

THE EXPRESSION AND INHERITANCE OF STEM STRENGTH IN IRRIGATION WHEAT

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ABBREVIATION LIST

1. FEB – *Fusarium* ear blight
2. GA – Gibberellic acid
3. GCA – General combining ability
4. MAS – Marker assisted selection
5. N – Nitrogen
6. QTL – Quantitative trait loci
7. SCA – Specific combining ability

CHAPTER 1

Introduction

Lodging is a yield barrier and has long been a problem in cereal cultivation. Because of lodging, whole fields of cereals are often flattened after storms (Crook & Enos, 1995). According to Bremmer (1969) and Widdowson (1962) lodging is promoted by an abundant supply of nitrogen (N). The increased yields of wheat (*Triticum aestivum* L.) over the past century have been accompanied by steady decreases in straw length (Gale et al., 1975). Austin et al. (1980) also reported that the yield of new wheat varieties, with shorter and stiffer straw and with increased amounts of N fertiliser, has doubled over this period. The optimum height for wheat grown under irrigation and high fertility is 70 cm (Gale et al., 1975). A yield penalty has been associated with the presence of major dwarfing genes (Richards, 1992). Studies done by Mesterhazy (1995) showed that in a naturally infected field trial, short straw wheat cultivars (below 70 cm) tended to have more symptoms of *Fusarium* ear blight than taller cultivars of above 1 m. Baltazar et al. (1990) suggested that there is a linkage between the *Rht2* dwarfing gene and resistance to *Septoria tritici* (Rob.) E. Desm. in wheat. Their studies showed that isogenic lines of wheat, containing the *Rht1* gene, were more susceptible than those with the *Rht2* gene. Scott et al. (1985) also reported that shorter cultivars have denser leaf canopies and produce a more favourable microclimate for the development of *Septoria nodorum* (Berk). In this complex interaction between straw length and susceptibility of diseases (*Fusarium*) and lodging, it is becoming more important to lengthen straw to semi-dwarf wheat and select stronger plants which enhance standing ability, with genes for solid stem. Thus sowing rates and fertilisation can be manipulated.

It is of strategic importance for wheat breeders to continuously progress in selection for yield improvement. With existing biotechnology, there are opportunities for stacking genes with markers for certain traits of interest. Most of the recent germplasm that are used in South African breeding programmes for irrigation spring type wheat have a CIMMYT background with short straw genes - *Rht1* and/or *Rht2*. In the northern province of South Africa where a significant percentage of irrigation

wheat is planted, lodging is a major concern often helped on by severe thunder storms, heavy rain and soils high in clay content. Lodging of the stem then occurs especially at the second or third internode. Short straw wheat with the solid stem background has a better standing ability. Limited information is available on the solid stem genes in connection to standing ability. The solid stem genes are used for enhancing resistance against diseases like eyespot and especially for resistance against saw flies (Miller et al., 1993). The present dominant South African irrigation wheat cultivars all have a combination of short straw genes with solid stem genes.

In the light of the complex interactions between optimising yield and removing physiological barriers like lodging and grain biomass ratios, it is becoming more important to increase straw length to semi-dwarf agrotypes and to select for those genes which enhance standing ability. In this respect it would be very important to combine genes for solid stems with genes which shorten straw length like semi-dwarf agrotypes. Thus it is important for the irrigation breeding programmes to focus on stem strength and on how to incorporate and manage this in present breeding programmes with other interactions such as plant density and fertilisation.

The aim of this study was to investigate the importance of heritable and environmental factors regulating stem strength in irrigation wheat.

CHAPTER 2

Literature review

2.1 Wheat production in South Africa

Today in South Africa, the wheat production environment can be divided into three different regions. Each of these suits different agrotypes to optimise adaptation (Jordaan, 2002). The first is the Mediterranean region around the Cape. This area is characterised by wet winters with very hot summers suitable for spring-winter type genotypes. It is sown in autumn and harvested in early summer. The second is the irrigation areas around the country, wherever water for irrigation from dams and rivers is available. It is sown during the winter season and adaptation requires spring agrotypes. For spring wheat agrotypes stability and yield potential is important. Spring wheat varieties are often high yielding with excellent quality and widely adapted. Lodging resistance is important and the reduced height genes *Rht1* and *Rht2* in combination with solid stem characteristics are used to improve standing ability of cultivars under conditions of overhead irrigation. They have a maturity range, disease resistance to rust diseases and eyespot. Spring wheat cultivars are photoperiod and vernalisation insensitive, have industrial processing quality and pre-harvest sprouting tolerance (Van Niekerk, 2001).

The dry land environment in the Free State is characterised by summer rainfall and dry, cold winters. The wheat agrotypes grown are winter types varying in vernalisation requirements and day length sensitivity (Jordaan, 2002). Winter wheat agrotypes are usually tall – no *Rht* semi-dwarfing. Coleoptile length exceeding 6 cm is necessary as seeds are sown deep to reach moisture and to ensure a good stand establishment. Cultivars should have lodging resistance and a high tillering ability, to compensate for very low seeding rates in combination with wide row spacing practices. Resistance to rust diseases and to the Russian wheat aphid are of importance (Van Niekerk, 2001).

In the regions described above, an average of 2 million ton of grain per year is produced (1990-1997) on approximately 1 million ha (Van Niekerk, 2001). In the South African production environment wheat is grown as dry land spring wheat (30%), winter wheat under dry land conditions (50%), and 20% spring wheat under irrigation. Although production has dropped during the past few years mostly because of the effect of market deregulation, the focus on new varieties and better production practises has improved the yield per hectare (Jordaan, 2002).

During the past few years, dry land winter wheat yields were very low with a dramatic drop in acreage. This environment is very variable with drought stress and heat posing a risk to the crop. The introduction of grain protein and falling number as grading specifications, created a negative attitude towards production. This caused producers to focus on better production technology and lower risk areas. The increased yield per hectare for winter wheat production under dry land conditions can clearly not be attributed to variety improvement only, but to improved production technology and selection of deeper soils with better moisture holding capacity (Jordaan, 2002). Cultivar release success can be attributed to the introduction of marketable traits into new varieties and the existence of a market structure for the seed business. In trials run by the South African wheat breeders, wheat varieties that were compared within the targeted agro-region of production were released during the past 30 years. These data confirm the sharp linear increase in production during the past 40 years. This improvement was due to a series of significant events which occurred during the past 100 years, more specifically during the past 20 years (Jordaan, 2002).

2.2 Adaptive changes

Wheat production was historically done under dry land conditions. Since the development of irrigation water schemes and better irrigation technology, wheat has become a major crop under irrigation. This has significantly improved yield per hectare and new production problems like lodging were generated (Jordaan, 2002). The Green Revolution was the cornerstone of the genetic control of straw length and of day length sensitivity. These genes were used to improve adaptation and to optimise performance (Satorre & Slafer, 1999).

All spring wheat varieties been grow in South Africa, and some winter wheat varieties, carry the height reducing genes, *Rht1* or *Rht2* or both. It was found that these genes have a significant effect on yield and in combination with the photoperiod insensitive genes *Ppd1* and *Ppd2* regulate the balance between vegetative growth and reproduction, to improve adaptation to both irrigation and stress in spring wheat (Jordaan, 2002). This enabled the South African breeders to breed for adaptation to very diverse environments (Jordaan, 2002). The most important phenotypic change in wheat plants has been the dramatic reduction in plant height from 150 cm to a current average height of 85 cm (Worland & Snape, 2001). This reduction is directly responsible for a large proportion of the increase in productivity experienced in recent years. In the past a tall plant was needed to compete with weed growth, but these tall plants were very susceptible to lodging, which reduced yield potential and quality, particularly under high fertilisation conditions (Worland & Snape, 2001). Reducing the height of plants contributes to increased lodging resistance, but also produces a more efficient plant that is able to divert assimilates into the production of grain rather than straw, and thus improving the harvest index (Austin et al., 1980). The genetic control of plant height in wheat is very complex. It is determined by a combination of major and/or minor genes on many chromosomes which act separately, to promote or suppress plant height (Worland & Snape, 2001). Semi-dwarf wheat has the potential of improving the harvest index and yield, and there is a correlation between reduced height and reduced yield. At present there are 21 height reducing (*Rht*) genes with major effects (Worland & Snape, 2001). Most of these genes were derived as mutants and probably have no breeding potential. Thus only a few major height reducing genes that break the correlation between reduced height and reduced yield remain. These are used in commercial breeding programmes. The two most important semi-dwarfing genes were brought into worldwide breeding programmes via a Japanese variety; Norin 10 (Worland & Snape, 2001). *Rht1* and *Rht2* are located on the short arms of chromosomes 4B and 4D respectively, and are known as gibberellic acid (GA) insensitive dwarfing genes, due to their insensitivity to exogenous application of low concentration of GA solution as seedlings (Gale et al., 1975). According to Flintham et al. (1997a) the GA insensitive genes reduce height by around 18%. In higher yielding environments the percentage increase in yield of the dwarf over the tall lines, gradually increased, until environments yielding around 6 t/ha were reached. The *Rht1* and *Rht2* genes are not the only GA insensitive dwarfing genes available to

plant breeders. The effective height reducing allele *Rht3* reduces height by 50% and causes a large increase in spikelet fertility. However, the phenotype produced by *Rht3* is too short for commercial acceptance (Worland & Snape, 2001).

A second main group of height reducing genes is GA responsive. They are difficult to identify and to study, as no detectable linked markers or diagnostic phenotypes are associated with these genes. Molecular markers can overcome this deficiency (Worland & Snape, 2001). Korzum et al. (1998) has associated a particular microsatellite marker with the main commercially GA responsive dwarfing gene, *Rht8*. It was originally introduced in breeding programmes via the Kavkaz genotypes in numerous crosses throughout the world between winter types and spring types, combining different *Rht* genes into the same genetic background (Worland & Snape, 2001). The height reduction achieved by Strampelli in his early varieties was due to genes located on chromosome 2D and 5BS-7B when compared to the standard Chinese Spring karyotype (Worland & Snape, 2001). Analyses of these two chromosomes showed that 2D carries two height reducing genes, *Rht8* and *Ppd-D1* which have pleiotropic effects. A single gene *Rht9* that is located on the 7BS arm of the 5BS-7BS translocated chromosome, also reduces height by 15%. An additional GA responsive dwarfing gene such as *Rht12*, a dominant dwarfing gene located on chromosome 5A, has been detected. It has been screened for commercial importance, but appears to be associated with reduction in yield (Worland & Snape, 2001). It is obvious that the genetic control of plant height is very complex and the task of breeders to obtain high yielding semi-dwarf varieties with good adaptability is difficult. Shortening and strengthening wheat straw and removing day length sensitivity were major trends in the study of wheat. At present, even though breeders are using short straw germplasm, lodging seems to be a major problem in raising yield levels under irrigation in South Africa. But the introduction of the solid stem trait into certain varieties in 1995, improved the standing ability on the dwarfing gene (*Rht*). It also has pleiotropic effects on crown root development, eyespot tolerance, take-all resistance and adaptation to environments from low yield to very high yield potential under pivot irrigation (Jordaan, 2002).

2.3 Removing yield barriers

Genetic improvement of wheat grain yield potential has played a significant role in increased wheat production in most of the wheat growing areas of the world. However, further increases in wheat grain yield would depend more upon genetic improvement than it did in the past. When the main objective of breeding programmes is to increase the grain yield of a crop which has suffered an intense selection pressure, it is necessary to understand its major morphological and physiological determinants, with the aim of developing new selection criteria (Slafer & Andrade, 1991).

2.4 Efficiency of selection

For maximum progress and efficiency in any breeding programme for any character, it would be advantageous if effective selection could be carried out in the earliest generations possible so that only the best lines would be retained for further testing (Whan et al., 1981). Theoretical evidence suggests that selection for yield should be done in F₂ derived lines, to prevent the loss of high yielding genotypes. However the testing of lines in an early generation is of little value, if it does not indicate the performance of selections which could be taken from those lines in a later generation (Whan et al., 1981). Therefore the development of alternative selection criteria to improve grain yield should involve physiologists, geneticists and breeders (Slafer & Andrade, 1991).

2.5 Physiological determinants

The genetic improvement effects on wheat grain yield were associated with those on harvest index (Slafer & Andrade, 1991). The plant height was reduced to 60 cm by breeders and this reduction, which is linear with yield, shows that the introduction of dwarfing genes was apparently just one step in this process (Calderini et al., 1995). A major reason for the continuous reduction in height is probably the search of lodging resistance associated with shorter culms. As much as 40% of yield can be lost due to lodging during grain filling. Grain yield has increased in association with a higher harvest index (Calderini et al., 1995). This indicated that during recent breeding,

harvest index was kept as the main attribute to be increased, in order to obtain further grain yield potential. The increase in harvest index was related to reductions in culm height, and indicated that the introduction of semi-dwarf genes has brought about increases in yield potential mainly as a result of their effect on culm height (Calderini et al., 1995). In the past it was relatively simple to balance increases in grain yield potential (increases in harvest index) with reductions in yield losses due to lodging, through reductions in height. Continuing the use of this relationship would depend on the optimum culm height for the highest yield potential and the values obtained in modern cultivars. The optimum height of wheat is between 70 and 100 cm indicating that modern cultivars already have a height close to the optimum. Thus future increases in harvest index should be independent of further decreases in culm height (Calderini et al., 1995). During the genetic improvement in both the harvest index and grain yield the changes were positively associated with changes in the number of grains per square meter, but not significantly related to individual grain weight (Slafer & Andrade, 1991). Even in modern cultivars the grain yield seems to be sink-limited during the grain-filling period. Future efforts should aim at increasing the number of grains per square meter, since it seems not to have an apparent ceiling, unlike breeding for increased harvest index (Slafer & Andrade, 1991), as the values of harvest index in modern wheat approach that upper limit (Calderini et al., 1995). Further genetic improvement of wheat grain yield potential should be done by increasing ability for producing biomass. The first requirement to achieve this goal will be to find variability in the physiological determinants of biomass production (Slafer & Andrade, 1991). It has not been established whether higher biomass was due to higher interception of solar radiation, greater efficiency of conversion of the intercepted radiation into new dry matter, or to a particular combination of simultaneous changes in both traits. The greater biological yield of lines was associated with taller stem (Slafer & Andrade, 1991). Law et al. (1978) reported that the positive relationship between height and grain yield of wheat, was probably due to a better light distribution within the leaf canopy of taller cultivars. This agrees with this positive association between biomass and height (Slafer & Andrade, 1991). Studies have shown that some modern varieties have slightly higher biomass than the older ones, although the former had even shorter stems (Austin et al., 1989). Brooking & Kirby (1981) found that semi-dwarf genotypes that present the taller phenotype had higher grain yield potential. The reduction in grain yield associated with increased

height can be attributed to a reduction in harvest index. In the case of the dwarf line with a dramatically reduced height, grain yield was lower than the semi-dwarf lines because of reduced biomass. Extreme dwarfism (main stems less than 45 cm) reduces final biomass in other genetic backgrounds also (Miralles & Slafer, 1995). These new varieties, having shorter and stiffer straw, permitted the use of increased amounts of nitrogen fertiliser - rates of application have more than doubled over the period (Austin et al., 1980). The increase in grain yield potential through tall lines could lead to an increased sensitivity to lodging (Slafer & Andrade, 1991). This argument suggests that breeders will need to detect and exploit genetic differences in total dry matter production, if there is to be a continued genetic gain in yield (Austin et al., 1980). Straw strength and number of ears will have to be increased or at least maintained. This implies a need to retain a distribution of dry matter between grain and straw, similar to that in the best of the present varieties (Austin et al., 1980). Increased dry matter production, by means other than increasing photosynthetic rate per unit leaf area, could be productive in optimal conditions.

2.6 Optimisation of the environments

The optimal conditions to cultivate wheat are under overhead irrigation with enough nitrogen (N) as N plays a crucial role in plant metabolism and more than 90% of the plant N is in protein. It only makes up a small portion of the total plant weight. Plants can only use specific forms of N and it could be the main factor limiting yield potential. The low N supply makes it necessary to optimise the management of N resources, to increase the efficiency of N use in crop systems (Satorre & Slafer, 1999). This can be achieved by increasing the proportion of soil N absorbed by the crop or by increasing the accumulation of N compounds in the edible part of the crop.

Increasing N fertiliser increases the amount of dry matter produced per unit of land linearly, up to a level where a plateau is reached. The biomass increase is associated with larger leaves, and plants stay greener for a longer period. They have taller stems as well as larger numbers of tillers surviving to maturity and bearing fertile spikes. The grain yield response to N parallels that of biomass, with three differences; the slope of the linear growth phase is lower; the biomass reaches a plateau at lower N rates after the ceiling, and grain yield decreases. The different reaction of N to

biomass and yield is described by the harvest index, which decreases with the increase of N rates. The high N rates have a negative effect on yield, due to the weakening of the vegetative organs which cause lodging (Satorre & Slafer, 1999). High N fertilisation will favour lodging due to the increased length of the lower internodes, a higher fresh weight of aerial parts of the plants, decreased culm stiffness, a lower number of coronal roots and less anchorage strength (Keller et al., 1999). Yield is affected not only by the rate of N, but also by the timing of N application. Deficiency at shooting time decreases the number of ear bearing tillers, spikelets per spike, kernels per spike and at flowering time, the reduction of seed setting. During grain filling only a limited amount of N is taken up from the soil (Satorre & Slafer, 1999).

Senescence is an organised process which follows a common pattern, which starts from the lower leaves and moves to the flag leaf. Yellowing begins at the point of the leaf and gradually reaches the leaf sheath. Culms and spikes remain green the longest and produce the energy for N remobilisation throughout photosynthesis. They are the last source of protein accumulation in the grain (Satorre & Slafer, 1999). Bread-making quality increases with N supply and reaches a peak at N supply level above that needed to achieve maximum yield. Thereafter protein quality decreases with the increase of protein content because the extra N accumulated in the grain is represented by gliadins, which are detrimental to the quality of bread made. The Green Revolution was the driving force of the optimal combination of new genotypes, sufficient water and higher N rates (Satorre & Slafer, 1999).

When the important contribution of N to grain yield became evident at the beginning of the last century, it was found that the available wheat varieties were not able to exploit the benefits of higher N levels because of their susceptibility to lodging. Breeders wanted to develop a new plant idiootype that is more tolerant to N. The attempt to improve lodging resistance by improving stem stiffness while keeping plant height constant did not have satisfactory results. This was because this approach was based on selection within the old local populations. The breakthrough was achieved by introducing the short-straw trait from a Japanese cultivar. This cultivar was a good source of earliness and dwarfism because of the genetic linkage between the *Ppd1* gene for earliness and the dwarfing gene *Rht8*. Using higher N rates increased the yield potential and ensured the success of the semi-dwarf high-input high-yielding

varieties that are more efficient in N use and are able to produce more grain per unit of N absorbed (Satorre & Slafer, 1999).

When the availability of N is lower than required to maximise grain yield, the hyperbolic response of yield to fertiliser occurs, whereby yield increases asymptotically to a maximum possible for a given environment (Satorre & Slafer, 1999).

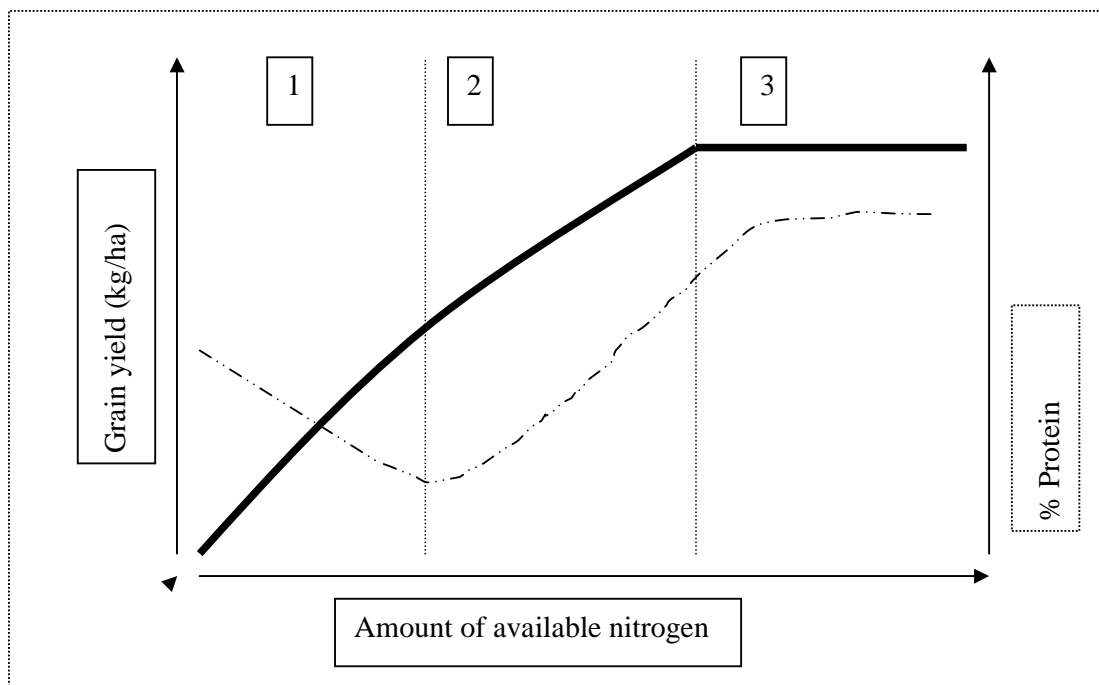


Figure 2.1 Diagrammatic representation of the response of yield (-) and protein percentage (-.-) to nitrogen fertiliser (Satorre & Slafer, 1999)

At the first increment (1) of N, (figure 2.1) at low N, the amount of starch and protein in the grain is increased. With the next increment the result is the frequently reported negative relationship between protein percentage and grain yield. Yield is increased, but protein percentage decreases. At the second region (2) with additional N, the yield accumulation is reduced but still with a positive effect, and it has a greater impact on protein accumulation. In the third region (3) with a greater amount of N added, maximum yield was attained but it increased the amount of grain protein. Protein percentage is highly responsive to N in this highly available region of N addition (Satorre & Slafer, 1999).

2.7 Lodging of wheat

Lodging can be defined as the state of permanent displacement of stems from the upright position. This has long been a problem in cereals (Verma et al., 2005). Whole fields of cereals are often flattened after summer storms (Crook & Ennos, 1995). Lodging can be classified into two types, the first being stem lodging, which is the bending or breaking of the lower culm internodes. This depends on the tensile failure strength of the first internodes, as well as on stem wall diameter and thickness (Verma et al., 2005). The second is root lodging, which refers to the straight and intact culms leaning from the crown, involving a certain disturbance of the root system. Anchorage in wheat is provided by a cone of rigid coronal roots which emerge around the stem base. Root plate spread and structural rooting depth are the components which determine anchorage strength (Verma et al., 2005).

Lodging can cause severe losses in wheat yield and quality (Al-Qaudhy et al., 1988). Lodging may reduce grain yield by up to 40%. It can also complicate harvesting and may cause deterioration in the quality of the grain (Zuber et al., 1999). In most studies lodging is so highly correlated with plant height that other morphological parameters influencing lodging are hard to identify (Verma et al., 2005). Despite the efforts of plant breeders to select cultivars with shorter and stiffer straw, lodging is still a serious cause of yield loss worldwide (Crook & Ennos, 1995). Through the use of dwarfing genes (*Rht1* and *Rht2*) which shorten stems, lodging resistance is improved. These act through reducing the leverage forces that contribute to both types of lodging. Even lines with the same height can differ in standing ability. It suggests that other traits must be important in determining lodging risk (Berry et al., 2003a). In previous studies it has been found that extreme dwarfism is also associated with several other undesirable characteristics, like decreased biomass, higher leaf density, shrunken kernels, premature senescence, increased incidence of diseases, thus resulting in an undesired increase of fungicide use (Hai et al., 2005). Modern high yielding cultivars are generally shorter with stronger straw and a higher harvest index, thus being responsive to high fertiliser input (Kelbert et al., 2004a). The newer varieties have higher harvest index and smaller root:shoot ratios than the older varieties. This may help to explain the higher frequency of root lodging in these modern varieties (Zuber et al., 1999). Scientists debate continuously on whether stem

lodging or root lodging predominates. However they agree that the form of lodging is due to an interaction of the plant with rain, wind and soil. Lodging is increased by rain through the decreasing of soil strength while increasing the load which the plant must bear. The wind acts as the force which pushes the plant over or buckles the stem (Sterling et al., 2003). The risk of lodging is strongly influenced by a number of husbandry decisions including variety choice, sowing date, drilling depth, soil fertility and the application of plant growth regulating chemicals (Sterling et al., 2003). Higher seed density will enhance lodging by increasing culm length and decreasing culm diameter as well as total root mass (Keller et al., 1999). Their influence on lodging risk has been shown to be through their ability to alter crop structure by affecting certain plant characteristics (Sterling et al., 2003).

