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INHERITANCE OF ROOT ROT RESISTANCE IN MAIZE (*ZEA MAYS* L.)

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CHAPTER 1

GENERAL INTRODUCTION

Maize (*Zea mays* L.) is one of the most important food crops among the world's cereal crops, such as wheat, rice, maize and sorghum. Maize ranks second after wheat in world production (FAO, 1992; Dowswell *et al*, 1996; Kling & Edmeandes, 1997). According to Purseglove (1975), maize is used for three main purposes, namely as a staple human food, feed for livestock and as raw material for many industrial products. In the tropics maize is a major source of human nutrition. In Latin America, Africa and Asia, several hundred million people depend on maize for their daily food. It is a source of dietary protein and is a major source of calories. Much of maize grown in the temperate and developed countries is used for animal feed (Purseglove, 1975; Kling & Edmeands, 1997). Animal feed accounts for 70% or more of total maize utilised in industrialised economies, including Eastern Europe and the former Soviet Union, and in certain middle-income and newly industrialised nations of the third world (Dowswell *et al*, 1996). In the industrial economies, maize is the feed ingredient of choice in formula feeds because of its low cost and high degree of consistency. As nutrient for human and animals, maize serves as a basic raw material for the production of starch, oil and protein, alcoholic beverages, food sweeteners and also more recently for the production of fuel (FAO, 1992; Dowswell *et al*, 1996).

Maize is grown on more than 100 million ha each year, with an annual production of about 250 million metric tons (FAO, 1992). Maize grows throughout the temperate, subtropical, and tropical zones where rainfall or irrigation is adequate. Maize has a fairly low water requirement per unit of dry matter produced, but also has low drought tolerance. Therefore it is important to maintain an adequate soil moisture regime through water conservation or irrigation. Maize is susceptible to a number of diseases that

can infect all plant organs and serve as a constraint in grain production. Reduction in grain production caused by diseases is estimated to an average of 9.4% (Agrios, 1978). Root rot of maize contributes to yield reduction and reduced grain quality (McKeen, 1953). In general, losses due to root rots are subtle and it is only when lodging and wilting occurs that these losses become conspicuous. Etiology is complex and includes several fungi and bacteria, the spectrum depending to a large extent on environmental conditions (Manns & Phillips, 1924; Mortimore & Ward, 1964).

Despite the paucity of research on maize root rot from 1940 until 1950, researchers have concluded that the majority of the fungi occurring in the root rot complex are soil inhabiting fungi that infect maize roots under various environmental conditions (Ho & Melhus, 1940). Factors such as soil, temperature, moisture, nutrients and soil physical properties could contribute to maize root rot (Manns & Phillips 1924). The severity of root rot is dependant to some extent on plant stress, most of which have yet to be quantified. Stress reduction can be achieved by ensuring optimum soil fertility, optimum tillage practices and relevant planting date. Effective weed and insect control are also necessary for optimum conditions and should be included in crop production (Mortimore & Ward, 1964). Effective root rot control is difficult because of the wide spectrum of pathogens associated with this disease. Chemical control is often not economically justifiable (Sumner *et al.*, 1990). Breeding for resistance is the only effective long-term control strategy (Whitney & Mortimore, 1961).

(Williams & Schmitthenner, 1963) found a high correlation between the severities of maize root rot and stalk rot. A number of authors have repeatedly called attention to the difficulty of evaluating stalk and root rot in the field. Some are concerned about visible symptom development while others are concerned about actual losses in yield and grain quality. Lodging has also been used to measure stalk and root rot resistance. In this regard

root rot has been neglected and the full impact of the disease on yield and grain quality has yet to be quantified (Mc Laren, personal communication).

The objective of this study was to review maize root rot research to determine susceptibility of commercial genotypes to root rot and to quantify the inheritance of resistance to root rot.

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CHAPTER 2

HOST PATHOGEN INTERACTION AND STABILITY OF RESISTANCE TO MAIZE ROOT ROT: AN OVERVIEW

ABSTRACT

This literature review discusses the principal aspects of host pathogen interactions and stability of resistance to maize *(Zea mays* L.*)* root rot. The pathogens involved in the maize root rot-complex, the symptoms of the disease predisposition and its role in the severity of the root rot complex, methods of quantifying maize root rot resistance, effects on yield and the control of the disease are also addressed.

Furthermore, different methods of disease management are reviewed with emphasis on genetic control. In general, more references were obtained from studies done on corn and wheat in the United States of America and South Africa where *Fusarium ssp.* are important pathogens of maize roots. Due to lack of information, only a few references addressing this disease throughout the Southern African region were included.

2.1 INTRODUCTION

Numerous fungal species are known to infect maize and cause roots to rot. Root discoloration is the most distinct symptom of root rot, and various forms of disease ratings have been based on this symptom (Manns & Philips, 1924). Despite statements that root rot is one of the most important diseases of maize, research on this disease has revolved mainly around the spectrum of fungi and disease symptoms (Manns & Philips, 1924; Thayer & Williams, 1960; Mohr & Le Roux, 1977). Several environmental factors play an important role in the incidence of the disease and may predispose the maize crop to disease. The views of Yarwood (1959), Colhoun (1973) and Schoeneweiss (1975) on the pathogenicity of the fungi differ considerably, and a distinct relationship between disease severity and yield has not yet been established. Various control measures seem promising in minimising the incidence and effect of root rot in maize. These include host plant resistance, chemical control, tillage practices and plant nutrition.

It is proposed that future research should identify the relative importance of the fungi associated with maize roots in order to focus research efforts on a few important pathogens and their effect on yield. Furthermore, an appropriate method to quantify the disease is essential to ensure satisfactory progress towards finding a solution to the root rot problem.

2.2. *PATHOGENS INVOLVED IN THE MAIZE ROOT ROT- COMPLEX*

Early research on the etiology of maize root rot indicated that there is no single causal organism, but that several fungi and even bacteria may be involved, the spectrum depending to a large extent on environment conditions (Manns & Phillips, 1924; Mortimore & Ward, 1964). The roots of maize plants grow in a milieu of high fungal populations for much of the season and are invaded by soil-borne fungal pathogens (Dodd, 1980). However, there is little agreement between researchers on the most important pathogens in the complex (Miller, 1964; Palmer & Kommedahl, 1969; Deacon & Scott, 1983). Chambers (1987) stated that fungi infecting maize roots are facultative parasites that occur in the soil and under the seed coat. He concluded that the ability of a fungus to cause maize root rot is an isolate rather than a species attribute. Due to the association of fungal flora with soil or debris, it is difficult to discern whether a fungal species is the primary disease causal agent, secondary invader or an entophyte (Leslie *et al*, 1990).

Pearson (1931) found hyphae of *F. graminearum* on maize to invade the ruptured area where adventitious roots emerge from the mesocotyl, but that hyphae did not pierce endodermal cells.

The contradictory results on the pathogenicity of *Fusarium spp.* emphasizes the complexity of the root rot problem. Many *Fusarium* species are viewed as opportunistic pathogens, capable only of attacking plants weakened by some stress factors (Leslie *et al*, 1990). The primary pathogen isolated from maize seedlings, collected in a commercial field in Mississippi, with poor stand problems was *F. moniliforme* (Futrell & Kilgore, 1969).

Rao *et al*, (1978) found *F. moniliforme* to be strongly pathogenic on maize roots in Ohio, USA. However, Chambers (1987) discovered this to be only weakly pathogenic in South Africa. Miller (1964) considered *F. graminearum*

as an important pathogen in the maize root rot-complex, while other researchers only occasionally isolated *F. graminearium.*

F. oxysporum causes wilting in many crops, but it is not a pathogen of maize roots except in sterile soil with a high inoculum potential (Palmer & Kommedahl, 1969). *F. oxysporum* and *Pyrenochaeta terrestris* were numerically dominant in rotten maize roots in the USA, throughout the season. Manns & Phillips (1924) observed that *Pythium spp.* have been common on maize roots since the early years of research on maize. Rao *et al* (1978) showed that *P. graminicola* is both a prevalent and virulent pathogen on maize roots. Hellinga *et al* (1983) found *Pythium spp.* to be the main cause of maize root rot while *Fusarium spp.* mainly contribute to root rot at a later growth stage.

Rhizoctonia spp. are also a major fungus in the maize root rot complex. Fowler (1980) found root rot caused by *R. solani* and several *Fusarium spp.* to be widespread in maize fields in New Zealand. *R. solani, R. zeae* and a binucleate *Rhizoctonia sp.* were isolated occasionally from lesions on maize roots in Georgia, USA. *Helminthosporium pedicellatum* was frequently associated with diseased maize and sorghum roots in California, USA, (Shepherd *et al*, 1962; Shepherd, *et al* 1967). Du Toit (1968) isolated *H. pedicellatum* in South Africa and found that it caused severe root rot of plants in inoculated soil.

