.33	0.07	1771.70	1458.70	1607.60	0.77	0.18	27.80	24.80	0.11	11.27	9.07	14.27	14.87	8.33	8.67
M1	G16835	37.33	37.33	66.67	63.33	0.05	1825.50	1366.10	1579.18	1.09	0.25	17.00	19.10	-0.12	11.67	10.13	13.10	11.53	8.67	8.33
M1	G19204	30.67	32.33	57.33	53.00	0.08	1536.30	1599.00	1567.34	-0.18	-0.04	25.83	25.23	0.02	9.80	10.00	9.80	6.13	10.33	9.67
M1	G2093	34.67	35.00	57.33	55.33	0.03	1721.10	1386.80	1544.93	0.84	0.19	24.73	22.63	0.08	11.53	9.40	10.80	4.60	10.33	8.67
M1	G3545	32.67	31.33	54.33	53.33	0.02	1664.50	1204.20	1415.77	1.20	0.28	23.23	19.63	0.15	9.73	7.80	4.53	2.27	9.67	9.33
M1	G3593	40.00	39.00	72.00	65.67	0.09	1444.90	1047.20	1230.08	1.20	0.28	19.07	20.67	-0.08	7.53	9.73	24.30	16.93	10.33	11.67
M1	G6450	37.67	38.33	63.33	66.33	-0.05	1653.40	864.47	1195.54	2.07	0.48	19.07	20.53	-0.08	12.53	8.27	13.50	11.77	9.67	9.33
M1	G955	36.33	33.67	60.33	58.00	0.04	1615.20	833.73	1160.45	2.10	0.48	25.20	22.80	0.10	12.93	8.67	26.03	10.23	10.00	9.67
M1	G3661	37.00	37.67	66.33	58.67	0.12	1608.30	662.60	1032.31	2.56	0.59	17.03	18.73	-0.10	11.67	8.20	20.00	12.20	8.33	7.67
M1	G4637	40.00	40.00	71.33	71.67	0.00	881.03	878.27	879.65	0.01	0.00	19.00	18.83	0.01	7.53	6.60	27.23	37.77	9.00	9.33
M1	G2445	42.00	43.67	68.00	67.33	0.01	1162.80	562.00	808.39	2.25	0.52	16.83	14.87	0.12	9.80	6.47	21.20	13.97	7.00	8.67
M1	G3595	38.67	39.00	72.33	67.33	0.07	826.73	429.10	595.61	2.09	0.48	19.10	19.43	-0.02	7.80	6.13	27.47	10.03	8.33	7.67
Mean		**35.79**	**35.57**	**62.73**	**59.51**	**0.05**	**1895.21**	**1374.91**	**1600.32**	**1.19**	**0.27**	**22.54**	**22.06**	**0.02**	**10.92**	**8.90**	**13.57**	**9.45**	**9.61**	**9.32**
M2	G3185	34.67	35.33	59.00	54.00	0.08	2723.40	1709.60	2157.76	1.62	0.37	26.37	23.70	0.10	12.20	8.20	7.70	3.40	10.33	10.00
M2	G11721	37.67	37.00	66.33	61.33	0.08	2192.10	2122.70	2157.12	0.14	0.03	20.33	18.53	0.09	12.20	7.80	4.63	3.37	9.67	9.00
M2	G18141	37.33	37.00	66.00	62.00	0.06	2679.50	1634.00	2092.44	1.70	0.39	20.77	21.93	-0.06	9.87	7.73	4.00	6.70	8.33	8.67
M2	G3005	37.00	36.33	65.33	62.00	0.05	2261.50	1774.20	2003.09	0.94	0.22	19.53	20.93	-0.07	11.13	10.87	3.47	1.43	9.00	8.67
M2	G1977	34.33	33.67	66.00	60.00	0.09	2212.10	1682.50	1929.21	1.04	0.24	20.80	23.90	-0.15	13.93	9.67	13.17	12.47	10.00	9.00
M2	G18454	35.33	34.67	59.00	56.00	0.05	2146.60	1623.10	1866.59	1.06	0.24	28.00	23.17	0.17	10.87	10.93	22.30	5.83	9.33	9.33
M2	G3017	29.33	26.67	51.33	49.00	0.05	1968.10	1762.30	1862.36	0.45	0.10	25.93	24.80	0.04	13.60	10.13	8.33	1.77	8.67	8.67
M2	G3586	37.00	37.00	65.00	63.67	0.02	1992.90	1714.70	1848.57	0.61	0.14	19.80	20.17	-0.02	9.20	9.73	6.53	8.40	9.00	8.67
M2	G4280	36.33	35.33	67.67	61.33	0.09	1778.50	1729.00	1753.58	0.12	0.03	20.13	23.87	-0.19	13.80	9.33	17.97	15.20	9.67	9.00
M2	G801	35.33	34.67	64.67	58.33	0.10	2125.90	1422.30	1738.87	1.44	0.33	33.37	24.70	0.26	13.87	8.60	26.97	12.23	10.33	10.67
M2	G3178	36.33	36.67	58.33	57.33	0.02	1983.40	1508.00	1729.44	1.04	0.24	22.90	24.93	-0.09	16.47	13.00	14.37	15.57	9.33	10.33
M2	G1264	37.33	38.00	65.00	65.33	-0.01	2005.40	1466.40	1714.85	1.17	0.27	19.67	22.87	-0.16	11.80	10.00	11.27	6.73	9.33	8.67
M2	G18451	29.00	29.33	54.33	52.00	0.04	1781.10	1562.40	1668.17	0.53	0.12	30.17	28.03	0.07	12.07	9.80	11.50	6.50	9.00	9.00
M2	G18157	33.00	30.00	57.00	53.33	0.06	1894.40	1370.60	1611.35	1.20	0.28	34.13	24.33	0.29	11.00	8.67	11.50	1.43	7.67	7.67
M2	G3217	38.33	38.33	67.33	65.67	0.02	1820.70	1355.40	1570.92	1.11	0.26	22.50	20.43	0.09	7.80	8.00	12.87	7.40	10.33	10.33
M2	G7952	37.67	38.67	66.00	65.67	0.01	2074.70	1059.20	1482.40	2.13	0.49	21.53	19.13	0.11	12.60	7.60	8.77	18.83	10.33	10.00
M2	G7765	34.67	34.33	66.00	57.00	0.14	1612.90	1288.10	1441.38	0.88	0.20	23.50	22.90	0.03	8.33	9.80	6.97	13.17	9.33	9.33
M2	G3990	37.67	37.00	66.33	58.00	0.13	1754.30	1180.40	1439.02	1.42	0.33	21.63	20.40	0.06	10.80	10.13	10.07	7.67	9.67	9.67
M2	G12806	39.33	39.00	69.00	65.67	0.05	1955.70	1025.90	1416.46	2.07	0.48	17.07	16.83	0.01	11.33	8.53	9.40	10.93	10.33	9.00
M2	G4258	34.00	33.33	60.67	55.33	0.09	1493.80	1300.00	1393.54	0.56	0.13	26.57	24.27	0.09	8.07	6.73	4.57	4.87	9.67	8.67
M2	G3142	37.00	38.33	68.00	66.67	0.02	1693.80	1130.90	1384.02	1.44	0.33	23.53	19.63	0.17	10.87	7.73	8.83	13.03	9.67	8.33
M2	G5733	31.33	31.67	52.33	52.67	-0.01	1455.70	1305.20	1378.40	0.45	0.10	24.87	24.13	0.03	7.40	7.07	11.33	13.53	10.00	9.00
M2	G16849A	34.00	33.67	57.00	52.67	0.08	1584.80	1197.60	1377.66	1.06	0.24	23.20	25.53	-0.10	10.13	6.00	18.37	8.37	9.67	9.33
M2	G803	28.67	29.33	50.67	50.33	0.01	1546.10	1222.60	1374.87	0.91	0.21	27.23	21.70	0.20	14.47	8.47	9.17	5.17	8.67	7.33
M2	G1957	36.00	36.00	65.67	58.67	0.11	1326.40	1372.70	1349.35	-0.15	-0.03	21.07	23.73	-0.13	12.87	12.13	15.13	7.33	10.67	9.33
M2	G7038	40.00	39.00	66.33	63.33	0.05	1790.30	988.33	1330.19	1.95	0.45	25.47	18.93	0.26	12.93	8.40	16.30	19.30	8.00	8.00
M2	G1358	35.67	36.00	64.67	58.67	0.09	1555.40	1036.80	1269.90	1.45	0.33	20.63	18.40	0.11	11.40	7.33	22.80	3.43	10.33	9.67
M2	G14163	37.00	36.67	69.00	66.33	0.04	1260.40	1266.30	1263.35	-0.02	0.00	21.33	19.77	0.07	10.67	12.73	33.37	20.30	9.67	10.00
M2	G15641	35.00	35.00	62.00	57.00	0.08	1458.00	1066.30	1246.86	1.17	0.27	18.53	17.50	0.06	11.07	11.87	20.87	30.93	9.33	8.67
M2	G7863	35.33	34.67	66.00	56.33	0.15	1158.50	761.17	939.05	1.49	0.34	24.03	22.97	0.04	8.53	7.33	13.60	12.30	9.67	8.67
M2	G17649	37.33	34.67	68.00	64.67	0.05	1375.40	492.90	823.37	2.79	0.64	25.00	17.67	0.29	13.13	7.80	15.90	25.27	9.33	8.00
M2	G7761	37.00	37.00	69.00	66.00	0.04	800.87	631.57	711.20	0.92	0.21	18.57	17.55	0.05	13.27	10.20	25.00	16.25	7.67	4.67
M2	G5712	38.33	38.33	72.33	70.33	0.03	520.47	200.30	322.88	2.67	0.62	23.23	20.90	0.10	4.93	3.40	31.97	22.53	7.67	8.67
Mean		**35.59**	**35.23**	**63.37**	**59.60**	**0.06**	**1757.06**	**1301.92**	**1504.49**	1.13	**0.26**	**23.38**	**21.76**	**0.07**	**11.29**	**8.96**	**13.91**	**10.96**	**9.38**	**8.91**
	G. mean	**34.59**	**34.19**	**63.11**	**59.26**		**1781.61**	**1377.32**				**25.88**	**24.51**		**10.83**	**9.14**	**14.53**	**11.46**	**9.13**	**8.86**
	lsd	**1.97**	**1.73**	**4.31**	**9.58**		**547.01**	**607.73**				**8.08**	**6.12**		**5.15**	**4.15**	**14.73**	**14.23**	**1.45**	**1.60**

M1 – Mesoamerica 1; M2 – Mesoamerica 2; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index; PR – Percent reduction

Appendix 3 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
check	BAT477	5.665	7.563	7.177	7.125	14.84	17.03	14.52	31.72
check	BAT93	4.046	3.439	8.133	5.743	15.37	9.89	15.01	19.07
check	DOR390	6.145	6.275	9.477	8.949	18.29	12.07	18.03	27.29
check	Maharagi Soya	4.439	4.112	7.811	5.347	13.54	8.72	13.23	18.18
check	Masaai Red	6.571	4.581	9.391	5.283	6.09	2.62	5.87	12.48
check	Pinto Villa	4.237	4.41	6.362	5.533	15.91	12.83	15.76	22.77
check	SXB418	3.897	4.782	5.903	5.423	15.61	13.14	15.16	23.35
check	G10971	4.388	4.402	7.691	5.896	18.81	16.84	18.72	27.14
check	G2866	4.455	4.002	7.229	4.71	18.3	13.84	17.98	22.55
check	G19012	3.639	4.882	6.886	6.162	14.7	16.92	14.37	27.97
check	G4278	5.67	5.843	11.147	7.181	16.9	9.82	16.59	22.85
check	G16835	5.839	6.044	8.407	6.484	14.89	11.06	14.77	23.59
check	G3017	5.291	4.768	8.919	6.877	15.35	12.41	14.73	24.05
	Mean	**4.94**	**5.01**	**8.04**	**6.21**	**15.28**	**12.09**	**14.98**	**23.31**
D1	G1797	7.293	5.895	13.145	8.903	12.23	6.79	12.14	21.59
D1	G2379	3.873	4.252	7.437	5.903	11.61	13.13	11.3	23.28
D1	G2778	4.247	3.841	7.808	5.317	17.32	14.64	16.93	23.79
D1	G14737	6.213	4.828	10.423	6.253	19.14	12.94	18.89	24.02
D1	G14914	3.749	4.385	7.605	5.993	16.83	10.67	16.63	21.05
D1	G22044	4.791	4.967	7.659	5.635	14.12	12.18	13.86	22.78
D1	G1356	4.107	4.403	8.611	5.488	3.88	1	8.01	10.9
D1	G22787	4.774	4.595	8.081	7.105	18.33	13.46	18.12	25.16
D1	G2660	2.827	4.517	4.937	5.318	8.97	13.36	8.74	23.19
D1	G4730	3.505	3.447	7.055	4.92	23.02	13.68	22.5	22.05
D1	G12778	3.523	3.393	5.675	3.937	14.38	12.53	14.03	19.86
D1	G4206	5.142	4.405	8.285	5.545	7.04	10.24	6.93	20.19
D1	G5694	3.866	3.347	5.907	4.763	13.88	6.61	13.78	14.72
D1	G2352	3.5	3.701	5.177	4.617	13.33	12.22	12.9	20.53
D1	G11721	3.234	4.041	6.87	5.421	16.17	13.54	15.79	23
D1	G3990	4.613	5.292	7.258	5.972	17.14	10.12	16.82	21.38
D1	G7761	7.244	4.739	11.227	6.338	18.61	12.73	18.38	23.8
	Mean	**4.50**	**4.36**	**7.83**	**5.73**	**14.47**	**11.17**	**14.46**	**21.25**
D2	SEA15	3.867	3.813	5.603	4.833	19.08	14.83	18.85	23.48
D2	SER16	7.937	8.185	11.789	8.969	0.42	0.9	20.146	18.06
D2	G13177	4.949	4.475	6.825	5.594	17.5	17.1	17.32	27.16
D2	G2635	6.953	5.989	9.835	6.594	9.19	4.99	8.77	17.57
D2	G7602	6.662	4.551	8.117	5.001	1.21	0.59	1.06	10.14
D2	G3331	3.568	4.787	6.385	6.053	10.31	10.64	10.01	21.48
D2	G3936	4.762	4.173	8.913	5.786	11.65	8.19	11.25	18.15
D2	G16072	3.145	4.393	4.877	4.591	15.17	9.97	14.26	18.95
D2	G5653	5.641	4.672	8.422	6.315	15.31	9.41	15.02	20.4
D2	DOR364	6.412	5.591	9.625	6.149	11.83	7	11.69	18.74
D2	G6450	5.815	4.408	10.112	5.943	16.61	9.69	16.32	20.04
D2	G15416	8.047	5.939	12.651	7.72	11.91	4.86	11.78	18.52
D2	G18147	5.461	4.168	9.541	6.117	11.13	5.58	10.9	15.86
D2	G2348	5.318	4.104	7.826	4.689	19.19	8.41	18.65	17.2
D2	G18454	4.663	7.205	7.115	7.507	6.27	3.4	6.08	18.11
D2	G17649	4.333	5.578	7.209	6.39	13.64	8.98	13.34	20.94
D2	G3178	4.375	3.703	8.263	6.313	15.87	13.3	15.32	23.31
D2	G7952	5.329	4.326	8.774	5.551	16.42	9.34	16.29	19.22
D2	G801	5.351	4.366	5.721	4.346	15.28	13.53	15.14	22.24
D2	G803	7.547	6.296	10.229	8.211	0.57	1.79	0.41	16.29
	Mean	**5.51**	**5.04**	**8.39**	**6.13**	**11.93**	**8.13**	**12.63**	**19.29**
G	G13696	5.364	4.374	8.666	5.789	4.06	1.61	3.72	11.77
G	G11656A	5.631	7.637	9.128	8.382	11.75	7.91	11.56	23.93
G	G5036	3.754	2.191	5.967	4.759	15	19.31	14.32	26.26
G	G16849A	6.981	6.331	10.389	7.269	11.19	5.39	11.08	18.99
G	G18451	4.363	5.837	7.819	8.619	5.11	3.14	4.9	17.6
G	G1977	5.335	5.024	10.421	7.317	9.08	9.18	8.72	21.52
G	G3586	5.892	6.333	8.127	6.631	10.54	7.29	10.43	20.25
G	G4258	8.916	8.381	11.619	9.953	5.43	2.09	5.18	20.43
G	G5712	4.959	5.919	9.296	6.937	8.22	5.75	8	18.61
G	G7038	5.425	3.157	9.204	4.456	6.56	1.58	6.23	9.19
	Mean	**5.66**	**5.52**	**9.06**	**7.01**	**8.69**	**6.33**	**8.41**	**18.86**

Appendix 3 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
M1	NCB280	7.136	5.469	8.763	6.32	10.09	11.33	9.8	23.12
M1	SER109	4.994	4.632	8.816	4.686	15.81	12.21	15.54	21.53
M1	G10945	5.046	6.688	10.245	8.894	12.99	12.77	12.38	28.35
M1	G11010	6.163	6.411	8.26	7.434	11.05	7.8	10.79	21.65
M1	G19941	3.665	4.914	6.203	5.455	15.55	8.07	15.43	18.44
M1	G2402	4.301	4.148	8.058	4.769	14.46	7.83	14.39	16.75
M1	G4342	4.241	5.067	6.196	5.217	10.77	10.03	10.41	20.31
M1	G4822	4.338	4.059	7.023	5.409	10.06	7.85	9.46	17.32
M1	G12796	4.233	6.542	7.364	5.603	12.89	8.28	12.44	20.43
M1	G15685	5.169	4.326	9.183	6.411	13.51	9.4	12.95	20.13
M1	G16026	5.663	6.003	8.261	6.939	14.32	7.97	13.53	20.91
M1	G278	6.63	6.691	8.593	7.606	10.1	9.25	7.56	23.55
M1	G1328	5.969	4.613	7.575	5.669	9.96	10.13	9.57	20.41
M1	G16400	7.575	8.673	11.159	9.107	2.59	2.65	2.45	20.43
M1	G2277	3.546	4.941	5.177	4.885	11.02	12	10.75	21.83
M1	G21212	3.545	3.834	6.543	4.711	11.45	8.25	11.23	16.8
M1	G2093	7.086	7.099	9.931	7.879	5.37	5.2	5.15	20.18
M1	G3545	7.711	6.891	11.043	7.703	4.12	2.57	3.81	17.16
M1	G4002	4.745	4.643	7.499	5.803	9.11	3.49	8.86	13.93
M1	G4495	6.201	5.441	8.86	6.11	16.54	9.58	16.13	21.13
M1	G2997	6.668	7.584	10.053	9.889	16.37	11.52	16.21	28.99
M1	G1358	7.45	6.635	11.375	8.135	18.87	11.52	18.62	26.29
M1	G14163	7.896	8.317	14.101	9.82	2.48	1.97	1.92	20.11
M1	G15641	6.533	5.232	9.491	5.019	9.33	7.05	8.98	17.3
M1	G18141	4.751	5.463	8.235	7.327	14.43	11.75	14.14	24.54
M1	G1957	7.961	8.331	11.142	8.575	13	6.01	12.41	22.91
M1	G3185	4.163	2.781	6.335	3.808	19.45	7.2	18.97	13.79
M1	G5733	5.5	5.229	7.231	5.361	10.64	7.99	10.28	18.58
	Mean	**5.67**	**5.74**	**8.67**	**6.59**	**11.65**	**8.27**	**11.22**	**20.60**
M2	Tio Canela 75	5.711	6.28	9.922	7.911	13.97	11.09	13.15	25.29
M2	VAX3	5.673	5.895	9.225	6.591	12.64	6.3	11.76	18.78
M2	G10982	6.661	5.973	10.15	6.946	11.95	5.91	11.6	18.82
M2	G18440	5.318	4.275	6.754	3.988	10.04	10.26	9.99	18.52
M2	G2775	6.426	4.795	8.617	6.217	11.78	11.18	11.11	22.19
M2	G3807	3.673	4.173	8.041	5.497	8.67	9.41	8.21	19.08
M2	G13578	4.429	3.13	6.949	5.047	10.72	11.14	10.52	19.32
M2	G11057	6.27	6.353	10.25	7.581	9.98	5.52	9.56	19.45
M2	G3334	6.214	5.681	10.504	6.193	17.83	8.28	17.53	20.16
M2	G4017	3.762	4.065	7.321	4.653	11.79	8.58	11.7	17.3
M2	G753	4.041	3.545	7.286	4.541	14.68	7.81	14.35	15.9
M2	G7742	3.959	5.774	6.126	6.631	11.94	11.02	11.72	23.43
M2	G16401	5.188	4.293	7.362	4.62	12.62	5.85	12.25	14.76
M2	G19204	5.999	6.724	9.354	6.419	16.61	8.98	16.09	22.12
M2	G3593	5.158	4.878	9.49	6.157	12.42	10.14	12.21	21.17
M2	G17648	3.769	3.026	4.653	3.87	13.4	11.51	13.2	18.4
M2	G2137	6.746	6.09	9.613	6.749	14.01	6.49	13.42	19.33
M2	G2199	4.564	5.314	7.583	5.725	12.25	11.91	11.66	22.95
M2	G2445	5.209	5.708	8.519	6.361	12.53	11.13	11.83	23.2
M2	G3595	5.103	6.721	8.271	7.984	8.14	9.55	7.87	24.26
M2	G3661	5.237	5.895	8.176	6.785	9.32	6.85	9.07	19.53
M2	G4637	4.658	5.762	7.449	6.44	9.74	5.89	9.23	18.09
M2	G7932	3.057	6.987	5.751	7.044	5.48	10.16	5.17	24.19
M2	G955	7.542	5.201	9.743	5.207	14.16	8.85	13.55	19.26
M2	G1264	6.928	5.563	10.411	7.387	2.81	0.58	2.71	13.53
M2	G12806	3.542	3.472	5.639	3.975	13.79	11.42	13.69	18.86
M2	G3005	7.198	6.269	10.049	7.577	8.11	3.93	8	17.77
M2	G3217	5.174	5.727	7.021	6.932	6.09	2.67	5.88	15.33
M2	G7765	4.276	4.041	7.625	6.732	10.84	12.89	10.58	23.67
M2	G18157	5.995	5.287	8.957	5.974	7.84	7.75	7.59	19.01
M2	G3142	6.24	6.914	10.143	8.863	11.99	3.83	10.68	19.61
M2	G4280	6.309	5.285	9.011	6.254	12.9	7.53	12.51	19.07
M2	G7863	3.907	3.455	5.323	4.625	13.56	6.74	13.24	14.82
	Mean	**5.27**	**5.23**	**8.22**	**6.17**	**11.35**	**8.22**	**10.96**	**19.61**
	Grand mean	**5.29**	**5.19**	**8.35**	**6.27**	**12.16**	**8.89**	**12.01**	**20.35**
	LSD	**1.40**	**1.46**	**1.67**	**2.13**	**4.34**	**4.16**	**4.89**	**5.36**

LSD – least significant difference

Appendix 4 Performance of 121 Mesoamerican genotypes evaluated under irrigated and rainfed treatments at Harare Research Station, 2011