A study on the effects of nitrogen and stem shorteners (growth regulators) on root and shoot characteristics, associated with lodging resistance in two winter wheat cultivars of contrasting lodging resistance showed that in both cultivars high levels of nitrogen increased the height of the stem, thereby increasing the self weight moment transmitted into the ground, which weakened both the stem and the anchorage coronal roots (Crook & Ennos, 1995). Cultivars resistant to lodging had strong anchorage that could resist the self weight moments generated by the stem. Cultivars susceptible to lodging either produced weak coronal root systems which conferred poor anchorage or generated greater self weight moments because their stems were tall. Growth regulators had little effect on the bending strength of the shoots and root systems but reduced plant height so that the lodging momentum generated by the weight of the shoot was less. Morphological and mechanical measures were used to calculate a safety factor against both stem and root lodging. In this process five factors were found that influence the safety factors: cultivar type, the type of lodging, the rate of N, growth regulators, application and time (Crook & Ennos, 1995). In their study they found that both nitrogen and growth regulators had significant effects on the plant height. N increased the height of the plants by around 2.5%, while growth regulators reduced it. The application of high N raised the height of the centre of gravity while growth regulators lowered it. High levels of N reduced the total bending strength of the coronal root system because the plants produced fewer and less rigid roots. However, the growth regulators had less effect on root development: while the number of coronal roots was increased, the total bending strength of the root system

remained unaltered. Thus for a plant to remain structurally intact, both the stem and the anchorage system must be strong enough to withstand the lodging momentum generated by the wind and by the weight of the plant (Crook & Ennos, 1995). Humphries (1968) concluded that growth regulators increase the stiffness of the stem. In many studies stiffness is assessed by using the snap test, in which a handful of culms are pulled over to a reclining position and then allowed to snap back into place. The force is recorded on a scale of one to ten (Murphy et al., 1958). The major effect of the growth regulators was to reduce stem height and as a result, the self weight moment generated by the stems was reduced because of the lower centre gravity. Hence the factor of safety was increased (Crook & Ennos, 1995). Lodging controlling cost has been shown to be very high. Plant growth regulator application has been found to have doubled (Clare et al., 1996), and applications often occurred regardless of lodging risk. It is shown that in years of severe lodging; even full commercial rates have not succeeded in preventing lodging completely (Clare et al., 1996). It has recently been shown that winter wheat cultivars have different rankings for root and stem lodging. Thus these findings would affect the way in which lodging risk is minimised. In this respect different crop management is required to reduce root lodging compared to stem lodging (Berry et al., 2003b). The risk of root lodging is reduced most effectively by the planting of fewer plants, while stem lodging is best reduced by delaying and reducing N fertiliser (Berry et al., 2003b). Widdowson (1962) found that an abundant N supply promotes lodging, but the application of growth regulators to the crop lowers the risk of lodging. Breeders use observations of naturally occurring lodging, to rank lines for lodging resistance on a scale from one to nine (Berry et al., 2003b). This method for assessing lodging has been used for many years but it does have two shortcomings. The first one relies on lodging events occurring within the cultivar trials, but these do not occur in significant amounts in most years. The disadvantage of this is that cultivars prone to lodging are not always identified before they are grown on a large scale. It is also difficult to assign the correct ranking to resistant cultivars when little lodging occurs. The second shortcoming is that it does not account for the different risks for the stem and root lodging, because the mechanism of lodging is not usually identified when the amount of lodging is assessed. The problem is that this means that the lodging rankings are a combination of stem and root lodging. In order to assess both types of lodging, breeders could begin to record the type of lodging (Berry et al., 2003b).

To understand lodging it is necessary to obtain a detailed measurement of plant, soil and weather conditions during the lodging process itself (Sterling et al., 2003). Artificially induced lodging has been described through various techniques (Kelbert et al., 2004b). Bauer (1964) and Harrington & Waywell (1950) made use of wind tunnels, while Laude & Pauli (1956) induced lodging by manually bending and pinching the stems between their fingers. Another technique was by completely flattening the middle rows of the plot by dragging a weighted plywood board over them (Kelbert et al., 2004b) and Jedel & Helm (1991) used a similar apparatus which pushed down the crop in one direction, with minimal stem breakage. Baker (1995) developed a conceptual model of the lodging process, in which the plant is considered to act as a harmonic oscillator. This model assumes that the dominant parameter affecting lodging is the wind-induced bending moment at the stem base. The value of this bending moment relative to the failure moment of the stem and the failure moment of the root/soil system indicates whether or not lodging occurs (Sterling et al., 2003).

While considering the adequacy of the simulation for qualitative observation of the lodging process it is found that stem lodging occurs more or less instantaneously, whilst root lodging occurs over a period of time. This happens under a discrete load. How this is actually produced should be of no importance (Sterling et al., 2003). Baker et al. (1998) showed that the base-bending moment of a shoot is determined by several factors, including the wind speed acting upon the ear and drag of the ear, together with the height at the centre of gravity and natural frequency of the shoot. Root lodging is caused by a series of discrete loads (Sterling et al., 2003). The peak bending-moment will occur when the arrival of the gust coincides with the motion of the crop in the same direction (Sterling et al., 2003). Berry et al. (2003b) stated that root lodging occurs when the wind induced base-bending moment of the shoots is larger than anchorage failure moment. In other words, the stem and anchorage failure moments may be approximated to the strength of the stem base and the anchorage system respectively. It was found that the failure of a single row usually occurred when the shoots were displaced by between 40° and 70° past the vertical (Berry et al., 2003b). They believe that root lodging may be promoted at the expense of stem lodging by reducing and delaying N fertiliser.

Other studies by Arora & Mohan (2001) have shown that high levels of soil N reduce root biomass and Berry et al. (2000) showed that the reduction in stem strength in response to high N was greater than the reduction in anchorage strength. The risk of stem lodging increases through the grain filling period, relative to the risk of root lodging because the stem bases become progressively weaker (Berry et al., 2003a). Wheat and other cereal crops produce slender flower stems bearing a relatively heavy tip inflorescence (Zebrowski, 1999). The apical location of the inflorescence had some adaptive importance in wild ancestors of the plants, increasing the success of their propagation. This is not optimal with respect to the mechanical stability of the shoot as a load-bearing structure. Many recent high-yielding varieties of wheat suffer from lodging when grown in dense canopies. Wheat is particularly prone to falling down at the stage when the inflorescence achieves its maximum weight. The *Gramineae* have been the subject of numerous biomechanical studies for at least two reasons, the economical severity of grain yield loss as a result of lodging and efforts of breeders to improve lodging resistance in cereals; and the capability of grasses to cope with strong winds without damage. Zebrowski (1999) stated that the effective spring constant, strongly biased by the compressive load due to the weight of the inflorescence, was found to be the dynamic attribute of a vertical stem, characterising its capability to resist wind loads, while it carries a relatively heavy tip inflorescence. The softening of the stem in lateral deflections and the further reduction of the natural frequency, in addition to the effect due to an increase in the inertia caused by the stems own mass, may explain to some extent the enhanced susceptibility of cereal crops to lodging. This was observed at the late milk stage of grain development. At this stage, cereals lodge more frequently than at earlier growth stages, e.g. during flowering, although the stems are then stiffer, have the same height and similar aerodynamics, and their anchoring in the soil is not inferior.

Zuber et al. (1999) conducted a study to determine the relationship of morphological traits to lodging resistance in spring wheat, to find easily measurable traits related to lodging resistance. A set of breeding lines representing a wide range of combinations of plant height and lodging resistance was evaluated (Zuber et al., 1999). In this study higher correlations were found for traits measured at anthesis than for traits measured at maturity. Plant height, stem length, stem diameter, ear weight, stem weight and

stem weight per centimetre, were measured at anthesis and correlated with the lodging score. Significant correlations between the lodging score and single morphological traits were found for stem diameter and stem weight per centimetre. Thus thicker and heavier stems (mg per cm) were indicative of better lodging resistance (Zuber et al., 1999). Also, wider basal culms diameter has been associated with lodging resistance in wheat (Kelbert et al., 2004a). It was also reported that lodging resistant genotypes exhibited thicker culm walls than those susceptible to lodging (Kelbert et al., 2004a). The presence of a reliable association between any easily measured culm character and lodging may enhance efficient selection of lodging resistant lines in early generations (Kelbert et al., 2004a). In literature it has been found that silica deposits in the epidermis of wheat culms were more abundant in a lodging resistant variety than in a variety susceptible to lodging (Zuber et al., 1999). Lignin is a phenolic cell wall polymer closely linked to cellulose and hemicelluloses (Ma et al., 2002). Mainly lignin deposits are in the walls of certain specialised cells such as tracheary elements, sclerenchyma and phloem fibres in plants. These deposits lead to a dramatic change in the cell wall properties, which impart rigidity and structural support to the wall, and assists in the transport of water and nutrients within the xylem tissue which decreases the permeability of the cell wall. It has long been proposed that lignin synthesis might be related to stem strength and this is important in crop plants where stem strength will lead to a lodging phenotype. These results suggest that the action of the wheat caffeic acid 3-O-methyltransferase (COMT) gene may be related to stem rigidity and lodging character in wheat (Ma et al., 2002). Many high correlations between plant parameters and lodging resistance were found but no single trait or group of traits has proven to be generally reliable as an index of lodging resistance (Zuber et al., 1999). Many studies have been done and many researchers have reported associations between plant height, number of internodes, adventitious roots, length and diameter of basal internodes, number of vascular bundles, culm wall thickness, lumen diameter and sclerenchyma thickness with lodging (Kelbert et al., 2004a). It was reported that short plants with fewer short, wide internodes with thick culm walls and a higher number of vascular bundles were characteristic of the lodging tolerant genotypes. Plant height and the length of the basal internodes were the two main culm characters closely associated with natural and artificially induced lodging for all genotype studies, while other culm characteristics did not appear to be related to lodging (Kelbert et al., 2004a). Stanca et al. (1979) found no association between the numbers

of vascular bundles stem diameter or culm wall thickness of the basal internodes and artificially induced lodging. Stem diameter explained almost half of the phenotypic variation in lodging resistance and Kelbert et al. (2004a) did not find stem diameter to be a significant character related to lodging resistance. A close correlation was calculated between the lodging resistance of wheat and the carrying capacity of the culms at maturity. This was calculated from the weight per unit length of the culms basis (g per 10 cm), plant height and the weight of the ear (Zuber et al., 1999). A greater diameter of the lower internodes and the greater weight per unit length of the stem basis of wheat was also suggested as a possible reason for better lodging resistance (Zuber et al., 1999). However Pinthus (1967) found no significant correlation between culm diameter and lodging resistance in wheat. This may be due to the fact that plant material in these studies had not been selected for plant height (Zuber et al., 1999). Therefore more of the variation for lodging resistance was caused by plant height and less by culm diameter than in their study. Stem weight per cm is of less importance for lodging resistance in plants shorter than 90 cm (Zuber et al., 1999).

Genotypes with heavier ears appear to reach the same level of lodging resistance compared to genotypes with lighter ears. This occurs only when their stem weight per centimetre values are higher, i.e. heavier ears increase lodging. Increased lodging caused by heavier ears was compensated for by heavier stems which help to reduce lodging (Zuber et al., 1999). The influence of ear weight on lodging can also vary depending on the stage of plant development. Certain studies have shown that longer, more rigid coronal roots, larger root spreading angles, or anchorage strength of root, usually increase lodging resistance. Morphological root parameters are difficult to measure and are highly influenced by environmental conditions such as nitrogen fertilisation and temperature. The suggestion is that besides plant height, stem weight per centimetre and culm diameter may be of value in breeding for better lodging resistance. If a simple method for scoring culm diameter in the field could be established, this could be an adequate selection criterion for lodging resistance among genotypes of similar height (Zuber et al., 1999). Berry et al. (2003a) suggested that breeders should opt for wider, deeper root plates and wide stems with thicker stem walls, for the greatest improvement in lodging resistance. Hai et al. (2005) suggested that more efforts to improve stem strength should be an important focus in wheat

breeding for lodging resistance. They reported that the heritability for culm length was relatively high, thus indicating selection for culm length would be effective.

Lodging resistance scoring is very difficult under natural field conditions (Hai et al., 2005). For wheat lodging resistance stem strength has been used as an index. This is a complex trait comprised of two characteristics; stem mechanical elasticity and rigidity of the stem, and is therefore closely associated with stem morphological and anatomical traits. The genetics of stem strength and related traits of basal stem internodes is very important for genetic improvement of lodging resistance. With the quantitative trait loci (QTL) mapping approach, it is feasible to analyse the genetic basis of the relationship between traits. This can be useful for genetic improvement of lodging resistance in wheat (Hai et al., 2005). They found a total of six QTL's for stem strength, culm wall thickness, pith diameter and stem diameter. Two QTL's were found for stem strength and two QTL's were associated with pith diameter, while only one QTL for stem diameter and culm wall thickness was detected (Hai et al., 2005). Li (1998) reported that stem strength, stem diameter and pith diameter were controlled by both additive and non-additive gene effects. Most of the QTL's for lodging were consistent over environments, but the additive effects of the simultaneous fit varied considerably between environments, but this can be explained by the effect of the year (Keller et al., 1999). The weather conditions which cause lodging plays an important role in the reaction of the genotypes. The degree of lodging is dependent on the stage of plant growth at which a critical weather event occurs, e.g. at sensitive growth stages such as milk development, grain filling or ripening (Keller et al., 1999). The results reported by Hai et al. (2005) on QTL mapping, show that stem strength can be improved by breeding for stem thickness and higher stem diameter/pith diameter ratio. Thus the combination of stem strength, stem diameter and culm wall thickness may be used as a selection index for lodging resistance with marker-assisted selection (MAS), to improve lodging resistance.

It is important to realise that stem strength is not only associated with morphological and anatomical traits of the stem, but is also with several physiological traits (Hai et al., 2005). According to Li (1998) the soluble carbohydrate content of basal internodes of the stem was significantly correlated with lodging resistance, and the lignin content of basal internodes of strong stems was higher than that of weak stems.

According to Keller et al. (1999) plant height is probably the best trait for an indirect assessment of lodging resistance. In their study they found that the mechanical parameter of culm stiffness was as highly correlated to lodging as to plant height, while culm stiffness is easy to assess by hand scoring. Some breeders use this trait as an indirect selection parameter for lodging resistance. The results for mechanical culm parameters, such as bending or breaking strength, are conflicting in the literature. In their study they found a total of nine QTL`s for lodging, seven coincided with QTL`s for morphological traits, thus reflecting the correlations between these traits and lodging (Keller et al., 1999). There were two QTL`s for lodging at the same place as the QTL for culm stiffness. There was no coincidence between these QTL`s and QTL`s for plant height. With MAS for these loci, lodging resistance could be increased without decreasing plant height, the latter being known to be determined by many genes. In wheat, almost all 21 chromosomes were found to contribute to genetic variation for plant height. About 20 major genes (dwarfing genes) for height reduction (*Rht* genes), are known. Five of the known dwarfing genes are located on chromosomes where they found QTL`s for plant height. On chromosome 2A there is *Rht7*, on 4BS there are *Rht1* and *Rht3* – these are two alleles of the same locus-, on 5AL there is *Rht12* and on 7BS, *Rht9*. Both *Rht1* and *Rht3* are GA genes. Dwarf mutants of this type showed a reduced response or complete insensitivity to applied GA. Besides these known GA-insensitive genes there are probably others on 5B and 7B, where the QTL`s for plant height were found. Keller et al. (1999) suggested that selection for lodging resistant genotypes can be done via indirect selection, based on the morphological traits of plant height and culm stiffness before flowering. Even though lodging resistance is a polygenic trait, single genes can still have major effects (Keller et al., 1999).

The reduction of yield components could be determined and analysed. It provides useful information for characterising environments subjected to numerous yield-limiting factors (Brancourt-Hulmel et al., 1999). Their study revealed that lodging affected yield more than the climatic variants, thus explaining genotype x environment interactions as central in a wheat breeding programme (Brancourt-Hulmel et al., 1999). According to Fischer & Stapper, (1987) culm lodging caused grain yield to be reduced by 7-35%, with the greatest effect in the first 20 days after anthesis. When lodging occurred just before anthesis, it was less deleterious, perhaps

because the crop was able to right itself quickly by node bending. Lodging after anthesis reduced crop growth rate. The adverse effect of lodging on grain yield is ascribed to this reduction in photo-assimilate supply (Fischer & Stapper, 1987). While kernel number per unit area tended to be reduced by early lodging, reduction in kernel weight accompanied by small increases in grain N percentage occurred by later lodging (Fischer & Stapper, 1987). When it rains and lodging occurs, ripening conditions increase grain sprouting. In the new high yielding semi-dwarf cultivars with higher kernel numbers and a tendency towards greater source limitation during grain filling, yield could be more sensitive to post-anthesis lodging. Yield reduction is caused by lodging, with the magnitude of the reduction depending on timing, season, variety and degree of lodging. In their study they found that artificial 80° lodging led to the greatest yield reduction of 20-30% in the period from anthesis. The initial degree of lodging is another factor which clearly affected the yield response to lodging: 45° lodging reduced yield by 9% while 80° lodging reduced it by 17% more (Fischer & Stapper, 1987). In times where lodging occurred one to two weeks before heading, the decrease in yield averaged 30 - 35% (Laude & Pauli, 1956). When lodging occurred during the five days just prior to heading it caused only half as much reduction in yield and did not consistently affect the number of fruiting tillers. During the heading period it was 27% while it increased to 35% when the plants were lodged during the next 10 days. This is an indication that some young kernels were aborted. The effect of lodging on yield and quality of wheat is associated with the capacity of the plant to recover from tissue damage and the extent to which materials have been translocated to the developing kernels, prior to the time the injury is inflicted. Injury to the stem, particularly during the periods of elongation and development of head in the boot, appeared to restrict further growth, which probably reduced the quantity of carbohydrate synthesised, and decreased grain production. They found in their studies that the greater reduction in yield resulted from injuries after mid-heading, possibly associated with the progressive hardening of the vascular tissue which lessens the capacity of the plant to recover (Laude & Pauli, 1956).

2.8 Genetic control of straw length

The cultivation of the semi-dwarf wheat has increased dramatically worldwide, since 1960 (Allen, 1980). Dwarf and semi-dwarf varieties have been cultivated in Asia for

more than a century (Worland et al., 1994). This successful introduction of the dwarf and semi-dwarf varieties into Europe was achieved early in the 20th century by the Italian breeder Strampelli. The pioneer work of Norman Borlaug, whose CIMMYT wheat germplasm features in the pedigree of most modern high yielding semi-dwarf wheat varieties, was accepted (Worland et al., 1994). The estimate is that 44% of the wheat produced in less-developed countries is composed of semi-dwarf wheat and probably 50% of the areas sown in the world (Allen, 1980). The origin of most of these cultivars was the Japanese semi-dwarf sources, Daruma and Akokomugi (Allen, 1980). Daruma has the capacity to transfer its short stature to the offspring of other wheat it was crossed with. It was extensively used by the Japanese breeders who were seeking higher yields (Hanson et al., 1982). Norin 10, which played the key role in the Green Revolution of wheat, was the parent of Daruma (Allen, 1980). The short stemmed Norin wheat has as many leaves and as big a manufacturing surface per stem as the other wheat. The difference is that they have shorter intervals between the leaves. They waste less effort on erecting an unproductive stalk and have many more stems per plant. It is meaningful that the Norin wheat has the capacity of taking up large amounts of soil nutrients and converting them to grain. The word Norin is an acronym made from the first letter of each word in the Romanised title of the Japanese Agricultural Experiment Station. Norin wheat is derived originally from Daruma, native wheat named after a kind of short, squat, Japanese tumbler doll. How and where Daruma originated must remain a mystery. Native short straw wheat varieties are found throughout Japan, China, Tibet, and Korea. Japanese plant breeders crossed Daruma with American wheat, Fultz. The resulting hybrid was later crossed with another American variety, Turkey Red, producing the Norin wheat (Paarlberg, 1970). Norin genes not only shortened the plant but resulted in higher tillering, more grains per head, and more grains per square meter as well as a more efficient use of fertiliser and moisture and a higher harvest index (Hanson et al., 1982). Rawson & Evans (1971) reported that the yield advantages of short wheat cultivars are largely due to their greater capacity for tillering. Another source of extreme dwarfism is Tom Thumb and it is controlled by a single gene – *Rht3* - but this variety has been less widely used in the production of commercial dwarfs (McVittie et al., 1978). *Rht3* has also been shown to cause a marked reduction in the rate of α -amylase synthesis during germination but can unfortunately not be used commercially because it results in plants with an agronomic unsuitable short straw (Mrva & Mares, 1996). Some of the

characteristics of the new short wheat are attributable to Norin 10 genes (Hanson et al., 1982). The wheat has short stature, height ranges from 50 to 100 cm, sturdy straw and strong crown roots. They have more fertile florets, the new semi-dwarfs can produce 120 to 150 fertile flowers per head under good management, which produces a high yield potential when it is properly spaced and adequately fertilised and watered. Plants are able to produce 25 to 100 tillers each. Semi-dwarf spring wheat can reach maturity days or even weeks sooner than the tall varieties can. If moisture is adequate, the wheat can produce 15 to 30 kilograms of additional grain for each kilogram of added N fertiliser, up to the first 50 to 70 kg/ha of N. They have higher harvest index, day length insensitivity, wide adaptation and disease resistance (Hanson et al., 1982).

The genetics of plant height in cereals is known to be complex and it is determined by many genes (Börner et al., 1996). Bread wheat ability ($2n = 6x = 42$), to tolerate aneuploidy, has led to the development of cytological techniques, whereby single pairs of chromosomes can be transferred from one variety to another (Snape et al., 1977). The substitution lines of these chromosomes provide a powerful tool for the genetical analysis of wheat crop, particularly with respect to the genetical variation for loci controlling quantitative characteristics of agronomic interest (Snape et al., 1977). Many attempts have been made to characterise the genetic system, controlling height in Norin 10 and its semi-dwarf derivatives. The estimation of the number of major genes involved and their chromosomal locations have been hampered by the quantitative nature of height variation (Gale et al., 1975). Plant height seemed to be additive. This could certainly be related to the presence of two major dwarfing genes, polymorphic in the population (Goldringer et al., 1997). In aneuploids it is possible to classify genes for height into those which increase or promote height and then those which reduce or suppress this character. Major genes for height reduction are designated as dwarfing genes. Because of this relation in their response to exogenously applied gibberellins, (GAs) dwarf mutants of several species can be divided into two categories (Börner et al., 1996): GA sensitive mutants, where the absence or modified spectrum of endogenous GAs result in dwarf plants, - normal growth can be restored by GA application and GA insensitive mutants, that show a reduced response or complete insensitivity to applied GA.

The GA insensitive dwarfing mutants (Table 2.1) usually exhibit a reduced internode length without reducing the length of the spikes. They are extensively used in agriculture and are therefore of economic importance (Börner et al., 1996). This GA insensitivity and the dwarf phenotypes have been described as being controlled by pairs of linked loci, e.g. *Rht2* linked to *Gai2* and *Rht3* to *Gai3* (McVittie et al., 1978). The genes *Rht1* and *Rht2* were introduced into many breeding programmes all over the world (Börner et al., 1996). The big advantages of *Rht1* or *Rht2* are that under optimal conditions, height is reduced by about 20%, a high level of spikelet fertility is promoted and yield increases by up to 20% (Worland et al., 1994). Certain genetic studies revealed that *Rht1* and *Rht2* were located near the centromere on the short arms of chromosome 4B and 4D respectively (Börner et al., 1996). On each of these two loci a series of multiple alleles (homoeologous set), that induce varying degrees of dwarfism have been identified. These two alleles *Rht3* on chromosome 4B and *Rht10* on chromosome 4D are very potent (Börner et al., 1996).

Table 2.1 GA insensitive dwarfing genes in wheat (Börner et al., 1996)

Dwarfing gene	Chromosomal location	Source	Inheritance	Newly proposed nomenclature
Rht1	4BS	Norin 10	Semi dominant	Rht-B1b
Rht2	4DS	Norin 10	Semi dominant	Rht-D1a
Rht3	4BS	Tom Thumb	Semi dominant	Rht-B1c
Rht10	4DS	Ai-bian 1	Semi dominant	Rht-D1c
Rht1S	4BS	Saitamara	Semi dominant	Rht-B1d
Rht <i>Krasnodari</i> 1	4BS	Kransnodari 1	Semi dominant	Rht-B1e
Rht <i>Aibian</i> 1a	4DS	Ai-bian 1a	Semi dominant	Rht-D1d
Rht <i>T.aeth.</i>	4BS	W6824D W6807C <i>T. aethiopicum</i>	Semi dominant	Rht-B1f

The alleles can be ranked in terms of their potency for reducing height as follows (Börner et al., 1996): Chromosome 4B: rht < Rht1S < Rht1 < RhtKransnodari 1 < Rht3
Chromosome 4D: rht < Rht2 < RhtAi-bian 1a < Rht10

GA insensitive dwarfing genes are more difficult to detect and to study than GA sensitive genes (Table 2.2) (Börner et al., 1996). There are two genes known to be located on homoeologous group 2 chromosomes. These are *Rht7* on chromosome 2A and *Rht8* on chromosome 2D (Börner et al., 1996). Possibly both genes are members of a homoeologous series on the group 2 chromosomes of wheat (Börner et al., 1996). *Rht9*, a third gene was localised on the short arm of chromosome 7B. Finally, a dominant dwarfing gene *Rht12* was located on chromosome 5A (Börner et al., 1996).