2.3. *SYMPTOMS ASSOCIATED WITH MAIZE ROOT ROT*

Symptoms associated with maize root rot, particularly aerial symptoms, can be very deceptive. It is therefore essential to inspect root systems for signs of discoloration and poor root development. The incidence of root rot is enhanced by environmental conditions such as strong winds, drought stress, shallow soil and tillage practices which result in soil compaction. Maize plantings subjected to root rot are characterized by poor stands and uneven growth, while older plants are stunted and chlorotic (Richardson, 1942). In such cases, root systems are often rotted to such an extent that only a few secondary roots are still functional. Eventually lodging of plants occur. Lodging may be caused either by root rot, or by stalk rot where the stalk usually snaps between the fourth and fifth internode. Dodd (1980) stated that root lodging is the condition in which maize plants are leaning, but not broken. Lodging of maize varies from season to season, the extent of lodging is dependant on the type of environmental stress that occurs (Thompson, 1972). Plants with crown and brace root rot lodge frequently and make machine harvesting difficult (Sumner & Bell, 1986).

Root rot symptoms on maize occur in the following sequence: seminal root rot, forming lens-shaped lesions, the onset of general browning, necrosis of root tips longitudinal fissuring of the cortex, decortication and eventually complete discoloration of the roots. Shepherd *et al* (1967) reported that the lesions on maize roots are initially light brown and somewhat water-soaked in appearance. Lesions enlarge and form elongated, dark, sunken areas on larger secondary roots. The cortex tissue is initially affected, but eventually the lesions will include the vascular tissue beneath the endodermis. Sumner & Bell (1982) found that rotted roots which disintegrated 2-5 cm below the soil surface resulted in symptoms such as lodging, stunting and chlorosis. Fungi associated with the maize root rot complex might predispose plants to

drought stress and thereby hasten the development of the main phase of the root rot stalk rot complex by inducing early senescence of the basal regions (Deacon & Scott, 1983).

Although various pathogens may invade maize roots at a relatively early plant growth stage, root and stalk rot is essentially a disease related to the onset of senescence and usually produces no visible symptoms until the plant has reached physiological maturity (Mortimore & Ward, 1964). Sumner & Bell (1982) found that diseased plants were occasionally stunted and chlorotic, but plants with severe crown and lateral root rot could not be distinguished from plants with well-developed root systems above ground, unless the plants were leaning. Odvody & Dunkle (1979) observed that roots of stressed male sterile sorghum plants from infested soil were symptomless in the greenhouse, but had a high percentage of infection by *Macrophomina phaseolina*.

Different fungi have been associated with specific root rot symptoms. *Fusarium spp.* had a distinctive, though considerably less pronounced parasitic effect resulting in the destruction of many lateral roots and occasionally causing light brown lesions on the larger roots (Richardson, 1942). *F. oxysporum* attacks roots by direct penetration of the epidermis and colonizes the cortex tissue vigorously (Du Toit,1968). Rao *et al* (1978) found that *F. roseum* produced scattered reddish-brown lesions. Infections by *Pythium ssp.* usually commences at the apex of the root and progresses rapidly as a light coloured, watery soft rot, destroying first the cortical tissues and later the vascular system (Richardson, 1942). Roots infected with *P. ultimum* exhibit very little external discoloration and internal symptoms include the presence of a dense material filling cells in the cortex and stele, the thickening of cell walls and necrosis of epidermal cells (Kisiel *et al*,1969). *P. graminicola* produces dark brown lesions, while *P. terrestris* causes pink root rot (Rao *et al*,1978).

Roots infected by *Helminthosporium spp.* are dark brown or black and leathery (Richardson, 1942). The fate of seedlings is determined by the speed of penetration of the outer sheaths of the embryo, either lesions form, plants are stunted or seedlings are killed. In initial pathogenicity tests with *H. pedicellatum* most of the smaller lateral and feeder roots were extensively damaged and practically all roots were discoloured. Plants, however, produced new secondary roots and no obvious signs of the disease appeared on the above ground plants (Shepherd *et al*, 1967).

Maize roots infected with *Rhizoctonia solani AG-2* showed large cankers or terminal decay on crown and brace roots. Plant height was significantly reduced in soil infected with *R. solani AG-2*, but stalk lodging occurred rarely (Sumner & Bell, 1986).

In several damaged plants infected with *Phialophora zeicola*, roots were blackened and rotted a few centimeters below their points of emergence. Plants were easily pulled from the ground. The adventitious roots showed pronounced dark streaks just above or below ground level (Deacon & Scott, 1983).

2.4. *PREDISPOSITION AND ITS ROLE IN THE SEVERITY OF THE ROOT ROT COMPLEX*

The occurrence of environmental conditions detrimental to optimal plant growth is considered to cause plant stress. It may influence plant disease through its effect on the pathogen, or on host susceptibility or on the host-pathogen interaction (Schoeneweiss, 1975). Stresses such as water stress, temperature stress, nutrient stress, and influence of tillage practices and other stresses seem to have pronounced effects, alone or in combination on the

susceptibility of plants to disease. Hartig (1882) realised the significance of the environment in disease severity and expanded the concept of predisposition to include many internal and external factors, such as proximity of inoculum to the host. Ward (1901) was a strong proponent of predisposition, although he excluded inherited variation from his concept and was primarily concerned with the influence of the environment. The concept of predisposition in the maize root rot complex was first introduced into the field of plant pathology by Sorauer (1974) as cited by Schoeneweiss (1975), who clearly recognised the importance of environmental factors in relation to plant diseases.

This section relates the influence of stress as a predisposing factor in plant disease.

2.4.1. Water stress

Water deficits and drought may influence plant disease through the effect on the pathogen, host susceptibility, and host-pathogen interaction. Variations in precipitation and the availability of moisture for plant growth occurs from year to year throughout the world, except in areas where irrigation is a regular practice. Major changes in climate over a period of years have been implicated as stress factors affecting the incidence and severity of many diseases (Schoeneweiss, 1975).

Ghaffar & Erwin (1969) reported that *Macrophomina phaseolina* produced root rot of cotton only on seedlings subjected to water stress prior to inoculation. Although water stress apparently has a predisposing effect on host susceptibility to disease, the ability of certain pathogens to grow or even increase growth *in vitro*, on media with low water potential, is a complicating factor. Cook *et al* (1972) reported that hyphal growth of *Fusarium roseum* "culmorum" was stimulated when the osmotic potential of the growth medium was decreased to 8-10 bars. In contrast few reports have appeared

on the predisposing effects of excess water. Tinsley (1953) reported that increasing the water supply of plants usually increased the amount of infection by viruses. Excess water and flooding, although not injurious directly, may produce a secondary oxygen-deficiency. This in turn may restrict root growth, resulting in an accumulation of toxic metabolites, which interfere with defence reactions of the host (Mc New, 1953).

2.4.2. Temperature stress

Temperature is considered the major factor that affects host susceptibility to disease. Root rot can be severe under conditions of high temperature or low temperature although the spectrum of fungi involved in each of these conditions will differ considerably. *Fusarium spp.* are known to favour dry conditions and *F. moniliforme* is particularly adapted to warm dry conditions. *F. subglutinans* is adapted to more temperate conditions and *F. graminearum* to intermediate conditions (Rheeder *et al,* 1990). Similarly, *Helminthosporium pedicellatum* is commonly found in maize grown on lighter soils, under irrigation in the United States of America (Shepherd, *et al.* 1967).

Sumner & Dowler (1983) found that the virulence of *Rhizoctonia zea* on maize roots increased with increased of temperature. *F. oxysporum* and *F. solani* cause root rot in maize when the temperatures are relatively high (Warren & Kommedahl, 1973). The effect of *R. solani AG-2* however is more severe at low temperatures (Sumner & Bell, 1982). Durrel (1923) observed more maize stalk rot in seasons of high temperature and rainfall.

2.4.3. Nutrient stress

Both increased and decreased susceptibility to root and stalk rots have been reported with major elements in plant nutrition, i.e. nitrogen, phosphorus, and potassium. This relationship between nutrition and disease development is extremely complex (Schoeneweiss, 1975). The effects of plant nutrients on disease may be attributed to (a) effects on plant vigour that can influence the microclimate in the crop and so affect infection by spores of the pathogen, (b) effects on cell walls and tissues as well the biochemical activities of the host, (c) the rate of growth of the host, which may enable seedlings to escape infection in the most susceptible stage, and (d) effects on the pathogen through alterations in the soil environment (Schoeneweiss, 1975). Colhoun (1973) found that alterations in plant nutrients may induce susceptibility of plant roots to a pathogen, but greatly increases the ability of the plant to produce new roots. Results of greenhouse studies by Schoeneweiss (1975) showed that nitrogen reduced severity of *F. graminearum* in wheat, thus increasing the number of seedlings in inoculated pots. Enzyme activity, free amino acids and protein were higher in treated plants than in those not treated. It is suggested that nitrogen influenced disease resistance by maintaining plant tissues in a juvenile state.