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	Genotype	Irr	Dro	Irr	Dro	PR	Irr	Dro	GMY	DSI	PR	Irr	Dro	PR	Irr	Dro	Irr	Dro	Irr	Dro
check	BAT477	38.00	39.00	100.00	98.33	0.02	1048.00	616.00	803.47	0.81	0.41	13.00	10.00	0.23	11.00	7.33	1.33	1.00	8.33	7.33
check	BAT93	41.33	40.67	98.00	83.67	0.15	696.00	176.00	349.99	1.46	0.75	8.67	6.33	0.27	11.00	5.33	2.33	3.00	8.00	5.33
check	DOR390	43.33	42.33	100.33	98.00	0.02	1624.00	560.00	953.65	1.28	0.66	12.33	9.33	0.24	15.00	11.33	1.33	3.00	8.00	7.00
check	Maharagi Soya	42.00	40.00	97.33	87.00	0.11	992.00	488.00	695.77	1.00	0.51	11.00	8.67	0.21	8.33	8.00	1.00	2.00	7.00	7.67
check	Masaai Red	35.33	37.67	100.00	94.00	0.06	1056.00	488.00	717.86	1.05	0.54	14.33	11.33	0.21	10.00	8.00	1.33	2.00	9.67	7.00
check	NCB280	33.00	32.00	76.67	72.67	0.05	504.00	160.00	283.97	1.34	0.68	10.00	7.33	0.27	7.67	6.33	2.33	3.00	6.67	7.33
check	Pinto Villa	32.67	32.33	76.33	72.33	0.05	576.00	712.00	640.40	-0.46	-0.24	15.33	13.67	0.11	8.33	10.33	4.33	3.67	6.33	7.33
check	SEA15	36.00	35.33	93.33	78.00	0.16	592.00	400.00	486.62	0.64	0.32	13.67	12.67	0.07	9.33	7.00	3.00	3.33	9.00	7.67
check	SER109	36.00	35.33	91.00	81.33	0.11	616.00	352.00	465.65	0.84	0.43	12.67	10.67	0.16	7.00	6.67	1.67	2.67	8.67	8.00
check	SER16	35.67	37.00	91.00	83.00	0.09	480.00	552.00	514.74	-0.29	-0.15	12.00	10.00	0.17	7.33	8.33	0.67	3.00	6.33	8.00
check	SXB418	43.00	39.00	89.00	85.67	0.04	448.00	416.00	431.70	0.14	0.07	9.00	7.33	0.19	7.33	6.67	1.67	3.00	8.33	8.33
check	Tio Canela 75	43.00	40.67	99.67	93.67	0.06	728.00	472.00	586.19	0.69	0.35	17.33	11.00	0.37	9.33	8.00	1.67	2.00	6.67	11.00
check	VAX3	36.33	37.00	92.33	88.67	0.04	1144.00	800.00	956.66	0.59	0.30	14.67	16.00	-0.09	8.33	11.00	1.00	3.00	8.67	9.67
Mean		**38.13**	**37.56**	**92.69**	**85.87**	**0.07**	**808.00**	**476.31**	**606.67**	**0.80**	**0.41**	**12.62**	**10.33**	**0.18**	**9.23**	**8.02**	**1.82**	**2.67**	**7.82**	**7.82**
D1	G10945	37.67	39.00	93.33	91.33	0.02	1024.00	536.00	740.85	0.93	0.48	15.33	13.00	0.15	8.67	8.00	2.33	2.00	7.67	8.67
D1	G10971	33.33	32.00	78.33	79.33	-0.01	848.00	584.00	703.73	0.61	0.31	19.00	15.33	0.19	9.67	7.00	3.67	2.33	7.67	7.00
D1	G10982	33.33	32.00	77.67	73.00	0.06	632.00	440.00	527.33	0.60	0.30	18.00	15.67	0.13	8.00	6.67	3.00	2.00	7.67	6.33
D1	G11010	34.67	37.33	93.33	79.67	0.15	1704.00	584.00	997.57	1.29	0.66	24.33	19.33	0.21	7.33	6.67	2.33	2.67	8.00	8.00
D1	G13177	33.00	32.00	78.67	73.00	0.07	560.00	224.00	354.18	1.18	0.60	18.67	9.00	0.52	5.67	4.33	3.00	4.00	6.67	6.00
D1	G13696	32.67	31.67	85.00	78.00	0.08	440.00	272.00	345.95	0.75	0.38	15.33	7.67	0.50	7.67	7.33	3.33	4.33	7.00	5.67
D1	G1797	38.00	36.00	98.67	99.33	-0.01	840.00	640.00	733.21	0.47	0.24	14.67	15.33	-0.04	8.67	7.67	1.67	1.67	7.33	6.67
D1	G18440	33.33	32.33	81.00	80.33	0.01	824.00	802.00	812.93	0.05	0.03	21.00	19.00	0.10	8.00	7.00	4.00	2.00	8.67	8.00
D1	G19941	32.00	31.33	75.33	73.67	0.02	496.00	344.00	413.07	0.60	0.31	18.33	13.00	0.29	7.00	6.33	3.33	3.33	7.67	5.67
D1	G2379	40.67	40.00	98.67	94.67	0.04	1872.00	616.00	1073.85	1.32	0.67	12.33	11.67	0.05	15.00	8.67	3.67	2.33	9.67	8.67
D1	G2402	32.00	31.33	77.00	72.00	0.06	480.00	328.00	396.79	0.62	0.32	14.00	9.67	0.31	10.33	9.00	4.00	5.33	7.00	7.33
D1	G2635	36.67	36.67	90.67	88.00	0.03	920.00	624.00	757.68	0.63	0.32	20.00	17.00	0.15	8.67	7.33	2.67	3.67	7.00	7.33
D1	G2775	32.67	32.33	76.67	76.67	0.00	736.00	344.00	503.17	1.04	0.53	20.00	11.00	0.45	7.00	5.00	3.67	3.33	7.33	7.00
D1	G2778	32.67	32.33	76.33	75.00	0.02	504.00	318.00	400.34	0.72	0.37	14.67	9.33	0.36	7.00	7.00	3.33	4.67	7.33	6.67
D1	G2866	33.00	32.67	82.00	80.00	0.02	1024.00	392.00	633.57	1.21	0.62	15.00	12.33	0.18	10.00	8.00	3.33	3.67	8.33	7.00
D1	G4342	35.00	34.33	95.33	84.33	0.12	544.00	312.00	411.98	0.84	0.43	13.00	12.00	0.08	8.67	5.67	3.67	2.33	8.67	7.00
D1	G7602	34.33	33.67	86.67	79.33	0.08	776.00	464.00	600.05	0.79	0.40	27.00	23.33	0.14	5.33	5.67	1.33	3.00	6.67	7.00
Mean		**34.41**	**33.94**	**84.98**	**81.04**	**0.05**	**836.71**	**460.24**	**612.13**	**0.88**	**0.45**	**17.69**	**13.74**	**0.22**	**8.39**	**6.90**	**3.08**	**3.10**	**7.67**	**7.06**
D2	G11057	33.67	33.00	78.33	72.33	0.08	328.00	264.00	294.27	0.38	0.20	12.67	10.00	0.21	5.33	5.33	3.33	1.67	7.67	6.33
D2	G11656A	40.33	40.67	93.67	94.00	0.00	648.00	186.00	347.17	1.40	0.71	6.00	7.33	-0.22	12.33	9.67	6.00	5.67	5.67	7.67
D2	G12796	34.33	34.67	87.00	79.67	0.08	600.00	584.00	591.95	0.05	0.03	11.33	10.00	0.12	8.00	9.67	2.00	2.67	7.00	6.67
D2	G13578	43.00	40.00	98.67	92.33	0.06	1008.00	376.00	615.64	1.23	0.63	14.33	10.33	0.28	11.67	7.00	2.67	2.00	7.67	7.33
D2	G14737	41.00	41.33	101.33	98.67	0.03	936.00	512.00	692.27	0.89	0.45	17.33	9.67	0.44	8.33	6.00	1.00	1.33	9.00	8.33
D2	G14914	39.33	38.33	99.67	88.67	0.11	992.00	120.00	345.02	1.72	0.88	10.67	5.00	0.53	11.33	4.67	4.00	3.33	7.00	5.67
D2	G15685	38.00	38.67	89.00	86.00	0.03	856.00	320.00	523.37	1.23	0.63	15.67	12.00	0.23	9.67	5.00	2.00	3.00	7.67	8.67
D2	G16026	33.67	33.00	82.33	73.33	0.11	232.00	264.00	247.48	-0.27	-0.14	9.33	9.33	0.00	3.33	4.33	1.33	5.00	6.33	8.00
D2	G19012	34.33	34.00	93.33	81.00	0.13	848.00	480.00	638.00	0.85	0.43	20.00	15.67	0.22	7.67	6.33	2.67	4.00	8.67	6.67
D2	G22044	34.67	34.33	96.67	89.00	0.08	616.00	568.00	591.51	0.15	0.08	11.33	13.67	-0.21	8.67	9.00	2.33	2.00	8.67	8.00
D2	G278	37.33	37.00	92.67	84.33	0.09	872.00	448.00	625.02	0.95	0.49	8.00	7.67	0.04	14.67	12.00	4.67	2.33	7.00	7.33
D2	G3331	36.67	37.67	98.67	89.33	0.09	1296.00	512.00	814.59	1.19	0.60	10.67	10.33	0.03	13.67	8.00	3.00	2.67	7.67	7.67
D2	G3334	34.67	34.00	98.67	90.67	0.08	1112.00	512.00	754.55	1.06	0.54	11.67	10.67	0.09	13.00	10.33	3.33	3.00	8.00	7.67
D2	G3807	38.67	41.33	94.00	81.33	0.13	744.00	368.00	523.25	0.99	0.51	10.67	7.67	0.28	9.33	7.33	1.33	4.00	7.33	8.33
D2	G3936	40.00	39.00	97.00	90.67	0.07	568.00	184.00	323.28	1.33	0.68	10.00	6.00	0.40	10.67	8.67	2.33	4.67	8.00	5.33
D2	G4017	43.67	42.33	99.00	92.33	0.07	1752.00	576.00	1004.57	1.32	0.67	12.00	11.33	0.06	14.67	7.67	1.00	2.67	6.33	9.33
D2	G4278	35.33	36.00	95.33	83.67	0.12	648.00	336.00	466.61	0.94	0.48	11.00	9.67	0.12	11.00	8.33	3.33	3.33	7.00	7.67
D2	G4822	41.67	38.00	97.00	88.33	0.09	1112.00	392.00	660.23	1.27	0.65	11.00	8.67	0.21	11.00	7.67	2.33	2.33	8.67	8.00
D2	G753	34.00	34.33	86.00	74.00	0.14	528.00	160.00	290.65	1.37	0.70	11.00	5.33	0.52	6.00	4.67	2.00	1.33	8.67	8.00
D2	G7742	41.00	41.00	94.67	98.67	-0.04	880.00	176.00	393.55	1.57	0.80	15.67	7.00	0.55	11.33	6.67	1.67	3.00	9.00	7.00
Mean		**37.77**	**37.43**	**93.65**	**86.42**	**0.08**	**828.80**	**366.90**	**537.15**	**1.09**	**0.56**	**12.02**	**9.37**	**0.22**	**10.08**	**7.42**	**2.62**	**3.00**	**7.65**	**7.48**
G	G1328	36.00	34.67	99.00	87.33	0.12	1040.00	336.00	591.13	1.33	0.68	13.00	11.00	0.15	13.33	9.00	3.67	4.67	7.33	6.33
G	G1356	41.33	41.67	101.00	92.33	0.09	1160.00	520.00	776.66	1.08	0.55	10.33	11.33	-0.10	12.67	9.33	1.67	3.00	6.33	7.00
G	G16072	32.67	32.67	78.67	72.67	0.08	760.00	424.00	567.66	0.87	0.44	15.67	7.67	0.51	7.33	8.33	5.00	2.33	7.67	7.33
G	G16400	37.00	38.00	98.33	89.00	0.09	760.00	472.00	598.93	0.74	0.38	11.33	10.33	0.09	10.33	8.67	2.67	3.00	7.33	6.00
G	G16401	34.33	36.00	95.67	89.00	0.07	1376.00	280.00	620.71	1.56	0.80	17.33	11.33	0.35	12.67	6.33	2.67	2.33	8.00	7.00
G	G2277	41.00	39.33	98.00	90.67	0.07	944.00	600.00	752.60	0.71	0.36	14.33	11.67	0.19	10.00	11.00	2.00	6.67	7.00	7.00
G	G22787	35.00	34.00	98.33	90.33	0.08	920.00	536.00	702.23	0.82	0.42	19.33	15.67	0.19	9.33	6.33	1.67	1.67	7.33	7.33
G	G2660	37.67	39.00	97.00	100.00	-0.03	744.00	512.00	617.19	0.61	0.31	11.67	11.33	0.03	8.00	9.33	0.67	3.00	7.33	7.00
G	G4730	41.00	40.00	100.00	99.67	0.00	800.00	344.00	524.60	1.12	0.57	10.33	6.00	0.42	15.33	11.33	3.33	2.67	6.67	6.00
G	G5653	37.67	35.33	94.67	89.33	0.06	1192.00	208.00	497.93	1.62	0.83	17.33	6.33	0.63	12.00	6.67	3.33	6.67	9.00	5.33
Mean		**37.37**	**37.07**	**96.07**	**90.03**	**0.06**	**969.60**	**423.20**	**624.96**	**1.10**	**0.56**	**14.07**	**10.27**	**0.27**	**11.10**	**8.63**	**2.67**	**3.60**	**7.40**	**6.63**

D1 – Durango 1; D2 – Durango 2; G – Guatemala; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index; PR – Percent reduction

Appendix 4 continued

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	**Genotype**	**Irr**	**Dro**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**GMY**	**DSI**	**PR**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**Irr**	**Dro**	**Irr**	**Dro**
M1	DOR364	43.00	42.00	100.33	88.67	0.12	1120.00	400.00	669.33	1.26	0.64	12.67	8.67	0.32	12.00	7.67	1.00	3.00	8.00	8.33
M1	G12778	34.67	33.33	84.00	77.67	0.08	472.00	296.00	373.78	0.73	0.37	10.67	9.33	0.13	5.00	7.33	1.67	4.33	8.67	6.00
M1	G15416	42.00	42.00	98.00	86.00	0.12	1336.00	320.00	653.85	1.49	0.76	11.33	5.67	0.50	16.00	6.67	2.33	2.67	7.33	6.67
M1	G16835	44.00	42.33	101.33	92.33	0.09	640.00	416.00	515.98	0.69	0.35	10.33	6.00	0.42	11.00	9.67	1.00	4.33	7.00	5.67
M1	G17648	34.00	33.67	94.33	83.00	0.12	544.00	256.00	373.18	1.04	0.53	8.67	8.00	0.08	6.67	5.67	0.67	1.67	8.67	7.33
M1	G18147	35.33	35.00	82.00	85.67	-0.04	1008.00	352.00	595.66	1.28	0.65	13.33	12.00	0.10	12.00	7.00	2.67	3.00	8.33	6.67
M1	G19204	35.33	34.67	94.67	80.67	0.15	792.00	464.00	606.21	0.81	0.41	12.00	9.00	0.25	10.67	8.67	2.00	3.00	7.33	9.00
M1	G2093	41.67	38.00	91.67	85.00	0.07	696.00	368.00	506.09	0.92	0.47	12.00	9.67	0.19	10.67	8.67	3.00	4.00	8.00	7.67
M1	G21212	38.00	36.67	95.67	87.33	0.09	1056.00	464.00	699.99	1.10	0.56	13.00	11.67	0.10	11.33	7.67	2.00	1.67	8.00	8.00
M1	G2137	40.33	39.33	98.00	89.00	0.09	720.00	696.00	707.90	0.07	0.03	12.00	10.67	0.11	9.33	10.33	3.67	5.67	7.67	6.67
M1	G2199	43.33	41.67	99.00	93.33	0.06	1064.00	312.00	576.17	1.39	0.71	10.33	9.33	0.10	8.33	6.33	0.67	3.33	8.33	7.33
M1	G2348	43.33	43.33	100.33	97.00	0.03	856.00	264.00	475.38	1.36	0.69	12.67	7.33	0.42	8.00	5.67	1.67	3.33	9.67	7.67
M1	G2352	39.33	38.00	99.33	98.67	0.01	1032.00	432.00	667.70	1.14	0.58	13.67	11.33	0.17	9.67	6.67	2.67	1.67	7.33	9.00
M1	G2445	43.00	42.67	98.33	91.67	0.07	768.00	544.00	646.37	0.57	0.29	7.33	10.67	-0.46	9.00	7.67	2.00	1.00	7.67	8.67
M1	G2997	36.33	34.33	85.00	75.33	0.11	592.00	232.00	370.60	1.19	0.61	10.33	7.33	0.29	8.67	6.00	1.67	2.33	7.67	7.33
M1	G3545	35.33	36.67	93.00	80.67	0.13	824.00	312.00	507.04	1.22	0.62	10.67	9.67	0.09	10.00	10.33	3.00	4.00	9.00	7.67
M1	G3593	43.00	43.33	100.00	95.00	0.05	1384.00	608.00	917.32	1.10	0.56	13.33	12.33	0.08	13.00	8.67	2.00	4.33	10.33	9.00
M1	G3595	43.33	41.67	100.67	97.33	0.03	896.00	224.00	448.00	1.47	0.75	11.00	6.67	0.39	13.33	7.67	2.67	3.00	10.00	8.33
M1	G3661	40.67	26.00	66.67	55.67	0.16	720.00	88.00	251.71	1.72	0.88	8.00	3.67	0.54	15.67	4.67	6.00	4.00	7.00	4.00
M1	G4002	42.00	39.00	89.00	80.67	0.09	568.00	184.00	323.28	1.33	0.68	9.33	7.00	0.25	11.33	7.33	2.67	4.67	9.67	7.67
M1	G4206	41.67	40.33	68.67	95.33	-0.39	960.00	728.00	835.99	0.47	0.24	14.33	10.00	0.30	10.00	12.33	1.67	3.00	7.00	7.67
M1	G4495	43.67	38.33	99.67	98.00	0.02	1032.00	192.00	445.13	1.60	0.81	12.67	6.67	0.47	9.67	7.33	1.00	3.33	7.67	7.33
M1	G4637	42.33	42.67	99.33	97.67	0.02	888.00	160.00	376.94	1.61	0.82	13.33	4.33	0.68	8.67	8.00	2.00	2.33	7.00	9.33
M1	G5036	43.00	44.00	100.00	92.67	0.07	960.00	368.00	594.37	1.21	0.62	11.00	7.00	0.36	10.00	6.67	1.67	2.00	7.67	5.67
M1	G5694	38.00	36.67	96.67	88.00	0.09	856.00	328.00	529.88	1.21	0.62	10.67	7.33	0.31	11.33	8.33	1.00	3.00	7.00	7.00
M1	G6450	43.00	44.00	100.00	99.33	0.01	848.00	600.00	713.30	0.57	0.29	11.00	10.33	0.06	10.67	10.33	2.33	5.00	8.33	8.67
M1	G7932	34.33	36.33	83.67	73.67	0.12	536.00	288.00	392.90	0.91	0.46	12.33	8.33	0.32	7.00	6.33	2.67	3.67	10.00	8.00
M1	G955	34.67	34.33	92.33	81.00	0.12	680.00	312.00	460.61	1.06	0.54	11.33	8.67	0.23	9.67	5.00	3.00	5.00	7.67	8.67
Mean		**39.95**	**38.58**	**93.27**	**87.37**	**0.06**	**851.71**	**364.57**	**544.09**	**1.12**	**0.57**	**11.40**	**8.52**	**0.25**	**10.31**	**7.67**	**2.16**	**3.30**	**8.14**	**7.54**
M2	G11721	42.67	44.33	99.67	95.33	0.04	824.00	864.00	843.76	-0.10	-0.05	10.33	8.33	0.19	13.67	13.67	3.33	3.00	7.00	7.67
M2	G1264	41.33	42.00	99.67	95.67	0.04	888.00	960.00	923.30	-0.16	-0.08	11.00	9.33	0.15	10.00	14.33	2.00	3.67	7.00	6.67
M2	G12806	43.00	40.67	100.00	94.33	0.06	800.00	320.00	505.96	1.18	0.60	9.33	7.33	0.21	12.00	8.33	1.33	2.67	8.00	7.33
M2	G1358	38.33	35.33	100.00	90.67	0.09	920.00	288.00	514.74	1.35	0.69	12.00	10.67	0.11	8.33	8.33	2.00	2.00	10.33	7.67
M2	G14163	43.00	40.00	98.00	92.00	0.06	1848.00	328.00	778.55	1.61	0.82	13.67	9.33	0.32	11.67	8.00	2.33	2.67	9.00	9.00
M2	G15641	40.67	40.33	95.33	88.67	0.07	816.00	680.00	744.90	0.33	0.17	13.33	9.33	0.30	12.00	11.67	4.67	5.67	7.67	7.00
M2	G16849A	34.67	35.67	85.67	77.33	0.10	400.00	184.00	271.29	1.06	0.54	11.00	6.33	0.42	8.00	6.67	3.00	4.67	8.00	7.00
M2	G17649	36.67	35.67	99.33	92.00	0.07	1168.00	512.00	773.31	1.10	0.56	11.33	9.00	0.21	15.67	10.33	3.33	4.33	5.67	5.33
M2	G18141	43.33	43.67	99.33	95.00	0.04	456.00	368.00	409.64	0.38	0.19	11.00	7.00	0.36	8.33	7.67	1.67	2.00	6.67	8.00
M2	G18157	34.33	34.67	93.67	75.67	0.19	280.00	248.00	263.51	0.22	0.11	11.00	9.67	0.12	6.00	6.00	2.67	1.00	8.00	7.33
M2	G18451	33.67	32.67	80.00	76.33	0.05	392.00	208.00	285.55	0.92	0.47	11.67	7.67	0.34	4.00	7.67	1.33	2.67	6.33	6.00
M2	G18454	39.33	35.00	97.67	85.00	0.13	608.00	368.00	473.02	0.77	0.39	11.67	9.00	0.23	7.67	5.33	1.00	2.67	9.33	6.67
M2	G1957	42.67	39.00	98.00	89.00	0.09	848.00	370.67	560.65	1.10	0.56	9.67	8.00	0.17	10.33	9.00	2.33	6.33	8.67	7.67
M2	G1977	35.67	37.00	95.33	90.67	0.05	776.00	440.00	584.33	0.85	0.43	13.00	14.33	-0.10	7.33	7.00	1.67	1.00	8.33	8.33
M2	G3005	43.33	43.33	99.33	93.33	0.06	1104.00	704.00	881.60	0.71	0.36	9.33	7.67	0.18	11.67	11.00	1.67	2.00	6.67	7.33
M2	G3017	33.33	32.33	77.33	72.33	0.06	480.00	488.00	483.98	-0.03	-0.02	8.67	9.33	-0.08	8.67	8.00	1.67	2.33	5.33	6.67
M2	G3142	42.67	41.33	96.67	94.67	0.02	1240.00	344.00	653.12	1.42	0.72	12.33	8.67	0.30	9.33	10.00	1.00	2.67	6.00	6.67
M2	G3178	40.67	38.33	91.33	85.67	0.06	720.00	224.00	401.60	1.35	0.69	9.33	7.33	0.21	12.67	7.67	2.33	3.67	8.00	5.67
M2	G3185	43.00	39.00	99.67	90.00	0.10	888.00	536.00	689.90	0.78	0.40	10.67	9.33	0.13	11.33	13.33	3.00	1.67	8.00	6.00
M2	G3217	41.00	37.67	100.00	91.33	0.09	1512.00	440.00	815.65	1.39	0.71	14.00	10.00	0.29	12.67	7.00	1.67	1.33	8.67	7.67
M2	G3586	43.67	39.00	100.67	93.00	0.08	944.00	360.00	582.96	1.21	0.62	10.67	8.33	0.22	11.67	8.33	0.67	2.33	8.00	7.00
M2	G3990	41.67	43.00	100.00	95.00	0.05	1368.00	928.00	1126.72	0.63	0.32	11.67	9.00	0.23	18.33	9.33	3.00	4.00	7.00	7.33
M2	G4258	33.33	33.00	90.33	80.33	0.11	552.00	360.00	445.78	0.68	0.35	12.00	12.00	0.00	5.33	5.00	1.00	2.33	7.00	8.67
M2	G4280	38.67	39.67	98.00	87.33	0.11	1232.00	456.00	749.53	1.24	0.63	12.00	9.00	0.25	10.33	8.33	1.67	4.67	6.67	7.00
M2	G5712	37.00	38.33	95.67	93.67	0.02	928.00	560.00	720.89	0.78	0.40	13.00	12.00	0.08	7.33	5.00	1.00	1.67	8.33	7.00
M2	G5733	34.33	33.67	87.00	81.33	0.07	584.00	200.00	341.76	1.29	0.66	13.00	7.33	0.44	7.67	4.67	1.33	3.00	8.33	7.00
M2	G7038	41.33	40.00	102.00	96.00	0.06	1152.00	280.00	567.94	1.48	0.76	12.00	8.00	0.33	13.00	9.00	1.67	3.67	5.67	6.33
M2	G7761	40.33	37.33	97.33	91.33	0.06	680.00	600.00	638.75	0.23	0.12	10.33	8.33	0.19	9.00	10.33	2.67	5.33	8.33	6.67
M2	G7765	37.33	36.67	99.33	83.00	0.16	704.00	208.00	382.66	1.38	0.70	12.67	8.33	0.34	11.33	7.33	1.33	3.33	8.00	5.67
M2	G7863	35.67	35.67	96.33	90.33	0.06	664.00	880.00	764.41	-0.64	-0.33	11.67	11.67	0.00	8.67	9.33	2.33	1.67	7.00	9.33
M2	G7952	44.00	43.67	101.00	95.33	0.06	848.00	272.00	480.27	1.33	0.68	11.00	6.33	0.42	13.00	8.67	3.67	3.33	7.33	6.67
M2	G801	38.00	38.33	96.00	85.33	0.11	808.00	504.00	638.15	0.74	0.38	13.00	12.33	0.05	5.67	6.33	1.33	1.33	8.33	7.33
M2	G803	34.00	36.00	81.67	85.67	-0.05	720.00	672.00	695.59	0.13	0.07	10.33	11.33	-0.10	11.00	11.33	5.33	3.67	7.67	7.67
Mean		**39.17**	**38.25**	**95.49**	**88.57**	**0.07**	**853.09**	**459.23**	**605.87**	0.91	**0.46**	**11.44**	**9.14**	**0.20**	**10.11**	**8.61**	**2.15**	**2.98**	**7.59**	**7.13**
	G. mean	**38.19**	**37.42**	**92.95**	**86.71**		**851.24**	**421.06**				**13.67**	**9.79**		**9.90**	**7.89**	**2.37**	**3.09**	**7.75**	**7.31**
	lsd	**2.83**	**4.60**	**13.00**	**9.54**		**653.27**	**385.41**				**4.47**	**5.12**		**6.23**	**4.69**	**2.58**	**3.09**	**2.74**	**2.44**

M1 – Mesoamerica 1; M2 – Mesoamerica 2; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index; PR – Percent reduction.

Appendix 4 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	Genotype	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed
check	BAT477	9.00	11.00	8.67	10.67	1.00	3.33	18.67	25.00
check	BAT93	8.33	7.33	7.00	6.33	2.33	3.33	17.67	17.00
check	DOR390	6.67	11.33	6.00	12.33	0.33	2.00	13.00	25.67
check	Maharagi Soya	9.00	7.67	10.33	7.00	5.33	5.33	24.67	20.00
check	Masaai Red	9.00	7.33	8.33	6.67	1.00	2.00	18.33	16.00
check	NCB280	6.00	6.67	6.00	7.67	6.67	6.67	18.67	21.00
check	Pinto Villa	5.67	9.33	8.67	10.00	12.33	28.67	26.67	48.00
check	SEA15	8.67	10.00	10.33	9.33	4.00	11.33	23.00	30.67
check	SER109	5.00	7.00	7.00	6.33	4.67	3.67	16.67	17.00
check	SER16	6.67	10.33	7.33	10.00	5.67	8.67	19.67	29.00
check	SXB418	7.67	10.00	9.00	10.33	2.33	3.33	19.00	23.67
check	Tio Canela 75	10.67	6.67	7.00	6.33	4.00	1.67	21.67	14.67
check	VAX3	7.33	9.33	9.33	10.00	3.00	1.33	19.67	20.67
	Mean	**7.67**	**8.77**	**8.08**	**8.69**	**4.05**	**6.26**	**19.80**	**23.72**
D1	G10945	8.33	12.33	12.33	15.33	5.33	3.33	26.00	31.00
D1	G10971	7.00	8.33	6.67	9.00	11.00	15.00	24.67	29.00
D1	G10982	5.33	6.67	6.67	8.33	6.33	8.00	18.33	23.00
D1	G11010	7.67	8.67	7.33	7.33	4.67	5.67	19.67	21.67
D1	G13177	9.00	5.00	10.00	6.67	7.67	5.67	26.67	17.33
D1	G13696	7.67	4.33	6.67	5.67	7.00	8.67	21.33	18.67
D1	G1797	9.33	11.67	11.33	10.00	1.33	4.67	22.00	26.33
D1	G18440	7.33	12.33	9.00	8.67	7.67	13.33	24.00	35.33
D1	G19941	5.67	8.00	7.00	6.00	10.00	4.33	22.67	21.67
D1	G2379	10.67	9.67	11.67	11.33	3.00	2.33	25.33	23.33
D1	G2402	6.33	5.67	7.33	5.67	17.00	8.33	30.67	19.67
D1	G2635	9.67	7.33	14.67	10.00	12.67	7.33	37.00	24.67
D1	G2775	7.67	9.00	7.33	5.00	14.67	9.33	29.67	23.33
D1	G2778	4.33	6.33	6.00	7.33	11.00	10.33	21.33	24.00
D1	G2866	5.00	9.33	7.00	10.00	8.67	4.00	20.67	23.33
D1	G4342	7.00	4.67	8.67	4.67	2.33	3.33	18.00	12.67
D1	G7602	7.33	7.67	11.00	8.00	11.67	12.33	30.00	28.00
	Mean	**7.37**	**8.06**	**8.86**	**8.18**	**8.35**	**7.41**	**24.59**	**23.71**
D2	G11057	8.67	9.00	7.00	10.00	9.00	12.33	24.67	31.33
D2	G11656A	8.33	8.33	8.00	9.33	1.33	1.33	17.67	18.33
D2	G12796	8.67	7.67	8.33	8.00	8.00	9.33	25.00	21.67
D2	G13578	8.33	7.33	5.33	6.00	0.67	1.00	14.33	14.33
D2	G14737	10.67	9.33	10.67	9.00	0.33	0.67	22.00	19.00
D2	G14914	10.00	9.00	11.67	9.00	5.33	4.00	27.00	22.00
D2	G15685	7.00	8.67	9.67	9.00	5.00	5.67	21.67	23.33
D2	G16026	3.33	5.33	5.00	4.00	7.67	10.00	16.00	19.33
D2	G19012	6.67	6.67	8.33	7.67	8.00	5.33	23.00	19.67
D2	G22044	7.67	12.00	9.00	13.67	3.67	9.67	20.33	35.33
D2	G278	8.00	4.67	10.33	5.00	4.67	2.33	23.00	12.00
D2	G3331	8.67	8.67	10.00	11.33	2.00	3.33	20.67	23.33
D2	G3334	7.33	4.33	9.33	4.67	6.00	4.33	22.67	13.33
D2	G3807	6.33	9.67	7.33	7.67	2.67	2.67	16.33	20.00
D2	G3936	7.00	8.33	7.33	6.33	2.67	4.00	18.00	18.67
D2	G4017	9.33	9.00	11.67	7.00	1.67	1.67	22.67	17.67
D2	G4278	6.67	6.67	6.67	7.33	3.00	4.00	16.33	18.00
D2	G4822	12.00	7.33	9.00	7.33	2.33	3.33	23.33	18.00
D2	G753	8.67	6.33	5.33	5.33	6.00	4.67	20.00	16.33
D2	G7742	13.00	7.67	11.00	8.67	2.67	1.67	26.67	18.00
	Mean	**8.32**	**7.80**	**8.55**	**7.82**	**4.13**	**4.57**	**21.07**	**19.98**
G	G1328	5.67	6.00	5.33	6.00	4.67	5.33	15.67	17.33
G	G1356	11.67	8.67	9.67	7.67	3.33	2.00	24.67	18.33
G	G16072	6.67	5.00	9.00	4.33	10.67	3.67	26.33	13.00
G	G16400	5.00	6.33	6.33	6.67	1.33	1.00	12.67	14.00
G	G16401	10.33	10.67	11.67	13.33	7.33	3.00	29.33	27.00
G	G2277	9.67	9.33	14.33	11.00	7.00	3.67	31.00	24.00
G	G22787	6.00	7.00	6.00	9.33	3.33	8.00	15.33	24.33
G	G2660	7.67	10.67	10.00	9.33	4.33	2.00	22.00	22.00
G	G4730	7.00	6.33	10.67	7.33	2.33	1.67	20.00	15.33
G	G5653	9.00	5.00	10.33	7.33	5.67	2.67	25.00	15.00
	Mean	**7.87**	**7.50**	**9.33**	**8.23**	**5.00**	**3.30**	**22.20**	**19.03**