Table 2.2 GA sensitive dwarfing genes in wheat (Börner et al., 1996)

Dwarfing gene	Chromosomal localisation	Inheritance
Rht4	?	Recessive
Rht5	?	Semi dominant
Rht6	?	Recessive
Rht7	2A	Recessive
Rht8	2DS	Semi dominant
Rht9	7BS	Semi dominant
Rht11	?	Recessive
Rht12	5A	Dominant
Rht13	?	Part. Dominant
Rht14	?	Semi dominant
Rht15	?	Part. Dominant
Rht16	?	Semi dominant
Rht17	?	Recessive
Rht18	?	Semi dominant
Rht19	?	Semi dominant
Rht20	?	Part. Dominant

In all the dwarfing genes that have been recognised in commercial varieties, all GA insensitive genes show varying degrees of yield instability associated with climatic stress. GA sensitive genes, under particular environmental conditions, can be associated with increases in yield (Worland et al., 1994). The *Rht12* gene has been described as having a few negative effects on yield and its components, while the gene is known to display dominance in reducing height by around 46%. There are some results obtained for plants grown under non-competitive spaced plant conditions, which suggest that *Rht12* should only be used with caution for in some varietal backgrounds yield was reduced by up to 67% (Worland et al., 1994). When the potential of *Rht12* is to be exploited in breeding programmes it will need to be combined with minor height promoting genes to maintain a plant height of no less than 60 cm. It must also be in a background where interactive effects do not reduce yield potential by reducing spikelet numbers. In most environments, adjustments

would have to be made to compensate for the delays in ear emergence time, associated with the gene, as these could interact with environmental conditions to produce noticeable drops in yield (Worland et al., 1994).

Rht12 has been located on the same locus as the awn inhibitor B1 or has been very tightly linked to this gene. Its position on the chromosome does not suggest any homoeologous relationship to the GA insensitive dwarfing genes *Rht1* and *Rht2* (Worland et al., 1994). Studies done by Sutka & Kovacs (1987) indicate that the near complete dominant dwarfing gene *Rht12* is located on the chromosome 5A. The tall genotypes are sensitive to exogenous GA and react with elongation of stem and leaf, while *Rht1*, *Rht2* and *Rht3* display a reduced response to GA (Hoogendoorn et al., 1990). It has been shown that GA affects growth by enhancing both cell division and cell elongation. It has been found that in both peduncles and in first leaves the *Rht1* and *Rht2* dwarfing genes significantly reduced cell length. It has become evident that these genes have different effects on vegetative and ear tissues. Indications from growth analyses have shown that the genes affect extension growth only in the stems and leaves. The growth of the ear is only indirectly affected by the genes, the reduced competition from the stem allowing the ear to attain greater mass at anthesis. These effects result in higher grain yield if overall plant biomass is maintained. *Rht3*, which has an even greater harvest index usually produces lower grain yield due to a reduced biomass associated with the extreme reduction in height. This corresponds with the effects of these genes on cell growth as described above, where a reduction in size is likely to have less effect on cell mass than a reduction in number of cells. It has been found that *Rht3* reduces biomass by an average of 20%, which are still much less than the 45% reduction of mature plant height. The commercial success of particularly the GA insensitive dwarfing genes, may be due to the unique effects of *Rht1* and *Rht2* on the reduction of cell length and plant height, but not, or only to a limited extent on the number of cells. Thus they have relatively small effects on plant biomass (Hoogendoorn et al., 1990).

Several studies have been conducted to determine the effects of the *Rht1*, *Rht2* and *Rht3* genes on agronomic, phenological, morphological and physiological characteristics (Ehdaie & Waines, 1994). These studies demonstrated that a major component of the genetic control of height also influences yield. This relationship is

possibly pleiotropic and therefore positive. This indicates that the mechanisms underlying this correlation are basic to the growth pattern and physiology of cereal plants. Tall plants would tend to have a greater biomass than shorter plants. The amount of biomass might be expected to be correlated with productive potential and final yield (Law et al., 1978).

Other genetic causes of increased yield are exploited in the production of high yielding varieties, but the variation in yield attributable to variation in height is likely to have a major influence on any breeding programme. Wheat has been selected for increased yield combined with shorter straw length. These selection aims counterbalance the observed positive genetic relationship between height and yield. Increased yield selections have a positive correlated effect on height. Selection for reduced height would tend to depress yield. In such selection pressure and genetic organisation, the highest yielding and acceptable varieties will be of intermediate height. To exploit fully the increased yields that certain genes can produce, lodging resistance might be achieved in other ways than through genes for reduced height (Law et al., 1978). Genes for short straw which have minimal or desirable effects on yield might be found without influencing the expression of the yield height genes. The dwarfing genes, *Rht1* and *Rht2*, may fall into this latter category. Some of their success results from their ability to remove the limitations to the exploitation of these correlated effects. It is important to introduce the dwarfing genes early in a breeding programme, while maintaining genetic variation within the populations and doing strict selection. Selecting for even shorter wheat would result in lower yields and what is perhaps more disastrous is the loss of allelic variation among the genes for increasing yield and height from the breeding population. This method of breeding for tall dwarfs should not be based upon selection for height alone, but must be carried out in conjunction with positive selection for yield and yield components. Easier measurement for height with its relative insensitivity to environmental variation is the major advantage of the selection (Law et al., 1978).

It has been found that the desirable features of the semi-dwarfs are increased tillering capacity and higher grain numbers. Studies of these classified derivatives have shown that the *Rht* genes do positively influence some of the yield components, and grain number per ear, while the relationship between height and yield within the

populations of *Rht* and *rht* homozygote is still positive (Law et al., 1978). A decrease in grain size has also been found, but the negative effect on grain size is less than the positive effect on the fertility of spikelets which results in an overall positive effect on grain yield (Hoogendoorn et al., 1988). It was found that the lines carrying the GA insensitive *Rht* genes yielded 10 to 25% more than the tall lines. This shows that in spring wheat germplasm adapted to low latitude climates, dwarfing genes do contribute to grain yield improvement due to reduced lodging. In their studies they found that the line with two dwarfing genes, *Rht1* and *Rht2*, yielded more than the tall lines and produced as high or higher yielding than the lines with a single dwarfing gene (Hoogendoorn et al., 1988). But these findings differ from those of Allen (1984) who found that the double gene genotypes had no advantage over the single dwarf lines but were equal in yield to the tall lines. In the case of the *Rht3* gene it did not confirm any clear yield advantage over comparable tall lines. However under the most favourable growing conditions the *Rht3* line out-yielded tall lines and was equal to the *Rht2* semi-dwarf. Furthermore it was found that the grain filling of the *Rht1*, *Rht2* and *Rht3* genotypes is likely to be more sensitive to heat stress. This confirms that very short varieties may be at a disadvantage when stress during grain filling is a common occurrence (Hoogendoorn et al., 1988). If the dwarf wheat yielded less than tall wheat under poor agricultural conditions, it might indicate a re-evaluation of breeding strategies, whereby selection for yield would be carried out only at high yielding sites (Hoogendoorn et al., 1988). It was reported that tall wheat was superior in yield to semi-dwarf wheat in dry areas. This may explain why semi-dwarf wheat is less common in areas with lower yield potentials (Miralles & Slafer, 1995). Semi-dwarf lines are well adapted to near optimal growing conditions though not so well adapted to environments where water or temperature stress are common features (Miralles & Slafer, 1995). The percentage yield reduction in response to water deficit was lowest in tall wheat, intermediate in semi-dwarf wheat and highest in dwarf wheat (Ehdaie & Waines, 1994). This could mean that this yield penalty might arise from a smaller biomass and water-use efficiency, where water is limited or, from poor establishment due to shorter coleoptiles and reduced early vigorous growth (Rebetzke & Richards, 2000). High soil temperatures also reduce coleoptile length to decrease seedling emergence. Wheat stands can also be reduced where stubble and / or hard seed bed restricts the growth of the coleoptiles through the soil surface, while slower rates of

emergence associated with *Rht1* and *Rht2* increase the likelihood for soil crusting prior to emergence (Rebetzke & Richards, 2000).

Ehdaie & Waines (1994) reported that tall wheat had greater total dry matter and transpiration efficiency than semi-dwarf and dwarf wheat. They also found that the dwarfing genes *Rht1*, *Rht2* and *Rht3* use water efficiently for dry matter (the ratio of aboveground dry matter to evaporation) and transpiration efficiency declined with plant height (Ehdaie & Waines, 1994). Richards (1992) concluded that tall and semi-dwarf lines had a similar ability for water extraction. Higher dry matter production and yield of tall wheat observed in dry field environments are mainly due to faster plant emergence, initial plant growth and higher water use efficiency associated with tall plants. The indication is that lower transpiration efficiency is associated with short lines. This is mainly due to consistently lower shoot dry matter produced by these lines (Richards, 1992). The relationship between plant heights or the natural logarithm of plant height with total dry matter and grain yield in certain experiments indicated that total dry matter and grain yield do not depend so much on the presence of the major dwarfing genes *Rht1*, *Rht2* and *Rht3* but rather on an optimum height (Richards, 1992). A negative relationship was found between plant height and harvest index under both wet and dry pot experiments. This indicated that harvest index might decrease at the optimum height determined for total dry matter and grain yield (Ehdaie & Waines, 1994). They found that the dwarfing genes *Rht1*, *Rht2* and *Rht3* had, in general, depressing effects on transpiration efficiency, water use efficiency, biomass and grain yield, especially in drought environments (Ehdaie & Waines, 1994). The beneficial effects of *Rht2* over *rht* genotypes were correlated with days to flowering. This might indicate that in order to realise the full potential of yield advantage of the semi-dwarfs, conditions conducive of high biomass production are required. Any advantage may be reduced if grain filling is restricted by drought or heat (Hoogendoorn et al., 1988).

In certain poor yielding environments where there is often a delay of sowing because of unfavourable soil and/or climatic conditions, it has been shown that the semi-dwarf cultivars out-yielded standard height cultivars after early, not late, sowing dates (Miralles & Slafer, 1995). In studies done by Fischer & Quail (1990) it was shown that the *Rht1* and *Rht2* dwarf genotypes gave the highest yields, while the *Rht3* group

yielded on average 3% lower, *Rht2* 9% lower, *Rht1* 11% lower and the tall group yielded 24% lower. These yield differences can positively be associated with harvest index, kernels per square meter and kernels per spike, but negatively with mature plant height. Even within major dwarfing gene classes, grain yield was significantly and negatively associated with height (Fischer & Quail, 1990).

Wheat breeders have successfully increased grain yield potential in a close positive association with the number of grains per square meter, but there have been only small changes in individual grain weight (Miralles & Slafer, 1996). Some modern cultivars could possess a high individual grain weight increase in the number of grain per square meter, often associated with small decreases in average grain weight, the net effect being an increased grain yield potential of wheat in most breeding situations. Several researchers have concluded that these genes affect the two major yield components, namely grain number per square meter and individual grain weight. It is reported that when semi-dwarf genes are introduced into a genotype, an increased grain number is negatively associated with, but not entirely compensated by a decreased grain size. The accepted explanation involves the competition for assimilates among growing grains, suggesting that the greater the number of grains per square meter produced by the line, the lower the availability of photo assimilates per grain, leading to decreases in individual grain weight. It suggests that due to the action of *Rht* genes, grain numbers increased independently of the number of spikelets. An increased proportion of grains are located in positions of low grain weight potential – in distal positions within the spikelets – reducing the average grain weight, irrespective of the level of availability of assimilates per grain. The higher number of grains per square meter of the *Rht* lines has been brought about by an increased grain set in distal florets, in apical spikelet positions. This occurred without any effect on the number of spikelets per spike, which is in agreement with previous studies showing no interference of these genes with plant development events (Miralles & Slafer, 1996). Especially younger leaves of the semi-dwarfs, may be reduced in size, but compensate with increased photosynthetic rates, so that overall biomass is similar to tall lines (Flintham et al., 1997b). Individual grain weights were strongly affected by the grain position within the spike where the basal grains were the heaviest and the fourth grains the lightest, and where the weight of the basal grains was not changed. The greater proportion of apical grains contributing to the total

number of grains per square meter reduced average grain weight (Miralles & Slafer, 1996). Particularly in the upper half of the spike – spikelets 11 to 19 – the contribution of basal grains accounted for 90% of the total number of grains in the standard height line, but for less than 70% in the dwarf line. This can explain most of the negative trend between the number of grains and their average weight. Basal grains of the standard height line tended to be heavier than those of the semi-dwarf and the dwarf lines although this difference was not consistent over all spikelets (Miralles & Slafer, 1996).

The fact that lines with *Rht* alleles had distal light grains with a much higher frequency of appearance than the standard height line could be the main reason for their lower average grain weight. The negative correlation between these grain yield components might not be reflecting a greater degree of competition for assimilates among grains in *Rht* lines than in the standard height line (Miralles & Slafer, 1996). Yield advantages of *Rht* semi-dwarf lines apparently derive from increased partitioning of assimilates to the developing ear as a consequence of reduced demand for stem elongation. This reduces pre-anthesis abortion of distal florets in each spikelet and increases the total number of florets viable at anthesis (Flintham et al., 1997b). Further reductions in assimilate demand for stem growth by increasingly potent combinations of *Rht* alleles, might thus be expected to increase spikelet fertility further (Flintham et al., 1997b).

It is shown that N deficiencies reduce both root and shoot growth, but root dry matter accumulation is less affected because more carbohydrates are translocated to the root, which is a highly active sink. Certain effects of N on root growth depend on the N concentration at the root surface. If the concentration is optimal the root growth is stimulated. If the N concentration is above optimal, root growth is reduced (Arora & Mohan, 2001). Root growth responds to N supply, depending on the genotype and stage of development while water stress reduces both root and shoots growth. However, during early plant growth, root growth is less sensitive to water deficit than shoot growth. In their study they found that tall types produced higher root biomass and maintained higher leaf N content than dwarf types under different N and water supply levels. The enlargement of the root system might not be under the control of the dwarfing genes, which could lead to the development of semi-dwarf cultivars that

are more resistant to moisture stress as a consequence of a greater expansion of the root system into the soil (Arora & Mohan, 2001). It could be rewarding to search for genetic backgrounds in which the surplus of assimilates produced by *Rht* alleles, were actually invested in new roots, thereby enlarging the root system (Miralles et al., 1997).

Certain diseases, like *Fusarium* ear blight (FEB), are caused by a range of pathogens. FEB is an important disease of wheat, causing yield losses up to 39% under conditions of high humidity, with a reduction in grain quality (Hilton et al., 1999). In a naturally infected field, short cultivars tended to have more symptoms of FEB than taller cultivars. However, when ears of the same cultivars were artificially inoculated, no significant difference in disease severity was observed. The differences in disease resistance between cultivars can be related to disease escape where taller cultivars, have ears held at greater distance from the primary source of inoculums. The severity of FEB is a quantitative character controlled by numerous genes. The suggestion is that disease severity in individual genotypes is not only affected by straw height, but also by other genes independent of height. Tall straw and resistance to FEB seems to co-segregate, suggesting that this relationship has a genetic basis that could be explained either by linkage between one or more genes, controlling resistance, and genes controlling straw height or by pleiotropy i.e. genes that promote shorter straw also promote susceptibility. The dwarfing genes, *Rht1* and *Rht2*, significantly increased severity of FEB in near isogenic lines (Hilton et al., 1999).

Linkage was found between the *Rht2* dwarfing gene and resistance to *Septoria*. Isogenic lines containing the *Rht1* gene were more susceptible than those with the *Rht2* gene (Hilton et al., 1999). They found that there was no indication that isogenic lines containing *Rht1* had more severe symptoms of FEB than those containing *Rht2*. As both straw height and severity of FEB are controlled by a number of genes, it seems difficult to postulate numerous linkages between height and resistance, to explain the observed link. One hypothesis for this pleiotropic association was that shorter cultivars have denser leaf canopies and produce a more favourable microclimate for the development of diseases. It was shown that leaf wetness lasted for a longer time on short cultivars than tall ones. The conclusion is that there are genes controlling resistance to *Septoria nodorum* that are independent of straw height.

Thus it would be possible to breed resistant cultivars of any height, but with increasing difficulty, as straw height is reduced (Hilton et al., 1999).

2.9 Germplasm for short, strong straw

Solid stem wheat is wheat in which most of the culms are filled with pith (Larson & MacDonald, 1959a). Combining solid stem with semi-dwarfness and higher grain yield in wheat is a plant breeding objective. There is a negative relationship between plant height and stem solidness and this indicates that selection of solid stemmed, semi-dwarf types should be possible (McNeal et al., 1974). Genes affecting solid stem are on several loci (Larson, 1959). The varieties of common wheat which are solid stemmed derive their solidness from the variety S-615, the genetics of solid stem in S-615 being of special interest (Larson & MacDonald, 1959a). In crosses of solid stemmed common wheat, with hollow stemmed wheat, the F₂ segregated in the ratio of one solid to 63 hollow or intermediate, indicating that solid stem is determined by three recessive genes (Larson, 1959). The F₃ verified these results. Further studies on inheritance of solid stem in tetraploid wheat showed solid stem to be due to a single dominant, and a single recessive gene, showing transgressive segregation, and of complementary recessive genes (Larson, 1959). Clark et al. (2002) reported that the expression of stem solidness fit the expected segregation ratios for a single dominant gene model in most of the crosses they did in their study, which suggests that stem solidness in the four durum wheat's they evaluated was controlled by a single dominant gene. Studies that were done on the genetics of solid stem in hybrids of tetraploid with hexaploids showed that solid stem varied from recessive through intermediate to dominant and F₂ segregations were interpreted as monohybrid or multifactor (Larson, 1959). Studies of the cytogenetics of solid stem in hybrids of tetraploids with hexaploids showed that in solid stemmed tetraploids the D genome tends to produce hollow culms, but that differences in solid stem between the two series are partly determined by genes in the A and B genomes (Larson, 1959). After extensive studies of interspecific hybrids between hollow and solid stemmed wheat, the following explanation of solid stem inheritance was postulated: The A genome has a gene for hollow stem – *ma*, that accounts for the hollowness of diploid wheat. There is no allele for this gene but it is hypostatic to all other genes for solid or hollow stem. On the B genome there is a gene, *Mb*, that affects the pith content of the stem and it

exists as an allelic series. Solid stem genes at the *Mb* locus are dominant to their alleles for less solid stem. *Od*, a gene for hollow stem, found on the D genome, is epistatic to genes for solid stem at other loci. In addition the A genome has a complementary gene, *C*, for pith in the lower internodes. It may be present in hollow stemmed varieties and species, its effect not shown in the absence of genes for pith in the B genome (Larson, 1959). Aneuploid analysis in common wheat, as developed and used by Sears, indicated that monosomics and nullisomics can be used to locate genes for a given characteristic and to study their actions and interactions (Larson, 1959). They have been used to determine the effects of each chromosome in common wheat on solid stem, and to resolve the interaction of chromosomes from solid and hollow stemmed varieties (Larson & MacDonald, 1966). Tests of solid stem in F₂ hybrids of all 21 monosomics of Chinese Spring by S-615 showed that these two varieties differ by at least four genes, affecting pith content of the culms (Larson & MacDonald, 1959a). The wheat variety S-615 culm phenotype in a given environment is apparently the result of interaction of genes that promote pith development and genes that suppress it (Larson & MacDonald, 1959a).

In a given environment, the amount and distribution of pith in the stem is determined by the balance of genes tending to make the stem solid, and those tending to make it hollow. The loss of either one of them tends to produce the opposite phenotype (Larson & MacDonald, 1959a). It is also seen that the loss of chromosomes in the variety Chinese Spring affects culm dimensions, most monosomics and nullisomics being shorter and thinner than normal, but at least one being taller and two coarser (Larson & MacDonald, 1959b). Some conflicting opinions on the relation of solid stem to culm dimensions have been expressed (Larson & MacDonald, 1959b).

The wheat culm growth develops by elongation from an intercalary meristem at the base of each internode (Larson & MacDonald, 1959b). In the order and degree of elongation and maturation of each internode, it is related to its rank in relation to the inflorescence, with no two internodes being alike in this respect. In their study they found that the influence of critical chromosomes on solid stem is specific, not a secondary result of gene action, that primarily governs culm growth (Larson & MacDonald, 1959b).

There was no consistent association of diameter and solid stem index in comparisons between monosomic lines critical for solid stem (Larson & MacDonald, 1959b). Within lines of genetically similar plants, there were correlations between culm dimensions and solid stem (Larson & MacDonald, 1959b), meaning that short culms tended to be more solid than long ones. It is shown that the top of internode I, and the region just below the top node of each of internodes three and four, tended to be most solid when they were thickest, while the centre and lower parts of internode one, were hollow when they were thickest (Larson & MacDonald, 1959b). The observations showed that short monosomic populations that are significantly more solid than normal, may be merely reflecting the results of decreased elongation, but short monosomics that are just hollow at the point of significance, have gone counter to the prevailing influence of elongation and must be considered seriously. Their studies also showed that lines with thin culms may be expected to be less solid in the tops of internodes one, three and four, and more solid in the lower parts of internode one. If they follow this trend to some degree, it may mean little, but if they reverse the trend to the same degree, the chromosome concerned must have a direct effect on pith production. Thick culms would show opposite trends (Larson & MacDonald, 1959b).

Internodes become progressively shorter toward the root and therefore probably have received smaller quantities of auxin. In a population of genetically similar plants, it was found that those that elongate the most, presumably under the influence of auxin, are least solid, probably because there are too few pith cells to fill the lengthened lumen (Larson & MacDonald, 1959b). The upper parts of internodes one, three and four were most solid in culms of the greatest diameter, because those of the internodes were laid down first by the intercalary meristem when the inflorescence was small, and before the culm had begun to elongate greatly. This is probably favoured in this period of cell division, with the low concentration of auxin from the immature inflorescence, though rapid cell division would result in a thicker culm and an increased number of pith cells (Larson & McDonald, 1959b).

The results of the study by McKenzie (1965) support the hypothesis that hollow (Red Bobs) and solid (C.T.715) differ by four genes for stem solidness. One allelic pair, *Ll*, has a major influence on solidness (McKenzie, 1965): the allele *L* for hollowness is partially epistatic when homozygous, and the allele *l* is twice as effective as any one

of the other three genes in promoting solidness. The other three allelic pairs *Mm*, *Nn* and *Oo* lack dominance and are equal in their influence on solidness (McKenzie, 1965). Cook et al. (2004) reported that four microsatellite markers were found linked to a single solid stem QTL (*Q_{ss.msub-3BL}*) on chromosome 3BL. Inheritance studies have shown that three or four genes cause stems to be solid, but one gene in particular appears to account for more than twice the genetic variation compared to the other two or three genes. The expression of stem solidness in durum has been described as being controlled by a single dominant gene, and studies using monosomic lines of S-615, a solid stem wheat, identified potential genes for stem solidness on chromosomes 3B, 3D, 5A, 5B and 5D (Cook et al., 2004).

McNeal (1956) found that the solid stem trait was controlled by one major gene, with several minor modifying genes. In the study of Larson & MacDonald (1959a) they found that at least five chromosomes carried genes promoting pith production, while at least three chromosomes carried genes inhibiting pith production. Environmental factors like cool temperatures, adequate moisture and low light intensity also affect and tend to reduce the degree of stem solidness (Hayat et al., 1995). Morrill et al. (1994) reported that stem solidness is affected by cloudy weather that encourages rapid stem growth causing stems not to fill with pith. Holmes (1984) also reported stem solidness to be negatively correlated with increased amounts of rainfall and decreased periods of sunshine, while shading the plants reduced stem solidness. Miller et al. (1993) found that plants sown at low densities had higher stem solidity than those sown at high densities. Competition between closely spaced plants for soil water, nutrients and light, possibly contributed to their more rapid maturation and lower stem solidness. Coupling the genetic control with varying environmental conditions, plant breeders have generally treated stem solidness as a quantitative trait (Hayat et al., 1995).

McNeal et al. (1965) found a highly significant negative relationship between grain yield and stem solidness in backcross derived lines from a solid stemmed x hollow stemmed wheat cross. Their explanation for the relationship between yield and stem solidness is that development of a solid pith must require food reserves that would otherwise be available to promote grain development. In the study of McNeal & Berg (1979) they found that the grain yield of the solid stem populations was significantly

lower than that of the hollow stemmed population. In contrast, Lebsock & Koch (1968) found no association between stem solidness and grain yield in two solid stemmed x hollow stemmed spring wheat crosses. They also showed that stem solidness tends to be negatively correlated with plant height. A relationship between grain protein concentrations and stem solidness was however not reported (Hayat et al., 1995). Previous studies investigating the relationship of stem solidness with grain yield have been contradictory. In their study they used random lines from six solid stemmed x hollow stemmed crosses, evaluated in three environments. No relationship was found between stem solidness and grain yield (Hayat et al., 1995). They anticipated that trait associations with stem solidness might change from inter-crossing during development of successive solid stemmed cultivars. Correlations of the evaluation of stem solidness with plant height and grain protein concentration, declined from early to recent solid stemmed parents in certain crosses. These changes in trait associations might have resulted from break-up of linkages and/or loss of genes for the solid stemmed trait in the sequential development of the solid stemmed cultivars. Their results show that the development of high yielding solid stemmed cultivars is not limited by undesirable associations between degree of stem solidness and other agronomic traits. The poor yield of solid stemmed cultivars compared with hollow stemmed cultivars of similar studies, cited by other authors, is more likely attributable to undesirable genes remaining from the original solid stemmed source S-615 (Hayat et al., 1995). High levels of solidness may be related to low yields in some genetic backgrounds. However it appears that if parents are chosen wisely and if sufficiently large populations are grown, high yielding solid stemmed lines should occur (Lebsock & Koch, 1968). Hayat et al. (1995) showed that solid stem is highly heritable and selection has been practised against the S-615 parent for traits other than stem solidness. It is not surprising that the solid stemmed cultivars may be poorer agronomically than comparable hollow stemmed cultivars. Heritability values for stem solidness ranged from 60% to 95% (Lebsock & Koch, 1968).

In the study of Cook et al. (2004) they found that a single chromosome region on chromosome 3BL, *Qss.msub-3BL*, controls most of the variation for stem solidness in wheat. This region is not associated with decreased yield potential, suggesting that high yielding solid stem cultivars can be developed. The tight linkage shown between microsatellite markers and *Qss.msub-3BL* in their population and in all solid stemmed

cultivars tested containing the same marker allele, suggests that the markers may be useful in a backcrossing program to help develop new solid stemmed wheat cultivars.