Lodging and stalk rots are frequently related to the level of potassium in the plant, but the mechanism by which potassium affects lodging and stalk rots is not clear. Phosphorus promotes root growth and seedling development and is beneficial against seedling diseases and certain root rots, where vigorous development of roots permits the plants to escape destruction (Mohr & Le Roux, 1977). Potassium may reduce disease severity through its effect on cell wall thickness, cell vigour, root excretions or through the effect on antagonistic soil microflora. Dodd (1980) found that the application of fertilisers, high in nitrogen and low in potassium often are associated with

increased stalk rot incidence. Maize root rot reacted in a similar way being more severe in the increasing levels of nitrogen and decreasing with added potassium (Mohr & Le Roux, 1977). Mc New (1953) also found that the addition of nitrogen to a phosphorous deficient soil, increased the susceptibility of maize roots to invasion by soil borne pathogens.

2.4.4. Tillage practices and crop rotation

Crop residues often associated with conservation-tillage practices have been shown to reduce soil surface temperature (Griffith *et al*, 1973), which in turn, affects the direction of root growth (Chaudhary & Prihar, 1974). They found that conventional tillage encouraged earlier and deeper penetration of roots into the soil profile than did no-tillage, but in no-tillage, corn had more roots in the upper (0.20 m) of soil during early growth stages. In Delaware experiments, *Fusarium spp* were isolated more frequently in rotted corn stalks taken from conventional tilled fields than from those collected in no-tilled fields (Lipps & Deep, 1991). It is clear that tillage systems alter the soil environment, thus affecting maize root distribution within the soil (Newell & Wilhelm, 1987).

Reduce tillage and crop rotation may affect the severity of maize and wheat stalk and root rots associated with *Fusarium spp*. Root and stalk rots are caused by numerous soil-borne and residue-borne fungi and are highly influenced by plant stress. In the cropping system, wheat sorghum-fallow rotation showed that minimal disturbance of crop residue and soil conserves soil moisture and reduces wheat stalk and root rot. Although tillage appears to affect stalk and root rot severity, the influence of crop rotation is not consistent. In Ohio root and stalk rot was most severe on plants in the plots planted after corn for seven years and least severe in plots following soybean (Lipps & Deep, 1991).

2.4.5. Other stresses

In addition to the major stresses, a number of other stresses have been associated with predisposition to root and stalk rot. Stresses that may induce or hasten the occurrence of maize root rot are listed as follows: prolificacy in an ordinarily single eared hybrid, severe stem borer damage, severe leaf disease severity, early frost, defoliation by chemical or mechanical means and high plant population (Ullstrup, 1977). He reported that the impositions of stress such as the removal or destruction of leaf or root tissue accelerated the spread of root infecting fungi in the stalks and roots of maize.

High light intensity and differences in light quantity have also been implicated in diseases (Schoeneweiss, 1975). He concluded that the quality and quantity of light available to host plants, affect photosynthesis and consequently nutrient reserves.

Toxic substances such as herbicides and other pesticides may cause undesirable side effects on crop plants but little research has been reported on the predisposing effects of toxins on diseases (Schoeneweiss, 1975). Although herbicides have numerous advantages, Percich & Lockwood (1975) reported that propagules of *Fusarium spp.* increased with Atrazine amendments. The use of Atrazine with continuous maize cropping or maize rotation with other *Fusarium* susceptible crops such as soybeans or vegetables can increase the inoculum potential. Sumner & Dowler (1983) found similar results with root rot caused by *R. solani* in soils treated with the herbicide Pendimethalin. Atmospheric pollutants also affect plants and may occasionally predispose plants to pathogenic organisms.

2.5. METHODS OF QUANTIFYING MAIZE ROOT ROT RESISTANCE

Various methods have been developed to quantify maize root rot resistance. Some of these are more creditable than others. Whitney & Mortimore (1957) assessed root rot at harvest on a rating scale of 0-4 where 0 = no disease; 1 = disease restricted to the tips of roots; 2= disease restricted to the lower half of the roots; 3 = roots totally diseased and the remaining roots only partly diseased; 4 = all roots totally diseased. Williams & Schmitthenner (1963) rated root rot on a 0-5 scale where 0 = no dead roots and little discolouration and 5 = all roots dead.

In vitro pathogenicity tests of maize root rot were done by Du Toit (1968), who rated the roots after 10 days on a seven-point scale according to the degree of discoloration. The percentage root rot was determined by measuring the total length (mm) of lesions on all affected roots per plant. A root rot index was calculated by multiplying the number of lesions of the different classes by a conversion factor pertaining to each class, divided by the total length (mm) of all the roots. The percentage root rot was determined as follows: Root rot = root rot index / total length of roots x 100. This method is not appropriate when large numbers of plants are being sampled since it requires qualified personnel and is labour intensive.

Sumner (1968) used dry root weight as an indication of root rot. However, rotten roots frequently disintegrated during washing and white, solid roots weighed more than discoloured, rotted roots. Fajemisin & Hooker (1974) rated plants for root rot eight weeks after planting by washing soil from the roots and recording the percentage of root browning or blackening. Roots were also air-dried and weighed. They found a negative correlation between dry root weight and root rot. Schmitthenner & Williams (1957) inoculated

three-week-old plants with *Gibberella roseun f. cereals.* Two weeks after inoculation the plants were removed and rated for root rot, considering only the adventitious roots. Thayer & Williams (1960) based their ratings on the percentage of roots with lesions. Futrell & Kilgore (1969) grew pure cultures of *Fusarium moniliforme* on Czapek's solution agar medium in petri dishes and placed sterile germinating kernels of inbred lines of maize on the living fungus. For comparative purposes the fungus was allowed to grow and cover the surface of agar, it was then heat killed and sterile maize seeds were placed on the medium. Ten days after the sterile maize seeds were placed in contact with both live and heat killed fungi, the number of secondary roots that had developed were counted and the longest primary root was measured. Check plants were grown on Czapek's solution agar medium under sterile conditions. An average of 8.7 roots per plant developed on check plants after 10 days, 3.7 developed on the live fungus and 1.8 on the heat killed *F. moniliforme.*

The presence of *Pythium* and *Fusarium spp.* on and in maize roots was investigated by Hellinga *et al* (1983). At each of seven sampling dates, pieces of roots (0.5mm long) were cleaned with sterile water and immediately plated out on selective medium for *Pythium spp.* Similarly, root pieces were sterilized for 1 min in a NaOCl solution, rinsed in sterile water and planted out on selective medium for the examination of *Fusarium spp.* After incubation at 25°C for 5 days, the pieces were examined for the presence of each fungus. Incidence of maize root rot was estimated by using a scale of 0 - 4 : 0 = <10%; 1=10 -25%; 2 = 25-50%; 3 = 50% - 75% and 4 = >75% of affected roots. Sumner *et al* (1985) removed maize roots with a shovel. After washing, these were rated on a per plant basis using a root disease index (RDI) on a scale of 1-5 where 1 = <2%; 2= 2- 10%; 3 = 11- 50%; 4 = > 50% discoloured and decayed roots and 5 = dead plants.

Root growth was rated using an empirical scale of 1-5 where 1 = very poor growth and 5 = excellent growth. Sumner & Dowler (1983) also used a similar RDI and found a significant negative correlation between root disease severity and both plant height (r = - 0.18) and root growth (r = - 0.36). Significant negative correlations were also recorded between the number of plants with hypocotyl lesions and both plant height (r = -0.27) and yield (r = - 0.28). The number of plants with swollen club shaped roots was correlated with root growth (r = - 0.31). There was also a significant positive correlation between yield and both root growth (r = 0.40) and plant height (r = 0.48) as well as disease severity and days to mid-tassel (r = 0.33) and mid-silking (r = 0.36).

Thompson (1968) reported that root size and root-clump mass were highly correlated with root lodging. Nass & Zuber (1971) found that total root mass, root volume and mass of nodal roots of seedlings were highly correlated with root-pulling resistance of mature plants.

2.5.1 Time of evaluation of resistance to maize root rot interaction

The time at which data are collected may influence root rot severity and the ease with which variety resistance can be determined Mc Laren (personal communication). He determined the optimum time for evaluation of diplodia stalk rot of maize in the greenhouse and observed it weekly after inoculation of roots and stalks. He concluded that the final data on root and stalk rot should not be taken until 3-4 weeks after inoculation. Pappelis & Miller (1984) found that in susceptible cultivars the rate of spread of inoculum was rapid in the first two weeks after inoculation. In intermediate resistant genotypes the rate of spread was constant during the four weeks interval following inoculation. In the resistant cultivars no spread occurred after the

first week following inoculation. They concluded, however, that later in the season after physiological maturity the rate of spread changes and all cultivars become susceptible to root and stalk rot.