Appendix 4 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	Genotype	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed
M1	DOR364	10.00	9.00	8.67	8.00	1.33	2.00	20.00	19.00
M1	G12778	5.33	5.67	7.67	6.67	10.00	6.67	23.00	19.00
M1	G15416	11.67	6.00	9.00	6.00	2.00	1.00	22.67	13.00
M1	G16835	8.00	9.00	7.67	6.00	4.67	1.00	20.33	16.00
M1	G17648	6.00	5.67	7.67	5.33	7.00	6.67	20.67	17.67
M1	G18147	8.33	9.00	9.67	9.67	6.67	10.67	24.67	29.33
M1	G19204	6.00	7.00	7.00	6.00	4.00	5.33	17.00	18.33
M1	G2093	11.33	7.00	7.33	10.00	2.67	1.67	21.33	22.00
M1	G21212	9.00	9.00	5.67	6.67	1.67	5.67	16.33	21.33
M1	G2137	10.00	10.67	12.33	10.33	4.33	3.67	26.67	24.67
M1	G2199	7.00	8.33	5.00	6.67	1.67	2.00	13.67	17.00
M1	G2348	10.00	8.33	7.67	9.33	1.67	1.67	19.33	19.33
M1	G2352	8.00	7.67	12.33	8.00	2.67	2.00	23.00	18.33
M1	G2445	7.00	6.67	5.33	7.67	3.33	1.33	15.67	15.67
M1	G2997	5.00	5.33	5.33	5.00	2.33	8.33	12.67	18.67
M1	G3545	5.67	7.00	4.00	7.00	2.67	9.33	12.33	23.33
M1	G3593	9.00	12.00	10.33	11.67	0.00	3.33	19.33	27.00
M1	G3595	10.00	10.00	8.67	7.67	2.67	1.00	21.33	18.67
M1	G3661	9.33	4.67	11.67	6.00	1.67	2.33	22.67	13.00
M1	G4002	7.33	6.00	5.00	5.67	3.33	3.67	15.67	15.33
M1	G4206	5.00	7.00	5.00	7.00	1.00	1.00	11.00	15.00
M1	G4495	5.33	7.67	7.67	8.33	1.00	6.67	14.00	22.67
M1	G4637	14.67	11.33	10.00	10.33	0.67	0.67	25.33	22.33
M1	G5036	7.67	6.67	5.33	5.67	0.67	1.00	13.67	16.67
M1	G5694	9.00	6.33	9.67	6.00	1.67	1.33	20.33	13.67
M1	G6450	10.33	11.67	8.00	9.00	0.67	0.67	19.00	21.33
M1	G7932	4.67	3.33	3.33	4.00	3.33	4.00	11.33	11.33
M1	G955	8.67	8.00	10.00	6.67	5.00	2.67	23.67	17.33
	Mean	**8.19**	**7.71**	**7.75**	**7.37**	**2.87**	**3.48**	**18.81**	**18.82**
M2	G11721	7.00	7.67	5.00	8.00	2.67	1.67	14.67	17.33
M2	G1264	9.33	7.67	8.00	6.67	3.33	1.00	20.67	15.33
M2	G12806	9.00	7.67	5.00	8.33	1.00	3.33	15.00	19.33
M2	G1358	9.33	9.33	9.67	8.33	3.33	2.33	22.33	20.00
M2	G14163	7.67	9.33	7.67	7.00	0.67	2.00	16.00	18.33
M2	G15641	8.67	12.00	9.33	10.00	3.67	7.67	21.67	29.67
M2	G16849A	7.00	5.67	9.33	5.00	3.00	8.00	19.33	18.67
M2	G17649	8.00	11.33	8.33	10.00	3.00	4.33	19.33	25.67
M2	G18141	11.67	11.00	8.00	8.00	1.67	1.33	21.33	20.00
M2	G18157	6.00	7.33	5.33	6.67	0.33	4.67	11.67	18.67
M2	G18451	5.67	5.33	5.67	6.67	7.00	11.00	18.33	19.67
M2	G18454	6.67	6.33	9.00	7.67	7.67	5.33	23.33	19.33
M2	G1957	7.67	6.67	6.00	7.67	3.33	2.67	17.00	17.00
M2	G1977	5.33	7.67	7.33	7.33	1.67	3.67	14.33	18.67
M2	G3005	9.67	5.33	8.33	4.33	1.00	2.00	19.00	11.67
M2	G3017	7.67	3.33	7.33	4.33	10.00	8.00	25.00	15.67
M2	G3142	10.33	9.00	5.67	8.33	5.00	1.67	17.67	19.00
M2	G3178	6.67	7.00	8.33	7.00	2.67	2.33	17.67	16.33
M2	G3185	6.00	7.33	5.67	7.00	1.33	8.00	13.00	22.33
M2	G3217	10.67	11.00	9.67	8.00	1.00	1.67	21.33	20.67
M2	G3586	10.33	12.67	7.67	8.33	1.33	2.00	19.33	23.00
M2	G3990	10.67	7.33	11.00	7.33	2.00	0.67	23.67	15.33
M2	G4258	7.33	7.67	9.00	5.67	10.33	7.67	26.67	21.00
M2	G4280	8.33	11.00	8.67	9.00	1.67	2.00	18.67	22.00
M2	G5712	8.67	7.67	8.33	6.67	4.67	1.67	21.67	16.00
M2	G5733	4.33	6.67	4.67	5.33	5.67	2.67	14.67	14.67
M2	G7038	9.33	7.00	9.00	7.67	3.67	1.67	22.00	16.33
M2	G7761	5.33	8.00	10.33	8.67	3.00	3.00	18.67	19.67
M2	G7765	6.00	4.67	6.33	6.33	1.33	1.67	13.67	12.67
M2	G7863	9.00	8.67	8.67	9.67	1.00	4.00	18.67	22.33
M2	G7952	8.00	8.00	7.67	6.00	1.00	1.00	16.67	15.00
M2	G801	8.67	10.67	9.00	9.67	1.33	3.67	19.00	24.00
M2	G803	7.67	8.67	8.00	6.67	11.00	5.33	26.67	24.00
	Mean	**7.99**	**8.08**	**7.79**	**7.37**	**3.37**	**3.63**	**19.05**	**19.07**
	Grand mean	**7.96**	**7.97**	**8.22**	**7.77**	**4.29**	**4.53**	**20.45**	**20.31**
	LSD	**5.09**	**5.29**	**4.86**	**5.16**	**5.36**	**5.25**	**11.13**	**12.20**

LSD – least significant difference

Appendix 5 Performance of 81 Andean genotypes evaluated under irrigated and rainfed treatments at CIAT-Palmira, 2009

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	**Genotype**	**Irr**	**Dro**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**GMY**	**DSI**	**PR**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**Irr**	**Dro**	**Irr**	**Dro**
check	AFR619	37.00	36.33	69.00	68.33	0.01	839.27	595.97	707.23	1.32	0.29	41.53	40.23	0.03	9.53	5.73	7.97	9.43	7.20	6.93
check	CAL143	35.33	34.67	67.67	65.00	0.04	1063.20	1113.80	1088.21	-0.22	-0.05	33.63	31.47	0.06	7.67	7.60	8.47	23.13	10.73	9.17
check	CAL96	31.67	32.67	64.00	58.33	0.09	1688.50	1527.30	1605.88	0.43	0.10	63.37	56.63	0.11	6.40	6.27	10.43	14.70	9.90	9.83
check	SAB258	27.67	28.00	54.00	53.33	0.01	1571.90	1672.40	1621.37	-0.29	-0.06	38.43	41.77	-0.09	9.47	9.53	10.80	6.83	8.47	7.70
check	SAB645	30.00	30.00	59.00	54.00	0.08	2075.50	1440.80	1729.27	1.39	0.31	38.83	34.63	0.11	10.93	7.87	16.60	17.90	9.40	9.67
check	SEQ1003	33.67	34.00	61.33	57.67	0.06	1648.50	1222.60	1419.67	1.17	0.26	46.60	39.83	0.15	7.73	7.47	19.17	16.33	11.00	10.10
check	SEQ1027	37.33	37.67	70.33	66.33	0.06	1521.10	1282.50	1396.71	0.71	0.16	46.90	37.23	0.21	8.67	7.00	11.83	12.53	9.40	9.97
Mean		**33.24**	**33.33**	**63.62**	**60.43**	**0.05**	**1486.85**	**1265.05**	**1366.91**	**0.68**	**0.15**	**44.18**	**40.26**	**0.09**	**8.63**	**7.35**	**12.18**	**14.41**	**9.44**	**9.05**
NG1	G17076	30.00	30.33	60.00	56.33	0.06	1894.20	1230.60	1526.76	1.59	0.35	57.30	50.33	0.12	9.00	9.93	9.37	24.17	10.20	9.80
NG1	G3157	30.00	30.00	64.00	58.00	0.09	1507.90	1139.40	1310.76	1.11	0.24	45.40	36.87	0.19	8.50	6.80	21.45	25.77	10.60	10.00
NG1	G4534	30.33	30.33	60.00	55.33	0.08	1700.60	1105.10	1370.89	1.59	0.35	51.27	45.33	0.12	9.53	7.60	21.00	19.23	10.53	9.37
NG1	G5625	29.33	30.00	61.00	57.67	0.05	1814.60	1668.20	1739.86	0.37	0.08	46.03	40.23	0.13	9.40	11.53	24.93	22.13	10.33	8.93
NG1	G13094	30.33	30.67	61.33	58.00	0.05	2026.50	955.90	1391.81	2.40	0.53	36.90	31.00	0.16	10.53	7.00	19.47	6.27	10.67	9.43
NG1	G16115	30.33	30.33	56.00	52.33	0.07	1944.90	1213.20	1536.08	1.71	0.38	41.37	33.67	0.19	11.93	8.07	27.87	20.90	9.60	8.87
NG1	G17070	31.33	31.00	58.33	53.33	0.09	1571.50	1809.30	1686.21	-0.69	-0.15	44.57	42.73	0.04	11.13	10.80	24.47	26.10	9.93	9.67
NG1	G18255	30.33	30.33	57.33	55.33	0.03	1966.70	1503.30	1719.46	1.07	0.24	44.07	40.83	0.07	9.67	8.67	17.90	21.77	10.10	9.67
NG1	G18942	30.33	30.67	63.33	63.33	0.00	2158.10	866.70	1367.63	2.72	0.60	44.73	36.53	0.18	10.40	7.33	14.93	43.80	13.57	11.80
NG1	G21210	33.67	33.00	66.33	64.33	0.03	1422.00	466.83	814.76	3.05	0.67	68.07	36.30	0.47	8.40	5.13	13.57	10.27	9.17	7.07
NG1	G4906	34.33	33.67	68.67	64.33	0.06	682.77	785.50	732.34	-0.68	-0.15	41.80	37.97	0.09	6.80	5.27	19.37	19.57	8.10	7.47
NG1	G6639	32.33	31.33	59.33	57.33	0.03	1270.30	613.33	882.67	2.35	0.52	37.90	26.97	0.29	8.20	5.73	10.87	22.37	10.27	8.00
NG1	G738	31.33	30.00	63.67	60.67	0.05	1395.10	846.80	1086.91	1.79	0.39	54.10	39.27	0.27	8.13	8.33	20.87	31.23	10.60	9.17
NG1	G7945	30.00	29.67	58.00	54.33	0.06	1533.60	1057.20	1273.31	1.41	0.31	42.90	33.70	0.21	8.40	6.87	15.13	18.30	10.23	9.30
NG1	G9846	37.00	41.67	71.00	60.00	0.15	279.87	67.83	137.78	3.44	0.76	21.80	26.80	-0.23	2.53	2.13	28.00	18.80	5.93	9.00
NG1	G11982	33.67	33.67	61.00	58.67	0.04	1383.50	1323.20	1353.01	0.20	0.04	53.40	39.70	0.26	7.27	9.00	13.07	15.10	9.80	10.33
NG1	G1688	33.67	33.33	60.33	54.00	0.10	1253.00	1339.40	1295.48	-0.31	-0.07	31.83	32.37	-0.02	7.93	8.87	8.13	26.43	7.53	7.63
NG1	G1836	34.00	35.00	64.00	57.00	0.11	1340.40	856.80	1071.66	1.64	0.36	37.93	26.70	0.30	10.67	10.47	16.37	20.80	8.67	8.07
NG1	G1939	33.67	34.00	61.67	56.33	0.09	1649.10	1211.80	1413.64	1.21	0.27	57.60	42.33	0.27	8.53	5.73	14.23	15.83	9.50	9.53
NG1	G22247	36.33	34.00	65.67	63.33	0.04	1280.30	1385.80	1332.01	-0.37	-0.08	40.93	31.73	0.22	7.27	9.00	15.43	28.43	8.30	7.17
NG1	G2875	34.00	34.00	60.33	56.33	0.07	1611.00	929.40	1223.63	1.92	0.42	56.07	36.90	0.34	7.27	7.27	14.20	12.70	10.80	9.87
NG1	G4001	34.67	35.67	63.33	61.33	0.03	1425.40	924.23	1147.78	1.60	0.35	38.67	30.77	0.20	10.53	8.27	8.90	17.77	10.53	8.30
NG1	G5142	33.33	33.67	58.33	56.00	0.04	1511.40	1595.80	1553.03	-0.25	-0.06	58.93	49.40	0.16	8.07	7.60	17.27	19.33	10.20	9.80
NG1	G5273	36.33	34.33	65.00	60.00	0.08	1341.70	1048.10	1185.85	0.99	0.22	45.00	31.90	0.29	8.13	10.00	16.43	29.87	11.47	8.80
NG1	G7776	40.67	42.00	80.33	83.67	-0.04	188.43	98.83	136.46	2.16	0.48	20.23	28.50	-0.41	2.53	1.07	39.43	44.43	5.47	7.67
NG1	G11957	34.00	34.00	61.00	58.00	0.05	1353.20	894.93	1100.46	1.54	0.34	52.33	30.73	0.41	4.80	5.40	7.87	21.30	10.07	10.23
NG1	G2563	30.33	29.67	59.00	55.00	0.07	1236.70	1517.20	1369.79	-1.03	-0.23	39.50	40.67	-0.03	12.73	9.80	4.57	6.13	9.00	8.87
Mean		**32.80**	**32.83**	**62.53**	**58.90**	**0.06**	**1434.92**	**1053.88**	**1213.33**	**1.21**	**0.27**	**44.84**	**36.30**	**0.19**	**8.45**	**7.54**	**17.23**	**21.81**	**9.67**	**9.03**
NG2	G11512	33.00	33.33	61.67	59.33	0.04	1234.30	928.30	1070.42	1.13	0.25	36.53	28.33	0.22	6.87	7.27	7.57	16.03	9.97	9.37
NG2	G11585	37.33	37.00	69.67	68.33	0.02	834.10	535.37	668.25	1.63	0.36	36.53	32.43	0.11	9.40	6.60	16.30	14.47	10.93	9.00
NG2	G14253	29.67	30.00	58.67	55.33	0.06	1492.10	1215.50	1346.72	0.84	0.19	39.90	34.93	0.12	8.33	8.27	8.90	7.27	8.47	8.30
NG2	G16104E	30.00	30.33	56.67	54.33	0.04	936.63	774.47	851.70	0.79	0.17	27.37	25.20	0.08	10.73	8.60	26.73	8.60	10.03	7.87
NG2	G4644	30.67	30.67	59.67	56.67	0.05	1383.40	841.33	1078.84	1.78	0.39	53.50	37.37	0.30	8.60	6.00	21.63	8.80	8.67	7.00
NG2	G5034	33.33	33.33	62.00	60.00	0.03	1269.30	976.53	1113.33	1.05	0.23	42.83	30.07	0.30	6.47	8.27	22.33	21.43	8.53	7.63
NG2	G5170	33.33	33.33	61.00	56.00	0.08	1432.90	1017.00	1207.17	1.32	0.29	40.70	27.63	0.32	8.20	7.13	14.93	28.97	10.83	9.53
NG2	G5708	33.00	33.67	63.33	64.00	-0.01	1452.40	855.00	1114.36	1.87	0.41	41.17	34.03	0.17	6.60	6.47	19.20	12.33	10.63	10.57
NG2	G6873	32.33	33.00	59.67	58.67	0.02	964.77	873.63	918.07	0.43	0.09	30.63	28.80	0.06	8.27	6.13	22.03	16.57	8.60	8.50
NG2	G7895	37.33	37.00	70.00	68.33	0.02	737.53	573.33	650.27	1.01	0.22	38.10	35.77	0.06	5.87	3.60	16.17	21.57	9.53	9.10
NG2	PVA1111	34.00	34.00	66.00	64.33	0.03	1601.40	1482.70	1540.91	0.34	0.07	36.83	32.83	0.11	9.13	8.40	8.67	18.67	8.80	7.40
NG2	AND1005	34.00	34.00	63.67	58.67	0.08	1430.60	1249.80	1337.15	0.57	0.13	46.77	40.40	0.14	5.20	6.47	2.17	13.37	9.40	9.47
NG2	G16110A	34.33	34.00	66.33	64.67	0.03	1303.70	1375.70	1339.22	-0.25	-0.06	45.33	36.70	0.19	8.27	10.20	23.83	34.13	12.37	10.87
NG2	G1678	35.33	35.00	64.00	62.33	0.03	1279.70	1158.10	1217.38	0.43	0.10	51.97	35.50	0.32	5.47	4.87	5.80	9.37	11.53	9.57
NG2	G23829	35.33	35.33	65.67	64.00	0.03	1127.00	1557.27	1324.78	-1.74	-0.38	20.80	19.07	0.08	12.53	17.13	8.07	16.40	7.20	6.90
NG2	G11564	40.67	40.33	81.67	78.00	0.04	265.83	366.23	312.02	-1.72	-0.38	21.10	18.33	0.13	5.80	4.27	58.50	60.50	7.53	7.13
NG2	G11759A	44.67	44.67	78.33	81.00	-0.03	301.20	125.07	194.09	2.66	0.58	21.00	31.10	-0.48	4.00	1.07	47.77	25.00	7.13	7.65
NG2	G16346	40.00	38.67	77.00	73.00	0.05	282.33	265.07	273.56	0.28	0.06	32.43	30.40	0.06	3.47	2.47	24.43	23.93	8.57	7.97
NG2	G9855	40.00	39.67	79.33	78.67	0.01	212.03	476.93	318.00	-5.68	-1.25	29.50	29.93	-0.01	1.00	3.07	63.33	17.23	7.87	7.27
NG2	G11727	43.33	44.33	80.00	76.00	0.05	250.00	238.13	243.99	0.22	0.05	29.60	30.80	-0.04	5.07	2.53	48.17	26.37	8.07	6.03
NG2	G12517	38.00	37.67	75.67	74.00	0.02	574.23	479.53	524.75	0.75	0.16	21.07	20.23	0.04	6.73	8.00	43.00	15.63	7.67	7.70
NG2	G13595	34.00	33.67	61.00	56.33	0.08	1488.70	1292.80	1387.30	0.60	0.13	39.37	31.97	0.19	8.07	8.00	9.57	15.60	9.70	8.93
NG2	G13910	36.33	35.33	69.00	68.00	0.01	818.57	821.03	819.80	-0.01	0.00	34.37	27.67	0.19	6.13	4.33	15.17	7.77	9.53	8.63
NG2	G13911	37.00	36.33	69.00	67.67	0.02	530.43	290.87	392.79	2.05	0.45	24.07	23.20	0.04	5.60	4.33	20.00	22.23	7.70	8.87
NG2	G18264	31.00	31.00	60.67	55.33	0.09	2047.70	1317.20	1642.32	1.62	0.36	47.47	39.87	0.16	8.53	6.40	9.77	3.00	8.70	8.43
NG2	G4672	43.33	42.67	77.33	78.67	-0.02	201.00	180.70	190.58	0.46	0.10	28.93	23.17	0.20	1.33	1.40	50.00	19.43	4.90	6.07
NG2	G5849	30.00	30.00	60.33	57.67	0.04	1513.90	1567.70	1540.57	-0.16	-0.04	40.87	39.43	0.04	10.07	9.20	10.50	15.43	7.47	7.63
NG2	G9335	34.33	33.67	62.00	57.00	0.08	1153.80	878.70	1006.90	1.08	0.24	32.03	26.83	0.16	8.07	6.60	13.17	21.50	7.40	7.10
NG2	G9603	37.33	35.33	66.67	65.00	0.03	863.03	797.53	829.63	0.34	0.08	39.20	31.57	0.19	6.00	5.60	19.87	27.03	9.93	8.17
NG2	G17168	43.33	43.67	85.67	85.67	0.00	164.63	124.20	142.99	1.12	0.25	30.57	20.07	0.34	2.20	1.40	30.13	26.20	7.07	7.90
Mean		**35.88**	**35.70**	**67.72**	**65.57**	**0.03**	**971.57**	**821.19**	**886.60**	**0.70**	**0.15**	**35.35**	**30.12**	**0.15**	**6.73**	**6.14**	**22.92**	**19.16**	**8.82**	**8.22**

NG1 – Nueva Granada 1; NG2 – Nueva Granada 2;PR – Percent reduction; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index

Appendix 5 continued

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	**Genotype**	**Irr**	**Dro**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**GMY**	**DSI**	**PR**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**Irr**	**Dro**	**Irr**	**Dro**
P	DRK47	33.67	31.00	68.00	66.33	0.02	1534.00	1411.30	1471.37	0.36	0.08	51.73	50.10	0.03	7.40	5.93	9.83	8.83	9.73	8.60
P	G11521	33.33	33.33	60.67	57.00	0.06	890.00	591.17	725.36	1.53	0.34	44.37	36.70	0.17	4.60	5.80	13.33	11.53	12.40	11.27
P	G22147	32.00	30.67	65.67	57.67	0.12	2060.10	1383.20	1688.06	1.49	0.33	55.00	51.37	0.07	7.07	6.27	10.33	12.70	10.53	9.33
P	G2686	36.00	34.67	68.00	60.67	0.11	1058.30	780.93	909.10	1.19	0.26	38.87	28.73	0.26	8.93	4.67	9.00	22.77	11.63	10.13
P	G4494	30.67	30.33	65.00	58.67	0.10	1818.10	1427.70	1611.12	0.98	0.21	50.67	47.87	0.06	9.13	7.47	7.77	9.73	10.10	9.87
P	G4547	39.33	38.67	81.00	80.50	0.01	101.87	41.30	64.86	2.70	0.59	26.73	21.90	0.18	4.53	1.20	52.53	45.85	8.07	7.55
P	PVA773	34.33	34.67	66.67	64.33	0.04	1570.10	1452.50	1510.16	0.34	0.07	47.67	38.27	0.20	7.40	5.60	7.73	12.10	11.03	10.10
P	G14016	41.67	42.00	84.67	82.67	0.02	99.13	135.37	115.84	-1.66	-0.37	17.13	24.15	-0.41	3.53	2.47	53.43	49.67	8.27	7.43
P	G19842	44.67	47.00	86.00	85.00	0.01	129.97	25.23	57.26	3.66	0.81	19.33	28.60	-0.48	1.53	1.53	37.80	74.37	9.33	7.67
P	G23604	39.33	38.33	71.00	72.00	-0.01	120.73	0.00	0.00	4.55	1.00	34.03	0.00	1.00	1.53	0.33	3.50	100.00	6.93	7.10
P	G2567	37.00	37.67	70.00	66.33	0.05	320.17	466.53	386.48	-2.08	-0.46	33.10	27.63	0.17	5.93	4.87	28.83	12.40	10.40	9.30
P	G4721	45.00	43.00	85.65	87.00	-0.02	16.53	51.90	29.29	-9.73	-2.14	20.00	21.70	-0.09	0.53	0.33	66.67	0.00	5.53	7.00
P	G4739	38.00	37.67	70.33	60.00	0.15	648.83	112.30	269.93	3.76	0.83	35.93	30.23	0.16	6.73	2.73	9.10	22.83	10.33	8.13
P	G12529	63.67	57.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P	G19833	55.33	51.67	0.00	88.00	0.00	0.00	8.75	0.00	0.00	0.00	0.00	17.00	0.00	0.00	0.20	0.00	66.70	0.00	10.00
P	G8209	45.67	52.00	79.33	81.00	-0.02	52.33	39.87	45.68	1.08	0.24	16.00	25.75	-0.61	1.53	1.40	72.53	59.27	8.60	9.47
P	G19860	50.33	46.67	0.00	80.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.50	0.00	0.00	0.13	0.00	100.00	0.00	5.00
Mean		**41.18**	**40.41**	**60.12**	**67.48**	**-0.12**	**612.95**	**466.36**	**522.62**	**1.09**	**0.24**	**28.86**	**27.44**	**0.05**	**4.14**	**3.00**	**22.49**	**35.81**	**7.82**	**8.11**
	G. mean	**35.74**	**35.53**	**64.03**	**59.75**		**1096.67**	**850.29**				**37.71**	**31.29**		**6.86**	**6.04**	**5.86**	**4.94**	**8.95**	**8.19**
	lsd	**2.23**	**3.32**	**3.96**	**21.91**		**387.46**	**426.86**				**9.14**	**10.77**		**3.20**	**3.60**	**6.66**	**6.06**	**1.70**	**2.59**

P – Peru; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index

Appendix 5 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
check	AFR619	4.01	5.05	6.09	5.52	6.33	2.33	16.67	12.33
check	CAL143	5.13	4.58	6.68	4.19	10.33	3.67	21.67	12.33
check	CAL96	2.90	3.57	4.51	3.92	10.67	5.00	18.00	12.33
check	SAB258	2.31	2.86	4.19	3.14	13.00	7.33	19.33	13.33
check	SAB645	3.55	2.60	5.28	3.38	15.33	6.00	24.00	12.00
check	SEQ1003	2.20	3.82	4.44	4.58	9.00	5.67	15.67	14.33
check	SEQ1027	5.08	5.62	7.05	5.01	7.33	2.00	19.67	12.67
	Mean	**3.60**	**4.01**	**5.46**	**4.25**	**10.28**	**4.57**	**19.29**	**12.76**
NG1	G17076	2.58	2.90	4.39	3.88	12.00	5.33	19.33	12.00
NG1	G3157	1.56	2.74	3.81	3.12	11.33	5.33	16.67	11.33
NG1	G4534	2.29	3.08	4.10	3.46	11.00	5.00	17.67	11.67
NG1	G5625	2.44	3.19	3.97	3.51	11.00	6.00	17.33	12.67
NG1	G13094	3.50	2.11	4.34	2.43	12.67	4.00	21.00	8.67
NG1	G16115	2.50	2.57	4.48	3.01	12.67	6.00	19.67	11.33
NG1	G17070	2.25	3.74	4.54	4.68	12.00	7.00	18.67	15.33
NG1	G18255	2.79	2.76	3.80	3.57	15.00	5.67	21.67	12.00
NG1	G18942	3.09	3.46	5.64	3.75	11.67	3.67	20.67	10.67
NG1	G21210	4.03	3.99	6.40	4.41	10.33	1.67	21.00	10.00
NG1	G4906	3.26	3.90	5.54	4.84	6.00	2.00	15.00	10.67
NG1	G6639	3.06	2.37	4.15	4.50	11.00	2.33	18.33	9.33
NG1	G738	3.38	2.80	5.38	3.25	11.00	4.00	19.33	10.00
NG1	G7945	2.44	3.15	3.45	3.62	9.67	5.33	15.33	11.67
NG1	G9846	6.96	5.72	10.61	6.27	4.67	1.00	22.00	13.00
NG1	G11982	2.30	4.69	5.12	6.07	9.33	6.67	16.67	17.33
NG1	G1688	2.23	2.80	3.43	3.42	7.33	4.33	13.33	10.67
NG1	G1836	2.70	3.71	4.24	3.39	7.67	3.00	14.67	9.67
NG1	G1939	2.60	2.99	6.03	3.95	15.00	3.33	23.67	10.33
NG1	G22247	2.73	4.11	4.96	4.47	7.67	3.33	15.33	12.00
NG1	G2875	3.03	3.07	5.56	4.33	11.00	3.67	19.67	11.33
NG1	G4001	4.15	4.00	6.48	4.09	10.33	3.00	21.00	11.67
NG1	G5142	3.10	3.83	5.62	4.99	10.67	5.00	19.33	13.67
NG1	G5273	2.32	2.82	5.03	4.31	5.33	2.33	13.00	9.33
NG1	G7776	5.82	4.48	7.86	4.99	9.33	0.00	23.00	9.33
NG1	G11957	2.84	2.70	5.15	3.76	8.67	3.00	16.67	9.67
NG1	G2563	2.08	3.62	4.13	3.73	11.33	6.67	17.67	14.00
	Mean	**3.04**	**3.38**	**5.12**	**4.07**	**10.21**	**4.02**	**18.43**	**11.46**