2.10 Diallel analysis

The diallel analysis has been the subject of more theoretical and practical application than any other mating design (Wright, 1985). The concept of the diallel can be defined as making all possible crosses among a group of genotypes (Saghroue & Hallauer, 1997). The diallel crossing concept was introduced by Sprague & Tatum (1942) to the field of plant breeding, by making mating possible among a set of maize inbred lines. Breeders have been using the analysis to obtain information on the value of varieties as parents, to assess the gene action involved in various characteristics, in order to develop appropriate selection procedures and understand heterotic patterns of the progenies at an early stage of the hybridisation program (Virmani & Edwards, 1983; Saghroue & Hallauer, 1997; Le Gouis et al., 2002; Egesel et al., 2003).

2.11 Combining ability

Combining ability is defined as the performance of a line in hybrid combinations. Assessments of the combining ability could be useful to define the contribution of a variety to the performance of its progeny and the mode of inheritance of a particular trait (Kambal & Webster, 1965). Sprague & Tatum (1942) developed the original theory of combining ability. Four methods to analyse combining ability were proposed by Griffing (1956) by using the genetic estimates of the parent and hybrid components of a diallel analysis, represented by general combining ability (GCA) and specific combining ability (SCA). GCA is expressed as the average performance of a line in hybrid combinations, where SCA is defined as a case in which certain combinations are relatively better or worse than would be expected, on the basis of average performance of the line involved (Sprague & Tatum, 1942). When considering the GCA and SCA effects, inferences can be made about additive and non-additive gene effects. It is shown that the GCA of each parent (g_i) is important to develop superior genotypes, while the SCA effect (s_{ij}) is important to provide information about hybrid performance (Cruz & Regassi, 1994). In studies done on the GCA:SCA ratio it was found that the GCA:SCA mean square ratio was an indicator

of the nature of genetic variability in a diallel analysis (Sayed, 1978; Quick, 1978). A high value of the ratio indicates the prevalence of additive genes, while a low value of the ratio indicates the prevalence of non-additive gene effects in determining a particular character. The relative importance of GCA and SCA could also be assessed from the components of variance, by expressing them as the $2\sigma^2_{GCA} / (2\sigma^2_{GCA} + \sigma^2_{SCA})$ ratio. The closer this ratio is to unity, the greater the magnitude of additive effects (Baker, 1978).

2.12 Variance components

Quantitative genetics is concerned with the inheritance of traits that show continuous variation or quantitative traits (Wricke & Weber, 1986). The amount of variation is measured in terms of variance according to Falconer & Mackey (1996). The total variance of a given character is its phenotypic variance (V_P) or the variance of phenotypic values. The partitioning of the variance into its components, allows the breeders to estimate the relative importance of the various determinants of the phenotype, in particular the role of heredity versus environment. Environmental variance (V_E) is that part of the phenotypic variance attributed to environmental conditions. The total variance of a given character is its phenotypic and environmental variance (Falconer & Mackey, 1996). The total genetic variance (V_G), also known as variance of genotypic value, is the part of phenotypic value which can be attributed to genotypic differences among the phenotypes (Dudley & Moll, 1969). It is also shown that the total genetic variance is further portioned into additive genetic variance (V_A), dominance genetic variance (V_D) and epistatic variance (V_I). The additive genetic variance, which is the variance of breeding values, is the important component. It determines the observable genetic properties of the population as well as the response of the population to selection. The plant breeders' goal in a breeding programme is to develop and identify high yielding transgressive segregants (Dudley & Moll, 1969).

2.13 Heritability

Allard (1960) used the term heritability to specify the genetic portion of the total variability, due to genetic causes. The relative importance of heredity in determining

phenotypic values is called the heritability of the character (Falconer & Mackey, 1996). The two types of heritability are the broad and the narrow sense heritability. The broad sense heritability can be defined as a consideration of total genetic variability in relation to genotypic variability. Narrow sense heritability can be defined as a consideration of only the additive portion of the genetic variability, in relation to phenotypic variability (Hanson, 1963). Wricke & Weber (1986) and Falconer & Mackey (1996) defined broad sense heritability as the ratio of genotypic to phenotypic variance, V_G/V_P . The ratio of V_A/V_P , narrow sense heritability, expresses the extent to which phenotypes are determined by the genes transmitted from parents (Falconer & Mackey, 1996). Heritability is not the measure of desirability. It determines the degree of resemblance between relatives and is therefore of the greatest importance in breeding programmes. The knowledge of the relative heritability of the various traits and their genotypic and phenotypic correlation, can aid in the design of efficient breeding systems, where many traits need to be improved simultaneously (Jones, 1986). The indication of the expected response to selection in a segregating population, is provided by heritability estimates, and is a useful tool in designing an effective breeding program (Burton & De Vane, 1953). When genetic variation in relation to environmental variation, is high, selection is more effective than when it is low. The net gain from selection depends upon the combined effects of the heritability, the amount of genetic variation present, and the selection intensity (Poehlman, 1987). Narrow sense heritability can be useful in making selection progress estimates. Characteristics with high narrow sense heritability values can be improved more rapidly with less intense evaluation, than those with low values. Hence they are useful in making selection progress estimates. While broad sense heritability includes non-additive effects, it overestimates the response to selection (Dudley & Moll, 1969). The estimates of heritability depend on the method used to estimate them, the population from which the estimates are derived and environmental conditions encountered during the test (Sidwell et al., 1976).

2.14 Heterosis

Heterosis or hybrid vigour was first introduced by Shull (1914) to denote the stimulation in size and vigour in a hybrid. Heterosis was defined by Rieger et al.

(1976) as “the superiority of heterozygous genotypes with one or more characteristics in comparison with the corresponding homozygotes”. Heterosis implies that there is dispersion for dominant alleles between parents, which may increase or decrease the character. The two theories of heterosis are the dominant and over dominance hypothesis. Under the dominant hypothesis, heterosis is produced by the masking of deleterious recessive in one strain, by dominant or partially dominant alleles in the second strain (Crow, 1952). There are several hypotheses to genetically explain the phenomenon of heterosis that is partial dominance of a large number of loci, over dominance of several loci, and several types of epistasis. It is indicated that for hybrid breeding, a substantial number of loci should show over dominance (Wricke & Weber, 1986). Furthermore it is shown that no heterosis can be detected, if genes controlling the trait, act in a strictly additive way.

Heterosis under the over dominance hypotheses, is due to heterozygote superiority and therefore, increased vigour is proportional to the amount of heterosis (Miranda Filho, 1999). It is stated by Burton (1968) that heterosis results from combined action and interaction of allelic and non-allelic factors. It is usually closely and positively correlated with heterozygosity. Heterosis is brought about by bringing together in the, F_1 the dispersed genes of dominant alleles showing directional dominance and non-allelic interactions, while it is not brought about by heterozygote superiority or complementary epistasis (Morgan, 1998). However according to Coors et al. (1999) dominance and epistasis are the principal genetic factors in the exploitation of heterosis. Heterosis can also be expressed as mid-parent, better-parent and standard heterosis. Mid-parent heterosis or hybrid vigour is defined as the difference between the hybrid and the mean of the two parents (Falconer & Mackey, 1996). Lamkey & Edward (1999) reported that mid-parent heterosis or a percentage of mid-parents are difficult to interpret from a quantitative genetics point of view. Their studies also indicated that high-parent heterosis, or the performance of F_1 hybrid over the better parent is preferred in some circumstances, particularly in self pollinated crops, for which the goal is to find a better hybrid than either of the parents.

CHAPTER 3

Combining ability and heritability of characteristics that influence stem strength in wheat

3.1 INTRODUCTION

Wheat, grown under dryland conditions with marginal rainfall and suboptimum fertilisation, does not lodge. The strength of the stem is not of major concern. Wheat production in South Africa was historically done under such conditions, using varieties with a long weak straw. Since the start of production of wheat under irrigation, this scenario has changed. At first wheat was flooded, but improvements in irrigation technologies lead to overhead precipitation. It was first done by means of changeable lines, and then by the use of pivots. This has changed the environment considerably, putting more pressure on the standing ability of the varieties. The focus in production research was the optimisation of the fertilisation requirements of wheat being grown under irrigation. Varieties were bred which responded to this environment, but soon yield became a limiting factor, mainly because of the damage caused by lodging. In South Africa, wheat under irrigation is grown in winter time and harvested in late spring and midsummer. Rainfall at this time of the year is characterised by stormy winds and high precipitation. This results in severe lodging, leading to harvesting delays, and degrading, caused by sprouting and weathering of the grain. This has resulted in breeding strategies improving standing ability, rather than maximum yield potential. Breeding genotypes, insensitive to day length, but, more importantly also resistant to lodging because of shorter and stiffer straw, were in line with the achievements of the Green Revolution (Paalberg, 1970). The CIMMYT germplasm was used to introduce these genes into South African bred varieties (Pienaar, 1980). A further improvement in standing ability was the use of solid stem characteristics in the SENSAKO breeding programme (Jordaan, 2002). In order to make decisions to further improve the standing ability of local wheat, it is necessary to look at the expression of the major and minor genes, which quantitatively regulate the expression of the standing ability trait. Although much is known of the major genes (*Rht*) regulating the length of the stem, and also about the quantitative effect of

the minor genes (Worland & Snape, 2001), limited data is available on the effect of the genes expressing solid stem, as far as the use of it to improve stem strength is concerned (Hai et al., 2005).

Breeding strategies in self pollinated crops like wheat are dependent on genes with additive effects or additive variation, within germplasm pools. This is in contrast to cross-pollinated crops like maize, where the breeding strategy depends on selection for hybrid vigour. In this case, interest is mainly on using genes with a dominance expression (Falconer, 1981). Selection improvement for traits like stem strength in wheat would thus depend on the significance of the additive part of genetic variation in the breeding population from which selection is to be done (Barbosa-Neto et al., 1997). The use of a diallel set of progeny from chosen parental lines generates information about the importance of additive and dominance variation in that population (Sprague & Tatum, 1942; Griffing, 1956). The measurement of the relative importance of additive genetic variance (the heritability) supplies information on the expected genetic gain for the selection of the traits (Griffing, 1956). It will also be possible to predict which of the parents will produce progeny (GCA effects) with the highest frequency of genes that will influence the expression of the trait (Jones, 1986). The aim of this first experiment was to determine whether there are significant differences among pure lines for the components of stem strength, as well as an index based on the length of the internode, thickness of the stem wall and the weight it takes to break the stem between two nodes.

3.2 MATERIALS AND METHODS

The parental material which was used is a selection of breeding lines from the AFGRI irrigation breeding programme (Table 3.1). The lines selected are of major interest because of their differences in straw strength, straw length and the expression or absence of solid stem characteristics. The gene or genes expressing stem solidness are believed to be of major importance to stem strength in wheat. The genotypes selected, also differ in straw length, which comply with the definition of short straw semi-dwarf genotypes, adapted to production under high fertilisation and irrigation. The dwarfing genes responsible for expressing this character in every parental genotype

are not known, but being derived from a CIMMYT background they are believed to have the *Rht* genes.

Table 3.1 Description of the parental material according to stem type and plant height

	Genotype	Stem type	Plant height
1	SST 57	Solid stem	Semi-dwarf
2	SST 55	Normal stem	Tall semi-dwarf
3	SST 806	Solid stem	Semi-dwarf
4	DH 24	Solid stem	Short semi-dwarf
5	DH 29	Solid stem	Short semi-dwarf
6	3-273	Solid stem	Tall semi-dwarf
7	BX	Normal stem	Tall semi-dwarf
8	SST 876	Solid stem	Tall semi-dwarf
9	36-8	Normal stem	Semi-dwarf

SST 57, SST 806 and SST 876, are expected to have *Rht* genes and also to express the solid stem character in the first three internodes. These genes, expressing the solid stem trait, originate from the *Aegilops ventricosa* (Tausch.) background. The genotypes DH 24 and DH 29 are double haploid (DH) lines derived from the AFGRI programme. Both have very short straw and also express the solid stem character at all the internodes of the stem. The genotype 3-273 (with a synthetic hexaploid background) is a tall semi-dwarf having one internode more than the rest of the parents, and remarkable stem solidness throughout all internodes up to the ear. Genotypes were selected from a synthetic hexaploid background derived from *Aegilops squarrosa* (L.) (personal communication, Jordaan, 2008).

Experiment 1

The nine parents were evaluated in a separate trial to test the differences in stem strength. This trial was planted in a tunnel in a complete randomised block design, with five replications. A plot consisted of four pots (23cm x 30 cm) with three plants per pot. A mature dry plant was selected to be evaluated for each replication. The following measurements were taken from the main stem (the wheat stem anatomy is shown in Figure 3.1) of each of the plants sampled per plot:

- I. Plant height (mm), measured from the crown to the tip of the spike, excluding awns
- II. Number of internodes, numbered from the ground upwards
- III. Length of each internode (mm), per digital calliper of 0.01 accuracy
- IV. Internode diameter (mm)
- V. Stem wall thickness (mm)
- VI. Pith thickness (mm), calculated as the wall thickness times two, divided by internode diameter
- VII. Breaking weight (g), (the weight that it took to break the stem between two nodes)
- VIII. Stem strength, defined as a function of the pressure it takes to break the stem, breaking weight (W), pith thickness (D) of the stem wall at breaking point, and the length (L) of the internode. The proposed index is $(W \times D) / L$. This is a simplified approach to a more mathematical possibility, as described by Berry et al. (2003).

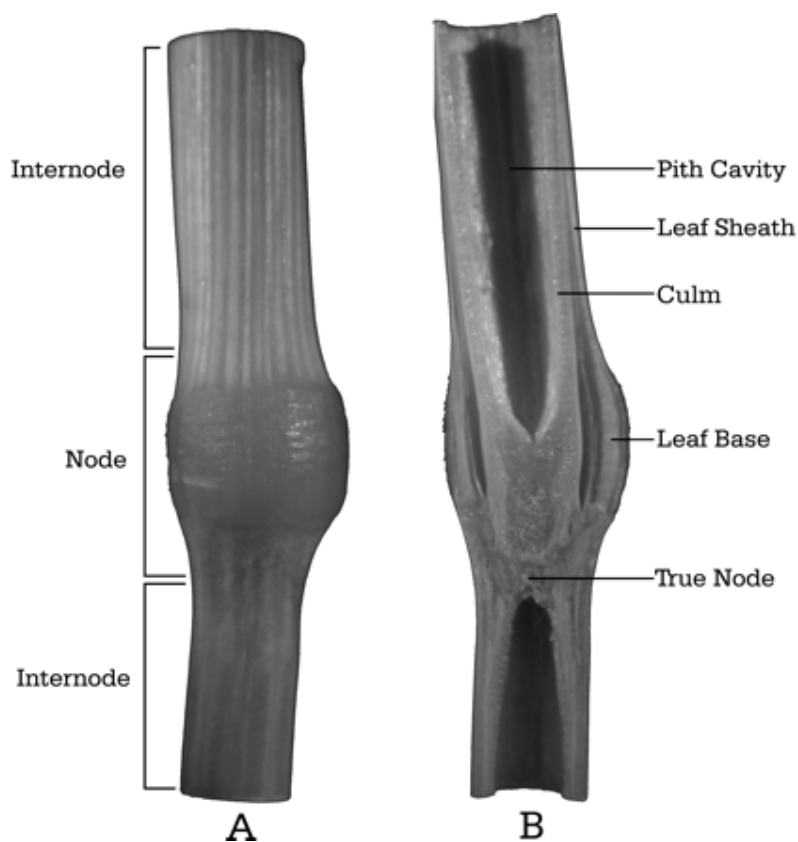


Figure 3.1. Wheat stem anatomy. A – Gross surface features. B – Longitudinal section (Guenther, 2005).

The instrument which was used is illustrated in Figure 3.2. Calculations were done for every internode separately, and then summarised. Statistical analyses were done on the average of all internodes per stem.

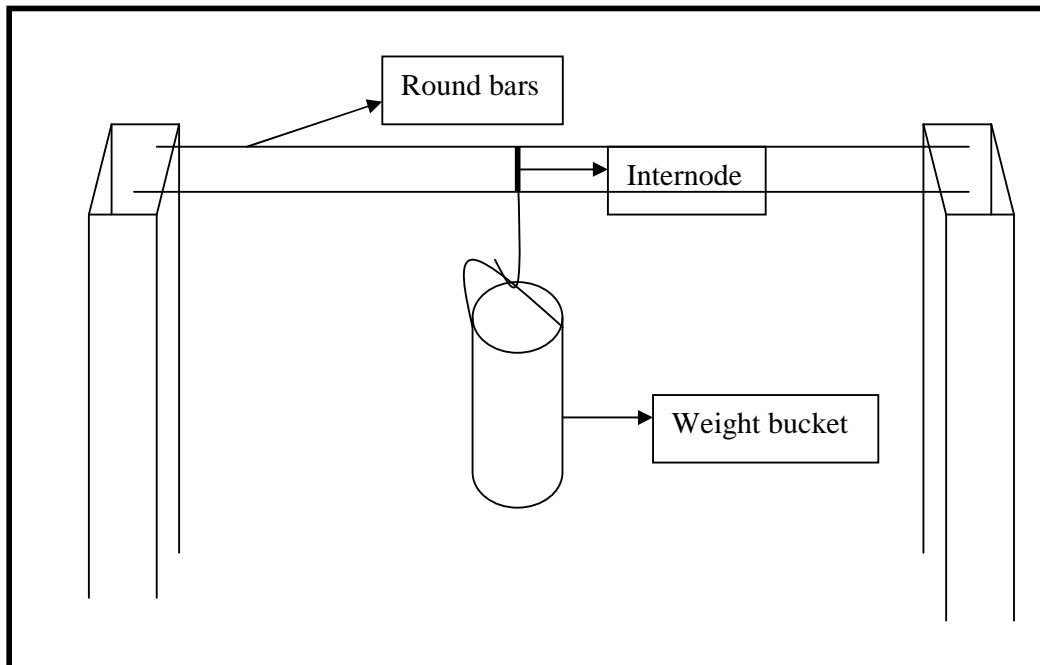


Figure 3.2 Design of an apparatus used to calculate the measurements defining stem strength.

Experiment 2

The nine parental genotypes were used to create a diallel set of progeny, where a diallel table is a square arrangement of p^2 measurements (where p refers to the parents, corresponding one on one to the crossing combinations of a diallel crossing block). The aim of this study was to use a diallel mating system to analyse the differences among progeny and relate significant differences to additive and non-additive variances. The nine parents were crossed in all combinations, ignoring reciprocal crosses, generating 36 F_1 crosses. The nine parents as well as the 36 crosses were planted in a tunnel, in a complete randomised design with five replications. Every plot consisted of four pots (23cm x 30cm) with three plants per pot. The data was taken on one plant per plot, selected from a pot with three plants. The selected plant was tagged at ear emergence of the main stem, the data being recorded at physiological maturity. Climatic conditions within the tunnel for the two experiments

were set at optimum watering, night temperature above 15°C, day temperature below 28°C, day length at 18 hours a day and fertility levels adequate for wheat plants growing in a tunnel based on soil tests (Table 3.2). At \pm 25 days after ear emergence, the tagged stem was removed and the same measurements were taken from the main stem of each of the plants sampled per plot, as described in experiment one.

Table 3.2 Soil analyses

	Content		Content
pH (KCL)	5.5	Sand %	79
S	>150	Silt %	12
P	75	Clay %	9
K	718	Zn	4.5
CA	810	Fe	135
Mg	196	Mn	10.6
Na	41	Cu	0.7
(Ca/Mg)	2.52	B	0.2

The data of experiment one, was statistically analysed according to the methods valid for a randomised block design.

Variances between entries were further divided into a variance for general combining ability (GCA), and specific combining ability (SCA) [Griffing Method 2, Model I (Fixed effect) and Model II (Random effects)]. Variances for GCA and SCA were further divided into GCA effects and SCA effects, associated with the parents and crosses respectively (Griffing, 1956). Only GCA was reported and discussed in the context of this study, as this is what is important to the breeding programme.

3.3 RESULTS

Table 3.3 Analyses of variance for stem strength (A) and plant height (B) in mature plants (Experiment 1)

Source of variance	Degrees of freedom	Sum of squares		Mean squares	
		A	B	A	B
Genotype	8	6478.06	711819.4	809.76**	88977.43**
Blocks	4	598.59	19407	149.65*	4851.73
Error	32	572.96	132574.6	17.91	4143.0

** $p \leq 0.01$, * $p \leq 0.05$

The mean squares for differences between parents were highly significant for both the stem strength characteristics and plant height. There was a significant block effect only for stem characteristics. This shows that combining the different components (internode length, pith thickness and breaking weight), describing stem strength, measures significant differences amongst the nine parents which were chosen to generate the F_1 progeny.

Table 3.4 Means of parental lines according to their stem strength and plant height

Genotypes		Stem strength (index^a)	Plant height (mm)
1	SST 57	15.46	549.61
2	SST 55	7.59	752.98
3	SST 806	4.80	650.62
4	DH 24	14.34	548.42
5	DH 29	21.47*	493.52
6	3-273	19.37	890.22
7	BX	2.90	772.17
8	SST 876	4.61	630.77
9	36-8	8.81	669.78
LSD (0.05)		5.47	83.05
CV		18.95 %	4.44 %
A (trial efficiency)		0.89	0.80

^aStem strength was defined as a function of the pressure it takes to break the stem, breaking weight (W), pith thickness (D) of the stem wall at breaking point and the length (L) of the internode. The proposed index is $(W \times D) / L$.

The parent with the strongest stem (DH 29) differed significantly from all parents except 3-273. DH 29 was also the shortest parent. This shows that shorter straw combined with solid stem throughout the whole stem, results in stem strength better than that of parents with longer straw, lacking solid stem (SST 55 and BX). The data clearly show that there are differences of stem strength amongst pure lines.

Table 3.5 Analyses of variance for components of stem strength (Experiment 2)

Internode	Variance components	Internode Length	Stem diameter	Stem wall thickness	Pith thickness	Breaking weight ¹	Stem strength ²
1	Genotypes ³	442.08 **	0.82 **	5.97 **	0.81 **	495778.28 **	1146.12 **
2		502.59 **	1.01 **	0.54 **	0.15 **	151473.86 **	82.94 **
3		1914.92 **	0.20 **	0.41 **	0.12 **	31810.61 **	5.02 **
4		6200.90 **	0.56 **	0.29 **	0.08 **	6449.91 **	0.21 **
1	Replications	104.17(-)	0.13(-)	1.59(-)	0.02(-)	445722.73 **	90.42(-)
2		141.56(-)	0.12(-)	0.03(-)	0.01(-)	32349.03(-)	1.87(-)
3		315.33(-)	0.08(-)	0.02(-)	0.01(-)	3293.39(-)	0.56(-)
4		2668.50 *	0.05(-)	0.11(-)	0.01(-)	2380.20(-)	0.07(-)
1	Error	57.47	0.09	0.05	0.02	128142.00	152.34
2		73.05	0.11	0.03	0.01	22905.55	7.09
3		238.29	0.09	0.04	0.01	5663.87	0.69
4		955.25	0.10	0.15	0.01	1817.23	0.05

* $P \leq 0.05$, ** $P \leq 0.01$, ¹ The pressure it takes to break the stem (g), ² Stem strength was defined to be a function of the pressure it takes to break the stem, breaking weight (W), pith thickness (D) of the stem wall at breaking point and the length (L) of the internode concerned. The proposed index is $(W \times D)/L$, ³ Genotypes including parents and F1 crosses

There were significant differences for internode length, stem diameter, stem wall thickness, pith thickness, breaking weight and stem strength between all the genotypes at all internodes (Table 3.5).

The data for all characteristics at every internode are summarised in Appendix 3.1a. A comparison of the means for internode length shows that there is a length increase from internode one to four of the parents as well as of the progeny. The shortest internodes for the parents were 30.52 mm (DH 29), 56.3 mm (SST 57), 107.09 mm (DH 29) and 196.8 mm (3-273) for internodes one to four respectively. For the crosses it was 19.16 mm (SST 57/SST 876), 48.35 mm (SST 57/SST 876), 97.21 mm (SST 57/SST 876) and 186 mm (DH 24/SST 876) for internodes one to four respectively. The data also shows that the mean internode length per internode of the crosses was shorter than for the parents.

In comparing the means for internode diameter (Appendix 3.1b), the thickest internode diameter for internodes one to four of the parents was respectively 4.01 mm (36-8), 4.3 mm (DH 29), 4.47 mm (36-8) and 3.54 mm (36-8). For the crosses it was 3.74 mm (3-273/BX), 4.55 mm (BX/36-8), 4.56 mm (BX/36-8) and 3.51 mm (DH 24/36-8) respectively for internodes one to four. The mean internode diameter of the parents for all four internodes was thicker than that of the crosses.

In comparing the means for stem wall thickness (Appendix 3.1c), the thickest stem walls were respectively 1.56 mm (SST 57), 1.54 mm (SST 57), 1.59 mm (SST 57) and 0.65 mm (SST 57 & DH 29) for internodes one to four of the parents. For the crosses it was 1.68 mm (SST 57/SST 55), 1.93 mm (SST 57/DH 29), 1.87 mm (SST 57/3-273) and 1.79 mm (3-273/SST 876) respectively for the four internodes. The means of the stem wall thickness for the four internodes of the crosses were thicker than that of the parents, except for internode one. The stem wall thickness of the parents decreased from internode one (1.08) to four (0.58), but internode two (1.09) of the crosses was thicker than internode one (1.07). A decrease for internodes three (0.89) and four (0.78) was observed.