2.6. EFFECTS ON YIELD AND CONTROL OF MAIZE ROOT ROT DISEASE

2.6.1. Effects on yield of root rot

Very little evidence of a direct association between root rot and yield loss is available. Le Roux (1977) stated: "Although we do not have factual data on the yield losses incurred by root and stalk rots, we are in agreement that this disease complex causes more losses than all other maize diseases put together". Channon & Farina (1991) are of the opinion that soil borne diseases result in yield losses, which are far greater than is generally recognized in South Africa. In New Zealand, maize root rot reduced grain yield by 10% in artificially inoculated trials and losses were estimated at 5% in commercial maize fields (Fowler, 1980). At the same locality, Blanquet *et al* (1990) found that the dry matter yield of plants affected by maize root rot was reduced by 12-21% in 1987 and 14-16% in 1988, compared with symptomless plants.

Yield was significantly lower in soil infected with *R. solani AG-2* and over a three year period an average yield loss of 22% was noted (Sumner & Bell, 1986). However they stated that more research is necessary to determine the relationship of crown and brace root rot on grain yield. Chambers (1987) found that rot of adventitious roots was correlated significantly with yield. Most of the above-mentioned data were obtained from greenhouse and microplot trials.

2.6.2. Control of maize root rot

Effective control of maize root rot is difficult mainly because of the wide spectrum of pathogens associated with the disease. Chemical control is often not economically justifiable. Therefore, alternative measures have to be sought in agricultural practices and breeding for resistance to the disease.

Hellinga *et al* (1983) found that fungicides such as Metalaxyl in combination with Captafol, delayed maize root rot. These fungicides markedly improved the quality of root systems of plants under continuous cropping. Soil fumigation with Methyl bromide reduced maize root disease severity in mature plants for up to five years after application (Sumner *et al*, 1985). Fumigation with DD-MENCS (20% methyl isothicynate + 80% chlorinated C_3 hydrocarbons) significantly reduced the percentage of maize plants with root rot and the percentage of crown and brace roots with lesions (Sumner *et al*, 1990).

Kruger & Du Plooy (1963) concluded that the variety of fungi involved in root and stalk rot of maize necessitates the employment of more than one control measure. Although fungicides could be used, they are expensive and alternative methods should be considered. They recommended two or more of the following control measures (i) maize stubble should be ploughed deep below the soil surface (ii) ploughing should be done as early as is practical, (iii) crop rotation can be effective but in severe cases a two to three year system has to be applied and (iv) breeding for host plant resistance. Thayer & Williams (1960) confirmed that high levels of phosphorus in the soil would assist in controlling root and stalk rot.

Doupnik & Boosalis (1980) developed a three year reduced tillage rotation system, known as ecofallow, that reduces the incidence and severity of disease

problems associated with other reduced tillage practices. Consistently more grain sorghum plants lodged in conventionally tilled plots than in ecofallow plots at harvest. They ascribed the lower incidence of stalk rot to soil moisture conservation and low soil temperatures associated with ecofallow. Soil water and temperature regimes and other soil physical factors can affect maize root growth (Newell & Wilhelm, 1987). These soil factors often differ among tillage systems. Summer & Bell (1986) found that tillage may influence plant residue distribution and soil compaction. The effects of maize crown and brace root rot on yield reduction may be greater if root growth is restricted by soil compaction.

Cropping systems had no effect on the distribution of *Rhizoctonia solani AG-2* (Sumner & Bell, 1986). However, Weller *et al* (1986) found that *R. solani* root rot on wheat occurred mainly in fields where minimum or no-tillage was used before sowing. Herman (1984) associated an increase of *Fusarium spp.* in wheat roots with no-tillage. Similarly *Fusarium spp.* in maize mesocotyls and crowns tended also to be higher in plants from no-tillage treatments than from ploughed treatments (Lipps & Deep, 1991).

Reduced tillage systems cause a decline in the total number of fungi with increasing depth, whereas with ploughed systems fungi are more evenly distributed (Norstadt & Mc Calla, 1968; Sumner et al, 1981). As a result of increased residue in the upper centimeters of soil, more fungi and micro-organisms will be present in reduced tillage systems compared to ploughed systems (Duley,1957). Continuous reduced tillage and monoculture of crops have been shown to increase the amount of inoculum for many disease (Boosalis & Doupnik, 1976; Sumner *et al* 1981).

Chemical control measures can be applied, however, these measures are usually not economically justifiable. Manipulation of agriculatural practices probably has the most merit with regard to the control of maize root rot. It is

essential to study the root systems occasionally, since above ground symptoms involved in the root rot complex are not specific. Preventive control measurements such as choice of cultivars are preferred.

Breeding for resistance to maize root rot probably offers the only economical and long-term solution to the problem. Whitney & Mortimore (1957) indicated that resistance to root rot also implies resistance to stalk rot.

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CHAPTER 3

INHERITANCE OF ROOT ROT RESISTANCE IN MAIZE

ABSTRACT

To determine the genetic variability and inheritance for root rot resistance in maize, an 8 X 8 full diallel was planted during 1999/2000. Infection was dependent on natural inoculum. Root discolouration, plant length, root volume, effective root volume and yield were measured. A diallel analysis was used to analyze the data and determine combining abilities, genetic correlations, heritabilities and correlated response.

The F1-hybrids showed significant differences for root rot discolouration, plant length, root volume, effective root volume and yield. Inbred line P28 and the cross B73XE739 had, respectively the highest general and specific combining abilities. Root discolouration had the highest genetic correlation (r_A = 0.47) with plant length. The broad and narrow sense heritabilities for root rot discolouration were respectively h^2 = 0.81 and h^2 = 0.51. Root rot discolouration had the highest correlated response (C_R = 0.14) with plant length.

INTRODUCTION

Most plant diseases are infectious. They result from interaction of two organisms: the host plant which is susceptible to the disease and the pathogen, which is the causal agent of the disease (Hooker & Saxena, 1971). According to them, in the resistant plant, host and pathogen are in conflict; pathogen growth and development are suboptimal. In maize (*Zea mays* L.) numerous fungal species are known to infect maize roots and stalks and eventually cause the roots and stalks to rot. The root and stalk rot complex is currently one of the major limiting factors in maize production in many countries in the world (Van der Watt, 1979; Chambers, 1983). The most effective way of combating the disease is by breeding for resistance. Resistance is the ability of an organism to exclude or overcome, completely or in some degree, the effect of pathogen or other damaging factors (Van Loon, 1997). Therefore resistance can take various forms and numerous genetic systems and are known to result in host resistance. Resistance to root and stalk rot is quantitatively inherited (Sprague, 1954; Hooker, 1956; Russell, 1961) and related to the physiology (Andrew, 1954).

Diallel analysis is an effective method to study the inheritance of quantitative characteristics like root rot resistance in maize. Inheritance of disease resistance embraces a wide and continuous array of patterns that are classified into three broad categories: aligogenic (Mendelian), polygenic and extrachromosomal. Polygenes are the main broad category that have been investigated in disease resistance studies (Hooker & Saxena, 1971). The two kinds of polygenes are additive and dominant genes. Diallel analyses identify their effects as general and specific combining ability effects respectively. The best way to develop root rot resistant hybrids in a hybrid breeding programme is to select simultaneously for GCA and SCA effects.

The main objective of this research was to study the genetic variability and the inheritance of root rot resistance in South African maize germplasm.

MATERIAL AND METHODS

3.1. Experimental material

Eight parental inbred lines P28, I137TN, MP706, E739, MO17, B37, B73 and B14 (Table 3.1) were planted during 1999 in the greenhouse at the ARC-Grain Crops Institute at Potchefstroom. The inbred lines were crossed in all combinations according to a complete Diallel (Model1) of Griffing (1956). The F1- hybrid seed were harvested after maturity. Data were analyzed using the analysis of variance in the Agrobase statistical programme version 1998.

3.2. Experimental design

The 56 F1-hybrid combinations and their eight parental lines were planted in a randomized complete block trial with three replications during December 1999 at Potchefstroom. Each plot consisted of 30 plants with an intra row spacing of 10 cm and an inter-row spacing of 1.2 meters. Fertilizer compound N,P,K was given using 300 Kg/ha 2:3:2. For top dressing, 250 Kg/ha LAN was applied 4-6 weeks after emergence. The trial was conducted under dry land conditions and irrigated only when absence of rain dictated. The total amount of rain received during the period of November1999 to March 2000 was 510.6 mm. Weed and insect control were applied as required.