NG1 – Nueva Granada 1

Appendix 5 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
NG2	G11512	2.35	3.41	3.77	3.84	7.33	4.33	13.33	11.33
NG2	G11585	3.49	4.86	4.25	5.33	5.33	1.00	13.00	11.00
NG2	G14253	3.04	2.56	3.64	3.10	11.33	4.33	18.00	9.67
NG2	G16104E	3.36	2.98	4.97	3.95	8.33	4.00	16.33	11.00
NG2	G4644	3.74	3.69	4.91	3.66	10.67	4.33	19.33	11.67
NG2	G5034	2.46	3.66	3.70	3.78	8.33	2.67	15.00	9.67
NG2	G5170	2.01	2.70	3.66	2.58	8.67	3.67	14.33	9.00
NG2	G5708	2.77	3.49	4.28	3.64	8.67	2.33	15.67	9.33
NG2	G6873	1.83	3.42	2.76	2.35	7.67	3.33	12.33	9.00
NG2	G7895	3.93	4.29	5.62	4.86	6.33	1.33	15.67	10.33
NG2	PVA1111	3.56	4.04	4.36	3.92	9.00	2.33	17.00	10.33
NG2	AND1005	3.84	4.40	6.76	4.64	11.33	3.67	21.67	12.67
NG2	G16110A	1.99	3.99	4.55	5.51	8.00	3.00	14.67	12.33
NG2	G1678	3.70	5.27	5.76	5.43	9.33	2.33	18.33	13.00
NG2	G23829	2.79	3.65	5.31	3.94	5.67	1.33	13.67	8.67
NG2	G11564	4.21	4.05	6.89	4.00	1.33	0.67	12.33	8.33
NG2	G11759A	5.02	4.95	8.03	4.83	1.00	0.33	14.00	10.00
NG2	G16346	5.36	4.63	6.20	4.86	4.67	0.00	15.67	9.67
NG2	G9855	5.40	4.10	8.73	4.82	2.33	0.00	16.33	9.00
NG2	G11727	4.05	6.26	6.85	6.01	0.33	0.00	11.33	12.33
NG2	G12517	4.60	3.30	8.14	3.83	5.00	0.00	18.00	7.33
NG2	G13595	3.28	3.86	4.88	3.69	10.33	4.67	18.33	12.33
NG2	G13910	2.94	4.30	5.82	5.75	4.67	2.00	13.67	12.00
NG2	G13911	4.76	7.67	7.75	10.82	6.33	3.67	19.00	22.00
NG2	G18264	2.29	3.43	3.94	3.32	11.67	5.67	18.33	12.33
NG2	G4672	4.74	3.74	7.99	3.77	7.67	0.00	20.67	7.33
NG2	G5849	2.26	3.35	5.37	4.10	20.00	8.00	28.00	15.00
NG2	G9335	3.63	3.16	5.14	3.27	12.33	3.33	21.00	9.67
NG2	G9603	3.55	3.95	5.69	3.96	6.67	1.67	16.00	9.67
NG2	G17168	5.08	4.05	8.21	4.30	0.33	0.00	13.67	8.33
	Mean	**3.53**	**4.04**	**5.60**	**4.40**	**7.36**	**2.47**	**16.49**	**10.81**
P	DRK47	3.72	4.13	5.06	4.37	9.00	5.00	18.00	13.33
P	G11521	4.31	4.78	6.43	5.38	9.00	4.00	19.33	14.00
P	G22147	1.57	3.06	3.75	3.25	8.67	3.67	14.00	10.00
P	G2686	3.29	3.75	4.42	3.94	5.67	2.33	13.67	10.00
P	G4494	3.68	3.17	5.51	3.44	9.33	3.67	18.67	10.00
P	G4547	6.93	3.66	7.51	3.20	1.00	0.00	15.33	6.67
P	PVA773	4.10	4.35	5.46	4.12	9.33	3.33	19.00	11.67
P	G14016	5.17	4.19	5.94	3.49	0.33	0.00	11.67	7.67
P	G19842	4.66	4.35	6.32	3.99	0.00	0.00	11.00	8.33
P	G23604	5.18	2.96	6.42	3.07	1.00	0.00	12.67	6.33
P	G2567	4.54	4.75	6.68	5.28	5.00	1.33	16.33	11.33
P	G4721	4.30	5.13	6.15	4.79	0.67	1.33	11.33	11.67
P	G4739	3.11	3.78	4.91	3.81	3.67	0.33	11.67	7.67
P	G12529	3.18	3.81	4.42	3.90	0.00	0.00	7.67	7.67
P	G19833	4.39	3.75	6.83	3.67	0.00	1.00	11.33	8.33
P	G8209	6.78	5.00	8.87	3.83	0.00	0.00	16.00	8.67
P	G19860	4.85	4.21	5.36	3.78	0.33	0.00	10.33	8.00
	Mean	**4.34**	**4.05**	**5.88**	**3.96**	**3.71**	**1.53**	**14.00**	**9.49**
	Grand mean	**3.54**	**3.82**	**5.49**	**4.18**	**7.79**	**2.97**	**16.86**	**10.92**
	LSD	**1.43**	**1.73**	**1.95**	**2.01**	**5.24**	**1.95**	**7.04**	**4.71**

NG2 – Nueva Granada 2; P – Peru; LSD – least significant difference

Appendix 6 Performance of 81 Andean genotypes evaluated under irrigated and rainfed treatments at Harare Research Station, 2011

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	Genotype	Irr	Dro	Irr	Dro	PR	Irr	Dro	GMY	DSI	PR	Irr	Dro	PR	Irr	Dro	Irr	Dro	Irr	Dro
check	AFR619	37.67	38.33	95.67	98.00	-0.02	696.00	488.00	582.79	0.73	0.30	35.00	17.00	0.51	6.00	10.33	1.00	4.33	8.33	7.00
check	CAL143	35.33	34.67	88.67	86.00	0.03	792.00	824.00	807.84	-0.10	-0.04	39.00	20.00	0.49	6.33	6.33	1.00	1.33	11.67	10.00
check	CAL96	33.67	35.00	87.33	82.00	0.06	736.00	344.00	503.17	1.30	0.53	36.00	18.00	0.50	5.67	5.33	1.33	2.00	8.67	8.00
check	SAB258	30.00	29.67	85.33	73.67	0.14	752.00	448.00	580.43	0.99	0.40	32.00	19.00	0.41	8.00	7.67	2.67	4.33	8.00	9.00
check	SAB645	34.33	32.33	87.33	76.33	0.13	1016.00	680.00	831.19	0.81	0.33	28.33	19.33	0.32	6.67	7.00	2.67	2.33	6.00	9.33
check	SEQ1003	38.33	37.67	97.67	87.67	0.10	1224.00	736.00	949.14	0.97	0.40	35.67	19.33	0.46	6.00	6.67	0.67	3.33	9.00	9.33
check	SEQ1027	42.67	44.67	96.67	94.67	0.02	1264.00	808.00	1010.60	0.88	0.36	36.33	20.33	0.44	9.67	10.33	1.33	3.33	9.67	10.33
Mean		**36.00**	**36.05**	**91.24**	**85.48**	**0.06**	**925.71**	**618.29**	**752.17**	**0.81**	**0.33**	**34.62**	**19.00**	**0.45**	**6.91**	**7.67**	**1.52**	**3.00**	**8.76**	**9.00**
NG1	G17076	33.67	32.67	85.33	74.00	0.13	1440.00	504.00	851.92	1.59	0.65	22.00	18.33	0.17	5.00	5.00	3.33	2.33	9.67	8.33
NG1	G3157	44.00	48.33	95.67	102.67	-0.07	744.00	77.67	240.39	2.18	0.90	29.00	16.67	0.43	9.33	3.00	5.00	1.33	11.67	6.67
NG1	G4534	34.00	33.67	89.33	75.00	0.16	688.00	672.00	679.95	0.06	0.02	35.00	19.33	0.45	5.00	6.33	2.33	1.67	8.67	9.33
NG1	G5625	42.00	43.67	106.00	101.67	0.04	552.00	213.33	343.16	1.50	0.61	25.33	18.33	0.28	10.67	7.00	5.33	2.33	10.00	8.33
NG1	G13094	34.67	33.33	88.67	76.00	0.14	552.00	528.00	539.87	0.11	0.04	26.33	18.00	0.32	5.33	5.67	1.33	2.67	8.33	8.00
NG1	G16115	31.33	32.00	85.67	72.33	0.16	744.00	640.00	690.04	0.34	0.14	36.00	17.00	0.53	7.00	7.33	2.00	6.33	6.67	7.00
NG1	G17070	33.00	32.67	84.67	72.67	0.14	528.00	304.00	400.64	1.03	0.42	31.33	19.00	0.39	6.67	7.33	2.67	4.67	8.00	9.00
NG1	G18255	33.00	31.33	85.67	72.33	0.16	656.00	416.00	522.39	0.89	0.37	31.33	15.67	0.50	4.67	6.67	1.67	2.33	8.33	5.67
NG1	G18942	33.00	32.67	83.67	75.00	0.10	792.00	808.00	799.96	-0.05	-0.02	33.33	21.00	0.37	5.33	8.67	1.33	2.33	10.67	11.00
NG1	G21210	35.67	33.67	88.33	81.33	0.08	632.00	552.00	590.65	0.31	0.13	33.67	17.33	0.49	5.00	4.67	1.00	1.67	7.67	7.33
NG1	G4906	35.67	36.33	90.00	87.33	0.03	776.00	744.00	759.83	0.10	0.04	35.33	15.33	0.57	6.00	5.00	1.00	2.67	7.33	5.33
NG1	G6639	33.67	33.67	87.33	72.33	0.17	808.00	648.00	723.59	0.48	0.20	33.67	18.00	0.47	6.33	6.33	1.67	3.00	8.33	8.00
NG1	G738	33.67	32.33	90.67	76.00	0.16	840.00	456.00	618.90	1.11	0.46	36.33	18.67	0.49	7.67	6.00	2.33	3.67	11.33	8.67
NG1	G7945	31.33	31.00	83.33	71.33	0.14	568.00	520.00	543.47	0.21	0.08	25.33	17.00	0.33	7.67	10.67	1.67	3.67	8.33	7.00
NG1	G9846	36.33	36.67	66.33	98.67	-0.49	888.00	736.00	808.44	0.42	0.17	34.00	18.67	0.45	6.33	6.00	1.00	1.67	9.67	8.67
NG1	G11982	36.67	37.33	89.33	87.33	0.02	952.00	480.00	675.99	1.21	0.50	34.67	19.67	0.43	7.33	6.00	4.00	1.67	9.67	9.67
NG1	G1688	36.33	36.33	87.33	78.67	0.10	848.00	528.00	669.14	0.92	0.38	26.00	17.33	0.33	7.67	7.33	2.00	2.33	6.00	7.33
NG1	G1836	37.33	37.67	95.67	91.67	0.04	1520.00	568.00	929.17	1.53	0.63	31.33	17.67	0.44	9.67	7.33	1.00	2.67	6.33	7.67
NG1	G1939	37.00	37.00	88.67	86.33	0.03	1256.00	656.00	907.71	1.17	0.48	36.67	19.33	0.47	8.67	6.33	1.00	1.33	11.00	9.33
NG1	G22247	38.67	38.00	98.67	92.67	0.06	1008.00	568.00	756.67	1.06	0.44	29.00	17.00	0.41	7.67	7.00	1.33	2.33	6.67	7.00
NG1	G2875	36.33	37.00	89.33	87.00	0.03	1256.00	600.00	868.10	1.27	0.52	36.00	17.67	0.51	9.00	5.00	0.67	1.67	9.67	7.67
NG1	G4001	38.00	38.33	95.33	89.33	0.06	1144.00	592.00	822.95	1.18	0.48	34.33	17.00	0.50	8.00	7.67	1.33	1.00	8.33	7.00
NG1	G5142	37.00	36.00	89.67	80.33	0.10	1472.00	720.00	1029.49	1.25	0.51	37.33	20.33	0.46	8.67	9.67	2.67	3.67	9.67	10.33
NG1	G5273	37.67	37.33	89.33	83.00	0.07	872.00	584.00	713.62	0.81	0.33	31.33	19.00	0.39	6.67	6.00	1.00	2.00	7.67	9.00
NG1	G7776	38.00	39.00	96.67	95.67	0.01	984.00	384.00	614.70	1.49	0.61	22.00	19.33	0.12	10.00	5.67	3.67	2.00	9.33	9.33
NG1	G11957	37.00	37.67	62.33	82.67	-0.33	1400.00	688.00	981.43	1.24	0.51	38.67	19.67	0.49	7.33	6.00	0.67	1.67	11.33	9.67
NG1	G2563	34.67	32.33	86.33	73.00	0.15	688.00	768.00	726.90	-0.28	-0.12	32.67	18.67	0.43	5.67	6.67	2.67	3.00	7.67	8.67
Mean		**35.91**	**35.85**	**84.20**	**82.83**	**0.02**	**911.41**	**553.89**	**696.63**	**0.96**	**0.39**	**31.78**	**18.19**	**0.43**	**7.20**	**6.53**	**2.06**	**2.51**	**8.82**	**8.19**
NG2	G11512	32.67	32.00	85.33	72.67	0.15	552.00	384.00	460.40	0.74	0.30	28.67	18.33	0.36	5.67	7.33	1.00	2.33	8.67	8.33
NG2	G11585	36.67	35.67	95.00	85.33	0.10	928.00	816.00	870.20	0.29	0.12	32.33	19.33	0.40	6.33	7.33	1.00	2.00	11.00	9.33
NG2	G14253	34.67	33.33	87.67	76.67	0.13	360.00	488.00	419.14	-0.87	-0.36	30.33	18.33	0.40	6.33	7.00	1.67	1.67	6.67	8.33
NG2	G16104E	35.00	33.67	88.33	72.00	0.18	568.00	352.00	447.14	0.93	0.38	27.00	18.67	0.31	6.67	6.00	2.67	2.00	8.00	8.67
NG2	G4644	34.00	34.00	88.00	78.67	0.11	688.00	560.00	620.71	0.45	0.19	33.33	16.67	0.50	5.33	5.33	2.33	2.00	6.00	6.67
NG2	G5034	34.67	34.00	87.00	79.33	0.09	728.00	720.00	723.99	0.03	0.01	34.00	18.33	0.46	6.33	7.00	1.67	1.67	8.67	8.33
NG2	G5170	35.33	35.00	86.67	76.33	0.12	760.00	440.00	578.27	1.03	0.42	32.67	20.00	0.39	5.00	7.00	1.33	6.00	9.00	10.00
NG2	G5708	34.00	33.00	84.67	72.67	0.14	608.00	440.00	517.22	0.67	0.28	30.33	19.33	0.36	5.33	6.00	1.00	1.33	10.33	9.33
NG2	G6873	34.67	35.33	87.33	75.67	0.13	640.00	448.00	535.46	0.73	0.30	32.33	16.00	0.51	4.33	5.33	1.33	1.33	6.67	6.00
NG2	G7895	36.67	37.00	99.33	86.33	0.13	736.00	384.00	531.62	1.17	0.48	32.67	18.67	0.43	6.33	5.00	1.33	2.67	12.00	8.67
NG2	PVA1111	36.33	37.00	92.67	87.67	0.05	1488.00	592.00	938.56	1.47	0.60	37.67	18.67	0.50	8.67	6.00	1.00	2.67	9.67	8.67
NG2	AND1005	37.67	37.67	93.00	95.33	-0.03	816.00	624.00	713.57	0.57	0.24	31.00	17.67	0.43	5.00	5.67	1.00	1.00	7.33	7.67
NG2	G16110A	37.00	38.00	63.00	91.00	-0.44	1104.00	840.00	963.00	0.58	0.24	37.33	21.33	0.43	8.67	7.00	2.33	2.67	12.00	11.33
NG2	G1678	38.00	37.67	94.33	91.33	0.03	1504.00	848.00	1129.33	1.06	0.44	37.67	21.33	0.43	6.67	5.33	0.33	1.00	12.00	11.33
NG2	G23829	36.00	36.00	93.33	89.33	0.04	616.00	448.00	525.33	0.67	0.27	20.33	17.33	0.15	9.67	6.33	4.33	2.33	5.67	7.33
NG2	G11564	39.67	41.67	100.67	99.67	0.01	552.00	244.67	367.50	1.36	0.56	22.67	21.00	0.07	9.00	9.00	2.67	3.00	6.33	11.00
NG2	G11759A	43.00	41.67	101.67	99.00	0.03	776.00	209.33	403.04	1.78	0.73	33.00	18.33	0.44	7.00	7.67	1.33	1.33	9.33	8.33
NG2	G16346	37.67	38.00	98.67	91.00	0.08	936.00	640.00	773.98	0.77	0.32	37.00	19.00	0.49	8.00	6.33	1.33	2.33	11.00	9.00
NG2	G9855	38.67	37.67	96.67	91.67	0.05	1080.00	608.00	810.33	1.07	0.44	34.67	20.00	0.42	6.33	5.67	1.67	2.00	11.33	10.00
NG2	G11727	42.67	44.33	100.67	101.00	0.00	360.00	72.67	161.74	1.95	0.80	39.00	17.00	0.56	9.67	5.67	1.67	2.67	10.00	7.00
NG2	G12517	37.67	38.67	97.67	97.67	0.00	840.00	680.00	755.78	0.46	0.19	27.33	16.67	0.39	10.33	12.33	2.00	4.67	7.33	6.67
NG2	G13595	37.33	37.33	97.00	90.00	0.07	1024.00	712.00	853.87	0.74	0.30	32.67	17.00	0.48	7.00	7.00	2.00	1.33	8.67	7.00
NG2	G13910	37.00	37.00	95.67	90.33	0.06	1296.00	1184.00	1238.73	0.21	0.09	33.00	17.67	0.46	6.67	7.67	0.67	1.33	10.00	7.67
NG2	G13911	37.00	37.33	93.33	92.33	0.01	1384.00	720.00	998.24	1.17	0.48	34.33	17.00	0.50	7.33	6.67	0.67	0.67	9.33	7.00
NG2	G18264	35.00	34.33	88.33	78.33	0.11	1280.00	416.00	729.71	1.65	0.68	37.00	17.67	0.52	8.33	4.33	1.00	2.67	9.33	7.67
NG2	G4672	39.33	37.33	99.33	98.00	0.01	1208.00	696.00	916.93	1.03	0.42	36.33	21.00	0.42	8.33	6.00	2.00	1.33	9.00	11.00
NG2	G5849	35.33	36.00	84.67	76.33	0.10	824.00	344.00	532.41	1.42	0.58	30.00	16.33	0.46	7.67	5.33	3.00	3.33	8.00	6.33
NG2	G9335	37.67	37.33	98.33	89.33	0.09	800.00	704.00	750.47	0.29	0.12	29.33	20.00	0.32	8.00	9.00	3.00	5.00	7.67	10.00
NG2	G9603	40.33	40.33	98.67	92.67	0.06	920.00	632.00	762.52	0.76	0.31	32.00	18.67	0.42	6.67	7.33	1.00	2.00	8.33	8.67
NG2	G17168	43.67	44.67	101.33	99.67	0.02	864.00	266.67	480.00	1.69	0.69	34.00	19.00	0.44	6.33	6.67	0.33	1.00	11.67	9.00
Mean		**37.18**	**37.10**	**92.61**	**87.24**	**0.06**	**874.67**	**550.44**	**683.64**	**0.90**	**0.37**	**32.33**	**18.54**	**0.43**	**7.10**	**6.68**	**1.62**	**2.24**	**9.03**	**8.54**

NG1 – Nueva Granada 1; NG2 – Nueva Granada 2; PR – Percent reduction; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index

Appendix 6 continued

	Trait	DF		Days to maturity			Yield (kg/ha)					100-seed weight (g)			NPP		EPP		Pod length (cm)	
Race	**Genotype**	**Irr**	**Dro**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**GMY**	**DSI**	**PR**	**Irr**	**Dro**	**PR**	**Irr**	**Dro**	**Irr**	**Dro**	**Irr**	**Dro**
P	DRK47	35.33	33.67	91.00	85.00	0.07	1064.00	448.00	690.41	1.41	0.58	42.00	18.67	0.56	6.67	5.67	2.33	2.00	9.33	8.67
P	G11521	35.67	35.00	89.33	91.67	-0.03	272.00	392.00	326.53	-1.08	-0.44	20.67	21.00	-0.02	2.67	3.33	1.00	0.67	8.33	11.00
P	G22147	34.33	33.00	91.33	84.00	0.08	968.00	560.00	736.26	1.03	0.42	40.00	20.33	0.49	6.00	5.33	0.33	1.00	10.67	10.33
P	G2686	36.67	36.67	92.00	90.67	0.01	816.00	568.00	680.80	0.74	0.30	32.33	20.00	0.38	4.67	5.33	0.33	1.00	9.33	10.00
P	G4494	34.33	33.33	89.00	81.33	0.09	616.00	352.00	465.65	1.05	0.43	32.33	20.00	0.38	4.67	5.00	1.00	2.00	7.67	10.00
P	G4547	36.67	37.00	100.00	97.67	0.02	928.00	406.67	614.32	1.37	0.56	40.67	22.33	0.45	5.00	5.33	0.33	0.33	11.67	12.33
P	PVA773	36.00	36.67	89.33	89.67	0.00	616.00	624.00	619.99	-0.03	-0.01	35.00	18.00	0.49	4.67	6.67	1.00	2.33	10.33	8.00
P	G14016	43.67	43.67	99.00	100.33	-0.01	792.00	205.33	403.26	1.81	0.74	33.00	17.33	0.47	9.33	7.00	0.67	2.00	9.00	7.33
P	G19842	41.00	39.67	100.00	97.00	0.03	984.00	317.00	558.51	1.65	0.68	26.33	21.33	0.19	7.33	7.67	2.00	2.00	12.33	11.33
P	G23604	38.67	39.67	100.00	96.00	0.04	648.00	185.33	346.55	1.74	0.71	23.33	16.00	0.31	7.67	8.67	3.67	2.00	7.00	6.00
P	G2567	38.00	40.33	97.00	92.67	0.04	1416.00	542.67	876.60	1.50	0.62	33.33	19.67	0.41	9.67	7.67	0.67	1.33	10.33	9.67
P	G4721	39.00	40.00	98.67	95.33	0.03	1048.00	488.00	715.14	1.30	0.53	28.33	17.00	0.40	9.00	5.67	2.67	1.67	10.33	7.00
P	G4739	41.33	43.67	97.67	96.00	0.02	1048.00	432.00	672.86	1.43	0.59	35.67	19.33	0.46	7.67	6.33	0.67	1.00	10.00	9.33
P	G12529	43.33	45.33	100.67	99.33	0.01	768.00	528.00	636.79	0.76	0.31	32.00	18.00	0.44	9.67	8.33	2.33	2.00	9.33	8.00
P	G19833	43.00	45.00	103.67	100.33	0.03	696.00	36.00	158.29	2.31	0.95	33.00	18.33	0.44	7.33	7.67	1.67	2.33	9.67	8.33
P	G8209	42.33	44.33	103.00	99.67	0.03	360.00	108.00	197.18	1.71	0.70	25.00	22.33	0.11	6.00	7.00	4.00	2.67	13.00	12.33
P	G19860	41.67	45.00	99.67	99.67	0.00	440.00	12.33	73.66	2.37	0.97	33.00	18.33	0.44	11.00	9.00	2.67	2.00	10.33	8.33
Mean		**38.88**	**39.53**	**96.55**	**93.90**	**0.03**	**792.94**	**365.02**	**516.05**	**1.32**	**0.54**	**32.12**	**19.29**	**0.40**	**7.00**	**6.57**	**1.61**	**1.67**	**9.92**	**9.29**
	G. mean	**37.01**	**37.10**	**90.51**	**87.02**		**873.58**	**518.54**				**32.40**	**18.62**		**7.10**	**6.69**	**1.76**	**2.28**	**9.12**	**8.62**
	lsd	**1.98**	**2.16**	**17.70**	**5.09**		**608.29**	**361.45**				**8.10**	**3.41**		**3.27**	**3.50**	**2.21**	**2.59**	**3.14**	**3.41**

P – Peru; GMY – Geometric mean for grain yield; DSI – Drought sensitivity index

Appendix 6 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
check	AFR619	3.47	4.67	4.53	4.20	3.00	2.67	12.00	10.67
check	CAL143	3.67	4.20	4.13	4.13	3.00	4.67	11.33	12.33
check	CAL96	3.60	4.07	4.27	3.13	3.67	4.00	11.67	10.67
check	SAB258	4.20	3.73	3.40	3.73	3.67	4.00	10.67	12.33
check	SAB645	4.27	3.33	3.73	4.33	4.33	6.00	12.00	14.67
check	SEQ1003	4.13	4.27	4.47	3.53	2.67	3.00	11.67	10.67
check	SEQ1027	5.00	4.27	4.07	4.40	2.00	2.00	10.33	11.67
	Mean	**4.05**	**4.08**	**4.09**	**3.92**	**3.19**	**3.76**	**11.38**	**11.86**
NG1	G17076	3.73	3.27	3.47	4.40	4.00	5.33	11.00	13.33
NG1	G3157	4.47	4.13	4.27	4.13	3.00	3.00	11.00	11.67
NG1	G4534	3.60	3.13	4.00	4.33	4.00	4.67	11.33	12.00
NG1	G5625	4.47	3.60	3.27	4.27	2.33	2.00	9.00	10.67
NG1	G13094	3.80	3.60	3.73	3.53	2.33	4.00	10.00	11.33
NG1	G16115	3.33	3.33	4.60	3.87	4.33	4.33	12.33	10.33
NG1	G17070	3.13	3.60	4.40	3.40	4.33	4.00	12.33	10.67
NG1	G18255	3.27	3.20	3.87	3.67	4.33	4.33	11.33	11.00
NG1	G18942	3.27	4.20	4.60	3.60	4.33	5.00	13.33	12.00
NG1	G21210	3.73	3.47	3.80	3.33	3.00	4.00	10.33	11.00
NG1	G4906	3.47	3.20	4.27	3.60	2.67	3.33	10.33	10.67
NG1	G6639	3.53	3.67	4.07	3.40	3.33	3.67	11.00	10.00
NG1	G738	4.07	3.07	3.87	4.33	4.00	4.67	10.67	13.33
NG1	G7945	3.67	3.93	3.87	3.87	4.00	4.33	11.67	12.00
NG1	G9846	3.73	3.53	4.40	3.67	2.67	3.67	10.67	10.67
NG1	G11982	3.93	3.73	4.33	4.47	3.67	3.33	12.00	11.67
NG1	G1688	4.33	4.13	4.87	4.47	4.33	4.33	13.33	13.33
NG1	G1836	4.40	4.27	4.53	3.93	3.33	4.00	12.33	12.33
NG1	G1939	3.73	4.20	5.13	4.20	4.00	3.00	13.33	11.00
NG1	G22247	4.07	3.87	4.27	4.00	2.67	3.33	10.67	11.33
NG1	G2875	4.47	2.80	3.93	5.07	3.00	4.00	9.67	13.67
NG1	G4001	3.13	3.87	3.80	3.40	2.67	2.67	10.67	9.33
NG1	G5142	4.00	3.93	5.20	4.47	4.00	3.67	13.33	12.00
NG1	G5273	4.60	3.13	4.00	5.27	2.67	3.67	9.67	12.67
NG1	G7776	4.60	3.87	4.00	4.33	3.00	2.67	10.67	11.33
NG1	G11957	4.00	3.87	4.93	4.00	3.00	3.00	11.67	11.00
NG1	G2563	3.87	3.60	3.80	3.60	4.33	4.67	12.00	12.00
	Mean	**3.87**	**3.64**	**4.20**	**4.02**	**3.46**	**3.80**	**11.32**	**11.57**