In comparing the means for pith thickness (Appendix 3.1d) the thickest pith of the parents for the four internodes was respectively 0.89 mm (SST 57), 0.81 mm (SST

57), 0.81 mm (SST 57) and 0.43 mm (SST 806 & BX). There was a significant decrease in pith thickness of the parents (0.6 to 0.38) and crosses (0.7 to 0.53) from internodes one to four. The thickest pith of the crosses at internodes one to four was 0.92 mm (SST 57/SST 55), 0.97 mm (SST 57/3-273 & SST 57/BX), 0.99 mm (SST 57/3-273) and 0.8 mm (SST 806/3-273) respectively. This shows that the expression of stem solidness in the crosses were significantly higher than in the parents.

In comparing the means for breaking weight (Appendix 3.1e) a significant decrease in breaking weight for internode one to four in the parents (1360.69 to 215.12) as well as in the crosses (1277.21 to 223.9) was observed. The biggest breaking weight per internode for the parents was 2040.36 g (DH 24), 1063.8 g (SST 57), 462.72 g (SST 57) and 247.24 g (36-8) respectively. In the crosses, the biggest breaking weight was 1763.4 g (SST 876/36-8), 1162.24 g (SST 876/36-8), 616.56 g (SST 57/36-8) and 299.04 g (BX/36-8) respectively for internodes one to four. The means for breaking weight in the parents was higher than for the crosses in internodes one and two. For internodes three and four, the mean of the crosses for breaking weight was higher than that for the parents.

In comparing the means for stem strength (Appendix 3.1f) it shows a decrease in stem strength from internodes one to four in the parents (23.85 to 0.36) as well as in the crosses (26.92 to 0.53). There was a significant difference in stem strength, especially between internodes one and two for the parents (23.85 and 6.54) as well as for the crosses (26.92 and 8.1). The biggest value for stem strength in the parents per internode one to four was 58.28 (SST 57), 15.71 (SST 57), 3.29 (SST 57) and 0.45 (DH 29) respectively. For the crosses the values were 83.45 (SST 57/SST 876), 19.29 (SST 57/DH 29), 4.42 (SST 57/3-273) and 1.17 (SST 57/SST 876) respectively for internodes one to four. The mean internode stem strength for the crosses was higher than for the parents in all four internodes.

Since the differences between the genotypes (parents and F₁) were significant, the genotype variances could be divided into variances for GCA and SCA (Griffing, 1956).

Significance of variance components

Table 3.6 Analysis of variance for GCA for measured characteristics

	Height	Internode Length	Internode diameter	Stem wall thickness	Pith thickness	Breaking weight	Stem strength
Whole plant	6582.84 **						
Internode 1		267.76 **	0.17 **	0.11 **	0.04 **	300236.15 **	798.02 **
Internode 2		258.92 **	0.29 **	0.33 **	0.81 **	91598.85 **	64.06 **
Internode 3		777.43 **	0.38 **	0.32 **	0.10 **	16833.88 **	3.71 **
Internode 4		2205.60 **	0.30 **	0.10 **	0.04 **	2466.64 **	0.04 **

** $P \leq 0.01$

Table 3.7 Analysis of variance for SCA for measured characteristics

	Height	Internode length	Internode diameter	Stem wall thickness	Pith thickness	Breaking weight	Stem Strength
	3069.33 **						
Internode 1		48.56 **	0.16 **	0.04 **	0.01 **	54471.10 **	102.82 **
Internode 2		65.32 **	0.18 **	0.06 **	0.01 **	16671.64 **	6.04 **
Internode 3		295.33 **	0.14 **	0.03 **	0.01 **	4035.07 **	0.40 **
Internode 4		1025.64 **	0.07 **	0.05 (-)	0.01 **	1028.50 **	0.04 **

** $P \leq 0.01$

There were statistically significant differences for GCA and SCA for all the characteristics and at all internodes which were measured to define stem strength, except for SCA for stem wall thickness of internode four. The implication of this is that both additive, and non-additive gene effects were involved in the expression of the traits. The magnitude of GCA mean squares (Table 3.6) was much larger than for SCA (Table 3.7), indicating that for this set of parental lines, differences in the progeny could largely be attributed to additive gene effects. The exception is for stem strength at internode four, where the SCA variance was larger than for GCA. This is

attributed to non-additive gene effect in the absence of the solid stem trait in internode four (parents SST 57, SST 806, SST 876, BX, SST 55 and 36-8) which lacks the expression of the genes for solid stem in internode four.

Combining ability

The calculated effects (except for SST 55) differed significantly from zero (table 3.8a). Parent five (DH 29) produced progeny with the shortest straw and differed significantly from parents three (SST 806) and four (DH 24), the second best performers.

Table 3.8a GCA effects for height

Parent		Height		Standard error
SST 57	1	18.797	Gi	4.579
SST 55	2	2.313	Gi – Gj	6.868
SST 806	3	-23.258		
DH 24	4	-21.232		
DH 29	5	-36.648		
3-273	6	30.488		
BX	7	32.241		
SST 876	8	6.441		
36-8	9	-9.144		

The GCA effects for all the components of stem strength were calculated at each internode and are summarised in Table 3.8b (internode length), Table 3.8c (internode diameter), Table 3.8d (stem wall thickness), Table 3.8e (pith thickness), Table 3.8f (breaking weight) and Table 3.8g (stem strength).

Table 3.8b shows that parent SST 57 had significantly shortened internodes one, two and three but internode four lengthened significantly. Parent SST 806 had a significant GCA effect only for internodes two and four. Parent DH 29 also had

significantly shortened internodes. The largest effect was experienced on internode length and contributed to shortening internode length throughout the stem. Parent 36-8 only showed reduced length at internode one (the bottom internode) and internode four (the top internode of the stem).

Table 3.8b GCA effects for internode length

	Parent	Internode			
		1	2	3	4
SST 57	1	-5.279	-4.893	-10.638	26.442
SST 55	2	2.884	-1.365	-0.276	2.928
SST 806	3	0.649	-0.971	0.77	-13.108
DH 24	4	-1.349	-1.353	-4.755	-18.072
DH 29	5	-6.825	-7.041	-13.833	-9.926
3-273	6	9.12	9.436	5.364	2.492
BX	7	4.12	4.295	11.362	13.637
SST 876	8	-0.235	0.287	4.043	4.787
36-8	9	-3.087	1.605	7.962	-9.181
		Standard error			
	Gi	0.964	1.087	1.962	3.93
	Gi – Gj	1.446	1.63	2.9437	5.894

The GCA effects for stem thickness (internode diameter) (Table 3.8c) were small and only significantly positive for parent 36-8 at internodes one (0.2659), two (0.3364), three (0.39) and four (0.3775).

Table 3.8c GCA effects for internode diameter

Parent		Internode			
		1	2	3	4
SST 57	1	-0.097	-0.164	-0.125	-0.0001
SST 55	2	-0.100	-0.105	-0.136	-0.095
SST 806	3	-0.115	-0.112	-0.189	-0.160
DH 24	4	-0.074	-0.120	-0.113	-0.179
DH 29	5	0.093	0.179	0.187	0.056
3-273	6	0.047	-0.045	-0.051	0.062
BX	7	-0.003	0.010	0.031	-0.053
SST 876	8	-0.016	0.020	0.004	-0.008
36-8	9	0.266*	0.336*	0.391*	0.378*
Standard error					
	Gi	0.038	0.041	0.038	0.040
	Gi – Gj	0.056	0.062	0.056	0.060

Parent SST 57 had a significant positive effect on stem wall thickness on internode one to four (Table 3.8d). Parent 3-273 had a significant positive effect on internodes two, three and four.

Table 3.8d GCA effects for stem wall thickness

Parent		Internode			
		1	2	3	4
SST 57	1	0.261	0.432	0.420	0.121
SST 55	2	-0.072	-0.094	-0.114	-0.067
SST 806	3	-0.035	-0.095	-0.111	-0.022
DH 24	4	-0.058	-0.127	-0.087	-0.065
DH 29	5	0.007	-0.003	-0.015	-0.004
3-273	6	-0.022	0.068	0.095	0.173
BX	7	-0.046	-0.080	-0.063	-0.103
SST 876	8	-0.036	-0.059	-0.077	0.053
36-8	9	0.001	-0.043	-0.050	-0.087
Standard error					
	Gi	0.027	0.022	0.025	0.049
	Gi – Gj	0.041	0.034	0.037	0.073

Table 3.8e GCA effects for pith thickness

Parent		Internode			
		1	2	3	4
SST 57	1	0.158	0.245	0.237	0.098
SST 55	2	-0.025	-0.038	-0.049	-0.014
SST 806	3	-0.002	-0.035	-0.038	0.023
DH 24	4	-0.008	-0.042	-0.029	0.009
DH 29	5	-0.014	-0.033	-0.032	-0.001
3-273	6	-0.021	0.037	0.053	0.048
BX	7	-0.025	-0.038	-0.034	-0.052
SST 876	8	-0.015	-0.028	-0.039	-0.012
36-8	9	-0.048	-0.068	-0.068	-0.099
Standard error					
	Gi	0.016	0.012	0.013	0.014
	Gi – Gj	0.024	0.018	0.020	0.022

Parent SST 57 had a significant positive effect for pith thickness at all the internodes (Table 3.8e). The GCA effect for parent 3-273 was positive at internode two, three and four because of the expression of the solid stem trait in these internodes.

Parents SST 57, DH 29 and 36-8 had a significant positive effect on breaking weight in internodes one, two, three and four (Table 3.8f). Parent DH 24 had a significant positive effect on internode one, while parent 3-273 had a positive effect on internodes three and four.

Table 3.8f GCA effects for the breaking weight

Parent		Internode			
		1	2	3	4
SST 57	1	234.79	168.75	80.76	5.20
SST 55	2	-143.91	-51.74	-6.78	0.86
SST 806	3	-128.76	-107.22	-57.95	-17.33
DH 24	4	135.38	-46.87	-18.76	-13.50
DH 29	5	194.52	112.05	30.48	2.11
3-273	6	-197.89	-53.40	6.29	18.02
BX	7	-153.57	-67.23	-25.73	-7.11
SST 876	8	-21.57	2.75	-16.38	-14.55
36-8	9	81.02	42.89	8.08	26.30
Standard error					
	Gi	45.51	19.24	9.57	5.42
	Gi – Gj	68.26	28.86	14.35	8.13

Table 3.8g showed that parent SST 57 had a significantly positive effect on all the internodes for stem strength, while parent DH 29 had a significantly positive effect on internode one and two, and parent 3-273 only on internode four.

Table 3.8g GCA effects for the stem strength

Parent		Internode			
		1	2	3	4
SST 57	1	18.349	5.972	0.237	0.071
SST 55	2	-5.954	-1.173	-0.049	-0.029
SST 806	3	-4.678	-1.613	-0.038	0.011
DH 24	4	0.349	-0.894	-0.030	0.007
DH 29	5	6.106	1.193	-0.032	0.015
3-273	6	-9.748	-1.288	0.053	0.098
BX	7	-7.096	-1.711	-0.034	-0.096
SST 876	8	1.369	-0.163	-0.039	-0.028
36-8	9	1.304	-0.326	-0.068	-0.049
Standard error					
	Gi	1.569	0.339	0.106	0.029
	Gi - Gj	2.354	0.508	0.159	0.044

SCA effects for each parental combination and all characters, are summarised in appendix 3.2(a-g). Although the SCA effects have been summarised in detail it is not of importance in the case of a self-pollinated crop like wheat, where breeding strategies do not include the development of hybrids.

Genetic variation

The genetic variances were calculated from the mean squares for general combining ability and specific combining ability (Griffing, 1956). The distribution of these variances are summarised in Table 3.9.

Table 3.9 Expected mean squares for combining ability

Source	Expected mean squares (Random effects, Model II)	Mean squares
GCA	$\Sigma^2_{e+(p+2)} \sigma^2 + \sigma^2_g$	Mg
SCA	$\Sigma^2_e + \sigma^2_s$	Ms
Error	Σ^2_e	Me

The expected variances for general combining ability (σ^2_g) and specific combining ability (σ^2_s) were calculated and summarised in Table 3.10.

Table 3.10 Summary of genetic variances of general and specific combining ability

	Sum of squares	Mean Squares	Estimated mean squares	Sum of squares	Mean squares	Estimated mean squares
Breaking weight						
Internode 1				Internode 2		
GCA	2401889.18	300236.15	22342.28	732790.79	91598.85	6811.56
SCA	1960959.71	54471.10	28842.70	600179.20	16671.64	12090.53
Error	22552992.21	25628.40	25628.40	4031377.00	4581.11	4581.11
Internode 3				Internode 4		
GCA	134671.00	16833.88	1163.53	19733.14	2466.64	130.74
SCA	145262.40	4035.07	2902.29	37026.06	1028.50	665.06
Error	996840.93	1132.77	1132.77	319832.63	363.45	363.45
Internode length						
Internode 1				Internode 2		
GCA	2142.04	267.76	19.93	2071.35	258.92	17.60
SCA	1748.26	48.56	37.07	2351.39	65.32	50.71
Error	10114.75	11.49	11.49	12856.73	14.61	14.61
Internode 3				Internode 4		
GCA	6219.46	777.43	43.83	17644.79	2205.60	107.27
SCA	10631.87	295.33	247.67	36923.09	1025.64	834.59
Error	41938.91	47.66	47.66	168123.28	191.05	191.059
Internode diameter						
Internode 1				Internode 2		
GCA	1.321	0.165	0.000	2.338	0.292	0.010
SCA	5.903	0.164	0.147	6.562	0.182	0.161
Error	15.337	0.017	0.017	18.607	0.021	0.021
Internode 3				Internode 4		
GCA	3.007	0.376	0.020	2.413	0.302	0.021
SCA	5.065	0.141	0.123	2.500	0.069	0.049
Error	15.429	0.018	0.018	17.206	0.020	0.020
Stem wall thickness						
Internode 1				Internode 2		
GCA	0.901	0.113	0.007	2.610	0.326	0.020
SCA	1.492	0.041	0.032	2.100	0.058	0.052
Error	8.013	0.009	0.009	5.478	0.006	0.006
Internode 3				Internode 4		
GCA	2.543	0.318	0.030	0.821	0.103	0.005
SCA	0.963	0.027	0.020	1.690	0.047	0.018
Error	6.552	0.007	0.007	25.905	0.029	0.029
Pith thickness						
Internode 1				Internode 2		
GCA	0.325	0.041	0.003	0.812	0.101	0.008
SCA	0.384	0.011	0.008	0.465	0.013	0.011
Error	2.681	0.003	0.003	1.548	0.002	0.002
Internode 3				Internode 4		
GCA	0.793	0.099	0.008	0.280	0.035	0.002
SCA	0.246	0.007	0.005	0.456	0.013	0.010
Error	1.937	0.002	0.002	2.279	0.003	0.003

Table 3.10 Summary of genetic variances of general and specific combining ability
(continued)

	Sum of squares	Mean Squares	Estimated mean squares	Sum of Squares	Mean squares	Estimated mean squares
Stem strength						
Internode 1				Internode 2		
GCA	6384.16	798.02	63.12	512.45	64.06	5.27
SCA	3701.66	102.82	72.36	217.46	6.04	4.62
Error	26812.08	30.47	30.47	1248.51	1.42	1.42
Internode 3				Internode 4		
GCA	29.700	3.713	0.300	0.310	0.039	-0.0002
SCA	14.513	0.403	0.260	1.518	0.042	0.031
Error	122.093	0.139	0.139	9.379	0.011	0.011
Plant height						
GCA	52663.07	6582.88	319.41			
SCA	110496.00	3069.33	2809.87			
Error	228325.43	259.46	259.46			

The genetic variance component (σ^2G) includes both the variance due to additive gene action ($\sigma^2A = \sigma^2g$) and non-additive gene action or gene action due to dominance effects ($\sigma^2D = \sigma^2s$). The ratio of the genotypic variance components (σ^2D) to the total phenotypic variance measured gives a measurement of the heritability of the trait. The higher the heritability the bigger the response, when selection for the trait is applied. These values were calculated and summarised in Table 3.11. Heritability was significantly larger than zero and relatively high. The repeatability for the different internodes was constant, showing that selection should be efficient regardless of the internode which was selected. The only exception was the heritability for stem wall thickness in internode four (0.49). Although lower, all the other heritability values for stem characteristics were still significant.

Table 3.11 Summary of genetic components and heritability for stem strength characteristics

Height				
$\Sigma^2A = 2\sigma^2g$	638.82			
$\Sigma^2D = \sigma^2s$	2809.87			
$\Sigma^2G = \sigma^2A + \sigma^2D$	3448.69			
$\Sigma^2P = \sigma^2G + \sigma^2e$	3708.15			
h^2	0.93			
Error	0.19			
Breaking weight	Internode 1	Internode 2	Internode 3	Internode 4
$\Sigma^2A = 2\sigma^2g$	44684.56	13623.12	2327.06	261.48
$\Sigma^2D = \sigma^2s$	28842.70	12090.53	2902.29	665.06
$\Sigma^2G = \sigma^2A + \sigma^2D$	73527.26	25713.65	5229.35	926.54
$\Sigma^2P = \sigma^2G + \sigma^2e$	99155.66	30294.76	6362.12	1289.99
h^2	0.74	0.85	0.82	0.72
Error	0.075	0.13	0.11	0.067
Internode length				
$\Sigma^2A = 2\sigma^2g$	39.86	35.2	87.66	214.54
$\Sigma^2D = \sigma^2s$	37.07	50.71	247.67	834.59
$\Sigma^2G = \sigma^2A + \sigma^2D$	76.93	85.91	335.33	1049.13
$\Sigma^2P = \sigma^2G + \sigma^2e$	88.42	100.52	382.99	1240.18
h^2	0.87	0.85	0.88	0.85
Error	0.143	0.13	0.15	0.13
Circumference				
$\Sigma^2A = 2\sigma^2g$	0.0002	0.020	0.040	0.040
$\Sigma^2D = \sigma^2s$	0.147	0.161	0.123	0.049
$\Sigma^2G = \sigma^2A + \sigma^2D$	0.150	0.181	0.163	0.089
$\Sigma^2P = \sigma^2G + \sigma^2e$	0.160	0.202	0.181	0.109
h^2	0.890	0.900	0.900	0.820
Error	0.160	0.160	0.160	0.110
Stem wall thickness				
$\Sigma^2A = 2\sigma^2g$	0.014	0.040	0.060	0.010
$\Sigma^2D = \sigma^2s$	0.032	0.052	0.020	0.018
$\Sigma^2G = \sigma^2A + \sigma^2D$	0.046	0.092	0.080	0.028
$\Sigma^2P = \sigma^2G + \sigma^2e$	0.055	0.098	0.087	0.057
h^2	0.840	0.940	0.920	0.490
Error	0.120	0.200	0.180	0.014
Pith thickness				
$\Sigma^2A = 2\sigma^2g$	0.006	0.016	0.016	0.004
$\Sigma^2D = \sigma^2s$	0.008	0.011	0.005	0.010
$\Sigma^2G = \sigma^2A + \sigma^2D$	0.014	0.027	0.021	0.014
$\Sigma^2P = \sigma^2G + \sigma^2e$	0.017	0.029	0.023	0.017
h^2	0.820	0.930	0.910	0.820
Error	0.110	0.190	0.170	0.110
Stem strength				
$\Sigma^2A = 2\sigma^2g$	126.24	10.54	0.60	-0.0004
$\Sigma^2D = \sigma^2s$	72.36	4.62	0.26	0.03
$\sigma^2G = \sigma^2A + \sigma^2D$	198.60	15.16	0.86	0.03
$\sigma^2P = \sigma^2G + \sigma^2e$	229.07	16.58	0.99	0.04
h^2	0.87	0.91	0.86	0.74
Error	0.14	0.17	0.14	0.08

Linear correlations

Linear correlations for all characteristics were calculated, based on the mean of all internodes (Table 3.12).

Table 3.12 Linear correlations between all the characteristics combined for all internodes

	Breaking weight	Internode length	Internode diameter	Stem wall thickness	Pith thickness
Internode length	-0.268**				
Diameter	0.355**	0.343**			
Stem wall thickness	0.571**	-0.042**	0.154		
Pith thickness	0.395**	-0.196**	-0.311**	0.873**	
Stem strength	0.741**	-0.505**	-0.101	0.760**	0.789**

** $p \leq 0.01$

There was a significant negative correlation between internode length and breaking weight (Table 3.12). Internode diameter was positively correlated with breaking weight and internode length. There was a positive correlation between stem wall thickness and breaking weight, and a negative correlation with internode length. Pith thickness was positively correlated with breaking weight and stem wall thickness and there was a negative correlation between internode length and diameter. Again stem strength of all the internodes was positively correlated with breaking weight, stem wall thickness and pith thickness, and negatively correlated with internode length.

Since crown lodging happens at internode one, the correlation between the different characteristics were calculated for internode one separately (Table 3.13).

Table 3.13 Linear correlations between all the characteristics of internode one

	Height	Breaking weight	Internode length	Internode diameter	Stem wall thickness	Pith thickness
Breaking weight	0.076					
Internode length	0.461**	-0.408**				
Diameter	0.348**	0.187**	0.287**			
Stem wall thickness	0.194	0.283**	-0.046	0.311**		
Pith thickness	-0.003	0.187**	-0.214**	-0.260**	0.811**	
Stem strength	-0.093	0.702**	-0.659**	-0.134	0.481**	0.580**

** $P \leq 0.01$

There was a positive correlation between internode length and height, but a negative correlation between breaking weight and internode length (Table 3.13). This correlation was expected. For internode diameter, there were positive correlations with height, breaking weight and internode length. There were positive correlations between breaking weight and internode diameter for stem wall thickness. For pith thickness there were positive correlations between breaking weight and stem wall thickness and negative correlations between internode length and internode diameter. Of utmost importance is the fact that there were positive correlations between the breaking weight, stem wall thickness and pith thickness and there was a negative correlation between internode length and stem strength.

3.4 DISCUSSION AND CONCLUSIONS

Up to now, resistance to lodging has been achieved by using single genes (Worland & Snape, 2001) which shorten the stem of the plant. There are also a large number of both the gibberellic acid insensitive and sensitive genes available, which have not been used in commercial breeding. However, some of the genes like *Rht3* are known to have a negative effect on yield (Worland & Snape, 2001). Continuous improvement of the standing ability of wheat in its resistance to lodging in an environment of high fertilisation and irrigation would depend on using marker technology to stack the major genes, as well as on the use of the genetic variability of a quantitative background to ensure selection gain for the trait. An investigation into the

components that regulate stem strength would support the development of strategies to improve resistance to lodging.

Although the solid stem character has been used to improve resistance to sawfly and also eyespot (Miller et al., 1993) it was also found to have a large influence on the standing ability of wheat under irrigation (Jordaan, 2002). These genes express themselves in a solid stem phenotype. The strength of the stem will then depend not only on the length of the internode, but also on the thickness of the pith and the thickness of the stem wall. The strength of the stem could then be measured by the power it takes to break the stem between two nodes. An index was developed combining these measurements into a single criterion to evaluate stem strength.

It was found that a chosen set of parental genotypes, which represents the available population of germplasm for improvement of resistance to lodging; differ significantly from one another for the components of stem strength as well as the index. This confirms the genetic background of the expression of stem strength. Looking into the genetic variability for the different components using Griffing's model for combining ability (Griffing, 1956), it was found that the contribution of GCA (additive genetic variance) was highly significant for all the components at all the internodes of the stem. The involvement of non-additive variation (specific combining ability) was also significant, but the magnitude thereof was much smaller than for the additive component. Genotypes also differed in their performance as parents. Parents with a shorter stem and solid stem phenotype, like SST 57 and DH 29, had higher breeding values (GCA effects) than longer stem and hollow stem phenotypes, like BX and SST 55. It is important to evaluate parents, to ensure the right populations to improve stem strength by means of pedigree or mass selection. The significance of variance for non-additive genes would also support a strategy for the development of hybrids showing stronger stems than the parents. This might be of importance, especially because of the complementary effect of genes derived from different parents.

The high and significant heritability which was calculated for all the components of stem strength as well as for plant height would, however, favour a breeding strategy based on selection of the additive variation. Although it is very important to look at

the components and to describe the phenotypes accordingly, it is impractical to measure these components in the field. A practical approach would be to select amongst progeny for shorter and harder stems (solidness).

An ideal phenotype for resistance to lodging could be described and idealised to have shorter stems (internodes, especially internodes two and three) and with a thicker pith throughout the stem, but especially at internodes one, two and three.

CHAPTER 4

The interaction of stem strength with plant density and nitrogen application in wheat

4.1 INTRODUCTION

In an environment where irrigation and fertilisation are optimised, the focus for standing ability is on the length of the straw. However, this ignores the complexity of the inheritance of short stiff straw and the genetic expression of the components. It is fair to reason that the length of the internodes, thickness and hardness of the stem and thickness of the culm play a major role in lodging resistance. It is also well known that the solid stem character expresses a thicker stem wall with no, or a very small opening, the pith. This explains the woody appearance of the stem. Making a study of the progeny of a selected set of parents which differ in genes for plant height and genes for solid stem, might give information on the inheritance of stem strength, and a possible response to selection of the characteristics, or most probably a strategy for combining the different components. Mechanical engineers simulate the strength of materials by combining length, thickness and breaking strength in an index (Shigley, 1986). It is argued that the strength of the stem is a function of the length of the internode. As breaking or snapping occurs between two nodes, it depends on the thickness of the wall, the degree of solid stem, and the power it takes to break or snap the stem between two nodes. Stem strength is thus defined to be a function of length of the internode, the thickness of the wall and the power it takes to break the stem. It has been observed in the field that the strength of the stem varies with environment and that nitrogen application, and especially plant density, plays a major role. More information on the interaction of stem strength with nitrogen application and plant density, would improve understanding of the genetic expression of the trait, and the aim of this study was therefore to study the effect of different N treatments and plant densities on stem strength of selected parents and their progeny.