Table 3.1. List of crosses made for a F1-diallel and their reciprocals

No	Pedigree	Code for crosses	No	Pedigree	Code for crosses
1	P28XI137TN	L8/L5	29	E739XP28	L4/L8
2	P28XMP706	L8/L7	30	E739XI137TN	L4/L5
3	P28XMO17	L8/6	31	E739XMP706	L4/L7
4	P28XE739	L8/L4	32	E739XMO17	L4/L6
5	P28XB37	L8/L2	33	E739XB37	L4/L2
6	P28XB14	L8/L1	34	E739XB14	L4/L1
7	P28XB73	L8/L3	35	E739XB73	L4/L3
8	I137TNXP28	L5/L8	36	B37XP28	L2/L8
9	I137TNXMP706	L5/L7	37	B37XI137TN	L2/L5
10	I137TNXMO17	L5/L6	38	B37XMP706	L2/L7
11	I137TNXE739	L5/L4	39	B37XMO17	L2/L6
12	I137TNXB37	L5/L2	40	B37XE739	L2/L4
13	I137TNXB14	L5/L1	41	B37XB14	L2/L1
14	I137TNXB73	L5/L3	42	B37XB73	L2/L3
15	MP706XP28	L7/L8	43	B14XP28	L1/L8
16	MP706XI137TN	L7/L5	44	B14XI137TN	L1/L5
17	MP706XMO17	L7/L6	45	B14XMP706	L1/L7
18	MP706XE739	L7/L4	46	B14XMO17	L1/L6
19	MP706XB37	L7/L2	47	B14XE739	L1/L4
20	MP706XB14	L7/L1	48	B14XB37	L1/L2
21	MP706XB73	L7/L3	49	B14XB73	L1/L3
22	MO17XP28	L6/L8	50	B73XP28	L3/L8
23	MO17XI137TN	L6/L5	51	B73XI137TN	L3/L5
24	MO17XMP706	L6/7	52	B73XMP706	L3/L7
25	MO17XE739	L6/L4	53	B73XMO17	L3/6
26	MO7XB37	L6/L2	54	B73XE739	L3/L4
27	MO17XB14	L6/L1	55	B73XB37	L3/L2
28	MO17XB73	L6/L3	56	B73XB14	L3/L1

L = Indicates the code of line used for crosses

3.3. Characters measured

The characters measured on single plants were: root discolouration (RRD), root volume (RV), plant length (PL), effective root volume (ERV) and yield.

3.3.1. Root discolouration (RRD)

Six weeks after planting, five randomized plants per plot, were selected. The roots of the plants were washed in running tap water to remove adhering soil. A visual assessment of the percentage of root discolouration was done on each plant separately. To quantify root discolouration a scale from one to five was used (Table 3.3.1), where 1 = < 2%; 2 = 2-10%; 3= 11-50%; 4 = > 50% discoloured and decayed roots and 5 = dead plants (Sumner *et al.*, 1985).

Table 3.3.1. Numerical and percentage values of the scale used for visualyzing root rot discolouraion (by Summer et al, 1985)

Numerical Value		Percentage value
1	= <	2%
2	=	2-10%
3	=	11-50%
4	= >	50%
5	=	dead plants

3.3.2. Root volume (RV)

Recovered root volume was determined using water displacement. A bucket of 10 litres with a small spout in the top of the bucket was used. The roots were put into the bucket filled with water and then covered with a lid. The water that runs through the spout was collected up in another small container. The amount of water in the container was measured in millilitres.

3.3.3. Plant length (PL)

Plant length was measured in centimeter using a tape measure. The lengths were measured from the crown to the tip of the upper leaf. Twenty random plants per replicate were measured and the mean per replicate was determined.

3.3.4. Effective root volume (ERV)

Effective root volume was calculated by putting the values for root rot severity and root volume in the following equation (Mc Laren, 1999).

$$ERV = (((100 - \text{root rot severity})/100) * \text{root volume}), \quad (1)$$

Where ERV i s the effective root volume (ml).

3.3.5. Yield (ton/ha)

Grain yield was calculated as shelled grain mass per plot adjusted to 12.5% grain moisture and converted to tons per hectare, according to the following formula:

$$GY = (Wt\ Kg / Np) * Pp * (100 - H\%) / 87.5\%) * 1t / 100Kg \qquad (2)$$

GY is grain yield in t /ha, Wt is grain mass in Kg, Np is final stand (number of harvested plants), Pp is plant population (total number of plants /hectare) calculated from plot size, H% is the moisture percentage taken after harvest and 87.5% is the moisture correction coefficient (100 – 12.5%).

3.4. *Statistical analysis*

The Agrobase 98 computer program was used to conduct various statistical analyses on the data. The following analyses were conducted:

3.4.1. Analysis of variance (ANOVA)

An analysis of variance was calculated on each data set for each of the five characters measured. To test for significant differences between means the LSD (0.05) of Tukey was used.

3.4.2. Diallel analysis of F1 progeny

The F1 data sets obtained for each of the five characters measured was analysed according to the variance analysis of Griffing (1956) model 1. The analysis measures the variances for general and specific combining abilities as well as the reciprocal effects. The complete analysis of variance is given in Table 3.4.2.

Table 3.4.2. Analysis of variance for a diallel cross model 1, method 3 (Griffing, 1956)

Source	d.f.	m.s.	E(m.s.)	Variance component
GCA	k-1	m1	$\sigma^2_e + 2r\sigma^2_{sca} + 2r(k-2)\sigma^2_{gca}$	$\sigma^2_{gca} = C(HS)$
SCA	k(k-3)/2	m2	$\sigma^2_e + 2r\sigma^2_{sca}$	$\sigma^2_{sca} = C(FS) - 2C(HS)$
RECIPROCALS	k(k-1)/2	m3	$\sigma^2_e + 2r\sigma_{rec}$	
BLOCKS	r-1	m4		
ERROR	(r-1)(k2 – k-1)	m5	σ^2_e	$\sigma^2_e = V_e$

V_A = the additive variance; V_D = dominance variance; V_E = environmental variance

VF1 = the variance of F1. The genetic variance (Vg) is calculated by subtracting the environmental variance (Ve) from the total variance, i.e. Vg = VF1 –Ve. The environmental Ve was calculated from the parental variances (Vp1, Vp2) by the formula:

$$Ve = \tfrac{1}{2} Vp1 + \tfrac{1}{2} Vp2 \qquad (3)$$

k = number of parents

$$HS = \text{half sib: } C(HS) = 1 + F/4 * \sigma^2\Lambda + \ldots\ldots \qquad (4)$$

$$FS = \text{Full sib: } C(FS) = 2 + Fm + Ff/4\,\sigma^2\,\Lambda + (1 + Fm)(1 + Ff)/4\,\sigma^2\,D + \ldots\ldots \qquad (5)$$

F = inbreeding coefficient of the genotypes tested

3.4.2.1. Combining abilities (general and specific)

The GCA and SCA, as well as the relationship between these two values, were calculated. In the combining ability analysis, the variety effects are considered in terms of GCA and SCA effects, such that:

$$V_{ij} = g_i + g_j + s_{ij} \qquad (6)$$

for those diallel crossing methods in which reciprocal F1's are not included.

Table. 3.4.2.1. ANOVA for method 2 giving expectations of mean squares for the assumptions of model 1.

Source	Df	Sum of squares	Mean squares	Expectation of mean squares
GCA	p - 1	S_g	M_g	$\sigma^2 + (p+2)(1/p-1)\Sigma g^2$
SCA	p(p -1)/2	S_s	M_s	$\sigma^2 + 2/p(p-1)\Sigma_i\Sigma_j S_{ij}^2$
ERROR	M	S_c	M_c	σ^2

Where:

$$S_g = 1/p + 2\{\Sigma_i (X_{i.} + X_{ii})^2 - 4/P X^2 \ldots\ldots \qquad (7)$$

$$S_s = \Sigma_i \leq \Sigma_j X_{ij}^2 - 1/p + 2_i \Sigma (X_i + X_{ij}^2 + 2/(p+1)(P+2) X^2 \ldots\ldots \qquad (8)$$

The mathematical model for the combining ability analysis is assumed to be

$$X_{ij} = u + g_i + g_j + S_{ij} + 1/bc \Sigma k \Sigma_i e_{ijkl} \qquad (9)$$

$i,j = 1, \ldots, p$ $\qquad$ u = population mean

$k = 1, \ldots, b$ $\qquad$ $(gi)gj$ = gca effect

$l = 1, ..., c$ $\quad$ sij = sca effect

The effects may be estimated as follows:

For GCA effects:

$$g_l - 1/p + 2 [X_{i.} + X_{ii} - 2/p X..] \qquad (10)$$

The LSD between GCA was calculated as

$$LSD = q\,\alpha;t,f.\sqrt{S^2_E}/r \qquad (t = 0.5) \qquad (11)$$

q α;t,f = α value at t treatment's degree of freedom and error degrees of freedom.

For SCA effects:

$$S_{ij} = X_{ij} - 1/p + 2 [X_i + X_{ii} + X_i + X_{jj}] + 2/(p + 1)(p + 2) X..... \qquad (12)$$

The LSD between SCA effects was calculated as

$$LSD = q\,\alpha;t,f.\sqrt{S^2_E}/r \qquad (t=0.5) \qquad (13)$$

q α;t,f = α value at t treament's degree of freedom and error's degrees of freedom.

3.4.2.2. GCA:SCA ratio's

The GCA:SCA ratio indicates whether GCA or SCA effects are predominant and which factor plays a more important role in exercising genetic control. This ratio also indicates whether a character is mainly under the control of additive / non-additive (dominant) gene action.