NG1 – Nueva Granada 1

Appendix 6 continued

	Trait	Leaf biomass (g)		Stem biomass (g)		Pod biomass (g)		Total biomass (g)	
Race	**Genotype**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**	**Irrigated**	**Rainfed**
NG2	G11512	3.53	3.07	3.07	3.40	3.33	4.33	9.67	11.00
NG2	G11585	3.80	3.60	4.00	3.53	2.33	2.67	10.00	10.00
NG2	G14253	4.20	3.13	3.93	3.60	4.00	4.33	10.67	12.00
NG2	G16104E	3.33	3.07	3.60	2.73	4.00	3.00	10.33	9.00
NG2	G4644	3.67	3.27	3.93	3.53	4.67	3.67	12.00	10.67
NG2	G5034	3.60	3.53	3.93	3.47	3.67	2.67	11.00	9.67
NG2	G5170	3.47	3.67	4.00	3.53	3.67	3.67	11.33	11.00
NG2	G5708	2.87	3.47	3.20	3.53	3.33	4.33	10.33	11.00
NG2	G6873	3.13	3.20	3.80	3.00	3.67	3.67	10.67	10.00
NG2	G7895	4.27	3.53	4.13	4.07	2.67	3.33	10.33	11.33
NG2	PVA1111	3.60	3.47	3.67	3.40	3.00	3.00	10.33	10.00
NG2	AND1005	4.93	3.93	4.60	4.53	3.33	3.00	11.67	12.67
NG2	G16110A	4.87	3.80	4.47	5.33	3.00	4.00	11.33	14.33
NG2	G1678	5.67	5.33	4.60	4.87	2.33	2.67	12.67	13.33
NG2	G23829	4.27	3.93	4.07	3.93	2.33	3.33	10.67	11.33
NG2	G11564	3.87	4.07	3.80	3.40	2.00	2.00	10.00	9.67
NG2	G11759A	4.93	4.20	4.53	4.53	2.00	2.00	11.00	11.33
NG2	G16346	4.00	4.07	4.27	4.13	3.33	2.33	11.33	10.67
NG2	G9855	4.07	4.27	4.47	3.80	3.00	2.67	11.33	10.67
NG2	G11727	4.33	3.93	4.27	3.93	2.00	2.33	10.33	10.67
NG2	G12517	4.07	3.27	3.80	4.27	2.67	2.67	10.00	11.00
NG2	G13595	4.33	4.33	4.20	4.07	3.00	3.00	11.67	11.67
NG2	G13910	3.80	4.20	4.47	3.67	2.67	2.67	11.33	10.00
NG2	G13911	3.73	4.27	5.00	3.93	3.33	3.33	12.67	10.67
NG2	G18264	4.27	4.07	4.13	3.73	4.00	3.33	12.00	11.33
NG2	G4672	4.47	3.53	4.33	4.60	2.33	2.33	10.00	11.67
NG2	G5849	3.53	3.07	3.73	3.20	4.00	2.33	10.33	8.67
NG2	G9335	4.73	3.40	3.33	4.00	2.33	2.67	9.33	11.67
NG2	G9603	4.00	3.87	3.67	3.80	2.33	3.00	10.00	11.00
NG2	G17168	4.00	3.60	3.60	3.87	2.67	2.33	9.67	10.00
	Mean	**4.04**	**3.74**	**4.02**	**3.85**	**3.03**	**3.02**	**10.80**	**10.93**
P	DRK47	3.67	3.87	3.87	3.60	3.67	3.33	11.33	10.33
P	G11521	4.27	3.33	3.87	4.33	2.67	3.33	10.33	11.67
P	G22147	3.73	3.87	4.33	4.27	3.67	4.33	11.67	12.33
P	G2686	3.53	3.47	4.13	3.20	3.00	3.33	10.33	10.00
P	G4494	3.60	4.00	3.47	3.87	3.33	4.33	11.00	11.33
P	G4547	4.20	3.60	3.67	3.93	2.00	2.33	9.67	10.67
P	PVA773	4.20	3.80	4.33	3.67	3.33	2.67	11.67	11.00
P	G14016	4.20	4.93	4.33	3.47	2.33	2.00	11.67	9.67
P	G19842	4.67	4.73	4.40	4.20	2.33	2.33	11.33	11.00
P	G23604	4.33	3.80	4.00	4.07	2.00	2.67	10.00	11.00
P	G2567	4.27	4.27	4.47	3.93	3.33	2.33	11.67	10.33
P	G4721	4.07	4.27	4.07	3.60	2.33	2.00	11.00	9.67
P	G4739	3.87	4.00	4.20	4.20	2.67	2.33	10.67	10.33
P	G12529	4.53	3.33	4.00	4.20	2.00	2.33	9.67	11.00
P	G19833	5.00	3.33	3.73	4.27	2.33	2.00	9.67	11.33
P	G8209	5.40	4.80	4.73	4.67	2.00	2.00	11.67	12.00
P	G19860	4.33	4.53	4.80	4.07	2.00	3.00	11.67	11.67
	Mean	**4.23**	**4.00**	**4.14**	**3.97**	**2.65**	**2.74**	**10.88**	**10.90**
	Grand mean	**4.02**	**3.79**	**4.11**	**3.94**	**3.11**	**3.29**	**11.04**	**11.22**
	LSD	**1.04**	**0.98**	**0.96**	**1.02**	**1.25**	**1.36**	**2.31**	**2.55**

NG2 – Nueva Granada 2; P – Peru; LSD – least significant difference

Appendix 7 Characteristics of microsatellite markers evaluated for population structure in a reference collection of common bean

Marker	Forward primer	Reverse primer	Motif size	AR (bp)	Panel	FL	Mg	Ta	LG
BM142	*TTC CGCTGA TTG GAT ATT AGA G*	*AGCCCGTTCCTTCGTTTAG*	(GA)10A(GA)15	155-162	0A	FAM	2 mM	52	b02
BM138	*TGT CCC TAA GAA CGA ATA TGG AAT C*	*GAATCAAGCAACCTTGGATCATAAC*	(GT)13	185-210	0A	NED	2 mM	50	b05
BM53	*AAC TAA CCT CAT ACG ACA TGA AA*	*AATGCTTGCACTAGGGAGTT*	(CT)21(CA)19(TA)9	90-130	0A	VIC	2 mM	55	b01
BMd33	*TAC GCT GTG ATG CAT GGT TT*	*CCTGAAAGTGCAGAGTGGTG*	(ATT)9	97-110	0A	PET	2 mM	47	b11
BM170	*AGC CAG GTG CAA GAC CTT AG*	*AGATAGGGAGCTGGTGGTAGC*	(CT)5CCTT(CT)12	148-192	0B	PET	2 mM	50	b06
GATS11	*CAC ATT GGT GCT AGT GTC GG*	*GAACCTGCAAAGCAAAGAGC*	(CT)8CA(CT)2GTTT(CT)4	226-233	0B	NED	2 mM	52	b10
BM185	*AAG GAG GTT TCT ACC TAA TTC C*	*AAAGCAGGGATGTAGTTGC*	(CT)12	100-117	0B	VIC	2 mM	52	b07
BMd36	*CAT AAC ATC GAA GCC TCA CAG T*	*ACGTGCGTACGAATACTCAGTC*	(TA)8	161-182	0B	FAM	2 mM	47	b03
BMc305	*CCA GAG AGA AGG GAA GAG GAA*	*AAC CCA AGT TGA GAA AGC TCC*	(GT)6	90-110	1A	FAM	1.5 mM	60	b03
BM199	*AAG GAG AAT CAG AGA AGC CAA AAG*	*TGAGGAATGGATGTAGCTCAGG*	(GA)15	270-320	1A	NED	2 mM	56	b04
BM157	*ACT TAA CAA GGA ATA GCC ACA CA*	*GTTAATTGTTTCCAATATCAACCTG*	(GA)16	96-130	1A	VIC	2 mM	52	b10
BMy06	*AAG GAT GGG TTC CGT GCT TG*	*CAC GGT ACA CGA AAC CAT GCT ATC*	(GAAT)5	160-166	1A	PET	2 mM	49	b04
BMd40	*AAC CTT CTT GCG CTG ATC TC*	*TAGTGGCCATTCCTCGATCT*	(AT)6	190-213	1B	FAM	2 mM	47	b07
BMd41	*CAG TAA ATA TTG GCG TGG ATG A*	*TGAAAGTGCAGAGTGGTGGA*	(ATT)9	232-255	1B	NED	2 mM	47	b11
BM152	*AAG AGG AGG TCG AAA CCT TAA ATC G*	*CCG GGA CTT GCC AGA AGA AC*	(GA)31	80-138	1B	VIC	2 mM	50	b02
BM161	*TGC AAA GGG TTG AAA GTT GAG AG*	*TTC CAA TGC ACC AGA CAT TCC*	(GA)7(GA)8	148-195	1B	PET	2 mM	52	b04
BMd03	*TGT TTC TTC CTT ATG GTT AGG TTG*	*TCA CGT TAT CAC CAG CAT CGT AGT A*	(AT)8	217-233	2A	FAM	2 mM	49	Na
BM188A	*TCG CCT TGA AAC TTC TTG TAT C*	*CCC TTC CAG TTA AAT CAG TCG*	(CA)18(TA)7	130-153	2A	NED	1.5 mM	50	b09
BM184	*AGT GCT CTA TCA AGA TGT GTG*	*ACA TAA TCA ATG GGT CAC TG*	(AC)11	150-167	2A	PET	2 mM	52	b11
BM98	*GCA TCA CAA AGG ACT GAG AGC*	*CCC AAG CAA AGA GTC GAT TT*	(CA)8(CT)3	242-255	2A	VIC	2 mM	55	b03
BM209	*CAA CCA ATG AAT GCT GAC AAT G*	*CAA TTT CTT GAT TGA AAG GCA AT*	(TA)4(TG)16	90-158	2B	FAM	2 mM	56	b07
BMd12	*CAT CAA CAA GGA CAG CCT CA*	*GCAGCTGGCGGGTAAAACAG*	(AGC)7	155-170	2B	NED	2 mM	47	b06
BM211	*ATA CCC ACA TGC ACA AGT TTG G*	*CCA CCA TGT GCT CAT GAA GAT*	(CT)16	140-220	2B	PET	2 mM	52	b08
BMd53	*TGC TGA CCA AGG AAA TTC AG*	*GGA GGA GGC TTA AGC ACA AA*	(GTA)5	95-112	2B	VIC	2 mM	47	b05
BMd42	*TCA TAG AAG ATT TGT GGA AGC A*	*TGAGACACGTACGAGGCTGTAT*	(AT)5	128-160	3A	PET	2 mM	49	b10
BM181	*ATG CTG CGA GTT AAT GAT CG*	*TGA GGA GCA AAC AGA TGA GG*	(CT)17	175-200	3A	NED	2 mM	50	b03
BMd45	*GGT TGG GAA GCC TCA TAC AG*	*ATCTTCGACCCACCTTGCT*	(AG)5	85-130	3A	VIC	2 mM	49	b01
BM151	*CAC AAC AAG AAA GAC CTC CT*	*TTA TGT ATT AGA CCA CAT TAC TTC C*	(TC)14	140-154	3A	FAM	2 mM	50	b08
BM165	*TCA AAT CCC ACA CAT GAT CG*	*TTC TTT CAT TCA TAT TAT TCC GTT CA*	(TA)3(CA)9	155-192	3B	PET	2 mM	52	Na
BM154	*TCT TGC GAC CGA GCT TCT CC*	*CTG AAT CTG AGG AAC GAT GAC CAG*	(CT)17	205-248	3B	NED	2 mM	50	b09
BM189	*CTC CCA CTC TCA CCC TCA CT*	*GCG CCA AGT GAA ACT AAG TAG A*	(CT)13	100-117	3B	VIC	2 mM	50	b08
BMd10	*GCT CAC GTA CGA GTT GAA TCT CAG*	*ATC TGA GAG CAG CGA CAT GGT AG*	(GA)8	135-144	3B	FAM	2 mM	48	b01
BMd07	*GGA TAT GGT GGT GAT CAA GGA*	*CATACCCAATGCCATGTTCTC*	(TGG)5	140-180	4A	NED	2 mM	49	b02
PV-at007	*AGT TAA ATT ATA CGA GGT TAG CCT AAA TC*	*CAT TCC CTT CAC ACA TTC ACC G*	(AT)9	145-215	4A	FAM	2 mM	49	b09
BM167	*TCC TCA ATA CTA CAT CGT GTG ACC*	*CCT GGT GTA ACC CTC GTA ACA G*	(GA)19	100-165	4A	VIC	2 mM	50	b02
BM153	*CCG TTA GGG AGT TGT TGA GG*	*TGA CAA ACC ATG AAT ATG CTA AGA*	(CA)5(TG)(CA)3CG(CA)10(TA)4	175-255	4A	PET	2 mM	52	Na
BMd22	*GGT CAC TTC CGG AGC ATT C*	*CGGGAAATGGAAGTCACAGT*	(TC)6	100-123	4B	NED	2 mM	47	b11
BM202	*ATG CGA AAG AGG AAC AAT CG*	*CCT TTA CCC ACA CGC CTT C*	(GA)9GT(GA)4	130-210	4B	FAM	2 mM	50	Na
BM114	*AGC CTG GTG AAA TGC TCA TAG*	*CAT GCT TGT TGC CTA ACT CTC T*	(TA)8(GT)10	220-275	4B	VIC	2 mM	50	b09
BMy11	*TTG ATG ACG TGG ATG CAT TGC*	*AAA GGG CTA GGG AGA GTA AGT TGG*	(AG)8	190-212	4B	PET	2 mM	48	b04
BMd08	*TTC ATC CTC TCT CCC GAA CTT*	*CTT TTG TGG CTG AGA CAT GGT*	(CT)7	176-190	5A	NED	1.5 mM	52	Na
BMd20	*GTT GCC ACC GGT GAT AAT CT*	*GTG AGG CAA GAA GCC TTC AA*	(TA)5	118-132	5A	VIC	2 mM	52	b05
BM172	*CTG TAG CTC AAA CAG GGC ACT*	*GCA ATA CCG CCA TGA GAG AT*	(GA)23	82-110	5A	PET	2 mM	50	b03
BMy02	*CAA TCC TCT CTC TCT CAT TTC CAA TC*	*GAC CTT GAA GTC GGT GTC GTT T*	(GA)11	150-164	5A	FAM	2 mM	47	b11
BM188B	*TCG CCT TGA AAC TTC TTG TAT C*	*CCC TTC CAG TTA AAT CAG TCG*	(CA)18(TA)7	160-200	5B	NED	1.5 mM	50	b09
BM175	*CAA CAG TTA AAG GTC GTC AAA TT*	*CCA CTC TTA GCA TCA ACT GGA*	(AT)5(GA)19	160-195	5B	VIC	1.5 mM	50	b05
BM200	*TGG TGG TTG TTA TGG GAG AAG*	*ATT TGT CTC TGT CTA TTC CTT CCA C*	(AG)10	227-295	5B	FAM	2 mM	54	b01
BM205	*CTA GAC CAG GCA AAG CAA GC*	*TGA GCT GGG ATT TCA TTT CTG*	(GT)11	135-153	5B	PET	2 mM	50	b07
BM139	*TTA GCA ATA CCG CCA TGA GAG*	*ACT GTA GCT CAA ACA GGG CAC*	(CT)25	84-118	6A	PET	2 mM	50	b02
BM156	*CTT GTT CCA CCT CCC ATC ATA GC*	*TGC TTG CAT CTC AGC CAG AAT C*	(CT)32	210-315	6A	FAM	1.5 mM	55	b02
PV-ctt001	*GAG GGT GTT TCA CTA TTG TCA CTG C*	*TTC ATG GAT GGT GGA GGA ACA G*	(CTT)5	152-172	6A	VIC	1.5 mM	50	b03
BM160	*CGT GCT TGG CGA ATA GCT TTG*	*CGC GGT TCT GAT CGT GAC TTC*	(GA)15(GAA)5	183-265	6A	NED	1.5 mM	55	b07
PV-ag003	*TCA CGT ACG AGT TGA ATC TCA GGA T*	*GGT GTC GGA GAG GTT AAG GTT G*	(AG)8	161-168	6B	NED	1.5 mM	50	b01
BMd01	*CAA ATC GCA ACA CCT CAC AA*	*GTC GGA GCC ATC ATC TGT TT*	(AT)9	165-199	6B	FAM	1.5 mM	50	b03
BMd02	*AGC GAC AGC AAG AGA ACC TC*	*CAA CAA ACG GTG ATT GAC CA*	(CGG)8	100-110	6B	PET	1.5 mM	50	b02
BMd16	*ATG ACA CCA CTG GCC ATA CA*	*CTC ACT GTC TTC CAT CCA AGC*	(CATG)4	135-150	6B	VIC	1.5 mM	50	b04
BM201	*TGG TGC TAC AGA CTT GAT GG*	*TGT CAC CTC TCT CCT CCA AT*	(GA)15	94-114	7A	PET	2 mM	50	b07
AG01	*CAT GCA GAG GAA GCA GAG TG*	*GAG CGT CGT CGT TTC GAT*	(GA)8GGTA(GA)5GGGGACG(AG)4	126-142	7A	VIC	2 mM	50	b03
BM140	*TGC ACA ACA CAC ATT TAG TGA C*	*CCT ACC AAG ATT GAT TTA TGG G*	(GA)30	160-210	7A	FAM	1.5 mM	50	b04
GATs54	*GAA CCT GCA AAG CAA AGA GC*	*TCA CTC TCC AAC CAG ATC GAA*	(GA)5AACAGAGT(GA)8	114-117	7A	NED	1.5 mM	50	b3
BM187	*TTT CTC CAA CTC ACT CCT TTC C*	*TGT GTT TGT GTT CCG AAT TAT GA*	(CT)10T(CT)14	150-226	7B	VIC	1.5 mM	52	b06
BMd17	*GTT AGA TCC CGC CCA ATA GTC*	*AGA TAG GAA GGG CGT GGT TT*	(CGCCAC)6	100-118	7B	PET	1.5 mM	50	b02
BM183	*CTC AAA TCT ATT CAC TGG TCA GC*	*TCT TAC AGC CTT GCA GAC ATC*	(TC)14	134-160	7B	NED	1.5 mM	52	b07
PV-at001	*GGG AGG GTA GGG AAG CAG TG*	*GCG AAC CAC GTT CAT GAA TGA*	(TA)22	170-330	7B	FAM	2 mM	55	b04
BM143	*GGG AAA TGA ACA GAG GAA A*	*ATG TTG GGA ACT TTT AGT GTG*	(GA)35	118-176	8A	PET	2 mM	55	b02
BM149	*CGA TGG ATG GAT GGT TGC AG*	*GGG CCG ACA AGT TAC ATC AAA TTC*	(TGC)6(TAG)3	242-258	8A	FAM	2 mM	50	Na
BM137	*CGC TTA CTC ACT GTA CGC ACG*	*CGC TTA CTC ACT GTA CGC ACG*	(CT)33	122-238	8A	VIC	2 mM	65	b06
BMd46	*GGC TGA CAA CAA CTC TGC AC*	*CTG GCA TAG GTT GCT CCT TC*	(TCT)4	320-330	8A	NED	1.5 mM	50	Na
BMd47	*ACC TGG TCC CTC AAA CCA AT*	*CAA TGG AGC ACC AAA GAT CA*	(AT)5	128-154	8B	PET	1.5 mM	50	b02
BM141	*TGA GGA GGA ACA ATG GTG GC*	*CTC ACA AAC CAC AAC GCA CC*	(GA)29	160-350	8B	FAM	2 mM	55	b09
PV-cct001	*CCA ACC ACA TTC TTC CCT ACG TC*	*GCG AGG CAG TTA TCT TTA GGA GTG*	(AT)12	137-158	8B	VIC	1.5 mM	50	Na
BMd15	*TTG CCA TCG TTG CTT AAT TG*	*TTG GAG GAA GCC ATG TAT GC*	(AG)6	163-202	8B	NED	1.5 mM	50	b04
BMy08	*AGT TAA ATT ATA CGA GGT TAG CCT AAA TC*	*CAT TCC CTT CAC ACA TTC ACC G*	(AT)12	190-196	16	VIC	2 mM	49	b09
BM67	*CCA ATG CTG CCA CAC AGA TA*	*CGC CCT TAT GAT CCA GTC CT*	(CA)31(CG)5(CA)10	280-298	16	NED	2 mM	50	Na

Appendix 7 continued

Marker	Forward primer	Reverse primer	Motif size	AR (bp)	Panel	FL	Mg	Ta	LG
BMd51	*CGC CAA TTC TTC AAC CCT AA*	*GTA GTT CGC CCG AGG ACT G*	(CT)5	107-118	9A	PET	1.5 mM	50	Na
BMd18	*AAA GTT GGA CGC ACT GTG ATT*	*TCG TGA GGT AGG AGT TTG GTG*	(TGAA)3	156-242	9A	FAM	1.5 mM	50	b02
PV-at003	*AAG GAT GGG TTC CGT GCT TG*	*GAA TGT GAA TAT CAG AAA GCA AAT GG*	(AT)4(T)2	156-166	9A	VIC	1.5 mM	50	b04
BMd56	*AAT GCG TGA GCA TGA TTA AGG*	*TCA TCT GTC AGC ACC AAA CC*	(AT)5	186-192	9A	NED	2 mM	50	b02
BMc206	*CTC TCA TCC ATT CGC ACC TT*	*ACCCCACTTGGTCTTCGTCT*	(TC)8	102-104	14	VIC	2 mM	47	b06
BMc161	*CCG CTC TTA ACC TGT CAC CT*	*ACCGTGTATTTGAGCGGTTG*	(TC)9	130-140	14	PET	2 mM	47	b06
BM213	*AAC CCT AAG CTT CAC GCA TTT G*	*GAGAGATTGACGACGGTTT*	(CTT)4(CT)5(CTT)(CT)(CTT)(CT)4	158-160	14	NED	2 mM	55	Na
BM197	*TGG ACT GGT CGA TAC GAA GC*	*CCCAGAAGATTGAGAACACCAC*	(GT)8	195-200	14	FAM	2 mM	53	b03
BMc283	*CAA AGT CCC ACT CTT CTC TCT C*	*TCAGCAAACCCTAATTGGAA*	(TC)12	96-113	15	VIC	2 mM	47	b06
BMd26	*CTT GCC TTG TGC TTC CTT CT*	*TCCATTCCCAACCAAGTTTC*	(GAT)6	90-125	15	NED	2 mM	55	b04
BM68	*TTC GTT CAC AAC CTC TTG CAT T*	*TGCTTGTTATCTTGCCCAGTG*	(CA)6TA(CA)4(TA)4(CA)5	90-100	15	FAM	2 mM	56	b04
BMd44	*GGC AGC TTA CTA ACC CGA AA*	*TTC CTT CCC CTT TCT TCT CC*	(AG)5		15	PET	2 mM	47	b08

AR – allele size range; bp – base pair; FL – fluorescent label; Mg – magnesium concentration; Ta – annealing temperature; LG – linkage group; mM – milli Molar; Na – unlinked

Appendix 8 Identified associations between SNP markers and grain yield under irrigated and rainfed treatments at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Across locations	Marker	linkage group	p value	Marker R^2	Across locations
Irrogated treatment				Rainfed treatment									
TOG895672_181	2	0.0011	0.0449	TOG913005_113	3	0.0013	0.0478	F	TOG901238_199	10	0.0013	0.0460	F
TOG907233_598	6	0.0014	0.0434	TOG916703_239	4	0.0013	0.0481	F	TOG900416_243	7	0.0020	0.0424	F
TOG895900_416	9	0.0014	0.0420	TOG904027_122	5	0.0013	0.0462	F	TOG894773_280	8	0.0032	0.0393	F
TOG896767_576	4	0.0015	0.0428	TOG903882_547	4	0.0025	0.0409	F	TOG897333_569	6	0.0039	0.0413	F
TOG900594_110	2	0.0016	0.0416	TOG896943_422	2	0.0028	0.0606	F	TOG910388_90	7	0.0047	0.0353	F
TOG910388_90	7	0.0022	0.0384	TOG906843_140	1	0.0028	0.0403	F	TOG898284_1682	8	0.0070	0.0343	F
TOG899600_703	9	0.0023	0.0388	TOG905343_279	2	0.0028	0.0411	F	TOG899600_703	9	0.0088	0.0309	F
TOG914633_385	7	0.0031	0.0484	TOG900594_110	2	0.0030	0.0398	F	TOG906600_415	9	0.0088	0.0311	F
TOG915832_137	7	0.0038	0.0348	TOG894986_609	2	0.0032	0.0393	F	TOG918299_615	6	0.0101	0.0380	F
TOG898024_443	5	0.0041	0.0351	TOG895672_181	2	0.0042	0.0369	F	TOG915832_137	7	0.0111	0.0289	F
TOG918946_209	8	0.0042	0.0345	TOG925468_198	3	0.0050	0.0363	F	TOG961366_282	11	0.0115	0.0284	F
TOG898304_707	6	0.0042	0.0349	TOG906936_331	2	0.0056	0.0359	F	TOG895747_525	8	0.0118	0.0283	F
TOG919452_184	4	0.0047	0.0328	TOG900221_555	3	0.0085	0.0412	F	TOG895245_245	8	0.0149	0.0266	F
TOG895846_60	7	0.0047	0.0333	TOG895899_315	5	0.0087	0.0320	F	TOG906530_971	8	0.0154	0.0276	F
TOG901215_645	1	0.0048	0.0340	TOG897521_498	1	0.0109	0.0298	F	TOG900220_648	11	0.0186	0.0250	F
				TOG901215_645	1	0.0162	0.0267	F	TOG895900_155	9	0.0195	0.0245	F
				TOG898353_150	4	0.0175	0.0253	F	TOG898284_346	8	0.0200	0.0256	F
				TOG898353_393	4	0.0175	0.0253	F	TOG900220_279	11	0.0232	0.0230	F
				TOG898302_727	2	0.0181	0.0261	F	TOG902611_789	8	0.0261	0.0224	F
				TOG897521_1471	1	0.0190	0.0269	F	TOG914633_385	7	0.0266	0.0299	F
				TOG899130_778	1	0.0212	0.0238	F	TOG896253_482	8	0.0274	0.0217	F
				TOG918275_1006	3	0.0216	0.0281	F	TOG896385_269	6	0.0278	0.0222	F
				TOG923111_969	3	0.0216	0.0281	F	TOG898489_619	9	0.0285	0.0221	F
				TOG900308_234	2	0.0240	0.0230	F	TOG896491_59	6	0.0294	0.0219	F
				TOG897579_687	5	0.0255	0.0383	F	TOG922990_288	7	0.0325	0.0215	F
				TOG943467_524	3	0.0259	0.0223	F	TOG910860_634	6	0.0329	0.0207	F
				TOG902879_375	1	0.0273	0.0225	F	TOG898075_168	7	0.0345	0.0207	F
				TOG896767_576	4	0.0280	0.0224	F	TOG922990_513	7	0.0353	0.0202	F
				TOG898024_443	5	0.0283	0.0221	F	TOG910860_172	6	0.0380	0.0194	F
				TOG894885_690	2	0.0330	0.0206	F	TOG916702_146	8	0.0383	0.0195	F
				TOG897323_74	5	0.0369	0.0200	F	TOG913042_449	9	0.0418	0.0189	F
				TOG895690_777	2	0.0379	0.0195	F	TOG907233_598	6	0.0423	0.0191	F
				TOG896943_500	2	0.0408	0.0190	F	TOG900332_1066	7	0.0459	0.0181	F
				TOG903712_258	3	0.0411	0.0190	F	TOG894037_604	9	0.0462	0.0178	F
				TOG901225_355	2	0.0442	0.0184	F	TOG914901_92	11	0.0492	0.0178	F
				TOG905371_69	3	0.0204	0.0245	T	TOG898046_230	7	0.0024	0.0420	T
				TOG905371_417	3	0.0219	0.0247	T	TOG894794_142	7	0.0059	0.0345	T
				TOG907013_1059	5	0.0424	0.0193	T	TOG913042_381	9	0.0284	0.0214	T