4.2 MATERIALS AND METHODS

Experiment three was concluded to interpret the interaction of stem strength with environmental factors. The factors analysed were plant density and N application. The genotypes were a selection of parents of experiment one, according to their status of solid stem and degree of dwarfism (Table 3.1). Crosses were made in all combinations between these five parents (SST 806, DH 24, DH 29, SST 55 and BX), ignoring reciprocal crosses, generating 10 F₁ crosses. The latter together with the parents, were used as experimental material for the study.

The 15 entries (parents and crosses) were planted in a tunnel in a complete randomised block design with three replications. Each plot consisted of eight pots (23 cm x 30 cm). The experiment included four treatments to determine the influence of the different environmental factors on stem strength.

The first treatment (D1/F1), consisted of one plant per pot (plant density, D1) with normal fertilisation (F1) which was adequate for growing wheat plants in the tunnel, based on soil tests (see Table 3.2).

The second treatment (D1/F2) consisted of one plant per pot (plant density, D1) and additional application of N amounting to 100 kilogram of nitrogen per hectare (F2). The additional N was given six weeks after planting; stage 31 of Zodoks et al. (1974), first node detectable (Eyal et al., 1987).

Treatment three (D2/F1) consisted of four plants (D2) per pot with normal fertilisation (F1).

The fourth treatment (D2/F2) consisted of four plants (D2) per pot, with additional N supplement as in treatment two (F2).

The data were taken on five plants per plot and mature dry plants were selected for evaluation. The following measurements were taken from the main stem (see wheat stem anatomy, Figure 3.1) of each of the plants sampled per plot:

1. Plant height (mm), measured from the crown to the tip of the spike, excluding awns
2. Number of internodes, numbered from the soil upwards
3. Length of each internode (mm), per digital calliper of 0.01 accuracy
4. Internode diameter (mm)
5. Stem wall thickness (mm)
6. Pith thickness (mm), calculated as the wall thickness times two, divided by internode diameter
7. Breaking weight (g), (the weight it took to break the internode)
8. Stem strength

Statistical analyses were done on the average of the five plants at each internode. The data were analysed to position the different sources of variation that are due to genotypes, blocks and the interaction of genotypes, and blocks with plant density and N application. The variance between genotypes were divided into variances for general combining ability (GCA) and specific combining ability (SCA) (Griffing Method 2, Model I, Fixed effects and Π Random effects). The variance for GCA and SCA were further divided into GCA effects and SCA effects, associated with the parents and crosses respectively (Griffing, 1956).

4.3 RESULTS

Table 4.1 Analysis of variance for stem strength for every internode and each treatment

Source of variance			Mean squares	
Internode	Treatment	Genotype	Replication	Error
2	1 (D1/ F1)	59.006 (-)	163.595 *	30.723
2	2 (D1/F2)	24.221 (-)	18.961 (-)	14.405
2	3 (D2/ F1)	10.244 (-)	6.873 (-)	8.084
2	4 (D2/ F2)	11.855 **	2.552 (-)	4.134
3	1 (D1/ F1)	0.405 (-)	0.331 (-)	0.23
3	2 (D1/F2)	0.400 (-)	0.169 (-)	0.286
3	3 (D2/ F1)	0.364 *	0.110 (-)	0.165
3	4 (D2/ F2)	0.354 **	0.339 (-)	0.111
4	1 (D1/ F1)	0.042 (-)	0.008 (-)	0.022
4	2 (D1/F2)	0.017 (-)	0.005 (-)	0.014
4	3 (D2/ F1)	0.034 **	0.012	0.011
4	4 (D2/ F2)	0.013 *	0.003 (-)	0.006
Combined	Combined	15.292 (-)	40.332 (-)	14.88

* $P \leq 0.05$, ** $P \leq 0.01$

There were no significant differences between genotypes for treatments one, two and three at each of the three internodes. For treatment four (higher plant density and higher N application), there were significant differences for internodes two, three and four. When all the data for internodes and genotypes were combined, the variance between genotypes was insignificant.

Table 4.2 Analysis of variance for interactions between genotypes and treatments combined for stem strength at each internode

	Internode 2	Internode 3	Internode 4
Replications	101.28 **	0.83 *	0.01 (-)
Genotypes	69.21 **	0.98 **	0.06 **
Treatments	215.36 **	18.09 **	21.03 **
Interaction	12.04 (-)	0.95 (-)	1.14 (-)
Variance error	15.15	0.19	0.01

** $P \leq 0.01$

When the genotype source of variance excludes the treatments (plant density and fertiliser components differ), the differences were significant at every internode (Table 4.2). The variance between treatments (plant density and fertiliser application) was also statistically significant at every internode. The variance component for the interaction between genotypes and treatments were insignificant for all the internodes.

Table 4.3 Summary of combined analyses for treatment ranks for combined internodes for stem strength

		Treatment^a	Averages		
			Internode 2	Internode 3	Internode 4
Treatments					
rank	1	1 D1 / F1	9.34	1.6	0.48
	2	2 D1 / F2	6.93	1.35	0.42
	3	3 D2 / F1	5.5	1.19	0.39
	4	4 D2 / F2	4.24	0.94	0.3
LSD (0.05)			6.29	0.7	0.18

^a D1 = Plant density one, F1 = Fertiliser application one

There was a tendency for stem strength to decline when either population or N application was increased (Table 4.3). This tendency is however only significant for the difference between treatment one and four for both internodes three and four.

The individual data for stem strength for all treatments are summarised in Appendix 4.1a for internode two, Appendix 4.1b for internode three and Appendix 4.1c for internode four.

The summary for stem strength for internode two for the four treatments (Appendix 4.1a), shows that there was a decrease in stem strength for treatments one to four, for the parents (7.428 to 3.704), as well as for the progeny (10.299 to 4.517). There was a significant difference between treatment one and two for the parents (7.428 and 4.942) and progeny (10.299 and 7.921). This shows that when N fertiliser was increased, stem strength was decreased. There was also a significant difference between treatment one and four for the parents (7.428 and 3.704) as well as for the progeny (10.299 and 4.517), thus showing that when plant density and N fertiliser increased, stem strength decreased. DH 29 had the best stem strength of all the parents for all four treatments. This genotype has the solid stem gene expression. The good stem strength of parent DH 29 corresponds with the evaluation of its progeny, resulting in the progeny with the best stem strength in combination with SST 806 (21.88) in treatment one, with SST 55 (11.21) in treatment two, with DH 24 (7.92) in treatment three and with SST 806 (8.03) in treatment four. This performance of DH 29 was repeated in all treatments at internode three (Appendix 4.1 b) and at internode four (Appendix 4.1 c).

Information on the gene action involved in the expression of the trait, can be derived from the variances for genotypes divided into GCA and SCA [Griffing Method 2 Model I (Fixed effects) and Model II (Random effects)].

Table 4.4 Analysis of variance for GCA (mean squares) of stem strength at each internode and treatment

Treatment	Stem strength		
	Internode 2	Internode 3	Internode 4
1 D1/F1	37.742 *	0.332 **	0.035 **
2 D1/F2	8.987 (-)	0.124 (-)	0.011 (-)
3 D2/F1	7.292 *	0.262 **	0.035 **
4 D2/F2	8.489 **	0.269 **	0.005 (-)

There were significant differences for GCA of internode two for treatments one, three and four. There was also a significant difference for internode three for treatments one, three and four. For internode four there only were significant differences at treatments one and three.

Table 4.5 Analysis of variance for SCA (mean squares) of stem strength at each internode and treatment

Treatment	Stem strength		
	Internode 2	Internode 3	Internode 4
1 D1/F1	12.439 (-)	0.056 (-)	0.006 (-)
2 D1/F2	7.708 (-)	0.137 (-)	0.003 (-)
3 D2/F1	1.864 (-)	0.065 (-)	0.002 (-)
4 D2/F2	2.137 (-)	0.055 (-)	0.004 *

The variance for SCA was insignificant for all the treatments at all the internodes (Table 4.5). The exception was treatment four (D2/F2) at internode four.

Combining ability

The significance of the variance for GCA allows for the calculation of GCA effects for the breeding value of each parent for the stem strength trait. These values are summarised in Table 4.6.

Table 4.6 GCA effects for stem strength characteristics of each parent for all internodes and all treatments

	Parents					Standard error	
	SST 806	DH 24	DH 29	SST 55	BX	Gi	Gi - Gj
	1	2	3	4	5		
Internode 2							
Treatment 1 D1/F1	0.672	-0.198	3.5806	-1.8932	-2.1613	1.08186	1.71057
Treatment 2 D1/F2	0.0479	-0.4845	1.7098	0.1265	-1.3997	0.74079	1.1713
Treatment 3 D2/F1	-0.0375	1.1639	0.8744	-0.8509	-1.1499	0.55496	0.87746
Treatment 4 D2/F2	0.592	-0.4885	1.4615	-0.1113	-1.4537	0.39687	0.6275
Internode 3							
Treatment 1 D1/F1	0.051	-0.0795	0.3557	-0.1443	-0.1829	0.09352	0.14787
Treatment 2 D1/F2	0.029	-0.121	0.1562	0.0876	-0.1519	0.10441	0.16509
Treatment 3 D2/F1	-0.0627	0.0807	0.2892	-0.0893	-0.2179	0.07939	0.12552
Treatment 4 D2/F2	0.2807	-0.1412	0.085	-0.0065	-0.2179	0.06515	0.10301
Internode 4							
Treatment 1 D1/F1	-0.0663	0.019	0.1113	-0.0515	-0.0125	0.02924	0.04623
Treatment 2 D1/F2	-0.0388	-0.0135	0.0598	-0.0278	0.0203	0.02269	0.03587
Treatment 3 D2/F1	-0.0539	0.0742	0.079	-0.0596	-0.0396	0.02045	0.03233
Treatment 4 D2/F2	0.0285	0.0004	0.0228	-0.0182	-0.0334	0.01471	0.02326

Only parent three (DH 29) contributed positively towards producing superior progeny for all four treatments and three internodes (Table 4.6). It was also significantly better than every other parent in all treatments and for all internodes. Parent two (DH 24)

had a significantly positive GCA effect for treatment three (higher plant density and normal N fertilisation) at all three internodes. Of significance is that parent one (SST 806) had a significant positive effect only for treatment four (higher plant density and higher N fertilisation) for all the internodes.

Because of the insignificance of the variance for SCA (Table 4.5), it can be expected that SCA effects would be insignificant. The exception was treatment four / internode four (Table 4.7).

Table 4.7 SCA effects for treatment four, internode four

		Parents					
Treatment 4		1	2	3	4		
Internode 4	2	-0.095					Standard Error
Internode 4	3	0.043	-0.023				Internode 4
Internode 4	4	-0.040	-0.002	0.039		Sii	0.03
Internode 4	5	-0.068	-0.033	-0.049	-0.025	Sij	0.03
						Sii - Sjj	0.04
						Sij - Sik	0.05
						Sij - Skl	0.05

Genetic variation

If the variance for general and specific combining is shown to be derived from random effects (Griffing, 1956 Method II Model II), the genetic variances can be calculated (Table 4.8).

Table 4.8 Genetic variances of general and specific combining ability

Internode	Treatment		Sum of squares	Mean squares	Estimated mean squares
2	1	GCA	150.969	37.742	3.61
		SCA	124.393	12.439	2.198
		Error	860.255	10.241	10.241
2	2	GCA	35.95	8.987	0.183
		SCA	77.08	7.708	2.906
		Error	403.351	4.802	4.802
2	3	GCA	29.168	7.292	0.78
		SCA	18.639	1.864	-0.83
		Error	226.362	2.695	2.695
2	4	GCA	33.956	8.489	0.9
		SCA	21.37	2.137	0.76
		Error	115.765	1.378	1.378
3	1	GCA	1.328	0.332	0.04
		SCA	0.564	0.056	-0.021
		Error	6.429	0.077	0.077
3	2	GCA	0.494	0.124	-0.002
		SCA	1.374	0.137	0.042
		Error	8.013	0.095	0.095
3	3	GCA	1.047	0.262	0.03
		SCA	0.65	0.065	0.01
		Error	4.632	0.055	0.055
3	4	GCA	1.074	0.269	0.03
		SCA	0.576	0.058	0.02
		Error	3.12	0.037	0.037
4	1	GCA	0.14	0.035	0.004
		SCA	0.056	0.006	-0.001
		Error	0.628	0.007	0.007
4	2	GCA	0.045	0.011	0.001
		SCA	0.032	0.003	-0.002
		Error	0.378	0.005	0.005
4	3	GCA	0.138	0.035	0.005
		SCA	0.025	0.002	-0.002
		Error	0.307	0.004	0.004
4	4	GCA	0.19	0.005	0.0001
		SCA	0.043	0.004	0.002
		Error	0.159	0.002	0.002

Using the values in Table 4.8, it was possible to calculate the variance for additive gene action (σ^2_A), for non-additive gene action (σ^2_D) and for error (σ^2_e). These values are summarised in Table 4.9 for every internode and treatment separately. This

allowed for the calculation of the heritability of stem strength. A standard error for the heritability was calculated by using the formula

$$h^2 = h^4 \frac{2}{p-1} \text{ (Robertson, 1959).}$$

The repeatability for the different treatments for the different internodes was relatively constant, showing that selection should be efficient regardless of the internode which was selected. Heritability, except for internode four, treatment two, was the largest for treatment four (high plant density and high N fertilisation).

Table 4.9 Genetic components for stem strength

Internode	Treatment	$\sigma^2A =$	$\sigma^2D =$	$\Sigma^2G = \sigma^2A +$	$\Sigma^2P = \sigma^2G +$	h^2	Error
		$2\sigma^2g$	σ^2s	σ^2D	σ^2e		
2	1 D1/F1	7.220	2.198	9.418	19.418	0.47	0.020
2	2 D1/F2	0.366	2.906	3.272	8.074	0.40	0.010
2	3 D2/F1	1.560	-0.830	0.730	3.430	0.21	0.001
2	4 D2/F2	1.800	0.760	2.560	3.940	0.65	0.090
3	1 D1/F1	0.080	-0.021	0.059	0.136	0.43	0.020
3	2 D2/F1	-0.004	0.042	0.038	0.133	0.29	0.004
3	3 D1/F2	0.060	0.010	0.070	0.125	0.56	0.050
3	4 D2/F2	0.060	0.020	0.080	0.117	0.68	0.110
4	1 D1/F1	0.008	-0.001	0.007	0.014	0.5	0.030
4	2 D2/F1	0.002	-0.002	0	0.005	0	0
4	3 D1/F2	0.010	-0.002	0.008	0.012	0.66	0.090
4	4 D2/F2	0.0002	0.002	0.002	0.004	0.52	0.040

Linear correlations

Since all the calculations so far have been done on the stem strength index, it is important to look at the correlations of the components thereof with the index (stem strength). The linear correlations were calculated and are summarised for all treatments on internode two (Table 4.10), internode three (Table 4.11), internode four (Table 4.12) and over treatments for each internode, and all internodes combined (Table 4.13).

All the characteristics, except internode diameter, measured to define stem strength for internode two, were highly correlated with stem strength (Table 4.10). Breaking weight was positively correlated with stem strength for all four treatments. Internode length was negatively correlated with stem strength in all four treatments; the shorter the internode, the stronger the stem. Stem wall thickness was also positively correlated with stem strength for all the treatments. This shows that the thicker the stem wall, the stronger the stem strength. That also applies to pith thickness- the thicker the pith, the stronger the stem of the plant.

Table 4.10 Linear correlation for stem strength for internode two for the four treatments

	Internode 2 Treatment	Plant height	Breaking weight	Internode length	Internode diameter	Stem wall thickness	Pith thickness
Breaking weight	1	-0.213					
	2	0.111					
	3	-0.195					
	4	-0.190					
Internode length	1	0.760**	-0.591**				
	2	0.624**	-0.379				
	3	0.682**	-0.423**				
	4	0.349	-0.409**				
Diameter	1	0.220	-0.037	0.192			
	2	0.380	-0.050	0.735			
	3	-0.010	0.238	0.073			
	4	-0.168	0.437**	0.386			
Stem wall thickness	1	-0.258	0.506**	-0.412**	-0.143		
	2	-0.021	0.301	-0.206	-0.233		
	3	-0.168	0.427**	-0.286	-0.053		
	4	-0.465**	0.376	-0.344	0.159		
Pith thickness	1	-0.358	0.476**	-0.490**	-0.489**	0.919**	
	2	-0.147	0.269	-0.436**	-0.568**	0.924**	
	3	-0.158	0.316	-0.325	-0.369	0.939**	
	4	-0.384	0.174	-0.485**	-0.2724	0.900**	
Stem strength	1	-0.446**	0.830**	-0.716**	-0.282	0.698**	0.756**
	2	-0.161	0.756**	-0.640**	-0.439**	0.691**	0.756**
	3	-0.352	0.801**	-0.599**	-0.072	0.720**	0.700**
	4	-0.369	0.775**	-0.672**	0.012	0.670**	0.633**

** $P \leq 0.01$

The data of Table 4.11 (internode three) shows that the characteristics that have been used to define stem strength were highly positively correlated with stem strength. Breaking weight was positively correlated with stem strength for all treatments. Internode length was negatively correlated with stem strength while internode diameter was not correlated. Stem wall thickness and pith thickness were both positively correlated to stem strength.

Table 4.11 Linear correlation between all the characteristics measured to define stem strength for internode three for the four treatments

	Internode 3 Treatment	Plant height	Breaking weight	Internode length	Internode diameter	Stem wall thickness	Pith thickness
Breaking weight	1	0.002					
	2	0.328					
	3	-0.255					
	4	-0.210					
Internode length	1	0.810 **	-0.034				
	2	0.826 **	0.019				
	3	0.848 **	-0.250				
	4	0.630 **	-0.182				
Diameter	1	0.433 **	0.568 **	0.372			
	2	0.513 **	0.405 **	0.515 **			
	3	0.099	0.444 **	0.196			
	4	-0.040	0.558 **	0.351			
Stem wall thickness	1	-0.080	0.275	-0.049	0.029		
	2	0.126	0.360	-0.071	0.097		
	3	-0.195	0.401 **	-0.194	0.053		
	4	-0.492 **	0.237	-0.347	0.274		
Pith thickness	1	-0.294	-0.058	-0.236	-0.502 **	0.845 **	
	2	-0.143	0.134	-0.336	-0.419 **	0.857 **	
	3	-0.245	0.191	-0.276	-0.326	0.917 **	
	4	-0.385	0.037	-0.564 **	-0.260	0.527 **	
Stem strength	1	-0.480 **	0.561 **	-0.581 **	-0.136	0.635 **	0.630 **
	2	-0.195	0.665 **	-0.545 **	-0.156	0.634 **	0.685 **
	3	-0.514 **	0.711 **	-0.647 **	-0.018	0.701 **	0.673 **
	4	-0.468 **	0.708 **	-0.688 **	0.082	0.447 **	0.597 **

** $P \leq 0.01$

Table 4.12 represents internode four with the four treatments. Again all the characteristics were significantly correlated with stem strength, except internode diameter.

Table 4.12 Linear correlation between all the characteristics measured to define stem strength for internode four for the four treatments

Internode 4	Treatment	Plant height	Breaking weight	Internode length	Internode diameter	Stem	
						wall thickness	Pith Thickness
Breaking weight	1	0.285					
	2	0.335					
	3	0.145					
	4	-0.067					
Internode length	1	0.833 **					
	2	0.843 **	0.299				
	3	0.798 **	0.201				
	4	0.699 **	0.038				
Diameter	1	0.478 **	0.638 **	0.428 **			
	2	0.603 **	0.437 **	0.315			
	3	0.044	0.009	0.072			
	4	0.076	0.442 **	0.046			
Stem wall thickness	1	-0.095	0.082	-0.154	-0.102		
	2	0.082	0.182	0.071	0.243		
	3	-0.279 **	0.171	-0.127	-0.011		
	4	-0.458 **	0.031	-0.31	0.329		
Pith thickness	1	-0.341	-0.232	-0.372	-0.542 **	0.871 **	
	2	-0.256	-0.069	-0.118	-0.33	0.831 **	
	3	-0.378 **	-0.006	-0.201	0.056	0.838 **	
	4	-0.521 **	-0.205	-0.357	-0.251	0.825 **	
Stem strength	1	-0.422 **	0.438 **	-0.441 **	-0.048	0.624 **	0.565 **
	2	-0.311	0.621 **	-0.371	0.073	0.548 **	0.496 **
	3	-0.418 **	0.599 **	-0.349 **	0.003	0.528 **	0.437 **
	4	-0.562 **	0.551 **	-0.457 **	0.265	0.585 **	0.462 **

** $p \leq 0.01$

Table 4.13 gives the linear correlations between the characteristics of stem strength over treatments for each internode, as well as over treatments across all internodes. These data again show that all these characteristics were significantly correlated with stem strength over treatments for each internode and over treatments for all internodes except for internode diameter.

Table 4.13 Linear correlation between stem strength characteristics for each internode over treatments and over internodes over treatments

Over treatments	Internode	Plant height	Breaking weight	Internode length	Internode diameter	Stem	
						wall thickness	Pith thickness
Breaking weight	2	-0.041					
	3	0.059					
	4	0.222 **					
	All	0.019					
Internode length	2	0.591 **	-0.404 **				
	3	0.789 **	-0.032				
	4	0.816 **	0.266 **				
	All	0.271 **	-0.688 **				
Diameter	2	-0.101	0.028	-0.022			
	3	0.222 **	0.627 **	0.279 **			
	4	0.049	0.016	0.061			
	All	-0.020	-0.005	0.057			
Stem wall thickness	2	-0.146	0.558 **	-0.311 **	0.077		
	3	-0.115	0.467 **	-0.136	0.401 **		
	4	-0.090	0.301 **	-0.052	-0.012		
	All	-0.093	0.723 **	-0.601 **	0.018		
Pith thickness	2	-0.223 **	0.356 **	-0.431 **	-0.004	0.879 **	
	3	-0.244 **	0.125	-0.337 **	-0.224 **	0.704 **	
	4	-0.327 **	-0.019	-0.215 **	0.020	0.768 **	
	All	-0.152 **	0.688 **	-0.730 **	-0.033	0.888 **	
Stem strength	2	-0.264 **	0.804 **	-0.586 **	0.004	0.722 **	0.692 **
	3	-0.323 **	0.726 **	-0.516 **	0.196	0.642 **	0.619 **
	4	-0.336 **	0.615 **	-0.305 **	-0.004	0.626 **	0.495 **
	All	-0.128 **	0.863 **	-0.645 **	-0.018	0.752 **	0.805 **

** p < 0.01

4.4 DISCUSSION AND CONCLUSIONS

Yield barriers may be caused by a large number of factors (Satore & Slafer, 1999), but where lodging is concerned, the main cause is the strength of the stem. This might

be due to the length of the internodes, the thickness of the stem, the thickness of the stem wall and the amount of “woodiness” or solidness of the stem. These characteristics have been combined into an index combining the length of the internode, pith thickness and the weight it takes to break or snap the internode. This index has proved to be a discriminative factor in measuring stem strength. Plant height is regarded as the main determinant of resistance to lodging (Bonjean & Angus, 2001), and has been shown to have a high and significant correlation with the index measuring stem strength. These factors influencing height are expected to influence stem strength. It has also been experienced in the field that lodging is mainly caused by either high seeding rates (high plant population) or high N fertilisation, or both. The significant difference between genotypes regarding their stem strength, would suggest that selection to improve the trait is possible. However, the expression of the trait is complicated by its significant interaction with treatments including plant density and N fertilisation. These results repeat themselves in internodes two, three and four, having a significant influence on the whole stem. It is also important to note that the combined effect of a higher plant density and higher N application is higher than when applied separately. On average, it reduces the stem strength of the whole stem by 47%. The genotype which performed the best in all internodes and all treatments was a double haploid derived from a cross with a synthetic hexaploid (Jordaan, personal communication), expressing the solid stem trait for all internodes. Parents and progeny with hollow stems performed the poorest. This confirms the importance of the solid stem trait in improving stem strength. It must be noted that these results were obtained under glasshouse conditions, and might differ under field conditions. However, it simulates responses under different plant populations and N levels.

It was shown that the differences in stem strength have a genetic base and that variances derived from combining ability effects, were mainly of an additive nature (general combining ability), while non-additive or dominance effects (specific combining ability) proved to be insignificant, except for internode four at a high population and a higher level of N application. This could be the result of the absence of the solid stem trait for internode four for most of the genotypes and their progeny.

The fact that genotypes differed in their genetic ability to produce progeny with strong stems, influence the use of such germplasm as parents. Considering that the genetic variances were mainly additive, it would be expected that the best individuals should be selected within the progeny population of the best parental lines. Information on the stem strength of parents is crucial in order to decide from which combinations it should be selected.

The calculated heritability for stem strength was high, and suggests the potential for highly effective selection. The highest heritability calculated was from genetic variances derived at high plant densities and high N levels. This would suggest that more selection progress will be made in an environment of high plant density (extreme inter plant competition) and high N fertilisation. A breeding strategy for lodging resistance should include evaluation in an environment where high population density and high N levels could be simulated.