3.4.2.3. Genetic correlations

The genetic correlation is the correlation between the additive variances of two characters. A genetic correlation matrix was calculated for all five characters measured. It was done using the additive variance components obtained from Griffing's (1956) analysis of variance. Genetic correlations can arise from pleiotropy, linkage or introduction of genes involved into a population.

3.4.2.4. Heritability

Heritability is in fact a regression coefficient of genotypic values G on phenotypic values P. It is defined as the ratio of genotypic variance thus the portion of phenotypic variation among individuals due to genetic differences between them. Broad and narrow sense heritability was determined.

The broad sense heritability is the extent to which the genotype influences the phenotype, and is therefore calculated from the ratio of the total genetic variance to the phenotypic variance according to the formula:

$$h^2 = \sigma^2_g / \sigma^2_P = v(G) / v(P) \qquad (14)$$

The narrow sense heritability expresses the extent to which the phenotypes are determined by the genes transmitted from the parents, and was estimated from the ratio of the additive portion of the genetic variance to the phenotypic variance according to the formula:

$$h^2 = \sigma^2_A / \sigma^2_p \qquad (15)$$

Where $\alpha^2_A - 2\ \alpha^2_{GCA}$

The variance components were calculated according to Griffing (1956):

$$\sigma^2_G = 2\sigma^2_{GCA} + 2\sigma^2_{SCA} \qquad (16)$$

Where:

$$\sigma^2_{GCA} = (MS_{GCA} - MS_{SCA}) / P\text{-}2 \qquad (17)$$

$$\sigma^2_{SCA} = MS_{SCA} - MS_E$$

$$\sigma^2_p = \sigma^2_G + 2\ \sigma^2$$

3.4.2.5. Correlated response

The main question breeders want to address is what will be the change in the correlated character Y when selection is applied for another character X. The response of character X, the character directly selected is equivalent to the mean breeding value of the selected individuals. The consequent change of character Y is therefore given by the regression of the breeding value of Y on the breeding value of X (Falconer, 1960).

The regression is:

$$b_{AYX} = Cova/\sigma^2_{AX} = r_A \sigma^2_{AY}/\sigma^2_{AX} \quad (18)$$

The response of character X, directly selected is:

$$R_X = ih^2_X \sigma_{AX} \quad (19)$$

Therefore the correlated response for character Y is:

$$CR_Y = ih^2_X r_A \sigma_{AY} \quad (20)$$

By putting $\sigma_{AY} = h^2_y \sigma_{PY}$ the correlated response becomes:

$$CR_Y = ih_X h_Y r_A \sigma_{PY} \quad (21)$$

Thus the response of a correlated character can be predicted if the heritabilities and genetic correlation of the two characters are known.

Since the selection intensity was constant from all characters, the value of i was taken as 1.

If the same intensity of selection can be achieved when selection for character *Y* as when selecting for character *X*, then the correlated response will be greater than the direct response if $r_A h_Y$ is greater than h_X. Therefore indirect selection cannot be expected to be superior to direct selection unless the secondary character has a substantially higher heritability than the desired character and the genetic correlation between the two is high; or, unless a substantially higher intensity of selection can be applied to the secondary character (Falconer, 1960).

RESULTS AND DISCUSSION

3.5. *Analysis of variance of root rot discolouration, plant length, root volume, effective root volume and yield*

The data set of each characteristic was submitted to a variance analysis. The analyses of variance with regard to root rot discolouration, plant length, root volume, effective root volume and yield are given in Table 3.5.

Highly significant differences between blocks existed for root rot discolouration, plant length, root volume, effective root volume and yield. Significant differences between entries were recorded for plant length, root volume, effective root volume and yield, but no significant differences existed among entries for root rot discolouration.

A highly positive correlation was found between root volume and plant length (R^2 = 0.53). A highly positive correlation between effective root volume and plant length was also recorded too (R^2= 0.50). Yield was poorly correlated with root discolouration, root volume, plant length and effective root volume, yielding no significant correlation coefficients (Figures. 3.51 to 3.5.7).

Table 3.5. ANOVA – Mean squares for root rot discolouration, plant length, root volume, and effective root volume

Yield

Source	Df	Characteristics				
		R.R.D	PL	R.V	E.R.V.	Yield
Total	191					
Block	2	1300.42**	4270.64**	2286.75**	927.25**	6.67**
Entry	63	34.24*	558.93**	494.53**	380.72**	4.37**
Residual	126	44.32	263.24	273.23	205.68	1.86
Grand mean		9.93	123.53	34.12	30.30	4.49
C.V.(%)		67.00	13.13	48.44	47.33	30.36

RRD-root rot discolouration, PL-plant length, RV-root volume, ERV-effective root volume

** indicates probability of highly significant differences

* indicates probability of significant differences

3.5.1. Mean differences for root rot discolouration, plant length, root volume effective root volume and yield

The mean root rot discolouration values of the 56 F1-hybrids (reciprocals included) and the eight parental inbred lines are given in Table 3.5.1(a) and Table 3.5.1(b). Although no significant differences were found in the F1-table for entries, significant differences occurred according to the t-values as measured by the LSD. This could be due to the large significance in block effects as well as the relatively high coefficient of variation calculated for root rot discolouration. No significant differences existed between the eight parental inbred lines for percentage root rot discolouration. The two parents with the lowest root rot discolouration were I137TN and MP706. Two of the F1-crosses MP706 X I137TN (3,33%) and B73 X B37 (3.67%) showed very little root rot discolouration. Their percentage of root rot discolouration were significantly lower than the crosses P28 X MP706, P28 X B73, I137 X B73, MP706 X P28, MP706 X MO17, B73 X P28, B73 X MO17 and B73 X E739, which seem to have had relatively high levels of root rot discolouration. The low percentage root rot discolouration of the cross MP706 X I137TN resulted from the low values of the two parents.

The mean values for plant length are given in the Table 3.5.1(a) and Table 3.5.1(b). Highly significant differences for plant length were recorded for both blocks and entries. Two parental inbred lines MO17, and B37 had lower plant lengths. Among the parental inbred lines B73 and P28 were the tallest, significantly taller than the rest of the maize inbreds. Among the crosses MO17 X I137TN, I137TN X MO17 and MO17 X MP706 had the lowest plant length combinations. The combination B14XMO17 had the tallest plant length among the crosses. According to the mean plant length of the combinations in which the parental line MO17 was used, it was quite clear that MO17 had a reducing effect on plant height.

Among the parental lines E739, P28, I137TN and B73 had relatively high root volumes. MO17 had the lowest root volume. Seven of the crosses B73 X P28, B14 X P28, B37 X B14, B14 X MO17, B37 X P28, B14 X B73 and B73 X MP706 had relatively high root volume and five of the crosses I137TN X E739, MO17 X MP706, MP706 X E739, B73 X E739 and I137TN X B73 had relatively low root volume ranging from 15(ml) to 17.33(ml) (Table 3.5.1(a) and Table 3.5.1(b)).

The parental inbred line E739 had the highest effective root volume while MO14 had the lowest effective root volume. Six of the crosses B37 X P28, B37 X B14, B14 X P28, B73 X P28, B14 X B73 and B14 X MO17 could be considered to have relatively high effective root volume values. The crosses MP706 X E739, MO17 X MP706, I137TN X E739 had relatively low effective root volume values (Tables 3.5.1(a) and 3.5.1(b)).

The mean values for yield are given in Tables 3.5.1(a) and Table 3.5.1(b). Among the parental inbred lines MP706 (6.89) had the highest mean yield. Parental line E739 (0.53) and P28 (0.53) had the lowest yield (Table 3.5.1(b)). MO17 X B14 (7.23) was the cross with the highest yield followed by other crosses such as P28 X I137TN (6.75), MP706 X B37 (6.15), MP706 X E739 (6.06) and B73 X MO17 (6.00), (Table.3.5.1 (a)).

The summary of general means and their rankings of root discolouration, plant length, root volume, effective root volume and yield evaluated in the field at Potchefstroom during the 1999/2000 season are presented in Tables 3.5.1 (c) and 3.5.1 (d).