Markers coloured red are common between the irrigated and rainfed treatments; T – markers are common between CIAT-Palmira and Harare Research Station under rainfed treatments; F – markers are not common between CIAT-Palmira and Harare Research Station under rainfed treatments

Appendix 9 Identified associations between SNP markers and grain yield under irrigated and rainfed treatments at Harare Research Station

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment			
TOG896888_794	11	0.0032	0.0497	TOG960456_224	1	0.0464	0.0212
TOG899382_247	2	0.0040	0.0477	TOG895871_64	2	0.0017	0.0520
TOG929859_500	1	0.0047	0.0454	TOG923884_128	2	0.0044	0.0475
TOG900259_705	7	0.0051	0.0451	TOG896567_73	2	0.0156	0.0309
TOG913042_381	9	0.0073	0.0409	TOG935639_446	3	0.0034	0.0460
TOG928182_453	2	0.0121	0.0365	TOG899072_215	3	0.0037	0.0443
TOG903324_447	2	0.0122	0.0363	TOG911121_130	3	0.0072	0.0393
TOG903898_287	2	0.0126	0.0360	TOG894987_722	3	0.0138	0.0321
TOG898304_552	6	0.0136	0.0350	TOG895572_269	3	0.0187	0.0296
TOG900129_79	2	0.0137	0.0375	TOG905371_417	3	0.0253	0.0277
TOG901841_376	3	0.0155	0.0339	TOG905371_69	3	0.0271	0.0264
TOG894885_690	2	0.0156	0.0338	TOG897306_218	3	0.0431	0.0222
TOG929271_717	2	0.0205	0.0311	TOG898271_99	4	0.0242	0.0274
TOG935983_331	8	0.0209	0.0313	TOG907013_1059	5	0.0352	0.0244
TOG897333_615	6	0.0223	0.0300	TOG898304_552	6	0.0026	0.0481
TOG895871_64	2	0.0237	0.0295	TOG897188_682	6	0.0181	0.0302
TOG903842_603	3	0.0238	0.0299	TOG900006_352	7	0.0012	0.0546
TOG901734_61	6	0.0248	0.0290	TOG894794_142	7	0.0109	0.0352
TOG923884_128	2	0.0262	0.0313	TOG898046_230	7	0.0149	0.0318
TOG899617_590	11	0.0265	0.0284	TOG935983_331	8	0.0088	0.0368
TOG898489_619	9	0.0269	0.0284	TOG907901_189	8	0.0450	0.0217
TOG899297_398	6	0.0297	0.0294	TOG913042_381	9	0.0211	0.0283
TOG918200_508	5	0.0335	0.0266	TOG901933_425	9	0.0381	0.0231
TOG899751_220	9	0.0369	0.0336	TOG908804_377	9	0.0381	0.0231
TOG912552_357	4	0.0378	0.0262	TOG901933_203	9	0.0474	0.0213
TOG902768_856	4	0.0417	0.0242	TOG899617_590	11	0.0020	0.0502
TOG900787_1237	11	0.0441	0.0237	TOG896372_529	11	0.0045	0.0428
TOG907902_589	4	0.0454	0.0231	TOG896372_451	11	0.0055	0.0409
TOG924531_275	4	0.0454	0.0231	TOG924872_53	11	0.0250	0.0269
TOG913108_139	7	0.0479	0.0226	TOG908034_427	11	0.0299	0.0256
TOG896103_318	11	0.0480	0.0228				
TOG900798_677	11	0.0480	0.0228				
TOG906599_51	11	0.0483	0.0227				

Markers coloured red are common between the irrigated and rainfed treatments; T – markers are common between CIAT-Palmira and Harare Research Station under rainfed treatments; F – markers are not common between CIAT-Palmira and Harare Research Station under rainfed treatments

Appendix 10 Identified associations between SNP markers and 100-seed weight under irrigated and rainfed treatments at CIAT-Palmira

Marker	LG	P-values	Marker R^2	Marker	LG	P-values	Marker R^2	Marker	LG	P-values	Marker R^2	Marker	LG	P-values	Marker R^2
			Irrigated treatment								Rainfed treatment				
TOG902879_375	1	<.0001	0.05256056	TOG894794_142	7	<.0001	0.096302321	TOG894042_842	1	<.0001	0.072633473	TOG894052_203	6	0.02515	0.02042888
TOG894042_842	1	<.0001	0.050603709	TOG898046_230	7	<.0001	0.071800378	TOG894818_243	1	<.0001	0.069515064	TOG918299_615	6	0.02677	0.02618366
TOG900375_652	1	<.0001	0.04715225	TOG900006_352	7	<.0001	0.052255107	TOG900375_652	1	<.0001	0.066295555	TOG897486_230	6	0.028	0.0194431
TOG896448_605	1	0.010223	0.027699274	TOG900416_243	7	0.00378	0.034085667	TOG894818_489	1	<.0001	0.072373905	TOG924576_145	6	0.02973	0.01893191
TOG903032_1755	1	0.01091	0.026111646	TOG899042_188	7	0.01912	0.022610866	TOG896448_605	1	<.0001	0.048706714	TOG902716_501	6	0.02973	0.01893191
TOG897724_419	1	0.01091	0.026111646	TOG900332_1066	7	0.02092	0.021611627	TOG895545_757	1	0.00469	0.032407522	TOG902716_610	6	0.02973	0.01893191
TOG898832_447	1	0.01091	0.026111646	TOG927609_1357	7	0.02641	0.020468403	TOG929859_500	1	0.01404	0.024104367	TOG897333_615	6	0.03145	0.01870738
TOG898832_568	1	0.01091	0.026111646	TOG894148_761	8	<.0001	0.113251807	TOG902879_375	1	0.01613	0.023896714	TOG910860_172	6	0.03154	0.01924102
TOG894818_243	1	0.012378	0.026646162	TOG925843_147	8	<.0001	0.082751057	TOG912381_118	1	0.03211	0.018428368	TOG901896_412	6	0.03211	0.01842837
TOG929859_500	1	0.016826	0.023164672	TOG907901_189	8	<.0001	0.078879293	TOG896584_248	1	0.04134	0.016900638	TOG897347_414	6	0.03382	0.01899673
TOG894818_489	1	0.025256	0.026247786	TOG898284_1682	8	0.00167	0.039354758	TOG894760_112	1	0.04226	0.016555241	TOG895876_107	6	0.03385	0.01817789
TOG895871_64	2	<.0001	0.140129384	TOG898284_346	8	0.00217	0.037481124	TOG895871_64	2	<.0001	0.082094599	TOG910860_634	6	0.03435	0.01884696
TOG896567_73	2	<.0001	0.080679632	TOG895245_245	8	0.00237	0.037467671	TOG896567_73	2	<.0001	0.052219472	TOG894516_506	6	0.03504	0.01791465
TOG906969_104	2	<.0001	0.055384415	TOG899729_79	8	0.04203	0.017490556	TOG928916_162	2	0.00233	0.037697695	TOG897347_125	6	0.0355	0.0179523
TOG895672_181	2	0.001575	0.04076711	TOG896253_482	8	0.0442	0.016493293	TOG896943_500	2	0.00426	0.032463048	TOG898304_707	6	0.03595	0.01765097
TOG895690_777	2	0.00165	0.040878251	TOG913042_381	9	<.0001	0.075745904	TOG895672_181	2	0.00432	0.032920987	TOG897646_1184	6	0.03596	0.01773846
TOG906764_376	2	0.007071	0.031117707	TOG906600_415	9	<.0001	0.049331453	TOG906764_376	2	0.00805	0.030116669	TOG896074_686	6	0.03753	0.01778031
TOG906764_834	2	0.007071	0.031117707	TOG898489_619	9	<.0001	0.047481937	TOG906764_834	2	0.00805	0.030116669	TOG931720_274	6	0.03766	0.01750653
TOG899382_247	2	0.012056	0.02613692	TOG895978_272	9	0.00927	0.027473252	TOG894755_654	2	0.01535	0.023986347	TOG902800_160	6	0.03972	0.01799258
TOG906936_331	2	0.012356	0.025444005	TOG901933_425	9	0.01264	0.025486855	TOG901225_355	2	0.0175	0.023088789	TOG897513_306	6	0.04203	0.0167446
TOG901225_355	2	0.019203	0.022649904	TOG908804_377	9	0.01264	0.025486855	TOG898302_727	2	0.02128	0.022298683	TOG899452_215	6	0.04205	0.01660719
TOG897172_226	2	0.020412	0.022166728	TOG901933_203	9	0.01507	0.024527257	TOG899382_247	2	0.0237	0.021138057	TOG897513_200	6	0.04292	0.01645213
TOG896943_500	2	0.021711	0.021169634	TOG905363_697	9	0.02167	0.022815993	TOG901772_360	2	0.03571	0.018462642	TOG896385_269	6	0.04517	0.0162149
TOG895690_643	2	0.028018	0.01933647	TOG899668_578	9	0.03025	0.020412595	TOG910927_147	2	0.036	0.017947683	TOG896850_232	7	<.0001	0.06867992
TOG928916_162	2	0.048024	0.016279928	TOG908646_276	9	0.04273	0.017040524	TOG906969_104	2	0.03853	0.017289688	TOG900006_352	7	<.0001	0.04774635
TOG899072_215	3	<.0001	0.09317495	TOG903088_74	9	0.04357	0.016870328	TOG895594_590	2	0.03998	0.017546558	TOG894794_142	7	0.00148	0.04016855
TOG943467_524	3	<.0001	0.076225389	TOG896504_1537	10	0.00381	0.033795778	TOG901960_1149	2	0.04018	0.016936203	TOG898046_230	7	0.01004	0.02704228
TOG894987_722	3	<.0001	0.073650333	TOG904927_660	10	0.00659	0.030426229	TOG896943_422	2	0.04135	0.031050501	TOG927609_1357	7	0.01188	0.02594988
TOG896609_245	3	<.0001	0.071154419	TOG894060_416	10	0.01938	0.022814864	TOG895739_547	2	0.04226	0.016555241	TOG894968_641	7	0.0155	0.0234206
TOG895163_666	3	<.0001	0.068999935	TOG894056_496	10	0.03796	0.01844719	TOG916436_325	2	0.04323	0.016543869	TOG899042_188	7	0.01983	0.02201869
TOG901547_185	3	<.0001	0.048231233	TOG907046_267	10	0.04181	0.01778173	TOG906936_331	2	0.04942	0.015891415	TOG894148_761	8	<.0001	0.06110233
TOG901547_549	3	<.0001	0.048231233	TOG900784_136	10	0.04622	0.01706982	TOG943467_524	3	<.0001	0.090438189	TOG907901_189	8	<.0001	0.05100021
TOG911121_130	3	0.003147	0.036126007	TOG908034_427	11	0.00135	0.041601638	TOG895163_666	3	<.0001	0.089496669	TOG894070_290	8	<.0001	0.05646359
TOG895572_269	3	0.006225	0.029909074	TOG899617_590	11	0.00209	0.038419619	TOG896609_245	3	<.0001	0.063434937	TOG894070_261	8	<.0001	0.05032347
TOG895984_205	3	0.01527	0.023487759	TOG894153_805	11	0.00337	0.034328884	TOG899072_215	3	<.0001	0.056002223	TOG925843_147	8	0.00114	0.04202687
TOG901675_241	3	0.022385	0.021166338	TOG895575_317	11	0.01372	0.025178331	TOG918275_1006	3	0.00119	0.044409414	TOG898284_1682	8	0.00176	0.03939359
TOG905123_751	3	0.026173	0.02026471	TOG900222_165	11	0.02277	0.021668406	TOG923111_969	3	0.00119	0.044409414	TOG896253_482	8	0.01497	0.02366037
TOG894864_431	3	0.027929	0.019218586	TOG906948_530	11	0.02798	0.021106865	TOG894196_495	3	0.0025	0.036607827	TOG906662_87	8	0.0221	0.02130218
TOG894712_181	3	0.035033	0.019327718					TOG905123_751	3	0.00961	0.026973547	TOG899689_445	8	0.0258	0.02033228
TOG916106_684	3	0.037732	0.017415479					TOG900241_1293	3	0.00986	0.026703413	TOG902629_253	8	0.02783	0.02001759
TOG896168_406	3	0.040202	0.017138896					TOG894987_722	3	0.01105	0.025771102	TOG898284_346	8	0.03049	0.01914303
TOG905443_301	3	0.045932	0.016049671					TOG901908_232	3	0.01324	0.024551048	TOG919333_731	8	0.04784	0.01588244
TOG896371_453	3	0.049876	0.015687581					TOG901037_215	3	0.01425	0.023986693	TOG899729_79	8	0.04825	0.01631096
TOG896767_576	4	0.017649	0.022703218					TOG912558_1306	3	0.01504	0.023602804	TOG946841_476	8	0.04853	0.01574148
TOG894658_115	4	0.04576	0.016527456					TOG919004_144	3	0.01549	0.0234889	TOG905363_697	9	<.0001	0.07294651
TOG904027_122	5	<.0001	0.091639983					TOG901032_412	3	0.01572	0.023500483	TOG901933_425	9	<.0001	0.06919505
TOG897323_74	5	0.001681	0.039569644					TOG899716_657	3	0.01656	0.022961887	TOG908804_377	9	<.0001	0.06919505
TOG904027_285	5	0.00199	0.042045402					TOG901908_188	3	0.0176	0.023072208	TOG901933_203	9	<.0001	0.0679185
TOG895899_315	5	0.004063	0.03249863					TOG896873_475	3	0.02141	0.021193796	TOG899668_578	9	<.0001	0.06300917
TOG907013_1059	5	0.004493	0.032755509					TOG895984_205	3	0.02715	0.019557247	TOG898489_619	9	<.0001	0.04967726
TOG898978_625	5	0.038038	0.017812086					TOG899518_974	3	0.02973	0.018931911	TOG895978_272	9	<.0001	0.04504663
TOG918200_347	5	0.038244	0.017714767					TOG901547_185	3	0.03018	0.01884837	TOG906600_415	9	0.00163	0.03923658
TOG897333_569	6	<.0001	0.059977834					TOG901547_549	3	0.03018	0.01884837	TOG895760_342	9	0.00184	0.03893108
TOG898304_707	6	0.001553	0.039481951					TOG895572_269	3	0.03555	0.017836573	TOG896197_226	9	0.00194	0.0398933
TOG896385_269	6	0.003645	0.033683416					TOG904255_224	4	0.01439	0.024334621	TOG908646_276	9	0.00417	0.03328461
TOG907233_598	6	0.028502	0.019654454					TOG904027_122	5	<.0001	0.054896116	TOG895760_820	9	0.00455	0.03662488
TOG896850_232	7	<.0001	0.101375233					TOG898978_625	5	0.00187	0.038934758	TOG913042_381	9	0.00637	0.02961442
								TOG918200_347	5	0.00917	0.02721752	TOG903088_74	9	0.00813	0.02835292
								TOG904027_285	5	0.01452	0.027268083	TOG894880_493	9	0.03556	0.01779661
								TOG897017_278	5	0.01923	0.023868777	TOG894022_713	9	0.04105	0.01676762
								TOG896089_391	5	0.0366	0.017793488	TOG894060_416	10	0.00621	0.03023079
								TOG897017_257	5	0.03697	0.023474209	TOG900784_136	10	0.00847	0.02907297
								TOG897333_569	6	<.0001	0.058957393	TOG896504_1537	10	0.01736	0.02273902
								TOG896074_553	6	0.00451	0.033899867	TOG907046_267	10	0.01823	0.0232753
								TOG901700_397	6	0.00495	0.034309332	TOG904927_660	10	0.02108	0.02176097
								TOG896306_360	6	0.0072	0.030019969	TOG906948_530	11	<.0001	0.06419114
								TOG900450_243	6	0.0072	0.030019969	TOG900222_165	11	<.0001	0.05941681
								TOG895876_339	6	0.0074	0.028746945	TOG908034_427	11	<.0001	0.05594331
								TOG896967_396	6	0.01138	0.025660091	TOG895575_317	11	0.00435	0.03306344
								TOG898441_398	6	0.01142	0.026633639	TOG917669_433	11	0.01652	0.02315271
								TOG895216_529	6	0.0115	0.025559276	TOG961366_282	11	0.0174	0.02262277
								TOG894483_1005	6	0.0115	0.025559276	TOG894153_805	11	0.01833	0.02315804
								TOG948068_208	6	0.01192	0.025213568	TOG898465_424	11	0.01844	0.02316501
								TOG902798_124	6	0.0121	0.025134758	TOG922096_428	11	0.01939	0.03112436
								TOG913325_673	6	0.01217	0.025234321	TOG899701_145	11	0.02315	0.02083382
								TOG894483_1190	6	0.01217	0.025234321	TOG896372_529	11	0.02376	0.0206018
								TOG905231_418	6	0.01217	0.025234321	TOG896372_451	11	0.02587	0.0200068
								TOG910602_439	6	0.0123	0.025798786	TOG919767_169	11	0.02679	0.01987087
								TOG913329_534	6	0.01252	0.025222271	TOG901894_233	11	0.03358	0.01815033
								TOG898575_586	6	0.01256	0.025224625	TOG902901_1102	11	0.03454	0.01791415
								TOG895237_557	6	0.01344	0.024776774	TOG902140_271	11	0.03494	0.01778604
								TOG896967_439	6	0.01384	0.024282117	TOG902140_336	11	0.03494	0.01778604
								TOG906318_220	6	0.02124	0.021692452	TOG907934_217	11	0.03494	0.01778604
								TOG902902_1027	6	0.02326	0.020604322	TOG899617_590	11	0.04676	0.01606563
								TOG897198_613	6	0.02412	0.020535929				

LG linkage group; Markers coloured red are common between the irrigated and rainfed treatments

Appendix 11 Identified associations between SNP markers and 100-seed weight under irrigated and rainfed treatments at Harare Research Station

Marker	LG	P-values	Marker R^2	Marker	LG	P-values	Marker R^2	Marker	LG	P-values	Marker_R2
			Irrigated treatment					Rainfed treatment			
TOG896448_605	1	<.001	0.016601932	TOG897347_125	6	0.00481	0.0060261	TOG900375_652	1	<.001	0.031868911
TOG900375_652	1	<.001	0.015676517	TOG897486_230	6	0.00498	0.00591853	TOG896448_605	1	<.001	0.028528788
TOG894042_842	1	<.001	0.012704317	TOG897347_414	6	0.00516	0.00619959	TOG894042_842	1	<.001	0.02304208
TOG894760_112	1	0.00207	0.007032855	TOG896306_360	6	0.00583	0.00586278	TOG906607_472	1	0.00803	0.009901877
TOG894002_95	1	0.00299	0.008548807	TOG900450_243	6	0.00583	0.00586278	TOG913321_535	1	0.01015	0.009587204
TOG899669_1293	1	0.00304	0.006574231	TOG896074_553	6	0.00593	0.00596433	TOG919160_653	1	0.01535	0.008417102
TOG912381_118	1	0.00309	0.006499718	TOG902800_160	6	0.01074	0.00544859	TOG896943_500	2	0.00228	0.012983668
TOG897762_708	1	0.00336	0.006390207	TOG899452_215	6	0.01079	0.00485831	TOG935004_879	2	0.00451	0.011288843
TOG927739_198	1	0.00336	0.006390207	TOG897513_306	6	0.012	0.00473326	TOG896681_173	2	0.01463	0.008938914
TOG946994_394	1	0.00371	0.006452666	TOG897513_200	6	0.01328	0.00459148	TOG928916_162	2	0.02456	0.007175118
TOG902692_40	1	0.00608	0.005679261	TOG897269_677	6	0.0141	0.0046328	TOG896943_422	2	0.02731	0.01449688
TOG929836_324	1	0.00781	0.005403759	TOG931720_274	6	0.01483	0.00447297	TOG902049_243	2	0.0289	0.006979509
TOG912105_1330	1	0.00781	0.005401118	TOG896074_686	6	0.01717	0.00442509	TOG897346_443	2	0.03621	0.005970711
TOG897242_420	1	0.00823	0.005253932	TOG899452_300	6	0.01791	0.00447824	TOG905638_273	2	0.04312	0.005740409
TOG900146_513	1	0.00887	0.005114952	TOG934079_228	6	0.01932	0.00412158	TOG897346_808	2	0.04483	0.005448958
TOG896584_248	1	0.009	0.005152246	TOG897188_821	6	0.01932	0.00412158	TOG899661_841	2	0.04597	0.005714748
TOG898020_461	1	0.01145	0.004785314	TOG911890_221	6	0.0198	0.00411588	TOG905123_751	3	<.001	0.023847746
TOG894925_279	1	0.01531	0.004526402	TOG897333_615	6	0.02212	0.003969	TOG894196_495	3	<.001	0.023554063
TOG896159_536	1	0.01563	0.004380541	TOG895876_339	6	0.02843	0.00365169	TOG895984_205	3	0.00298	0.012397809
TOG896159_332	1	0.01592	0.004352982	TOG900006_352	7	0.00139	0.00766049	TOG935639_446	3	0.00392	0.011894402
TOG896186_314	1	0.01594	0.004416907	TOG898095_396	7	0.00323	0.00722486	TOG894712_405	3	0.0069	0.010306669
TOG896975_539	1	0.01594	0.004416907	TOG894812_176	7	0.00346	0.00647678	TOG901675_241	3	0.00709	0.010313024
TOG903989_184	1	0.01594	0.004416907	TOG901045_327	7	0.00418	0.00629605	TOG943467_524	3	0.00775	0.009940804
TOG895545_757	1	0.01986	0.004242792	TOG896540_336	7	0.01109	0.00487491	TOG895163_666	3	0.00892	0.009673562
TOG894224_229	1	0.01987	0.004065819	TOG901549_339	7	0.01109	0.00487491	TOG896276_59	3	0.01726	0.008305354
TOG895458_231	1	0.01988	0.00409934	TOG915832_137	7	0.01188	0.00475118	TOG918275_1006	3	0.02413	0.005765659
TOG894224_719	1	0.02	0.004061637	TOG896540_627	7	0.01245	0.00481564	TOG923111_969	3	0.02413	0.005765659
TOG963076_539	1	0.02	0.004061637	TOG901549_630	7	0.01245	0.00481564	TOG929136_76	3	0.02781	0.006823101
TOG963076_226	1	0.02059	0.004021291	TOG907173_734	7	0.015	0.00442929	TOG905443_301	3	0.03144	0.006563083
TOG923884_128	2	<.001	0.01087669	TOG919337_759	7	0.01592	0.00435298	TOG900221_555	3	0.03926	0.005117918
TOG895871_64	2	<.001	0.008816659	TOG910203_883	7	0.01592	0.00435298	TOG900261_152	3	0.03959	0.006096773
TOG928916_162	2	<.001	0.008708912	TOG895846_143	7	0.01592	0.00435298	TOG900261_206	3	0.03959	0.006096773
TOG899661_642	2	<.001	0.008192373	TOG898599_949	7	0.01623	0.00438874	TOG904255_224	4	<.001	0.020742004
TOG894755_654	2	0.001	0.008156971	TOG894812_593	7	0.01623	0.00438874	TOG912552_357	4	0.03395	0.00648422
TOG895202_277	2	0.00102	0.008194064	TOG896981_525	7	0.01623	0.00438874	TOG903882_547	4	0.03525	0.006257066
TOG895202_298	2	0.00102	0.008194064	TOG913485_147	7	0.02045	0.00402972	TOG898978_625	5	<.001	0.022751955
TOG899127_233	2	0.00109	0.008101519	TOG898824_662	7	0.02045	0.00402972	TOG918200_347	5	0.00129	0.01342177
TOG901960_1149	2	0.00185	0.007177794	TOG895578_468	7	0.02181	0.00413244	TOG899033_1374	5	0.01481	0.008574651
TOG896943_500	2	0.00187	0.007263887	TOG895578_922	7	0.02181	0.00413244	TOG915697_119	5	0.02864	0.006706411
TOG895594_590	2	0.00196	0.007432256	TOG927609_1357	7	0.03616	0.00338137	TOG910602_439	6	<.001	0.016296722
TOG902049_243	2	0.00207	0.007275989	TOG905290_760	7	0.04764	0.00295375	TOG896306_360	6	0.00138	0.014525801
TOG895739_547	2	0.00207	0.007032855	TOG898285_318	8	<.001	0.00906646	TOG900450_243	6	0.00138	0.014525801
TOG916436_325	2	0.00214	0.007060198	TOG894070_290	8	0.00118	0.00891505	TOG894052_203	6	0.00979	0.009656329
TOG910927_147	2	0.00236	0.007051262	TOG907901_189	8	0.00196	0.0072688	TOG906318_220	6	0.01024	0.009324703
TOG906764_376	2	0.00242	0.007396672	TOG894070_261	8	0.00286	0.00707524	TOG896074_553	6	0.02937	0.007079792
TOG906764_834	2	0.00242	0.007396672	TOG919333_731	8	0.00509	0.00589675	TOG897362_457	6	0.02984	0.006727662
TOG897999_309	2	0.00253	0.006551764	TOG946841_476	8	0.00532	0.00583887	TOG897362_571	6	0.03243	0.006575677
TOG896681_173	2	0.00293	0.007495118	TOG902629_253	8	0.00574	0.00583288	TOG900006_352	7	<.001	0.026549247
TOG907177_474	2	0.00309	0.006505054	TOG899689_445	8	0.00574	0.0057983	TOG894812_176	7	<.001	0.015589782
TOG905479_729	2	0.00382	0.006319611	TOG894320_172	8	0.01787	0.00426663	TOG898095_396	7	0.00138	0.016532184
TOG896940_329	2	0.00404	0.006235365	TOG918273_446	8	0.01787	0.00426663	TOG896540_627	7	0.01319	0.008457009
TOG902130_272	2	0.00645	0.005674505	TOG896253_88	8	0.02238	0.00393068	TOG901549_630	7	0.01319	0.008457009
TOG897132_587	2	0.0075	0.005408441	TOG923107_319	8	0.02313	0.00392559	TOG896540_336	7	0.03447	0.006213108
TOG901840_596	2	0.00761	0.005390821	TOG909835_665	8	0.02677	0.0036843	TOG901549_339	7	0.03447	0.006213108
TOG896190_354	2	0.00783	0.005429621	TOG899729_79	8	0.02919	0.00372808	TOG899998_203	7	0.03921	0.005942452
TOG896190_237	2	0.00798	0.005467568	TOG910318_239	8	0.03153	0.00349546	TOG897558_103	8	0.00415	0.012512435
TOG919131_1127	2	0.00815	0.005458748	TOG896253_482	8	0.04246	0.00309912	TOG894070_290	8	0.00877	0.010446473
TOG961505_49	2	0.01408	0.004520043	TOG915502_68	8	0.04278	0.00338832	TOG902611_789	8	0.01583	0.008266007
TOG938494_409	2	0.01503	0.004428009	TOG915502_64	8	0.04363	0.00332117	TOG894070_261	8	0.0204	0.008060285
TOG903957_676	2	0.01563	0.004380541	TOG902906_149	8	0.0487	0.00303421	TOG935983_331	8	0.02472	0.007147711
TOG896498_574	2	0.01827	0.00423377	TOG901933_203	9	<.001	0.02112083	TOG896613_235	8	0.02695	0.007072078
TOG896567_73	2	0.02594	0.003775942	TOG901933_425	9	<.001	0.02099827	TOG901166_767	8	0.03933	0.006167863
TOG928843_388	2	0.02677	0.003684295	TOG908804_377	9	<.001	0.02099827	TOG894201_269	8	0.03939	0.004500545
TOG902063_602	2	0.02727	0.003712002	TOG899668_578	9	<.001	0.01927305	TOG901933_425	9	<.001	0.027463274
TOG902999_172	2	0.02766	0.003842017	TOG905363_697	9	<.001	0.01403862	TOG908804_377	9	<.001	0.027463274
TOG898302_727	2	0.02776	0.003831316	TOG895978_272	9	<.001	0.01378907	TOG901933_203	9	<.001	0.027607558
TOG899661_841	2	0.03044	0.003602486	TOG895760_820	9	0.00181	0.00800662	TOG905363_697	9	<.001	0.024692015
TOG897680_202	2	0.0307	0.003560344	TOG894880_493	9	0.00185	0.00723767	TOG895978_272	9	<.001	0.024151166
TOG896907_533	2	0.03387	0.003482325	TOG896197_226	9	0.00209	0.00747421	TOG899668_578	9	<.001	0.024933953
TOG901772_360	2	0.04005	0.003341089	TOG899482_348	9	0.00304	0.00657423	TOG903088_74	9	0.00886	0.009634782
TOG896943_422	2	0.04243	0.007418598	TOG918373_273	9	0.00304	0.00657423	TOG908646_276	9	0.00926	0.009662492
TOG897956_500	2	0.04496	0.003127752	TOG946792_836	9	0.00304	0.00657423	TOG895900_155	9	0.01657	0.008090259
TOG943467_524	3	<.001	0.011083586	TOG894248_243	9	0.00304	0.00657423	TOG896197_226	9	0.01906	0.008264233
TOG894196_495	3	<.001	0.009253644	TOG900046_135	9	0.00304	0.00657423	TOG898007_380	9	0.02126	0.006804112
TOG901908_232	3	0.00222	0.00703748	TOG917794_636	9	0.00304	0.00657423	TOG895760_820	9	0.03367	0.006208744
TOG905123_751	3	0.00231	0.006894038	TOG918373_668	9	0.00336	0.00639021	TOG896504_1537	10	<.001	0.015486028
TOG919004_144	3	0.00235	0.006858498	TOG898489_619	9	0.00394	0.0062703	TOG894060_416	10	0.02047	0.007682285
TOG912558_1306	3	0.00242	0.006829097	TOG896050_646	9	0.00465	0.00606648	TOG907046_267	10	0.03567	0.006348788
TOG901037_215	3	0.00251	0.006874729	TOG895505_185	9	0.00504	0.00595909	TOG900784_136	10	0.04749	0.005748307
TOG899716_657	3	0.00265	0.00670229	TOG901096_444	9	0.00504	0.00595909	TOG908034_427	11	<.001	0.018602934
TOG899518_974	3	0.00285	0.006610715	TOG896050_731	9	0.00549	0.00579885	TOG917669_433	11	0.00109	0.014673844
TOG901908_188	3	0.00294	0.006825449	TOG895760_342	9	0.00596	0.00552948	TOG924872_53	11	0.00254	0.012804148
TOG895163_666	3	0.00627	0.005617405	TOG894037_604	9	0.0115	0.00477529	TOG916151_413	11	0.00384	0.012394922
TOG901841_376	3	0.00682	0.005522574	TOG900136_127	9	0.01444	0.00501253	TOG900222_165	11	0.01395	0.009097941
TOG900241_1293	3	0.0101	0.005017289	TOG894965_25	9	0.01752	0.00422359	TOG900991_671	11	0.01497	0.008265001
TOG935699_696	3	0.01424	0.004501484	TOG897326_365	9	0.01758	0.0042654	TOG961354_444	11	0.04029	0.005899835