CHAPTER 5

General conclusions and recommendations

Improvement of yield under optimum conditions depends on overcoming several yield barriers which have been identified. Lodging was shown to be one of these barriers. This is caused mainly by improved irrigation and fertilisation technology. In the past, major genes were used to shorten the stem of the plant. However, for further improvement we should look at all genes which have an effect on the length and the strength of the stem. Breeding strategies will depend on knowledge about the genetic basis of components that regulate stem strength. The solid stem character was found to have a positive effect on the standing ability of wheat under irrigation. The solid stem phenotype varies, depending on the genes involved. It depends not only on the length of the internode but also on the thickness of the pith and stem wall. The strength of the stem was measured by the weight it took to break the internode between two nodes. The different components were combined into an index to evaluate the stem strength by means of a single criterion. Stem strength was defined to be a function of the length of the internode, the thickness of the stem wall and the power it takes to break the stem. It was shown that the chosen set of parental genotypes differed significantly from each other in plant height but also in the components measuring the strength of the stem. These components were correlated highly significantly with each other and also with plant height. Parents differed significantly from each other in their ability to produce progeny with stronger stems. This variance proved to be of an additive nature and although the variance for non-additive effects was also significant, it was much lower, suggesting that selection based on the components of stem strength would result in genotypes with improved standing ability. It is known that plant density and N fertilisation have a negative effect on the standing ability of a wheat crop. These interactions were simulated by evaluating progeny at higher plant densities and higher N application, planted in pots in the tunnel. Both major components showed significant interactions with the characters of stem strength. Again genotypes were found to differ in their ability to produce progeny with strong stems under these conditions. Genetic variances were mainly of an additive nature and parents with solid stems and stronger stems produced

progeny resembling the parental phenotypes. Selection amongst plants and crosses from parents with the best stem strength would ensure improvement for the stem strength trait. Heritability for stem strength and the components thereof were high and significant at all internodes. However, the highest heritability calculated was from genetic variances at high plant densities and high N levels. These results would suggest that more selection progress is to be made in an environment of high population density and high N fertilisation. It is also important to describe the phenotype according to the stem strength components and it is impractical to measure stem thickness, pith thickness and wall thickness in the field. A more practical approach would be to select amongst progeny plants for shorter and solid stems. Phenotypes for resistance to lodging could be idealised to have shorter internodes with thicker pith throughout the stem but especially at internodes one, two and three. A breeding strategy for lodging resistance would induce evaluation and selection in an environment where higher population densities and higher N levels would be simulated.

CHAPTER 6

Summary

The aim of this study was to determine the inheritance and environmental factors that regulate stem strength in irrigation wheat. The strength of the stem is defined by its length and as an index of the function of the pressure which it takes to break the stem, the pith thickness of the stem wall at breaking point and the length of the internodes. In the first experiment a set of parents was evaluated to determine the differences amongst parents for stem strength and its components. The parents significantly differed in stem length and strength. Some parental genotypes had shorter and more solid stems.

For the second experiment the same parental genotypes were used to create a diallel set of progeny. The progeny and the parents were planted in pots in the tunnel in a replicated experiment to evaluate plant height and stem strength. It was found that the variances for all characteristics were significant, but the additive component (general combining ability) was higher than the dominance component. The parents differed significantly in their ability to produce F_1 progeny with stronger stems. The calculated heritability was high and significant, which showed that the best way to select for improved stem strength is to select amongst plants in the progeny of the parents with the highest combining ability for the desirable traits.

The third experiment was done to determine the interaction of higher plant density and higher N fertilisation on the expression of stem strength. This experiment (parents and progeny) was planted in pots in a tunnel. It was found that genotype, plant density and N fertilisation had a highly significant effect on stem strength. The ability of the parents to produce progeny with strong stems differed. The parents with the solid stem phenotype and shorter stems generally produced progeny with stronger stems. The variance for general combining ability (additive genetic variance) is significant. The heritability for all characteristics was high, but higher in increased plant density or increased nitrogen application but with the highest expression where both plant density and nitrogen application were increased. This indicates that selection for stem

strength should be more successful in populations with a higher plant density under high N conditions.

Opsomming

Die studie is onderneem om die oorerflikheid van stamsterkte en die eienskappe wat dit bepaal by verskillende omgewingstoestande, te ondersoek. Die sterkte van die stam is gedefinieer as die lengte daarvan, en word weergegee in terme van 'n indeks wat 'n funksie is van die krag wat benodig word om die stam te breek, die kerndikte van die stam by breekpunt en die litemte. In die eerste eksperiment is 'n stel ouers ondersoek om die verskille tussen ouers vir die stamsterkte en die komponente daarvan te meet. Daar is gevind dat die ouers betekenisvol in lengte en die sterkte van die stam verskil. Hierdie ouer genotipes het 'n soliede en korter stam.

In die tweede eksperiment is 'n dialeel stel kruisings van hierdie ouers gegenereer. Die kruisings, sowel as die ouerlyne, is in 'n eksperiment met herhalings in potte geplant in 'n tunnel en vir planthoogte en stamsterkte geëvalueer. Daar is gevind dat die variasie vir alle eienskappe betekenisvol is, maar dat die additiewe (algemene kombineervermoë) komponent heelwat hoër is. Ouers het betekenisvol van mekaar verskil in hul vermoë om F₁ nageslag met sterk strooi te produseer. Die oorerflikheid was hoog en betekenisvol, wat aandui dat die aangewese manier om stamsterkte te verbeter, sou berus tussen plante binne die nageslag van ouers met die beste kombineervermoë vir die eienskap.

Die derde eksperiment is uitgevoer om te bepaal wat die interaksie van verhoogde plantestand en verhoogde stikstofbemesting op die uitdrukking van stamsterkte is. Die eksperiment (ouers sowel as hul nageslag) is in potte in 'n tunnel aangeplant. Daar is gevind dat die drie hoofkomponente naamlik genotipe, stand en stikstofbemesting 'n hoogs betekenisvolle effek op stamsterkte gehad het. Die ouers het verskil in hul vermoë om nageslag te lewer met sterk stamme. Die ouers met die soliede stam fenotipe en korter strooi het deurgaans 'n nageslag gelewer met sterker stamme. Die variasie vir algemene kombineervermoë (additiewe genetiese variasie) was betekenisvol. Die berekende oorerflikheid was vir alle eienskappe hoog, maar hoër by 'n verhoogde plantestand of verhoogde stikstofbemesting met die hoogste uitdrukking waar beide plantestand en stikstofvoeding verhoog is. Dit beklemtoon 'n strategie

waar seleksie vir stamsterkte beloof om meer suksesvol te wees in populasies wat aan 'n hoër stand en hoër stikstofbemesting onderwerp is.

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Appendix 3.1a Summary for internode length in millimetre (mm) for the diallel trial

		Mean internode length			
Parents		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	31.32	56.3	129.97	329
38	SST 55	59.47	67.9	141.16	263.8
39	SST 806	38.11	69.98	134.53	227.4
40	DH 24	40.12	70.73	138.7	233.6
41	DH 29	30.52	63.55	107.09	222.2
42	3-273	47.33	78.6	128.72	196.8
43	BX	49.6	61.81	140.5	249.8
44	SST 876	45.14	74.46	151.97	251.4
45	36-8	41.11	78.61	147.81	203.8
	Mean for parents	42.52	69.104	135.605	241.97
	Crosses				
1	SST 57 / SST 55	40.21	68.17	117.99	276.6
2	SST 57 / SST 806	33.54	64.61	130.66	271.4
3	SST 57 / DH 24	33.65	66.54	98.37	244.4
4	SST 57 / DH 29	26.69	51.77	106.3	227.2
5	SST 57 / 3-273	54.51	74.67	100.56	292.4
6	SST 57 / BX	34.95	58.78	111.88	212.2
7	SST 57 / SST 876	19.16	48.35	97.21	219.85
8	SST 57 / 36-8	32.06	60.57	108.08	287.8
9	SST 55 / SST 806	37.68	62.5	134.97	262.2
10	SST 55 / DH 24	34.92	64.97	122.31	230
11	SST 55 / DH 29	31.55	54.44	112.77	214.4
12	SST 55 / 3-273	45.04	65.26	111.34	233.2
13	SST 55 / BX	45.63	70.16	117.19	240
14	SST 55 / SST 876	39.09	66.44	135.02	243
15	SST 55 / 36-8	34.12	57.13	111.07	204.2
16	SST 806 / DH 24	41.7	62.92	113.04	202.2
17	SST 806 / DH 29	31.87	50.19	109.34	228.4
18	SST 806 / 3-273	50.26	68.94	122.59	186.8
19	SST 806 / BX	40.88	67.67	128.7	263
20	SST 806 / SST 876	49.01	69	127.73	191.6
21	SST 806 / 36-8	41.43	63.41	120.39	194.4
22	DH 24 / DH 29	33.42	51.38	111.23	220.2
23	DH 24 / 3-273	39.42	64.46	105.24	247.8
24	DH 24 / BX	42.53	72.54	124.66	190.2
25	DH 24 / SST 876	40.06	53.54	104.95	186
26	DH 24 / 36-8	34.69	67.18	138.51	212.2
27	DH 29 / 3-273	44.44	76.67	119.41	230
28	DH 29 / BX	32.89	57.67	111.82	273.4
29	DH 29 / SST 876	31.8	63.27	102.59	239.2
30	DH 29 / 36-8	26.68	49.95	108.2	212.6
31	3-273 / BX	69.98	96.93	177	286.4
32	3-273 / SST 876	58.07	77.87	160.81	293.2
33	3-273 / 36-8	39.42	81.68	152.64	263
34	BX / SST 876	34.63	77.5	139.95	322
35	BX / 36-8	40.08	82.26	180.8	262.2
36	SST 876 / 36-8	30.81	58.15	120.29	254
	Mean for crosses	38.801	65.209	122.1	239.379
	LSD (0.05)	7.928	8.938	16.143	32.322

Appendix 3.1 b Summary for internode diameter in millimetre (mm) for the complete diallel including parent values

Parents		Mean internode diameter			
		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	3.27	3.72	3.66	3.05
38	SST 55	3.81	4.11	3.94	3.1
39	SST 806	3.39	3.91	3.79	2.94
40	DH 24	3.59	3.85	3.78	2.81
41	DH 29	3.74	4.3	4.27	3.07
42	3-273	3.46	3.57	3.5	2.76
43	BX	3.21	3.59	3.47	2.5
44	SST 876	3.57	3.99	3.95	3.07
45	36-8	4.01	4.28	4.47	3.54
	Mean for parents	3.56	3.92	3.87	2.98
	Crosses				
1	SST 57 / SST 55	3.58	3.97	3.89	3.21
2	SST 57 / SST 806	3.25	3.61	3.68	2.96
3	SST 57 / DH 24	2.41	2.6	2.85	2.33
4	SST 57 / DH 29	3.09	3.49	3.64	2.93
5	SST 57 / 3-273	3.16	3.41	3.58	3.11
6	SST 57 / BX	2.6	2.61	3.05	2.42
7	SST 57 / SST 876	2.57	2.96	3.15	2.7
8	SST 57 / 36-8	3.15	3.6	3.97	3.16
9	SST 55 / SST 806	2.68	3.11	3.4	2.52
10	SST 55 / DH 24	3.03	3.46	3.68	2.59
11	SST 55 / DH 29	2.59	3.07	3.23	2.5
12	SST 55 / 3-273	2.49	2.85	2.92	2.62
13	SST 55 / BX	2.83	3.34	3.51	2.75
14	SST 55 / SST 876	2.82	3.29	3.36	2.72
15	SST 55 / 36-8	2.66	3.04	3.13	2.78
16	SST 806 / DH 24	2.88	3.24	3.15	2.45
17	SST 806 / DH 29	2.82	3.31	3.6	2.62
18	SST 806 / 3-273	2.8	3.14	3.2	2.71
19	SST 806 / BX	2.63	2.99	3.16	2.47
20	SST 806 / SST 876	3.21	3.45	3.29	2.52
21	SST 806 / 36-8	3.14	3.59	3.37	3.05
22	DH 24 / DH 29	3.3	3.7	3.79	2.9
23	DH 24 / 3-273	2.57	3.07	3.44	2.77
24	DH 24 / BX	2.91	3.28	3.37	2.61
25	DH 24 / SST 876	2.78	3.04	3.14	2.35
26	DH 24 / 36-8	3.58	4.08	4.28	3.32
27	DH 29 / 3-273	3.5	3.88	3.95	3.19
28	DH 29 / BX	3.26	3.77	3.89	3.01
29	DH 29 / SST 876	2.99	3.64	3.58	2.73
30	DH 29 / 36-8	3.39	4.01	4.33	3.51
31	3-273 / BX	3.74	3.98	4.1	3.32
32	3-273 / SST 876	3.21	3.61	3.69	3.03
33	3-273 / 36-8	3.54	3.92	4.06	3.33
34	BX / SST 876	3.33	3.91	4.27	3.26
35	BX / 36-8	3.65	4.55	4.56	3.5
36	SST 876 / 36-8	3.21	3.85	4.16	3.39
	mean for crosses	3.037	3.456	3.595	2.87
	LSD (0.05)	0.308	0.34	0.309	0.327

Appendix 3.1 c Summary for stem wall thickness in millimetre (mm) for the complete diallel including parent values

		Mean stem wall thickness			
Parents		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	1.56	1.54	1.59	0.65
38	SST 55	1.03	0.99	0.72	0.62
39	SST 806	1	0.99	0.68	0.64
40	DH 24	1.13	1.04	0.7	0.54
41	DH 29	1.07	0.98	0.76	0.65
42	3-273	0.82	0.75	0.67	0.5
43	BX	1.08	0.82	0.65	0.55
44	SST 876	1.06	0.9	0.74	0.56
45	36-8	1.02	0.85	0.67	0.52
Mean for parents		1.085	0.98	0.797	0.581
Crosses					
1	SST 57 / SST 55	1.68	1.8	1.17	0.98
2	SST 57 / SST 806	1.53	1.61	1.22	0.92
3	SST 57 / DH 24	0.6	0.69	0.77	0.75
4	SST 57 / DH 29	1.6	1.93	1.44	1.09
5	SST 57 / 3-273	1.45	1.89	1.87	1
6	SST 57 / BX	1.06	1.37	1.23	0.74
7	SST 57 / SST 876	1.2	1.49	1.15	1.04
8	SST 57 / 36-8	1.36	1.6	1.36	0.93
9	SST 55 / SST 806	0.87	0.8	0.65	0.51
10	SST 55 / DH 24	1.08	0.94	0.77	0.74
11	SST 55 / DH 29	0.87	0.83	0.7	0.62
12	SST 55 / 3-273	0.62	0.71	0.64	0.64
13	SST 55 / BX	0.91	0.82	0.73	0.63
14	SST 55 / SST 876	0.97	0.96	0.7	0.73
15	SST 55 / 36-8	0.89	0.86	0.69	0.62
16	SST 806 / DH 24	0.9	0.74	0.68	0.67
17	SST 806 / DH 29	0.94	0.94	0.7	0.7
18	SST 806 / 3-273	1.05	1	0.88	1.1
19	SST 806 / BX	1.05	0.84	0.67	0.57
20	SST 806 / SST 876	0.99	0.8	0.68	0.78
21	SST 806 / 36-8	1.02	0.94	0.69	0.67
22	DH 24 / DH 29	1.16	0.96	0.79	0.77
23	DH 24 / 3-273	1.12	1.17	1.15	0.99
24	DH 24 / BX	0.86	0.81	0.68	0.56
25	DH 24 / SST 876	1.08	0.92	0.72	0.59
26	DH 24 / 36-8	1.06	1	0.84	0.56
27	DH 29 / 3-273	1.3	1.35	1.09	1.08
28	DH 29 / BX	0.94	0.85	0.75	0.52
29	DH 29 / SST 876	0.79	0.82	0.72	0.68
30	DH 29 / 36-8	1.06	1.03	0.88	0.64
31	3-273 / BX	1.31	1.57	1.19	1.02
32	3-273 / SST 876	0.93	1.24	0.86	1.79
33	3-273 / 36-8	1.08	1.03	0.77	0.7
34	BX / SST 876	0.99	0.94	0.73	0.57
35	BX / 36-8	0.97	0.99	0.77	0.62
36	SST 876 / 36-8	1.27	1.1	0.85	0.7
Mean for crosses		1.07	1.092	0.893	0.783
LSD (0.05)		0.223	0.184	0.201	0.401

Appendix 3.1 d Summary for pith thickness of the internode in millimetre (mm) for the complete diallel including parent values

		Mean internode pith thickness			
Parents		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	0.89	0.81	0.81	0.42
38	SST 55	0.54	0.48	0.36	0.4
39	SST 806	0.59	0.51	0.36	0.43
40	DH 24	0.63	0.54	0.37	0.38
41	DH 29	0.58	0.46	0.36	0.41
42	3-273	0.48	0.42	0.38	0.37
43	BX	0.67	0.46	0.37	0.43
44	SST 876	0.59	0.45	0.38	0.36
45	36-8	0.51	0.4	0.3	0.3
	Mean for parents	0.608	0.503	0.41	0.388
	Crosses				
1	SST 57 / SST 55	0.92	0.88	0.6	0.62
2	SST 57 / SST 806	0.91	0.89	0.66	0.62
3	SST 57 / DH 24	0.57	0.59	0.56	0.7
4	SST 57 / DH 29	1	1	0.78	0.75
5	SST 57 / 3-273	0.87	0.97	0.99	0.64
6	SST 57 / BX	0.82	0.97	0.8	0.61
7	SST 57 / SST 876	0.88	0.95	0.73	0.77
8	SST 57 / 36-8	0.81	0.85	0.68	0.59
9	SST 55 / SST 806	0.65	0.51	0.39	0.4
10	SST 55 / DH 24	0.71	0.55	0.42	0.62
11	SST 55 / DH 29	0.68	0.54	0.43	0.5
12	SST 55 / 3-273	0.49	0.5	0.44	0.52
13	SST 55 / BX	0.65	0.5	0.42	0.46
14	SST 55 / SST 876	0.69	0.59	0.42	0.54
15	SST 55 / 36-8	0.67	0.57	0.44	0.45
16	SST 806 / DH 24	0.63	0.46	0.43	0.55
17	SST 806 / DH 29	0.67	0.57	0.39	0.53
18	SST 806 / 3-273	0.75	0.64	0.55	0.8
19	SST 806 / BX	0.74	0.56	0.42	0.46
20	SST 806 / SST 876	0.61	0.47	0.42	0.63
21	SST 806 / 36-8	0.64	0.52	0.41	0.44
22	DH 24 / DH 29	0.7	0.52	0.42	0.53
23	DH 24 / 3-273	0.87	0.76	0.67	0.71
24	DH 24 / BX	0.6	0.5	0.41	0.43
25	DH 24 / SST 876	0.8	0.61	0.46	0.51
26	DH 24 / 36-8	0.6	0.49	0.39	0.33
27	DH 29 / 3-273	0.74	0.7	0.55	0.68
28	DH 29 / BX	0.57	0.45	0.39	0.34
29	DH 29 / SST 876	0.53	0.45	0.38	0.53
30	DH 29 / 36-8	0.63	0.51	0.4	0.36
31	3-273 / BX	0.7	0.79	0.58	0.61
32	3-273 / SST 876	0.59	0.69	0.46	0.47
33	3-273 / 36-8	0.61	0.53	0.38	0.42
34	BX / SST 876	0.59	0.48	0.34	0.35
35	BX / 36-8	0.53	0.44	0.34	0.35
36	SST 876 / 36-8	0.78	0.57	0.41	0.41
	Mean for crosses	0.7	0.626	0.498	0.534
	LSD (0.05)	0.129	0.098	0.109	0.119

Appendix 3.1 e Summary for the breaking weight of the internode in gram (g) for the complete diallel including parent values

		Mean internode breaking weight			
Parents		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	1702.76	1063.8	462.72	204.08
38	SST 55	1174.88	865.08	405	245.92
39	SST 806	1318.44	731.76	313.72	220.24
40	DH 24	2040.36	801.64	334.52	206.32
41	DH 29	1708.56	1026.76	436.72	233.44
42	3-273	925.52	585.2	313.92	208.48
43	BX	1106.2	641.6	307.08	182.32
44	SST 876	1119.76	723.36	319.36	188.04
45	36-8	1149.76	639.28	309.24	247.24
	Mean for parents	1360.693	786.497	355.808	215.12
	Crosses				
1	SST 57 / SST 55	1626.88	1027.88	523.28	232.56
2	SST 57 / SST 806	1671.44	910.28	485	214.2
3	SST 57 / DH 24	1657.6	811.48	399.64	223.28
4	SST 57 / DH 29	1552.28	995.32	482.08	235.04
5	SST 57 / 3-273	972.08	854.76	534.64	248.8
6	SST 57 / BX	1258.9	754.84	470.92	182.76
7	SST 57 / SST 876	1745.54	927.72	463.72	275.4
8	SST 57 / 36-8	1631.52	1174.2	616.56	256.28
9	SST 55 / SST 806	1042.72	635.72	344.12	173.44
10	SST 55 / DH 24	1301.72	648	416.88	237.92
11	SST 55 / DH 29	1161.56	610.16	327.28	179.04
12	SST 55 / 3-273	935.72	621.52	408.08	227.92
13	SST 55 / BX	843.2	624.6	375.88	229.84
14	SST 55 / SST 876	974.78	647.94	328.8	194.76
15	SST 55 / 36-8	1119.72	612.84	404.04	261.44
16	SST 806 / DH 24	805.16	520.2	286.56	152.44
17	SST 806 / DH 29	1233.6	719.24	344.8	189.8
18	SST 806 / 3-273	917.82	564.16	319.52	260.6
19	SST 806 / BX	1105.98	522.56	329.08	150.68
20	SST 806 / SST 876	812.64	513.92	293.08	191.72
21	SST 806 / 36-8	1296.48	698.84	345.84	255.24
22	DH 24 / DH 29	1609.68	901.28	440.04	222.68
23	DH 24 / 3-273	1324.72	708.88	470.52	209.72
24	DH 24 / BX	995.92	542.08	328.76	205.16
25	DH 24 / SST 876	1092.76	701.56	395.4	175.76
26	DH 24 / 36-8	1560	775.48	399.72	231.13
27	DH 29 / 3-273	1575.72	960.12	560.8	278.72
28	DH 29 / BX	1108.68	854.52	385.96	203.88
29	DH 29 / SST 876	1694.44	798.92	422.6	203.4
30	DH 29 / 36-8	1725.68	1067.28	511.2	263.04
31	3-273 / BX	1048.64	838.96	455.56	316
32	3-273 / SST 876	1002	776.96	373.08	221.92
33	3-273 / 36-8	1134.56	644.72	332.16	236.88
34	BX / SST 876	1376.72	782.12	406.56	189.08
35	BX / 36-8	1299.32	785.44	363.04	299.04
36	SST 876 / 36-8	1763.4	1162.24	510.76	231.04
	Mean for crosses	1277.21	769.353	412.665	223.905
	LSD (0.05)	374.364	158.277	78.705	44.581

Appendix 3.1 f Summary for internode stem strength for the complete diallel including parent values

		Mean internode stem strength			
Parents		Internode 1	Internode 2	Internode 3	Internode 4
37	SST 57	58.28	15.71	3.29	0.27
38	SST 55	10.84	6.13	1.11	0.38
39	SST 806	21.05	5.45	0.86	0.41
40	DH 24	32.19	7.56	0.91	0.39
41	DH 29	33.85	7.69	1.47	0.45
42	3-273	9.39	3.24	0.95	0.39
43	BX	16.04	4.86	0.98	0.34
44	SST 876	14.69	4.4	0.8	0.27
45	36-8	18.32	3.89	0.65	0.35
	Mean for parents	23.85	6.547	1.224	0.361
	Crosses				
1	SST 57 / SST 55	39.17	13.53	2.66	0.51
2	SST 57 / SST 806	46.44	12.53	2.43	0.5
3	SST 57 / DH 24	29.74	7.18	1.8	0.6
4	SST 57 / DH 29	58.37	19.29	3.64	0.78
5	SST 57 / 3-273	16.33	11.19	4.42	0.55
6	SST 57 / BX	33.05	12.72	3.39	0.57
7	SST 57 / SST 876	83.45	19.2	4.33	1.17
8	SST 57 / 36-8	41.83	16.52	3.99	0.56
9	SST 55 / SST 806	17.93	5.28	0.97	0.29
10	SST 55 / DH 24	27.8	5.86	1.46	0.65
11	SST 55 / DH 29	24.82	6.32	1.3	0.42
12	SST 55 / 3-273	10.08	4.86	1.67	0.6
13	SST 55 / BX	13.92	4.51	1.36	0.43
14	SST 55 / SST 876	19.11	6.05	1.02	0.44
15	SST 55 / 36-8	23.09	6.33	1.62	0.58
16	SST 806 / DH 24	12.68	3.94	1.09	0.42
17	SST 806 / DH 29	26.81	8.35	1.25	0.45
18	SST 806 / 3-273	13.65	5.37	1.46	1.16
19	SST 806 / BX	20.66	4.4	1.09	0.26
20	SST 806 / SST 876	10.86	3.48	0.96	0.63
21	SST 806 / 36-8	20.52	5.91	1.19	0.59
22	DH 24 / DH 29	33.45	9.23	1.67	0.56
23	DH 24 / 3-273	30.27	8.71	3.03	0.7
24	DH 24 / BX	14.09	3.79	1.06	0.47
25	DH 24 / SST 876	22.7	8.38	1.72	0.51
26	DH 24 / 36-8	31.83	5.85	1.16	0.39
27	DH 29 / 3-273	26.72	8.74	2.62	0.88
28	DH 29 / BX	19.24	6.68	1.35	0.25
29	DH 29 / SST 876	30.21	5.89	1.64	0.45
30	DH 29 / 36-8	42.95	11.15	1.95	0.48
31	3-273 / BX	10.91	6.9	1.52	0.68
32	3-273 / SST 876	11.04	6.92	1.14	0.36
33	3-273 / 36-8	18.11	4.56	0.83	0.37
34	BX / SST 876	25.01	5.78	0.98	0.21
35	BX / 36-8	16.08	4.58	0.68	0.4
36	SST 876 / 36-8	46.41	11.62	1.75	0.38
	Mean for crosses	26.925	8.1	1.838	0.534
	LSD (0.05)	12.908	2.785	1.716	0.241