Table 3.5.1 (a) Mean values for root discolouration, plant length, root volume, effective root volume and yield of crosses and parental inbred lines planted at Potchefstroom during the 1999/2000 season

Entry	Cross	Designation	RRD	PL	RV	ERV	Yield
1	P28XI137TN	L8/L5	10.33	125.33	39.33	35.33	6.75
2	P28XMP706	L8/L7	13.33	126.00	25.00	21.33	5.49
3	P28XMO17	L8/L6	9.67	122.67	21.33	18.00	5.30
4	P28XE739	L8/L4	8.33	108.67	27.00	25.00	4.38
5	P28XB37	L8/L2	11.33	126.00	40.33	35.00	5.65
6	P28XB14	L8/L1	12.00	129.33	29.33	25.33	3.04
7	P28XXB73	L8/L3	14.00	125.00	29.00	23.67	5.76
8	I137TNXP28	L5/L8	10.67	119.33	35.00	30.67	5.63
9	I137TNXMP706	L5/L7	11.00	138.33	36.33	31.67	4.60
10	I137TNXMO17	L5/L6	9.33	97.67	20.00	18.33	4.00
11	I137TNXE739	L5/L4	6.67	113.33	15.00	14.00	5.06
12	I137TNXB37	L5/L2	9.67	104.00	24.33	21.33	5.68
13	I137TNXB14	L5/L1	5.00	124.33	37.33	35.67	4.47
14	I137TNXB73	L5/L3	16.00	122.33	17.33	14.67	5.40
15	MP706XP28	L7/L8	16.67	124.00	31.33	25.67	5.06
16	MP706XI137TN	L7/L5	3.33	114.00	22.67	21.67	3.69
17	MP706XMO17	L7/L6	16.00	140.33	44.00	36.33	4.67
18	MP706XE739	L7/L4	6.00	108.33	16.33	15.33	6.06
19	MP706XB37	L7/L2	13.67	128.67	40.33	34.00	6.15
20	MP706XB14	L7/L1	13.00	141.33	36.67	31.33	2.78
21	MP706XB73	L7/L3	6.67	133.33	20.33	18.67	3.98
22	MO17XP28	L6/L8	12.67	131.67	37.33	32.00	5.13
23	MO17XI137TN	L6/L5	9.33	99.00	20.00	18.33	3.85
24	MO17XMP706	L6/L7	9.00	97.00	15.67	14.33	4.49
25	MO17XE739	L6/L4	7.33	124.00	34.00	31.00	5.76
26	MO17XB37	L6/L2	9.67	140.67	42.00	3.00	5.40
27	MO17XB14	L6/L1	10.67	140.67	47.33	42.00	7.23
28	MO17XB73	L6/L3	6.33	136.33	44.33	41.33	4.87
29	E739XP28	L4/L8	10.33	112.00	34.33	30.33	3.78
30	E739XI137TN	L4/L5	9.00	124.00	25.67	23.33	5.07
31	E739XMP739	L4/L7	7.00	139.00	34.00	32.33	3.52
32	E739XMO17	L4/L6	5.67	118.33	37.33	34.67	4.60
	Grand mean		9.94	123.54	34.12	30.30	4.49
	LSD (p=0.05)		9.08	22.00	22.40	19.40	1.84
	CV (%)		67.00	13.13	48,44	47,33	30.36

Table 3.5.1(b). Mean values for root rot discolouration plant length, root volume, effective root volume and yield of crosses and parental inbred lines planted at Potchefstroom-1999/2000 season

Entry	Cross	Designation	RRD	PL	RV	ERV	Yield
33	E739XB37	L4/L2	11.33	102.00	29.00	25.33	3.61
34	E739XB14	L4/L1	10.00	137.33	43.00	38.67	4.72
35	E739XB73	L4/L3	13.00	135.67	46.00	38.00	4.22
36	B37XP28	L2/L8	11.00	139.33	66.00	58.00	4.23
37	B37XI137TN	L2/L5	6.33	122.00	33.00	31.00	3.60
38	B37XMP706	L2/L7	5.33	126.67	41.67	40.00	4.61
39	B37XMO17	L2/L6	13.00	127.33	30.67	27.00	3.92
40	B37XE739	L2/L4	4.33	124.00	25.67	24.67	3.48
41	B37XB14	L2/L1	7.33	124.33	60.33	56.33	4.60
42	B37XB73	L2/L3	5.33	127.00	46.67	44.00	4.48
43	B14XP28	L1/L8	9.00	133.67	62.33	55.00	4.66
44	B14XI137TN	L1/L5	11.00	129.33	34.33	28.00	4.93
45	B14XMP706	L1/L7	8.00	127.67	31.33	29.00	4.37
46	B14XMO17	L1/L6	17.67	156.67	59.33	48.33	4.17
47	B14XE739	L1/L4	7.33	131.00	49.00	45.00	4.43
48	B14XB37	L1/L2	9.67	130.00	33.67	29.67	5.09
49	B14XB73	L1/L3	10.67	147.00	55.33	50.00	4.93
50	B73XP28	L3/L8	15.67	136.67	59.00	51.33	5.30
51	B73XI137TN	L3/L5	8.33	120.00	23.33	22.33	3.88
52	B73XMP706	L3/L7	12.00	122.67	51.00	43.33	4.31
53	B73XMO17	L3/L6	16.67	135.33	47.00	36.67	6.00
54	B73XE739	L3/L4	14.00	119.33	18.67	16.67	4.19
55	B73XB37	L3/L2	3.67	129.00	42.67	41.00	4.35
56	B73XB14	L3/L1	10.33	118.33	30.00	24.67	3.74
57	P28	L8	11.33	123.67	29.33	25.33	0.53
58	I137TN	L5	6.67	109.33	25.67	24.00	3.85
59	MP706	L7	5.67	108.33	7.00	16.00	6.89
60	MO17	L6	12.00	85.33	13.67	12.00	3.81
61	E739	L4	10.67	106.33	37.67	32.33	0.55
62	B37	L2	12.00	97.67	19.67	18.00	3.43
63	B14	L1	7.33	108.67	19.67	18.00	2.14
64	B73	L3	9.67	129.67	21.00	19.00	3.38
	Grand mean		9.94	123..54	34.12	30.30	4.49
	LSD(p=0.05)		9.08	22.00	22.40	19.40	1.84
	CV (%)		67.00	13.13	48.44	47.33	30.36

Table 3.5.1(c). Summary of general means and their rankings of root discolouration, plant length, root volume, effective root volume and yield evaluated in the field at Potchefstroom-1999/2000 season

Entry	Cross	Desig.	Yield	Rank	RRD	Rank	PL	Rank	RV	Rank	ERV	Rank
27	MO17XB14	L6/L1	7.23	1	10.67	26	140.67	4	47.33	9	42.00	10
59	MP706	L7	6.89	2	5.67	58	108.33	56	17.00	60	16.00	59
1	P28XI137TN	L8/L5	6.75	3	10.33	29	125.33	32	39.33	21	35.33	20
19	MP706XB37	L7/L2	6.15	4	13.67	9	129.00	23	40.33	20	34.00	23
18	MP706XE739	L7/L4	6.06	5	6.00	56	106.33	57	16.33	61	15.33	60
53	B73XMO17	L3/6	6.00	6	16.67	2	137.33	10	47.00	10	36.67	17
25	MO17XE739	L6/L4	5.76	8	7.33	46	124.00	35	34.00	31	31.00	30
7	P28XB73	L8/L3	5.76	7	14.00	7	125.00	31	29.00	42	23.67	45
12	I137TNXB37	L5/L2	5.68	9	9.67	33	102.00	59	24.33	48	21.33	49
5	P28XB37	L8/L2	5.65	10	11.33	19	126.00	30	40.33	19	35.00	21
8	I137TNXP28	L5/L8	5.63	11	10.67	27	120.00	44	35.00	28	30.67	31
2	P28XMP706	L8/L7	5.49	12	13.33	10	126.00	29	25.00	47	21.33	50
26	MO17XB37	L6/L2	5.40	14	9.67	34	140.67	5	42.00	17	38.00	15
14	I137TNXB73	L5/L3	5.40	13	16.00	4	122.00	43	17.33	59	14.67	61
50	B73XP28	L3/L8	5.30	16	15.67	6	136.33	12	59.00	5	51.33	4
3	P28XMO17	L8/6	5.30	15	9.67	37	122.33	42	21.33	51	18.00	57
22	MO17XP28	L6/L8	5.13	17	12.67	14	131.67	17	37.33	23	32.00	26
48	B14XB37	L1/L2	5.09	18	9.67	35	130.00	20	33.67	33	29.67	33
30	E739XI137TN	L4/L5	5.07	19	9.00	41	124.00	39	25.67	46	23.33	46
15	MP706XP28	L7/L8	5.06	21	16.67	3	124.00	37	31.33	36	25.67	37
11	I137TNXE739	L5/L4	5.06	20	6.67	51	113.33	50	15.00	63	14.00	63
49	B14XB73	L1/L3	4.93	23	10.67	25	147.00	2	55.33	6	50.00	5
44	B14XI137TN	L1/L5	4.93	22	11.00	24	130.00	19	34.33	29	28.00	35
28	MO17XB73	L6/L3	4.87	24	6.33	54	135.67	13	44.33	13	41.33	11
34	E739XB14	L4/L1	4.72	25	10.00	32	136.67	11	43.00	15	38.67	14
17	MP706XMO17	L7/L6	4.67	26	16.00	5	140.33	6	44.00	14	36.33	18
43	B14XP28	L1/L8	4.66	27	9.00	40	133.67	15	62.33	2	55.00	3
38	B37XMP706	L2/L7	4.61	28	5.33	59	127.33	26	41.67	18	40.00	13
41	B37XB14	L2/L1	4.60	31	7.33	47	124.00	38	60.33	3	56.33	2
32	E739XMO17	L4/L6	4.60	30	5.67	57	118.33	47	37.33	25	34.67	22
9	I137TNXMP706	L5/L7	4.60	29	11.00	22	139.33	7	36.33	27	31.67	27
24	MO17XMP706	L6/7	4.49	32	9.00	42	97.00	63	15.67	62	14.33	62