LG Linkage group; Markers coloured red are common between the irrigated and rainfed treatments

Appendix 12 Identified associations between SNP markers and days to flowering under irrigated and rainfed treatments at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment				Rainfed treatment			
TOG895245_245	8	0.0011	0.0559	TOG925843_147	8	0.0012	0.0541	TOG895900_416	9	0.0048	0.0410
TOG902879_375	1	0.0011	0.0571	TOG911121_130	3	0.0013	0.0539	TOG961354_444	11	0.0050	0.0405
TOG907233_598	6	0.0013	0.0548	TOG900006_352	7	0.0017	0.0511	TOG901238_199	10	0.0062	0.0391
TOG895672_181	2	0.0015	0.0530	TOG896385_269	6	0.0018	0.0506	TOG895900_155	9	0.0100	0.0348
TOG894987_722	3	0.0017	0.0515	TOG900416_243	7	0.0027	0.0461	TOG904927_660	10	0.0139	0.0317
TOG894042_842	1	0.0017	0.0513	TOG895846_60	7	0.0028	0.0460	TOG896397_349	9	0.0161	0.0302
TOG903882_547	4	0.0019	0.0505	TOG894818_243	1	0.0032	0.0482	TOG928931_192	9	0.0161	0.0302
TOG896385_269	6	0.0024	0.0487	TOG894818_489	1	0.0042	0.0518	TOG900136_127	9	0.0168	0.0325
TOG901547_185	3	0.0028	0.0467	TOG900259_705	7	0.0043	0.0422	TOG897326_365	9	0.0208	0.0279
TOG901547_549	3	0.0028	0.0467	TOG894042_842	1	0.0044	0.0419	TOG901001_164	9	0.0208	0.0279
TOG895899_315	5	0.0029	0.0476	TOG900308_234	2	0.0045	0.0421	TOG896602_1693	9	0.0208	0.0282
TOG925843_147	8	0.0029	0.0468	TOG907233_598	6	0.0052	0.0410	TOG904656_460	9	0.0213	0.0275
TOG907901_189	8	0.0030	0.0469	TOG895899_315	5	0.0054	0.0408	TOG904224_491	9	0.0213	0.0278
TOG911121_130	3	0.0033	0.0464	TOG899382_247	2	0.0062	0.0392	TOG894965_25	9	0.0216	0.0276
TOG900006_352	7	0.0051	0.0415	TOG906764_376	2	0.0063	0.0417	TOG896702_457	9	0.0217	0.0278
TOG894818_489	1	0.0055	0.0498	TOG906764_834	2	0.0063	0.0417	TOG897350_248	9	0.0218	0.0275
TOG894818_243	1	0.0060	0.0430	TOG895747_525	8	0.0063	0.0385	TOG897350_381	9	0.0218	0.0275
TOG961354_444	11	0.0064	0.0390	TOG899729_237	8	0.0067	0.0400	TOG915278_1019	9	0.0218	0.0275
TOG900416_243	7	0.0064	0.0391	TOG895163_666	3	0.0071	0.0378	TOG915884_316	9	0.0218	0.0275
TOG895846_60	7	0.0075	0.0377	TOG900268_798	6	0.0081	0.0371	TOG895666_623	9	0.0218	0.0278
TOG899729_237	8	0.0076	0.0395	TOG897521_498	1	0.0087	0.0373	TOG913415_529	9	0.0218	0.0278
TOG901238_199	10	0.0080	0.0374	TOG897333_569	6	0.0134	0.0338	TOG895666_144	9	0.0219	0.0283
TOG895900_416	9	0.0090	0.0360	TOG909801_195	3	0.0136	0.0314	TOG915278_553	9	0.0222	0.0275
TOG895747_525	8	0.0097	0.0353	TOG894141_219	8	0.0154	0.0307	TOG902883_235	9	0.0228	0.0274
TOG906969_104	2	0.0099	0.0354	TOG929859_500	1	0.0173	0.0293	TOG902778_470	9	0.0231	0.0278
TOG904027_285	5	0.0104	0.0465	TOG901700_397	6	0.0203	0.0307	TOG915884_396	9	0.0234	0.0272
TOG899382_247	2	0.0105	0.0350	TOG894171_240	7	0.0207	0.0277	TOG906506_244	11	0.0239	0.0278
TOG895163_666	3	0.0106	0.0347	TOG903155_410	7	0.0207	0.0277	TOG906600_415	9	0.0255	0.0262
TOG897333_569	6	0.0108	0.0366	TOG896767_576	4	0.0211	0.0281	TOG896504_1537	10	0.0256	0.0259
TOG900308_234	2	0.0115	0.0341	TOG897172_226	2	0.0217	0.0278	TOG894037_604	9	0.0302	0.0244
TOG904927_660	10	0.0138	0.0325	TOG895412_225	8	0.0218	0.0274	TOG894314_478	11	0.0306	0.0243
TOG901700_397	6	0.0165	0.0333	TOG910388_90	7	0.0242	0.0266	TOG894098_359	11	0.0315	0.0242
TOG906764_376	2	0.0187	0.0317	TOG906936_331	2	0.0255	0.0267	TOG924126_523	11	0.0315	0.0242
TOG906764_834	2	0.0187	0.0317	TOG918200_508	5	0.0256	0.0266	TOG903109_489	9	0.0315	0.0240
TOG900268_798	6	0.0198	0.0294	TOG916106_551	3	0.0275	0.0256	TOG897887_661	9	0.0315	0.0240
TOG897521_498	1	0.0199	0.0300	TOG894844_1048	3	0.0276	0.0253	TOG897062_494	9	0.0315	0.0240
TOG895900_155	9	0.0203	0.0288	TOG900332_1066	7	0.0277	0.0256	TOG913047_460	9	0.0315	0.0240
TOG900259_705	7	0.0205	0.0286	TOG896390_287	3	0.0281	0.0253	TOG902031_422	9	0.0315	0.0240
TOG906600_415	9	0.0211	0.0284	TOG925468_198	3	0.0284	0.0256	TOG915277_583	9	0.0322	0.0240
TOG918200_508	5	0.0213	0.0287	TOG895412_564	8	0.0284	0.0253	TOG914920_329	9	0.0322	0.0240
TOG929859_500	1	0.0268	0.0259	TOG906969_104	2	0.0285	0.0252	TOG901255_247	9	0.0322	0.0240
TOG897172_226	2	0.0273	0.0262	TOG915832_137	7	0.0308	0.0243	TOG899744_93	11	0.0328	0.0240
TOG909801_195	3	0.0283	0.0254	TOG963076_226	1	0.0315	0.0240	TOG906506_612	11	0.0332	0.0252
TOG894171_240	7	0.0293	0.0251	TOG894224_229	1	0.0320	0.0240	TOG897062_123	9	0.0334	0.0238
TOG903155_410	7	0.0293	0.0251	TOG894224_719	1	0.0322	0.0240	TOG894314_171	11	0.0334	0.0240
TOG898284_1682	8	0.0304	0.0257	TOG963076_539	1	0.0322	0.0240	TOG900220_648	11	0.0361	0.0232
TOG896397_349	9	0.0318	0.0246	TOG895458_231	1	0.0329	0.0239	TOG894153_805	11	0.0419	0.0231
TOG928931_192	9	0.0318	0.0246	TOG894141_709	8	0.0330	0.0236	TOG896972_596	9	0.0425	0.0218
TOG913042_381	9	0.0329	0.0241	TOG940321_64	5	0.0350	0.0235	TOG901894_395	11	0.0442	0.0217
TOG918200_347	5	0.0336	0.0244	TOG896361_260	2	0.0353	0.0236	TOG913042_381	9	0.0453	0.0208
TOG896767_576	4	0.0348	0.0240	TOG894196_495	3	0.0361	0.0238	TOG900220_279	11	0.0494	0.0205
TOG925468_198	3	0.0389	0.0232	TOG894236_303	5	0.0378	0.0226				
TOG900220_648	11	0.0394	0.0228	TOG898353_150	4	0.0379	0.0224				
TOG906506_244	11	0.0406	0.0233	TOG898353_393	4	0.0379	0.0224				
TOG894060_416	10	0.0410	0.0232	TOG894564_431	4	0.0390	0.0222				
TOG894141_219	8	0.0422	0.0222	TOG908913_664	3	0.0392	0.0224				
TOG898489_619	9	0.0423	0.0222	TOG904027_285	5	0.0483	0.0275				
TOG906948_530	11	0.0467	0.0223								
TOG898284_346	8	0.0491	0.0212								

Markers coloured red are common between the irrigated and rainfed treatments

Appendix 13 Identified associations between SNP markers and days to flowering under irrigated and rainfed treatments at Harare Research Station

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Across locations
Irrigated treatment				Rainfed treatment				
TOG919227_1306	8	0.0014	0.0497	TOG896850_232	7	0.0012	0.0565	F
TOG894986_609	2	0.0016	0.0494	TOG898075_168	7	0.0014	0.0539	F
TOG894081_362	7	0.0016	0.0493	TOG922990_513	7	0.0014	0.0532	F
TOG897579_687	5	0.0023	0.0732	TOG918946_209	8	0.0016	0.0523	F
TOG898075_168	7	0.0028	0.0445	TOG900268_798	6	0.0019	0.0515	T
TOG922990_513	7	0.0029	0.0440	TOG919227_1306	8	0.0019	0.0505	F
TOG906843_140	1	0.0030	0.0438	TOG916151_413	11	0.0026	0.0508	F
TOG903898_287	2	0.0033	0.0426	TOG896078_808	7	0.0032	0.0480	F
TOG894196_495	3	0.0033	0.0438	TOG899072_215	3	0.0039	0.0434	F
TOG919160_653	1	0.0037	0.0416	TOG899382_247	2	0.0040	0.0436	T
TOG900006_352	7	0.0037	0.0410	TOG899729_237	8	0.0041	0.0450	T
TOG916151_413	11	0.0039	0.0443	TOG895871_64	2	0.0042	0.0429	F
TOG922990_288	7	0.0040	0.0417	TOG919160_653	1	0.0043	0.0430	F
TOG900848_206	10	0.0046	0.0400	TOG902879_375	1	0.0050	0.0421	F
TOG902879_375	1	0.0051	0.0391	TOG902611_789	8	0.0064	0.0389	F
TOG896078_808	7	0.0068	0.0385	TOG906843_140	1	0.0072	0.0382	F
TOG906575_146	2	0.0076	0.0373	TOG900006_352	7	0.0074	0.0376	T
TOG905123_751	3	0.0084	0.0342	TOG894986_609	2	0.0083	0.0371	F
TOG902611_789	8	0.0098	0.0329	TOG895984_205	3	0.0084	0.0366	F
TOG899072_215	3	0.0101	0.0324	TOG935983_331	8	0.0094	0.0362	F
TOG895876_339	6	0.0101	0.0330	TOG922990_288	7	0.0103	0.0354	F
TOG896850_232	7	0.0104	0.0332	TOG905363_697	9	0.0123	0.0342	F
TOG900222_165	11	0.0106	0.0332	TOG894081_362	7	0.0125	0.0332	F
TOG896504_1537	10	0.0107	0.0321	TOG896361_260	2	0.0130	0.0331	T
TOG918200_347	5	0.0129	0.0308	TOG899600_703	9	0.0147	0.0315	F
TOG895871_64	2	0.0150	0.0292	TOG899701_145	11	0.0149	0.0311	F
TOG894070_261	8	0.0153	0.0309	TOG912981_1529	6	0.0164	0.0321	F
TOG906575_68	2	0.0158	0.0305	TOG897579_687	5	0.0178	0.0493	F
TOG905363_697	9	0.0159	0.0295	TOG894196_495	3	0.0180	0.0305	T
TOG895163_666	3	0.0161	0.0287	TOG895545_505	1	0.0187	0.0302	F
TOG896448_605	1	0.0174	0.0286	TOG894794_142	7	0.0206	0.0286	F
TOG899600_703	9	0.0181	0.0278	TOG911121_130	3	0.0230	0.0278	T
TOG896361_260	2	0.0190	0.0277	TOG902692_40	1	0.0235	0.0275	F
TOG898978_625	5	0.0227	0.0258	TOG905123_751	3	0.0238	0.0270	F
TOG900375_652	1	0.0230	0.0258	TOG896276_59	3	0.0243	0.0280	F
TOG905443_301	3	0.0245	0.0250	TOG900987_506	9	0.0281	0.0256	F
TOG895978_272	9	0.0265	0.0245	TOG906764_376	2	0.0294	0.0269	T
TOG901675_241	3	0.0293	0.0237	TOG906764_834	2	0.0294	0.0269	T
TOG898302_727	2	0.0297	0.0247	TOG903872_356	10	0.0294	0.0262	F
TOG895846_60	7	0.0298	0.0234	TOG906575_146	2	0.0302	0.0261	F
TOG900308_234	2	0.0301	0.0234	TOG895163_666	3	0.0346	0.0237	T
TOG905343_279	2	0.0307	0.0238	TOG919767_169	11	0.0363	0.0233	F
TOG894153_805	11	0.0320	0.0241	TOG894060_416	10	0.0366	0.0240	F
TOG894818_489	1	0.0322	0.0289	TOG898046_230	7	0.0378	0.0232	F
TOG915832_137	7	0.0327	0.0227	TOG895876_339	6	0.0390	0.0229	F
TOG895877_63	7	0.0334	0.0229	TOG898304_552	6	0.0390	0.0225	F
TOG894060_416	10	0.0345	0.0232	TOG894070_261	8	0.0398	0.0234	F
TOG904255_224	4	0.0363	0.0218	TOG894141_219	8	0.0413	0.0230	T
TOG897521_498	1	0.0366	0.0228	TOG896504_1537	10	0.0423	0.0218	F
TOG894070_290	8	0.0368	0.0229	TOG897707_1718	8	0.0431	0.0219	F
TOG897346_443	2	0.0369	0.0218	TOG894818_243	1	0.0437	0.0231	T
TOG897346_808	2	0.0389	0.0212	TOG905443_301	3	0.0442	0.0215	F
TOG896276_59	3	0.0399	0.0219	TOG895877_63	7	0.0457	0.0215	F
TOG894712_405	3	0.0401	0.0210	TOG916702_146	8	0.0487	0.0211	F
TOG901933_203	9	0.0441	0.0201	TOG904255_224	4	0.0499	0.0206	F
TOG897521_1471	1	0.0452	0.0214					
TOG895984_205	3	0.0471	0.0195					
TOG894141_219	8	0.0473	0.0206					
TOG894818_243	1	0.0485	0.0207					
TOG895900_416	9	0.0493	0.0192					

Markers coloured red are common between the irrigated and rainfed treatments; T - markers are common between CIAT-Palmira and Harare Research Station under rainfed treatments; F - markers are not common between CIAT-Palmira and Harare Research Station under rainfed treatments.

Appendix 14 Identified associations between SNP markers and days to maturity under irrigated and rainfed treatments at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Across locations
Irrigated treatment				Rainfed treatment				
TOG895545_757	1	0.0049	0.0450	TOG894818_489	1	0.0095	0.0451	T
TOG894818_243	1	0.0050	0.0481	TOG906969_104	2	0.0100	0.0361	T
TOG894818_489	1	0.0077	0.0483	TOG906764_376	2	0.0122	0.0368	T
TOG902879_375	1	0.0272	0.0283	TOG906764_834	2	0.0122	0.0368	T
TOG895871_64	2	0.0018	0.0534	TOG897188_682	6	0.0013	0.0563	T
TOG894885_690	2	0.0066	0.0411	TOG901700_397	6	0.0412	0.0243	T
TOG923884_128	2	0.0240	0.0317	TOG894818_243	1	0.0053	0.0467	F
TOG895572_269	3	0.0118	0.0358	TOG894042_842	1	0.0463	0.0218	F
TOG894987_722	3	0.0210	0.0296	TOG894885_690	2	0.0051	0.0428	F
TOG894864_431	3	0.0345	0.0257	TOG894864_431	3	0.0256	0.0282	F
TOG899072_215	3	0.0415	0.0232	TOG916106_684	3	0.0348	0.0248	F
TOG916106_684	3	0.0444	0.0230	TOG896609_245	3	0.0380	0.0236	F
TOG912552_357	4	0.0139	0.0354	TOG898271_99	4	0.0022	0.0517	F
TOG904027_285	5	0.0031	0.0665	TOG905831_497	4	0.0341	0.0251	F
TOG897323_74	5	0.0072	0.0405	TOG897323_74	5	0.0024	0.0506	F
TOG907013_1059	5	0.0120	0.0364	TOG904027_122	5	0.0031	0.0476	F
TOG900416_243	7	0.0014	0.0561	TOG907013_1059	5	0.0045	0.0454	F
TOG910862_232	7	0.0182	0.0309	TOG904027_285	5	0.0055	0.0581	F
TOG895846_60	7	0.0286	0.0268	TOG900332_1066	7	0.0069	0.0398	F
TOG900332_1066	7	0.0303	0.0264	TOG895846_60	7	0.0197	0.0296	F
TOG925843_147	8	0.0207	0.0302	TOG895245_245	8	0.0126	0.0338	F
TOG899729_237	8	0.0424	0.0241	TOG896253_482	8	0.0133	0.0331	F
TOG896253_482	8	0.0455	0.0223	TOG895747_525	8	0.0436	0.0222	F
TOG894022_713	9	0.0166	0.0318	TOG899729_237	8	0.0450	0.0229	F
TOG895900_416	9	0.0374	0.0243	TOG913042_381	9	0.0159	0.0314	F
TOG901238_199	10	0.0110	0.0362	TOG925794_230	9	0.0349	0.0250	F
TOG900787_1237	11	0.0266	0.0281	TOG895900_416	9	0.0463	0.0217	F
TOG961354_444	11	0.0305	0.0261	TOG899617_590	11	0.0017	0.0528	F

Markers coloured red are common between the irrigated and rainfed treatments; T – markers are common between CIAT-Palmira and Harare Research Station under rainfed treatments; F – markers are not common between CIAT-Palmira and Harare Research Station under rainfed treatments

Appendix 15 Identified associations between SNP markers and days to maturity at Harare Research Station in 2011

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Marker	linkage gr	p value	Marker R^2
Irrigated treatment				Rainfed treatment				Rainfed treatment			
TOG894042_842	1	0.0013	0.0563	TOG906607_472	1	0.0161	0.0321	TOG898974_591	5	0.0320	0.0255
TOG894818_243	1	0.0067	0.0429	TOG929859_500	1	0.0185	0.0305	TOG899509_584	5	0.0320	0.0255
TOG906936_331	2	0.0011	0.0597	TOG894818_489	1	0.0192	0.0375	TOG902765_214	5	0.0372	0.0242
TOG895871_64	2	0.0070	0.0401	TOG905303_749	1	0.0284	0.0268	TOG898304_552	6	0.0061	0.0413
TOG896567_73	2	0.0076	0.0392	TOG913321_535	1	0.0339	0.0254	TOG908483_524	6	0.0081	0.0387
TOG894885_690	2	0.0191	0.0306	TOG895142_874	1	0.0396	0.0234	TOG894262_306	6	0.0137	0.0385
TOG901225_355	2	0.0322	0.0259	TOG924275_542	1	0.0396	0.0234	TOG901700_397	6	0.0157	0.0359
TOG899382_247	2	0.0323	0.0257	TOG896309_1245	1	0.0479	0.0216	TOG900268_798	6	0.0174	0.0319
TOG896609_245	3	0.0015	0.0551	TOG896567_73	2	0.0014	0.0557	TOG907233_598	6	0.0214	0.0297
TOG899072_215	3	0.0064	0.0408	TOG899382_247	2	0.0037	0.0467	TOG897333_569	6	0.0220	0.0312
TOG943467_524	3	0.0091	0.0375	TOG900308_234	2	0.0051	0.0434	TOG897188_682	6	0.0242	0.0283
TOG894987_722	3	0.0139	0.0332	TOG894044_453	2	0.0111	0.0367	TOG900339_308	6	0.0409	0.0241
TOG895572_269	3	0.0155	0.0325	TOG906764_376	2	0.0223	0.0312	TOG903058_351	6	0.0454	0.0232
TOG901032_412	3	0.0232	0.0287	TOG906764_834	2	0.0223	0.0312	TOG900416_243	7	0.0028	0.0490
TOG895163_666	3	0.0324	0.0255	TOG896234_245	2	0.0372	0.0245	TOG915832_137	7	0.0078	0.0389
TOG895984_205	3	0.0446	0.0225	TOG894986_609	2	0.0435	0.0231	TOG896850_232	7	0.0105	0.0376
TOG901547_185	3	0.0458	0.0221	TOG906969_104	2	0.0472	0.0220	TOG910388_90	7	0.0283	0.0269
TOG901547_549	3	0.0458	0.0221	TOG896943_422	2	0.0488	0.0331	TOG898046_230	7	0.0339	0.0253
TOG903882_547	4	0.0125	0.0345	TOG901547_185	3	0.0017	0.0532	TOG922990_513	7	0.0393	0.0238
TOG897333_569	6	0.0216	0.0314	TOG901547_549	3	0.0017	0.0532	TOG898075_168	7	0.0395	0.0239
TOG907233_598	6	0.0242	0.0284	TOG895572_269	3	0.0037	0.0464	TOG935983_331	8	0.0050	0.0441
TOG900259_705	7	0.0306	0.0261	TOG903842_603	3	0.0041	0.0461	TOG918946_209	8	0.0087	0.0381
TOG896850_232	7	0.0364	0.0252	TOG925468_198	3	0.0057	0.0429	TOG899729_237	8	0.0134	0.0353
TOG900006_352	7	0.0428	0.0228	TOG901032_412	3	0.0065	0.0411	TOG919227_1306	8	0.0156	0.0323
TOG925843_147	8	0.0073	0.0398	TOG900261_152	3	0.0106	0.0371	TOG907901_189	8	0.0179	0.0314
TOG961354_444	11	0.0088	0.0377	TOG900261_206	3	0.0106	0.0371	TOG895412_225	8	0.0333	0.0251
TOG900222_165	11	0.0203	0.0310	TOG943467_524	3	0.0220	0.0290	TOG925843_147	8	0.0341	0.0250
TOG894153_805	11	0.0250	0.0292	TOG909801_195	3	0.0222	0.0288	TOG895900_155	9	0.0018	0.0540
				TOG895163_666	3	0.0442	0.0226	TOG894338_478	9	0.0326	0.0259
				TOG901841_376	3	0.0445	0.0226	TOG898007_380	9	0.0384	0.0261
				TOG903882_547	4	0.0122	0.0347	TOG904927_660	10	0.0156	0.0327
				TOG898353_150	4	0.0189	0.0304	TOG901238_199	10	0.0192	0.0305
				TOG898353_393	4	0.0189	0.0304	TOG961354_444	11	0.0156	0.0321
				TOG895899_315	5	0.0082	0.0391	TOG903002_997	11	0.0192	0.0314
				TOG918200_508	5	0.0150	0.0335	TOG896251_193	11	0.0490	0.0216

Markers coloured red are common between the irrigated and rainfed treatments

Appendix 16 Identified associations between SNP markers and total shoot biomass at CIAT-Palmira

Marker	linkage group	p value	Marker R^2
Irrigated treatment			
TOG899130_778	1	0.0062	0.0422
TOG894818_489	1	0.0070	0.0506
TOG894818_243	1	0.0159	0.0358
TOG894042_842	1	0.0307	0.0266
TOG894925_279	1	0.0453	0.0230
TOG900594_110	2	0.0014	0.0582
TOG905343_279	2	0.0083	0.0404
TOG896567_73	2	0.0111	0.0365
TOG896109_664	2	0.0156	0.0331
TOG908531_728	2	0.0170	0.0322
TOG906969_104	2	0.0373	0.0246
TOG906764_376	2	0.0397	0.0255
TOG906764_834	2	0.0397	0.0255
TOG900342_110	3	0.0073	0.0406
TOG908913_664	3	0.0095	0.0381
TOG900342_587	3	0.0109	0.0371
TOG913005_113	3	0.0473	0.0228
TOG896746_651	5	0.0173	0.0320
TOG897579_687	5	0.0196	0.0518
TOG904027_285	5	0.0318	0.0369
TOG897017_257	5	0.0473	0.0300
TOG898441_398	6	0.0019	0.0551
TOG901700_397	6	0.0086	0.0438
TOG912981_1529	6	0.0101	0.0396
TOG897188_682	6	0.0327	0.0260
TOG894052_203	6	0.0451	0.0232
TOG894254_243	6	0.0470	0.0232
TOG910860_634	6	0.0470	0.0230
TOG899042_188	7	0.0011	0.0596
TOG896850_232	7	0.0079	0.0414
TOG895846_60	7	0.0428	0.0234
TOG894794_142	7	0.0430	0.0236
TOG908356_281	8	0.0015	0.0593
TOG918946_209	8	0.0048	0.0452
TOG906530_971	8	0.0097	0.0397
TOG895412_225	8	0.0147	0.0338
TOG895412_564	8	0.0203	0.0308
TOG916702_146	8	0.0322	0.0265
TOG902872_249	8	0.0399	0.0248
TOG894148_761	8	0.0403	0.0251
TOG899600_703	9	0.0253	0.0285
TOG897374_829	9	0.0328	0.0265
TOG895900_416	9	0.0471	0.0224
TOG904927_660	10	0.0051	0.0446
TOG920339_544	10	0.0499	0.0223
TOG894539_444	11	0.0368	0.0258
TOG906506_244	11	0.0416	0.0242
TOG906506_612	11	0.0438	0.0239