Appendix 3.2a Specific combining ability effects for internode length

	Parents	1	2	3	4	5	6	7	8
Internode 1		3.06							
Internode 2	2	8.44							
Internode 3		4.1							
Internode 4		7.33							
Internode 1		-1.38	-5.4						
Internode 2	3	4.49	-1.16						
Internode 3		15.73	9.67						
Internode 4		18.17	32.48						
Internode 1		0.73	-6.16	2.85					
Internode 2	4	6.8	1.7	-0.74					
Internode 3		-11.04	2.54	-7.77					
Internode 4		-3.87	5.24	-6.52					
Internode 1		-0.75	-4.05	-1.5	2.04				
Internode 2	5	-2.29	-3.14	-7.79	-6.22				
Internode 3		5.97	2.08	-2.4	5.02				
Internode 4		-29.21	-18.5	11.54	8.3				
Internode 1		11.12	-6.51	0.94	-7.9	2.6			
Internode 2	6	4.14	-8.8	-5.52	-9.61	8.28			
Internode 3		-18.97	-18.55	-8.35	-20.17	3.08			
Internode 4		23.57	-12.12	-42.48	23.48	-2.46			
Internode 1		-3.44	-0.92	-3.43	0.21	-3.95	17.2		
Internode 2	7	-6.61	1.24	-1.64	3.61	-5.57	17.21		
Internode 3		-13.65	-18.69	-8.23	-6.75	-10.51	35.47		
Internode 4		-67.78	-16.46	22.57	-45.26	29.79	30.37		
Internode 1		-14.88	-3.11	9.05	2.1	-0.69	9.63	-8.81	
Internode 2	8	-13.03	1.53	3.69	-11.38	4.04	2.16	6.93	
Internode 3		-21	6.45	-1.89	-19.14	-12.42	26.6	-0.25	
Internode 4		-51.28	-4.61	-39.98	-40.61	4.44	46.02	63.68	
Internode 1		0.88	-5.22	4.32	-0.42	-2.95	-6.16	-0.5	-5.42
Internode 2	9	-2.13	-9.1	-3.21	0.94	-10.61	4.65	10.37	-9.73
Internode 3		-14.04	-21.42	-13.14	10.5	-10.73	14.51	36.67	-16.51
Internode 4		30.64	-29.45	-23.21	-0.45	-8.19	29.79	17.84	18.49
Standard Errors									
		Internode 1	Internode 2	Internode 3	Internode 4				
Sii		2.74	3.09	5.58	11.18				
Sij		3.1	3.49	6.31	12.64				
Sii-Sjj		3.82	4.31	7.78	15.59				
Sij-Sik		4.57	5.15	9.3	18.63				
Sij-Skl		4.33	4.88	8.83	17.68				

Appendix 3.2b Specific combining ability effects for internode diameter

	Parents	1	2	3	4	5	6	7	8
Internode 1		0.637							
Internode 2	2	0.6863							
Internode 3		0.5003							
Internode 4		0.4086							
Internode 1		0.3261	-0.2412						
Internode 2	3	0.3396	-0.2272						
Internode 3		0.347	0.0719						
Internode 4		0.2237	-0.1212						
Internode 1		-0.5632	0.0595	-0.0714					
Internode 2	4	-0.6628	0.1305	-0.0783					
Internode 3		-0.567	0.2759	-0.1993					
Internode 4		-0.3794	-0.0243	-0.1072					
Internode 1		-0.0483	-0.5396	-0.2945	0.1363				
Internode 2	5	-0.0759	-0.5546	-0.3093	0.0943				
Internode 3		-0.0701	-0.4672	-0.0504	0.0656				
Internode 4		-0.0148	-0.3537	-0.1687	0.1323				
Internode 1		0.0717	-0.6016	-0.2765	-0.5477	0.2232			
Internode 2	6	0.0667	-0.5461	-0.2528	-0.3112	0.1957			
Internode 3		0.1012	-0.5439	-0.2152	-0.0472	0.1677			
Internode 4		0.157	-0.2399	-0.0888	-0.0019	0.1826			
Internode 1		-0.4419	-0.2092	-0.3901	-0.1574	0.0255	0.5595		
Internode 2	7	-0.7823	-0.117	-0.4537	-0.1621	0.0268	0.4654		
Internode 3		-0.5083	-0.0333	-0.3326	-0.1986	0.0183	0.4736		
Internode 4		-0.4217	0.0013	-0.2116	-0.0467	0.1179	0.4217		
Internode 1		-0.4608	-0.2061	0.199	-0.2923	-0.2234	0.0386	0.207	
Internode 2	8	-0.4486	-0.1793	-0.0061	-0.4064	-0.1055	0.081	0.3261	
Internode 3		-0.3795	-0.1606	-0.1779	-0.3999	-0.265	0.0903	0.5828	
Internode 4		-0.1843	-0.0712	-0.2021	-0.3592	-0.2147	0.0832	0.4264	
Internode 1		-0.161	-0.6423	-0.1552	0.2455	-0.1096	0.0864	0.2508	-0.1821
Internode 2	9	-0.121	-0.7397	-0.1884	0.3132	-0.0539	0.0767	0.6517	-0.0528
Internode 3		0.0496	-0.7735	-0.4808	0.3532	0.1041	0.0674	0.4899	0.1187
Internode 4		-0.1121	-0.399	-0.0639	0.227	0.1815	-0.0067	0.2786	0.1301
Standard Errors									
		Internode 1	Internode 2	Internode 3	Internode 4				
Sii		0.1	0.11	0.1	0.11				
Sij		0.12	0.13	0.12	0.12				
Sii-Sjj		0.14	0.16	0.14	0.15				
Sij-Sik		0.17	0.19	0.17	0.18				
Sij-Skl		0.16	0.18	0.16	0.17				

Appendix 3.2c Specific combining ability effects for stem wall thickness

	Parents	1	2	3	4	5	6	7	8
Internode 1		0.4137							
Internode 2	2	0.3858							
Internode 3		-0.0121							
Internode 4		0.1828							
Internode 1		0.2343	-0.0943						
Internode 2	3	0.2051	-0.0849						
Internode 3		0.0328	0.0011						
Internode 4		0.0823	-0.1479						
Internode 1		-0.6806	0.1328	-0.0806					
Internode 2	4	-0.6884	0.0876	-0.1051					
Internode 3		-0.4416	0.0968	0.0017					
Internode 4		-0.045	0.1288	0.0123					
Internode 1		0.2599	-0.1346	-0.1021	0.135				
Internode 2	5	0.4336	-0.1424	-0.0311	0.0215				
Internode 3		0.1584	-0.0472	-0.0523	0.0193				
Internode 4		0.2259	-0.0563	-0.0208	0.0959				
Internode 1		0.133	-0.3615	0.031	0.1241	0.2447			
Internode 2	6	0.3182	-0.3398	-0.0445	0.162	0.21			
Internode 3		0.4784	-0.2152	0.0197	0.2633	0.1373			
Internode 4		-0.0368	-0.207	0.2084	0.1412	0.1701			
Internode 1		-0.225	-0.0495	0.059	-0.1099	-0.0993	0.3037		
Internode 2	7	-0.052	-0.074	-0.0607	-0.0522	-0.1402	0.5144		
Internode 3		-0.0051	0.0353	-0.0318	-0.0441	-0.0421	0.2819		
Internode 4		-0.0232	0.0546	-0.0519	-0.0192	-0.1203	0.203		
Internode 1		-0.0946	0.0028	-0.0146	0.0985	-0.253	-0.0819	-0.0059	
Internode 2	8	0.0471	0.0371	-0.1136	0.0329	-0.1931	0.1595	0.0073	
Internode 3		-0.0676	0.0208	-0.0083	0.0093	-0.0667	-0.0307	-0.0081	
Internode 4		0.1272	-0.001	0.0104	-0.1368	-0.1099	0.8233	-0.125	
Internode 1		0.0227	-0.1079	-0.0173	0.0437	-0.0177	0.0274	-0.0606	0.2277
Internode 2	9	0.1389	-0.0771	0.0102	0.0987	0.0027	-0.0687	0.0371	0.1342
Internode 3		0.1139	-0.0198	-0.0229	0.1008	0.0668	-0.1452	0.0093	0.1048
Internode 4		0.157	0.0288	0.0323	-0.031	-0.0141	-0.1328	0.0648	-0.0108
Standard Errors									
		Internode 1	Internode 2	Internode 3	Internode 4				
Sii		0.07	0.06	0.06	0.13				
Sij		0.08	0.07	0.07	0.15				
Sii-Sjj		0.1	0.08	0.09	0.19				
Sij-Sik		0.12	0.1	0.11	0.23				
Sij-Skl		0.12	0.1	0.11	0.21				

Appendix 3.2d Specific combining ability effects for pith thickness

	Parents	1	2	3	4	5	6	7	8
Internode 1		0.1027							
Internode 2	2	0.0743							
Internode 3		-0.0711							
Internode 4		0.0272							
Internode 1		0.0715	-0.0033						
Internode 2	3	0.0735	-0.0176						
Internode 3		-0.0215	-0.0075						
Internode 4		-0.0061	-0.1096						
Internode 1		-0.2582	0.0631	-0.0442					
Internode 2	4	-0.2136	0.0233	-0.0614					
Internode 3		-0.1329	0.0171	0.0167					
Internode 4		0.0879	0.1184	0.0152					
Internode 1		0.1716	0.0329	0.0016	0.04				
Internode 2	5	0.1839	0.0108	0.0361	-0.007				
Internode 3		0.0905	0.0305	-0.0238	0.0007				
Internode 4		0.1437	0.0063	0.003	0.021				
Internode 1		0.0484	-0.1424	0.0944	0.2207	0.0925			
Internode 2	6	0.0897	-0.0994	0.0319	0.1648	0.0903			
Internode 3		0.2215	-0.0485	0.0531	0.1616	0.0511			
Internode 4		-0.0096	-0.023	0.2257	0.1497	0.1235			
Internode 1		0.0009	0.0202	0.0889	-0.0527	-0.0689	0.0638		
Internode 2	7	0.1646	-0.0265	0.0308	-0.0223	-0.0808	0.191		
Internode 3		0.1164	0.0184	0.016	-0.0095	-0.026	0.0809		
Internode 4		0.0564	0.021	-0.0143	-0.0323	-0.1105	0.1103		
Internode 1		0.0505	0.0498	-0.0515	0.1369	-0.1253	-0.0545	-0.048	
Internode 2	8	0.1286	0.0515	-0.0732	0.0817	-0.0888	0.077	-0.0561	
Internode 3		0.0533	0.0273	0.0129	0.0475	-0.0271	-0.0322	-0.0693	
Internode 4		0.179	0.0595	0.1103	0.0063	0.0341	-0.0752	-0.0892	
Internode 1		0.0216	0.0649	0.0116	-0.03	0.0078	-0.0015	-0.0769	0.1587
Internode 2	9	0.0683	0.0772	0.0244	-0.0047	0.0108	-0.0414	-0.0605	0.0675
Internode 3		0.038	0.076	0.0376	0.0082	0.0236	-0.0835	-0.0425	0.0364
Internode 4		0.0843	0.0608	0.0095	-0.0805	-0.0427	-0.0299	-0.0019	0.0166
Standard errors									
		Internode							
		1	Internode 2	Internode 3	Internode 4				
Sii		0.04	0.03	0.03	0.04				
Sij		0.05	0.03	0.04	0.04				
Sii-Sjj		0.06	0.04	0.05	0.05				
Sij-Sik		0.07	0.05	0.06	0.06				
Sij-Skl		0.07	0.05	0.06	0.06				

Appendix 3.2e Specific combining ability effects for breaking weight

	Parents	1	2	3	4	5	6	7	8
Internode 1		242.1							
Internode 2	2	138.1							
Internode 3		48.01							
Internode 4		4.57							
Internode 1		271.5	21.5						
Internode 2	3	76	21.9						
Internode 3		60.9	7.56						
Internode 4		4.41	-32.02						
Internode 1		-6.5	16.3	-495.4					
Internode 2	4	-83.2	-26.2	-98.5					
Internode 3		-63.65	41.13	-38.02					
Internode 4		9.66	28.63	-38.65					
Internode 1		-170.9	-183	-126.1	-14.1				
Internode 2	5	-58.3	-222.9	-58.4	63.3				
Internode 3		-30.45	-97.71	-29.02	27.03				
Internode 4		5.8	-45.86	-16.9	12.15				
Internode 1		-358.7	-16.4	-49.4	93.3	285.2			
Internode 2	6	-33.4	-46.1	-48	36.4	128.7			
Internode 3		46.29	7.27	-30.12	81.69	122.73			
Internode 4		3.65	-12.89	37.98	-16.73	36.66			
Internode 1		-116.2	-153.2	94.4	-279.8	-226.2	106.2		
Internode 2	7	-119.5	-29.2	-75.8	-116.6	36.9	186.8		
Internode 3		14.6	7.1	11.47	-28.04	-20.08	73.7		
Internode 4		-37.26	14.16	-46.81	3.85	-13.05	83.16		
Internode 1		238.4	-153.6	-330.9	-315	227.6	-72.4	258	
Internode 2	8	-16.6	-75.9	-154.4	-27.1	-88.7	54.8	73.8	
Internode 3		-1.95	-49.33	-33.88	29.25	7.21	-18.13	47.38	
Internode 4		62.83	-13.47	1.68	-18.11	-6.08	-3.47	-11.18	
Internode 1		21.8	-111.3	50.3	49.7	156.2	-42.5	78	410.1
Internode 2	9	189.8	-151.1	-9.6	6.7	139.6	-117.6	37	343.8
Internode 3		126.43	1.45	-5.58	9.11	71.35	-83.51	-20.6	117.77
Internode 4		2.85	12.35	24.35	-3.6	12.7	-29.37	57.92	-2.63
Standard errors									
		Internode 1	Internode 2	Internode 3	Internode 4				
Sii		129.51	54.75	27.22	15.42				
Sij		146.4	61.89	30.78	17.43				
Sii-Sjj		180.6	76.35	37.96	21.5				
Sij-Sik		215.86	91.26	45.38	25.7				
Sij-Skl		204.78	86.58	43.05	24.38				

Appendix 3.2f Specific combining ability effects for stem strength

	Parents	1	2	3	4	5	6	7	8
Internode 1		0.46							
Internode 2	2	0.938							
Internode 3		-0.255							
Internode 4		-0.0284							
Internode 1		6.46	2.25						
Internode 2	3	0.381	0.277						
Internode 3		-0.291	-0.024						
Internode 4		-0.0808	-0.1924						
Internode 1		-15.27	7.1	-9.3					
Internode 2	4	-5.688	0.133	-1.345					
Internode 3		-1.162	0.223	0.044					
Internode 4		0.0172	0.1716	-0.0988					
Internode 1		7.6	-1.64	-0.93	0.68				
Internode 2	5	4.338	-1.495	0.979	1.143				
Internode 3		0.356	-0.267	-0.124	0.062				
Internode 4		0.1897	-0.0699	-0.0783	0.0377				
Internode 1		-18.59	-0.53	1.76	13.35	4.05			
Internode 2	6	-1.283	-0.466	0.479	3.104	1.042			
Internode 3		1.111	0.086	0.066	1.395	0.665			
Internode 4		-0.1155	0.0308	0.5525	0.0985	0.269			
Internode 1		-4.51	0.66	6.12	-5.47	-6.08	1.45		
Internode 2	7	0.672	-0.395	-0.064	-1.395	-0.595	2.108		
Internode 3		0.552	0.251	0.17	-0.1	-0.132	0.019		
Internode 4		0.0941	0.0585	-0.1559	0.0541	-0.1673	0.1794		
Internode 1		37.42	-2.62	-12.14	-5.33	-3.57	-6.89	4.43	
Internode 2	8	5.601	-0.406	-2.535	1.646	-2.93	0.579	-0.135	
Internode 3		1.332	-0.251	-0.118	0.404	-0.002	-0.517	-0.206	
Internode 4		0.6301	-0.0015	0.1441	0.0321	-0.0353	-0.2146	-0.169	
Internode 1		-4.14	1.43	-2.42	3.87	9.23	0.25	-4.44	17.42
Internode 2	9	3.085	0.034	0.061	-0.716	2.494	-1.615	-1.171	4.32
Internode 3		1.06	0.408	0.172	-0.095	0.367	-0.774	-0.451	0.459
Internode 4		0.0392	0.1556	0.1312	-0.0668	0.0177	-0.1795	0.0401	-0.039
Standard errors									
		Internode 1	Internode 2	Internode 3	Internode 4				
Sii		4.46	0.96	0.3	0.08				
Sij		5.04	1.08	0.34	0.09				
Sii-Sjj		6.22	1.34	0.42	0.11				
Sij-Sik		7.44	1.6	0.5	0.13				
Sij-Skl		7.06	1.52	0.47	0.13				

Appendix 3.2g Specific combining ability effects for plant height

Parents	1	2	3	4	5	6	7	8	
2	21.4								
3	39.3	35.9							
4	18.1	1.7	-13.5						
5	-33.6	-37.7	1.1	3.5					
6	37.6	-48.8	-57.7	-13.2	-4.6				
7	-106.9	-33.4	9.6	-49.1	22.3	121.4			
8	-73.3	-8	-36.9	-88.5	-7.8	84	64.1		
9	7	-80.3	-44	9.9	-34	42.8	66	11.1	
		Standard errors							
Sii	13.03								
Sij	14.73								
Sii-Sjj	18.17								
Sij-Sik	21.71								
Sij-Skl	20.61								

Appendix 4.1a Summary for stem strength for internode two for the four treatments for the complete diallel including parent values

		Mean stem strength			
		Internode 2	Internode 2	Internode 2	Internode 2
		Treatment 1	Treatment 2	Treatment 3	Treatment 4
Parents					
11	SST 806	8.08	7.29	5.5	5.83
12	DH 24	6.94	3.12	7.7	1.85
13	DH 29	12.56	8.39	5.6	6.67
14	SST 55	4.7	3.02	2.44	2.71
15	BX	4.86	2.89	2.43	1.46
Mean for parents		7.428	4.942	4.734	3.704
Crosses					
1	SST 806 / DH 24	8.85	4.91	4.18	4.03
2	SST 806 / DH 29	21.88	10.65	7.83	8.03
3	SST 806 / SST 55	7.31	7.53	5.66	3.05
4	SST 806 / BX	6.55	4.23	4.48	2.84
5	DH 24 / DH 29	15.72	9.83	7.92	5.12
6	DH 24 / SST 55	8.9	9.08	7.36	5.92
7	DH 24 / BX	7.32	8.11	6.26	3.3
8	DH 29 / SST 55	9.14	11.21	6.2	6.64
9	DH 29 / BX	9.26	5.06	6.4	2.58
10	SST 55 / BX	8.06	8.6	2.93	3.66
Mean for crosses		10.299	7.921	5.922	4.517
LSD (0.05)		9.27	6.34	4.75	3.4

Appendix 4.1b Summary for stem strength for internode three for the four treatments for the complete diallel including parent values

		Mean stem strength			
		Internode 3	Internode 3	Internode 3	Internode 3
		Treatment 1	Treatment 2	Treatment 3	Treatment 4
Parents					
11	SST 806	1.53	1.73	1.07	1.68
12	DH 24	1.26	0.82	0.99	0.65
13	DH 29	2.06	1.79	1.48	0.99
14	SST 55	1.17	1.15	0.84	0.7
15	BX	1.27	1.19	0.67	0.67
Mean for parents		1.458	1.336	1.01	0.938
Crosses					
1	SST 806 / DH 24	1.59	1.01	1.05	0.96
2	SST 806 / DH 29	2.51	1.61	1.61	1.53
3	SST 806 / SST 55	1.48	1.29	1.04	0.97
4	SST 806 / BX	1.3	0.95	0.85	0.79
5	DH 24 / DH 29	2.06	1.28	1.74	0.78
6	DH 24 / SST 55	1.57	2.2	1.62	1.01
7	DH 24 / BX	1.29	1.15	1.3	0.62
8	DH 29 / SST 55	1.71	1.55	1.44	1.4
9	DH 29 / BX	1.68	1.18	1.39	0.55
10	SST 55 / BX	1.48	1.39	0.72	0.82
Mean for crosses		1.667	1.361	1.276	0.943
LSD (0.05)		0.8	0.89	0.68	0.55

Appendix 4.1c Summary for stem strength for internode four for the four treatments for the complete diallel including parent values

		Mean stem strength			
		Internode 4	Internode 4	Internode 4	Internode 4
		Treatment 1	Treatment 2	Treatment 3	Treatment 4
Parents					
11	SST 806	0.32	0.41	0.31	0.43
12	DH 24	0.51	0.36	0.53	0.37
13	DH 29	0.64	0.57	0.54	0.34
14	SST 55	0.38	0.37	0.30	0.27
15	BX	0.44	0.52	0.29	0.32
Mean for parents		0.458	0.446	0.39	0.346
Crosses					
1	SST 806 / DH 24	0.32	0.31	0.31	0.23
2	SST 806 / DH 29	0.66	0.43	0.43	0.39
3	SST 806 / SST 55	0.37	0.36	0.31	0.27
4	SST 806 / BX	0.43	0.32	0.31	0.22
5	DH 24 / DH 29	0.71	0.51	0.59	0.3
6	DH 24 / SST 55	0.48	0.45	0.41	0.28
7	DH 24 / BX	0.48	0.43	0.49	0.23
8	DH 29 / SST 55	0.47	0.39	0.36	0.34
9	DH 29 / BX	0.55	0.47	0.44	0.24
10	SST 55 / BX	0.45	0.4	0.26	0.22
Mean for crosses		0.492	0.407	0.39	0.272
LSD (0.05)		0.25	0.19	0.173	0.12

Appendix 4.2 SCA effects for all the internodes in all treatments

		Parent				Standard Error			
Treatment 1		1	2	3	4	Internode 2	Internode 3	Internode 4	
Internode 2	2	-0.963				Sii	2.20	0.19	0.05
Internode 3		0.025				Sij	2.79	0.24	0.07
Internode 4		-0.114				Sii - Sjj	2.96	0.25	0.08
Internode 2	3	8.288	2.991			Sij - Sik	4.19	0.36	0.11
Internode 3		0.503	0.184			Sij - Skl	3.82	0.33	0.10
Internode 4		0.133	0.101						
Internode 2	4	-0.811	1.645	-1.887					
Internode 3		-0.027	0.197	-0.098					
Internode 4		0.003	0.034	-0.075					
Internode 2	5	-1.300	0.340	-1.499	2.772				
Internode 3		-0.165	-0.044	-0.086	0.211				
Internode 4		0.030	-0.008	-0.031	0.036				
Treatment 2						Standard Error			
Internode 2	2	-1.581				Internode 2	Internode 3	Internode 4	
Internode 3		-0.250				Sii	1.51	0.21	0.04
Internode 4		-0.055				Sij	1.91	0.26	0.05
Internode 2	3	1.964	1.677			Sii - Sjj	2.02	0.28	0.06
Internode 3		0.073	-0.111			Sij - Sik	2.86	0.4	0.08
Internode 4		-0.011	0.047			Sij - Skl	2.61	0.36	0.08
Internode 2	4	0.424	2.513	2.449					
Internode 3		-0.182	0.878	-0.046					
Internode 4		0.003	0.068	-0.062					
Internode 2	5	-1.346	3.063	-2.181	2.942				
Internode 3		-0.279	0.071	-0.173	0.099				
Internode 4		-0.078	-0.0003	-0.034	-0.013				
Treatment 3						Standard Error			
Internode 2	2	-2.439				Internode 2	Internode 3	Internode 4	
Internode 3		-0.152				Sii	1.13	0.16	0.04
Internode 4		-0.100				Sij	1.43	0.2	0.05
Internode 2	3	1.050	0.382			Sii - Sjj	1.51	0.21	0.05
Internode 3		0.193	0.183			Sij - Sik	2.14	0.3	0.07
Internode 4		0.009	0.051			Sij - Skl	1.96	0.28	0.07
Internode 2	4	1.049	1.548	0.684					
Internode 3		0.0044	0.441	0.056					
Internode 4		0.0306	0.006	-0.056					
Internode 2	5	0.175	0.750	1.180	-0.565				
Internode 3		-0.0603	0.253	0.134	-0.157				
Internode 4		0.0106	0.066	0.011	-0.034				
Treatment 4						Standard Error			
Internode 2	2	-0.322				Internode 2	Internode 3		
Internode 3		-0.123							
Internode 2	3	-0.247	-0.101			Sii	0.81	0.13	
Internode 3		0.228	-0.107			Sij	1.02	0.16	
Internode 2	4	-1.676	2.272	1.045		Sii - Sjj	1.08	0.17	
Internode 3		-0.247	0.215	0.378		Sij - Sik	1.53	0.25	
Internode 2	5	-0.543	0.994	-1.673	0.977	Sij - Skl	1.4	0.23	
Internode 3		-0.216	0.036	-0.254	0.101				