Marker	linkage group	p value	Marker R^2
Rainfed tr			
TOG898369_503	1	0.0028	0.0419
TOG924240_197	1	0.0038	0.0399
TOG903904_203	1	0.0041	0.0393
TOG960456_435	1	0.0042	0.0392
TOG937860_202	1	0.0079	0.0336
TOG894818_243	1	0.0108	0.0338
TOG960456_224	1	0.0120	0.0297
TOG896448_605	1	0.0123	0.0304
TOG901928_200	1	0.0179	0.0265
TOG894078_375	1	0.0186	0.0266
TOG929859_500	1	0.0208	0.0252
TOG903032_1755	1	0.0402	0.0203
TOG897724_419	1	0.0402	0.0203
TOG898832_447	1	0.0402	0.0203
TOG898832_568	1	0.0402	0.0203
TOG897521_1471	1	0.0420	0.0214
TOG898376_688	1	0.0473	0.0188
TOG928916_162	2	0.0017	0.0481
TOG900594_110	2	0.0034	0.0422
TOG935004_879	2	0.0049	0.0377
TOG900308_234	2	0.0157	0.0282
TOG895871_64	2	0.0265	0.0235
TOG906764_376	2	0.0276	0.0251
TOG906764_834	2	0.0276	0.0251
TOG896567_73	2	0.0323	0.0219
TOG906936_331	2	0.0378	0.0214
TOG899661_841	2	0.0488	0.0189
TOG895163_666	3	0.0014	0.0488
TOG897306_218	3	0.0058	0.0364
TOG935639_446	3	0.0075	0.0348
TOG901032_412	3	0.0080	0.0339
TOG894712_405	3	0.0080	0.0336
TOG903842_603	3	0.0114	0.0315
TOG896276_59	3	0.0120	0.0311
TOG905443_301	3	0.0120	0.0303
TOG894196_495	3	0.0148	0.0287
TOG927660_524	3	0.0191	0.0267
TOG918275_1006	3	0.0202	0.0305
TOG923111_969	3	0.0202	0.0305
TOG925468_198	3	0.0252	0.0247
TOG911121_130	3	0.0346	0.0218
TOG901547_185	3	0.0468	0.0188
TOG901547_549	3	0.0468	0.0188
TOG903882_547	4	0.0088	0.0328
TOG905629_486	4	0.0373	0.0210
TOG910676_123	5	0.0046	0.0391
TOG896746_651	5	0.0046	0.0383
TOG895899_315	5	0.0056	0.0376
TOG918200_347	5	0.0433	0.0195
TOG897362_571	6	0.0076	0.0341
TOG897362_457	6	0.0076	0.0338
TOG910860_634	6	0.0094	0.0325
TOG910860_172	6	0.0108	0.0311
TOG918299_615	6	0.0205	0.0327
TOG895846_60	7	0.0019	0.0452
TOG906952_58	7	0.0020	0.0457
TOG900006_352	7	0.0159	0.0277
TOG914633_385	7	0.0201	0.0352
TOG902016_103	7	0.0214	0.0261
TOG895877_63	7	0.0243	0.0247
TOG898046_230	7	0.0461	0.0194
TOG908356_281	8	0.0018	0.0482
TOG897558_389	8	0.0054	0.0363
TOG895747_525	8	0.0105	0.0310
TOG906530_971	8	0.0144	0.0298
TOG905195_605	8	0.0177	0.0270
TOG894148_761	8	0.0206	0.0270
TOG908646_276	9	0.0040	0.0399
TOG903088_74	9	0.0092	0.0324
TOG895760_820	9	0.0159	0.0312
TOG901933_425	9	0.0183	0.0266
TOG908804_377	9	0.0183	0.0266
TOG901933_203	9	0.0195	0.0262
TOG899668_578	9	0.0222	0.0259
TOG895760_342	9	0.0324	0.0224
TOG895900_416	9	0.0389	0.0204
TOG897374_829	9	0.0468	0.0194
TOG898489_619	9	0.0496	0.0188
TOG900784_136	10	0.0049	0.0386
TOG896504_1537	10	0.0163	0.0274
TOG902834_623	10	0.0185	0.0272
TOG904927_660	10	0.0487	0.0186
TOG900222_165	11	0.0069	0.0366
TOG908034_427	11	0.0082	0.0337
TOG906948_530	11	0.0222	0.0256
TOG895575_317	11	0.0371	0.0207
TOG914901_92	11	0.0495	0.0190

Markers coloured red are common between the irrigated and rainfed treatments

Appendix 17 Associations between markers and total shoot biomass at Harare Research Station

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2	Across locations
Irrigated treatment				Rainfed treatment				
TOG900375_652	1	0.0013	0.0198	TOG897362_457	6	0.0028	0.0242	T
TOG895545_505	1	0.0055	0.0156	TOG897362_571	6	0.0030	0.0240	T
TOG894002_95	1	0.0297	0.0138	TOG895575_317	11	0.0049	0.0217	T
TOG894042_842	1	0.0369	0.0085	TOG914633_385	7	0.0059	0.0347	T
TOG899661_841	2	0.0034	0.0160	TOG900222_165	11	0.0102	0.0191	T
TOG928916_162	2	0.0147	0.0113	TOG906530_971	8	0.0165	0.0144	T
TOG901167_256	2	0.0227	0.0102	TOG908034_427	11	0.0203	0.0150	T
TOG906941_330	2	0.0231	0.0100	TOG925468_198	3	0.0299	0.0132	T
TOG894986_609	2	0.0243	0.0101	TOG894712_405	3	0.0327	0.0125	T
TOG897516_505	2	0.0454	0.0080	TOG895163_666	3	0.0340	0.0125	T
TOG897306_218	3	0.0032	0.0157	TOG910860_172	6	0.0343	0.0125	T
TOG905371_417	3	0.0152	0.0112	TOG910860_634	6	0.0404	0.0117	T
TOG905123_751	3	0.0169	0.0109	TOG900594_110	2	0.0460	0.0103	T
TOG927660_524	3	0.0184	0.0106	TOG895760_342	9	0.0482	0.0109	T
TOG897579_687	5	0.0083	0.0202	TOG897017_278	5	0.0010	0.0281	F
TOG922036_169	5	0.0236	0.0099	TOG897017_257	5	0.0017	0.0307	F
TOG898978_625	5	0.0239	0.0098	TOG918864_542	5	0.0024	0.0255	F
TOG918200_347	5	0.0254	0.0100	TOG894007_1101	8	0.0032	0.0241	F
TOG915697_119	5	0.0263	0.0095	TOG900221_555	3	0.0037	0.0295	F
TOG895150_1434	5	0.0293	0.0094	TOG894254_243	6	0.0067	0.0200	F
TOG896103_114	5	0.0305	0.0093	TOG901894_395	11	0.0069	0.0198	F
TOG938507_670	5	0.0317	0.0090	TOG918864_641	5	0.0089	0.0189	F
TOG901015_898	5	0.0317	0.0090	TOG922092_304	5	0.0095	0.0182	F
TOG922188_1448	5	0.0337	0.0093	TOG896078_808	7	0.0099	0.0186	F
TOG922092_304	5	0.0346	0.0090	TOG896103_114	5	0.0100	0.0178	F
TOG897017_278	5	0.0383	0.0086	TOG895030_340	8	0.0105	0.0204	F
TOG898024_443	5	0.0401	0.0083	TOG938507_670	5	0.0106	0.0174	F
TOG897017_257	5	0.0457	0.0089	TOG901015_898	5	0.0116	0.0175	F
TOG918864_641	5	0.0461	0.0079	TOG922188_1448	5	0.0118	0.0178	F
TOG897362_571	6	0.0021	0.0177	TOG895150_1434	5	0.0127	0.0172	F
TOG897362_457	6	0.0028	0.0168	TOG903058_351	6	0.0131	0.0155	F
TOG896074_553	6	0.0036	0.0168	TOG895142_874	1	0.0146	0.0162	F
TOG894262_473	6	0.0045	0.0153	TOG924275_542	1	0.0146	0.0162	F
TOG910860_172	6	0.0053	0.0149	TOG896933_796	3	0.0147	0.0163	F
TOG895876_339	6	0.0073	0.0136	TOG900220_648	11	0.0148	0.0163	F
TOG910860_634	6	0.0082	0.0131	TOG898978_625	5	0.0151	0.0162	F
TOG894262_306	6	0.0273	0.0116	TOG922990_513	7	0.0152	0.0163	F
TOG903058_351	6	0.0330	0.0082	TOG898075_168	7	0.0155	0.0164	F
TOG914633_385	7	0.0022	0.0329	TOG900992_94	8	0.0158	0.0159	F
TOG901985_670	7	0.0026	0.0179	TOG901731_934	8	0.0170	0.0156	F
TOG896540_627	7	0.0047	0.0156	TOG924872_53	11	0.0178	0.0156	F
TOG901549_630	7	0.0047	0.0156	TOG901731_631	8	0.0216	0.0144	F
TOG896540_336	7	0.0053	0.0148	TOG908776_41	8	0.0224	0.0148	F
TOG901549_339	7	0.0053	0.0148	TOG896074_553	6	0.0225	0.0132	F
TOG899998_203	7	0.0085	0.0125	TOG927609_1357	7	0.0227	0.0144	F
TOG899042_188	7	0.0263	0.0095	TOG900375_652	1	0.0229	0.0142	F
TOG900006_352	7	0.0275	0.0095	TOG906941_330	2	0.0233	0.0144	F
TOG894081_362	7	0.0475	0.0076	TOG899751_220	9	0.0233	0.0142	F
TOG894070_290	8	0.0023	0.0164	TOG894773_280	8	0.0237	0.0142	F
TOG900987_506	9	0.0024	0.0177	TOG897521_498	1	0.0252	0.0141	F
TOG899668_578	9	0.0148	0.0120	TOG899452_215	6	0.0278	0.0132	F
TOG901933_203	9	0.0233	0.0100	TOG899130_778	1	0.0280	0.0132	F
TOG901933_425	9	0.0341	0.0088	TOG895578_468	7	0.0281	0.0124	F
TOG908804_377	9	0.0341	0.0088	TOG895578_922	7	0.0281	0.0124	F
TOG898007_380	9	0.0379	0.0093	TOG913042_449	9	0.0281	0.0134	F
TOG900784_136	10	0.0102	0.0129	TOG899033_1374	5	0.0283	0.0137	F
TOG900848_206	10	0.0112	0.0123	TOG897346_443	2	0.0285	0.0129	F
TOG900222_165	11	0.0065	0.0148	TOG901675_241	3	0.0294	0.0131	F
TOG924872_53	11	0.0075	0.0140	TOG899729_79	8	0.0316	0.0130	F
TOG898465_424	11	0.0104	0.0131	TOG897486_230	6	0.0324	0.0126	F
TOG908034_427	11	0.0115	0.0125	TOG900220_279	11	0.0325	0.0127	F
TOG917669_433	11	0.0485	0.0075	TOG937303_617	8	0.0332	0.0130	F
				TOG908913_664	3	0.0337	0.0125	F
				TOG937303_228	8	0.0364	0.0123	F
				TOG901045_327	7	0.0366	0.0121	F
				TOG894262_473	6	0.0376	0.0111	F
				TOG905123_751	3	0.0378	0.0118	F
				TOG922990_288	7	0.0399	0.0119	F
				TOG922036_169	5	0.0405	0.0115	F
				TOG899452_300	6	0.0431	0.0114	F
				TOG894070_290	8	0.0454	0.0118	F
				TOG901734_61	6	0.0454	0.0112	F
				TOG897346_808	2	0.0468	0.0108	F
				TOG913485_147	7	0.0471	0.0107	F
				TOG898824_662	7	0.0471	0.0107	F
				TOG918556_344	3	0.0476	0.0107	F
				TOG913272_94	3	0.0477	0.0108	F
				TOG897306_61	3	0.0477	0.0108	F
				TOG897621_157	3	0.0477	0.0108	F
				TOG898231_46	3	0.0479	0.0107	F
				TOG930271_685	3	0.0481	0.0109	F
				TOG898231_269	3	0.0483	0.0107	F
				TOG907078_337	3	0.0484	0.0109	F
				TOG935618_510	3	0.0484	0.0109	F
				TOG897032_106	3	0.0486	0.0108	F
				TOG898883_986	6	0.0491	0.0106	F

Markers coloured red are common between the irrigated and rainfed treatments; T – markers are common between CIAT-Palmira and Harare Research Station under rainfed treatments; F – markers are not common between CIAT-Palmira and Harare Research Station under rainfed treatments

Appendix 18 Association between markers and number of pods per plant at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment			
TOG902879_375	1	0.0011	0.0393	TOG895142_874	1	0.0283	0.0192
TOG894818_489	1	0.0258	0.0228	TOG924275_542	1	0.0283	0.0192
TOG895142_874	1	0.0266	0.0180	TOG894818_489	1	0.0355	0.0223
TOG924275_542	1	0.0266	0.0180	TOG900308_234	2	0.0015	0.0399
TOG896234_245	2	0.0029	0.0320	TOG895672_181	2	0.0074	0.0294
TOG896567_73	2	0.0034	0.0316	TOG906936_331	2	0.0133	0.0259
TOG895672_181	2	0.0041	0.0307	TOG906969_104	2	0.0353	0.0179
TOG923884_128	2	0.0100	0.0275	TOG896109_664	2	0.0416	0.0164
TOG904064_307	2	0.0170	0.0217	TOG961505_49	2	0.0435	0.0161
TOG906936_391	2	0.0288	0.0175	TOG905371_417	3	0.0331	0.0189
TOG906936_331	2	0.0313	0.0178	TOG935639_446	3	0.0356	0.0185
TOG896109_664	2	0.0371	0.0155	TOG905371_69	3	0.0363	0.0180
TOG894987_722	3	0.0015	0.0363	TOG900261_152	3	0.0385	0.0174
TOG901547_185	3	0.0024	0.0335	TOG900261_206	3	0.0385	0.0174
TOG901547_549	3	0.0024	0.0335	TOG894712_405	3	0.0480	0.0156
TOG896609_245	3	0.0025	0.0336	TOG896276_59	3	0.0480	0.0166
TOG911121_130	3	0.0029	0.0330	TOG898271_99	4	0.0141	0.0245
TOG894864_431	3	0.0202	0.0206	TOG898353_150	4	0.0365	0.0176
TOG916106_684	3	0.0232	0.0194	TOG898353_393	4	0.0365	0.0176
TOG898271_99	4	0.0017	0.0366	TOG895899_315	5	0.0065	0.0304
TOG901711_650	4	0.0352	0.0163	TOG910676_123	5	0.0346	0.0187
TOG904027_122	5	0.0334	0.0169	TOG896746_651	5	0.0462	0.0159
TOG895899_315	5	0.0367	0.0167	TOG904027_285	5	0.0479	0.0254
TOG898974_591	5	0.0465	0.0148	TOG896385_269	6	0.0014	0.0409
TOG899509_584	5	0.0465	0.0148	TOG897333_569	6	0.0038	0.0359
TOG896385_269	6	0.0032	0.0324	TOG898441_398	6	0.0055	0.0311
TOG894262_306	6	0.0234	0.0225	TOG901700_397	6	0.0091	0.0295
TOG897333_569	6	0.0293	0.0194	TOG906841_475	6	0.0343	0.0179
TOG896074_553	6	0.0363	0.0165	TOG898304_707	6	0.0480	0.0159
TOG894794_142	7	0.0035	0.0316	TOG897198_293	6	0.0500	0.0158
TOG898046_230	7	0.0039	0.0314	TOG895846_60	7	0.0016	0.0394
TOG915832_137	7	0.0062	0.0274	TOG898046_230	7	0.0025	0.0374
TOG908017_73	7	0.0304	0.0170	TOG915832_137	7	0.0054	0.0309
TOG894171_240	7	0.0359	0.0162	TOG914633_385	7	0.0060	0.0397
TOG903155_410	7	0.0359	0.0162	TOG894794_142	7	0.0106	0.0263
TOG896850_198	7	0.0487	0.0143	TOG894171_240	7	0.0118	0.0253
TOG898284_1682	8	0.0033	0.0330	TOG903155_410	7	0.0118	0.0253
TOG894148_761	8	0.0103	0.0259	TOG910388_90	7	0.0242	0.0202
TOG902611_789	8	0.0110	0.0239	TOG896850_198	7	0.0354	0.0178
TOG898284_346	8	0.0139	0.0232	TOG910796_209	7	0.0373	0.0179
TOG896253_482	8	0.0261	0.0181	TOG913108_139	7	0.0397	0.0166
TOG895245_245	8	0.0278	0.0178	TOG910796_459	7	0.0492	0.0187
TOG935983_331	8	0.0399	0.0159	TOG895747_525	8	0.0012	0.0418
TOG897374_829	9	0.0133	0.0230	TOG895245_245	8	0.0048	0.0315
TOG898489_619	9	0.0333	0.0170	TOG898284_1682	8	0.0073	0.0301
TOG895900_416	9	0.0448	0.0148	TOG898284_346	8	0.0334	0.0191
TOG901238_199	10	0.0052	0.0291	TOG895747_228	8	0.0343	0.0179
TOG961354_444	11	0.0046	0.0292	TOG896253_482	8	0.0345	0.0179
				TOG902802_1031	8	0.0400	0.0174
				TOG906600_415	9	0.0016	0.0395
				TOG895900_416	9	0.0020	0.0379
				TOG894037_604	9	0.0073	0.0286
				TOG895900_155	9	0.0149	0.0238
				TOG896972_596	9	0.0208	0.0219
				TOG898489_619	9	0.0345	0.0182
				TOG897326_365	9	0.0439	0.0161
				TOG901001_164	9	0.0439	0.0161
				TOG896602_1693	9	0.0440	0.0163
				TOG900136_127	9	0.0454	0.0179
				TOG904927_660	10	0.0079	0.0281
				TOG916065_221	10	0.0445	0.0167
				TOG961354_444	11	0.0089	0.0272

Markers coloured red are common between the irrigated and rainfed treatments.

Appendix 19 Association between markers and number of pods per plant under irrigated and rainfed treatments at Harare Research Station

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment			
TOG929859_500	1	0.0033	0.0377	TOG894042_842	1	0.0130	0.0319
TOG906607_472	1	0.0363	0.0196	TOG894755_654	2	0.0134	0.0319
TOG897521_498	1	0.0383	0.0206	TOG906936_391	2	0.0282	0.0248
TOG899130_778	1	0.0415	0.0185	TOG899382_247	2	0.0388	0.0221
TOG899382_247	2	0.0021	0.0424	TOG897956_500	2	0.0468	0.0203
TOG929271_717	2	0.0098	0.0297	TOG897306_218	3	0.0141	0.0318
TOG903898_287	2	0.0136	0.0272	TOG943467_524	3	0.0266	0.0254
TOG896943_500	2	0.0339	0.0199	TOG913005_113	3	0.0458	0.0208
TOG943467_524	3	0.0019	0.0421	TOG915697_119	5	0.0044	0.0414
TOG908913_664	3	0.0217	0.0234	TOG922990_513	7	0.0128	0.0323
TOG897618_377	3	0.0362	0.0199	TOG898075_168	7	0.0130	0.0323
TOG905123_751	3	0.0439	0.0181	TOG927609_1357	7	0.0184	0.0291
TOG894564_431	4	0.0403	0.0188	TOG910862_232	7	0.0249	0.0259
TOG897017_257	5	0.0089	0.0383	TOG935983_331	8	0.0264	0.0263
TOG897017_278	5	0.0159	0.0266	TOG894773_280	8	0.0412	0.0221
TOG915697_119	5	0.0255	0.0220	TOG906948_530	11	0.0396	0.0231
TOG895899_315	5	0.0385	0.0191				
TOG927703_239	5	0.0474	0.0181				
TOG894081_362	7	0.0027	0.0402				
TOG927609_1357	7	0.0056	0.0347				
TOG922990_513	7	0.0227	0.0235				
TOG898075_168	7	0.0231	0.0234				
TOG922990_288	7	0.0234	0.0232				
TOG899042_188	7	0.0252	0.0223				
TOG895877_63	7	0.0277	0.0221				
TOG901985_670	7	0.0500	0.0173				
TOG935983_331	8	0.0042	0.0371				
TOG918946_209	8	0.0062	0.0335				
TOG899729_237	8	0.0327	0.0216				
TOG896348_940	8	0.0397	0.0196				
TOG895030_430	8	0.0469	0.0180				
TOG901933_203	9	0.0056	0.0345				
TOG901933_425	9	0.0060	0.0338				
TOG908804_377	9	0.0060	0.0338				
TOG899668_578	9	0.0242	0.0239				
TOG896504_1537	10	0.0206	0.0238				
TOG894056_496	10	0.0428	0.0199				
TOG900222_165	11	0.0121	0.0290				
TOG901894_395	11	0.0242	0.0233				

Markers coloured red are common between the irrigated and rainfed treatments

Appendix 20 Associations between markers and canopy temperature depression under irrigated and rainfed treatments at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment			
TOG898084_434	1	0.0062	0.0299	TOG895571_1208	1	0.0184	0.0278
TOG895142_874	1	0.0213	0.0210	TOG895571_420	1	0.0188	0.0278
TOG924275_542	1	0.0213	0.0210	TOG906843_140	1	0.0194	0.0279
TOG894557_593	1	0.0247	0.0207	TOG896309_1245	1	0.0276	0.0243
TOG896940_329	2	0.0048	0.0315	TOG907937_1292	1	0.0379	0.0281
TOG905479_729	2	0.0050	0.0316	TOG895142_874	1	0.0409	0.0210
TOG896498_574	2	0.0061	0.0299	TOG924275_542	1	0.0409	0.0210
TOG898584_416	2	0.0182	0.0223	TOG894044_453	2	0.0023	0.0467
TOG933812_137	2	0.0216	0.0272	TOG898302_727	2	0.0026	0.0464
TOG897956_500	2	0.0255	0.0205	TOG923884_128	2	0.0094	0.0368
TOG902049_243	2	0.0276	0.0193	TOG906936_391	2	0.0312	0.0233
TOG895202_277	2	0.0355	0.0175	TOG895690_777	2	0.0495	0.0201
TOG895202_298	2	0.0355	0.0175	TOG908913_664	3	0.0145	0.0303
TOG899127_233	2	0.0362	0.0173	TOG925468_198	3	0.0331	0.0234
TOG899661_642	2	0.0377	0.0169	TOG913005_113	3	0.0366	0.0225
TOG897132_587	2	0.0379	0.0169	TOG918200_508	5	0.0011	0.0536
TOG901840_596	2	0.0382	0.0168	TOG900268_798	6	0.0045	0.0411
TOG896190_354	2	0.0391	0.0168	TOG901734_61	6	0.0050	0.0393
TOG894986_609	2	0.0399	0.0172	TOG898441_398	6	0.0265	0.0255
TOG896190_237	2	0.0399	0.0168	TOG918299_615	6	0.0402	0.0265
TOG919131_1127	2	0.0404	0.0168	TOG896540_336	7	0.0013	0.0516
TOG895672_181	2	0.0426	0.0167	TOG901549_339	7	0.0013	0.0516
TOG905371_417	3	0.0139	0.0251	TOG896540_627	7	0.0023	0.0471
TOG905371_69	3	0.0190	0.0224	TOG901549_630	7	0.0023	0.0471
TOG909801_195	3	0.0262	0.0196	TOG894081_362	7	0.0275	0.0252
TOG902776_217	5	0.0049	0.0314	TOG960856_776	8	0.0061	0.0390
TOG918864_641	5	0.0203	0.0220	TOG894007_849	8	0.0085	0.0430
TOG896089_391	5	0.0370	0.0179	TOG918946_209	8	0.0165	0.0292
TOG894262_473	6	0.0011	0.0427	TOG908356_281	8	0.0186	0.0294
TOG903058_351	6	0.0018	0.0393	TOG960856_596	8	0.0275	0.0249
TOG900339_308	6	0.0071	0.0295	TOG910318_239	8	0.0316	0.0232
TOG894262_306	6	0.0160	0.0267	TOG897374_829	9	0.0320	0.0236
TOG901700_397	6	0.0193	0.0256	TOG913042_449	9	0.0431	0.0212
TOG912981_1529	6	0.0347	0.0191	TOG897466_231	10	0.0099	0.0353
TOG906841_475	6	0.0357	0.0175	TOG897171_759	10	0.0297	0.0241
TOG896074_553	6	0.0426	0.0174	TOG901894_395	11	0.0088	0.0351
TOG905558_83	6	0.0460	0.0161	TOG900991_671	11	0.0147	0.0306
TOG910862_232	7	0.0094	0.0266	TOG894153_805	11	0.0385	0.0224
TOG922990_288	7	0.0117	0.0268				
TOG894171_240	7	0.0156	0.0231				
TOG903155_410	7	0.0156	0.0231				
TOG898826_427	7	0.0226	0.0211				
TOG908473_409	7	0.0260	0.0202				
TOG910796_459	7	0.0271	0.0239				
TOG901985_670	7	0.0341	0.0183				
TOG898075_168	7	0.0400	0.0175				
TOG922990_513	7	0.0400	0.0173				
TOG901047_1097	7	0.0461	0.0161				
TOG900992_94	8	0.0065	0.0295				
TOG899411_366	8	0.0105	0.0277				
TOG897558_103	8	0.0147	0.0258				
TOG960856_596	8	0.0180	0.0229				
TOG894148_761	8	0.0239	0.0208				
TOG899241_138	8	0.0284	0.0191				
TOG899241_222	8	0.0299	0.0188				
TOG895747_228	8	0.0357	0.0175				
TOG899411_252	8	0.0437	0.0167				
TOG902802_1031	8	0.0453	0.0166				
TOG913042_449	9	0.0161	0.0240				
TOG900848_206	10	0.0410	0.0175				
TOG898135_831	10	0.0481	0.0158				
TOG907127_775	10	0.0481	0.0158				
TOG906506_612	11	0.0145	0.0250				
TOG906506_244	11	0.0157	0.0244				
TOG961354_444	11	0.0293	0.0189				
TOG922096_428	11	0.0378	0.0222				
TOG894539_444	11	0.0484	0.0166				

Markers coloured red are common between the irrigated and rainfed treatments

Appendix 21 Identified associations between markers and leaf temperature under irrigated and rainfed treatments at CIAT-Palmira

Marker	linkage group	p value	Marker R^2	Marker	linkage group	p value	Marker R^2
Irrigated treatment				Rainfed treatment			
TOG910683_736	1	0.0448	0.0225	TOG894557_593	1	0.0265	0.0271
TOG923884_128	2	0.0230	0.0312	TOG901675_241	3	0.0064	0.0409
TOG906941_330	2	0.0318	0.0263	TOG897306_218	3	0.0078	0.0390
TOG894986_609	2	0.0352	0.0247	TOG896276_59	3	0.0135	0.0350
TOG895538_815	4	0.0074	0.0402	TOG905371_417	3	0.0193	0.0307
TOG899042_188	7	0.0128	0.0343	TOG905371_69	3	0.0252	0.0275
TOG901731_934	8	0.0355	0.0244	TOG894712_405	3	0.0335	0.0246
TOG901731_631	8	0.0440	0.0226	TOG903058_351	6	0.0196	0.0303
TOG900987_506	9	0.0221	0.0291	TOG894052_203	6	0.0249	0.0279
TOG894965_186	9	0.0324	0.0260	TOG906318_220	6	0.0315	0.0257
TOG895978_272	9	0.0406	0.0234	TOG901700_397	6	0.0355	0.0264
TOG908034_427	11	0.0422	0.0231	TOG898304_552	6	0.0493	0.0210
				TOG914633_385	7	0.0278	0.0369
				TOG908017_73	7	0.0305	0.0256
				TOG901985_670	7	0.0307	0.0261
				TOG898489_619	9	0.0026	0.0491
				TOG903872_356	10	0.0029	0.0504
				TOG900848_206	10	0.0084	0.0386