Table 3.5.1(d). Summary of general means and their rankings of root discolouration plant length, root volume, effective root volume and yield evaluated in the field at Potchefstroom-1999/2000 season

Entry	Cross	Desig.	Yield	Rank	RRD	Rank	PL	Rank	RV	Rank	ERV	Rank
42	B37XB73	L2/L3	4.48	33	5.33	60	126.67	28	46.67	11	44.00	8
13	I137TNXB14	L5/L1	4.47	34	5.00	61	124.33	34	37.33	24	35.67	19
47	B14XE739	L1/L4	4.43	35	7.33	49	131.00	18	49.00	8	45.00	7
4	P28XE739	L8/L4	4.38	36	8.33	44	108.67	53	27.00	43	25.00	41
45	B14XMP706	L1/L7	4.37	37	8.00	45	127.67	25	31.33	35	29.00	34
55	B73XB37	L3/L2	4.35	38	3.67	63	129.33	22	42.67	16	41.00	12
52	B73XMP706	L3/L7	4.31	39	12.00	18	124.33	33	51.00	7	43.33	9
36	B37XP28	L2/L8	4.23	40	11.00	23	139.00	8	66.00	1	58.00	1
35	E739XB73	L4/L3	4.22	41	13.00	13	135.33	14	46.00	12	38.00	16
54	B73XE739	L3/L4	4.19	42	14.00	8	119.33	45	19.67	56	16.67	58
46	B14XMO17	L1/L6	4.17	43	17.67	1	156.67	1	59.33	4	48.33	6
10	I137TNXMO17	L5/L6	4.00	44	9.33	38	97.67	62	20.00	55	18.33	54
21	MP706XB73	L7/L3	3.98	45	6.67	53	133.33	16	20.33	53	18.67	52
39	B37XMO17	L2/L6	3.92	46	13.00	12	127.00	27	30.67	37	27.00	36
51	B73XI137TN	L3/L5	3.88	47	8.33	43	119.33	46	23.33	49	22.33	47
58	I137TN	L5	3.85	49	6.67	52	109.33	52	25.67	44	24.00	44
23	MO17XI137TN	L6/L5	3.85	48	9.33	39	97.97	61	20.00	54	18.33	53
60	MO17	L6	3.81	50	12.00	16	85.33	64	13.67	64	12.00	64
29	E739XP28	L4/L8	3.78	51	10.33	31	112.00	51	34.33	30	30.33	32
56	B73XB14	L3/L1	3.74	52	10.33	30	118.33	48	30.00	38	24.67	43
16	MP706XI137TN	L7/L5	3.69	53	3.33	64	114.00	49	22.67	50	21.67	48
33	E739XB37	L4/L2	3.61	54	11.33	20	104.00	58	29.00	41	25.33	38
37	B37XI137TN	L2/L5	3.60	55	6.33	55	122.67	40	33.00	34	31.00	29
31	E739XMP739	L4/L7	3.52	56	7.00	50	138.33	9	34.00	32	32.33	24
40	B37XE739	L2/L4	3.48	57	4.33	62	124.00	36	25.67	45	24.67	42
62	B37	L2	3.43	58	12.00	15	99.00	60	19.67	57	18.00	56
64	B73	L3	3.38	59	9.67	36	129.33	21	21.00	52	19.00	51
6	P28XB14	L8/L1	3.04	60	12.00	17	128.67	24	29.33	39	25.33	39
20	MP706XB14	L7/L1	2.78	61	13.00	11	141.33	3	36.67	26	31.33	28
63	B14	L1	2.14	62	7.33	48	108.67	54	19.67	58	18.00	55
61	E739	L4	0.55	63	10.67	28	108.33	55	37.67	22	32.33	25
57	P28	L8	0.53	64	11.33	21	122.67	41	29.33	40	25.33	40

3.5.2. General and specific combining abilities of the parents and crosses

General and specific combining effects were investigated in this study. The ANOVA for combining ability effects for root discolouration, plant length, root volume, effective root volume and yield are given in Table 3.5.2.1.

No significant differences for both combining ability effects, GCA and SCA, were observed for root rot discolouration. Highly significant differences for general combining ability effects were found for plant length, root volume and effective root volume. Significant differences for general combining ability effects were observed for yield. Highly significant differences for specific combining ability effects were observed for plant length, yield, root volume and effective root volume.

No significant differences for reciprocal effects were observed for root rot discolouration. Significant differences for reciprocal effects were observed for plant length, root volume and effective root volume. Highly significant differences for reciprocal effects were observed for yield.

Table 3.5.2. ANOVA for combining abilities effects for root rot discolouration, plant length,root volume, effective root volume and yield

		Characters				
Source	Df	RRD	PL	RV	ERV	Yield
Total	63					
GCA	7	19.80	33339.23**	280.6**	213.4**	1.31*
SCA	28	9.80	209.67**	151.90*	115.50*	2.20**
Reciprocal	28	10.94	123.78*	147.10*	17.00*	1.68**
Residual	126	14.80	88.40	92.50	68.90	0.62

** P=0.01
* P=0.05

3.5.2.1. *General combining ability effects (GCA)*

The general combining ability effects for root rot discolouration plant length, root volume, effective root volume and yield are listed in Table 3.5.2.1.

The inbred lines I137TN (-1.22) and E739 (-1.08) had the lowest general combining ability effects for root rot discolouration thus indicating that they are probably the best to use for the improvement of root rot resistance in maize. The inbred line P28 (1.77) had the highest general combining ability effect of the parental lines for root rot discolouration. The use of P28 in F1-hybrids will probably lead to an increase in root rot discolouration. However no significant differences existed between the eight inbred lines with regard to their general combining ability effects. This could be explained by the low repeatability for discolouration in this trial.

The inbred lines B14 (6.66) and B73 (5.81) had respectively the highest general combining abilities for plant length. These two inbreds can therefore be successfully used to increase plant length maize hybrids. The inbred line with the lowest general combining ability effect for plant length was I137TN. It could therefore be successfully used in crosses to reduce plant height. The general combining ability of I137TN differs significantly from inbred lines B14 and B73.

For root volume the inbred line B14 (6.17) had the highest general combining ability effect of the inbred lines. The general combining ability effect of B14 inbred line exceeded that of inbred line I137TN (-6.86) significantly.

The highest general combining ability effect for effective root volume was found in inbred line B14 (5.42) followed by B37 (3.59). Their general

combining ability effects were significantly higher than the inbred line I137TN (-5.59). According to these data the inbred lines B14 and B37 would probably be the best to use in crosses to reduce root discolouration in a maize resistance breeding programme.

The inbreds E739 (-0.49) and B14 (-0.28) had the lowest general combining ability effects for yield followed by P28 (-0.04) and B37 (-0.01). The inbred lines with the highest general combining ability effects for yield were MP706 (0.35), MO17 (0.31) followed by I137TN (0.15). These results indicate that these inbred lines are probably the best to use in a maize breeding programme for increasing yield.

Table 3.5.2.1. General combining ability effects for root rot discolouration, plant length, root volume, effective root volume and yield

		Characteristics				
Entry	Parent	RRD	PL	RV	ERV	Yield
1	B14	-0.18	6.66	6.17	5.42	-0.28
2	B37	-0.83	-1.62	3.25	3.59	-0.01
3	B73	0.82	5.81	1.79	1.30	0.01
4	E739	-1.08	-3.98	-2.00	-1.55	-0.49
5	I137TN	-1.22	-6.60	-6.86	-5.59	0.15
6	MO17	1.13	-2.35	1.08	-1.46	0.31
7	MP706	-0.41	0.60	-3.53	-3.30	0.35
8	P28	1.78	1.47	2.35	1.59	-0.04
	LSD(p=0.05)	8.11	8.92	9.13	7.88	0.74

3.5.2.2. Specific combining ability effects (SCA)

The specific combining ability effects of the crosses for root rot discolouration, plant length, root volume, effective root volume and yield are listed in Table 3.5.2.2.

For root rot discolouration the cross B37XB73 (-5.42) had the lowest specific combining ability effect, followed by the cross E739XMO17 (-3.48). These results indicate that these crosses are the best crosses for developing F1-hybrids resistant to maize root rot disease. The crosses B73XE739 (3.82), MP706XP28 (3.70) and B14XMO17 (3.28) followed by B73XI137TN (2.64) and B73XP28 (2.30) showed the highest specific combining ability effects for root rot of all the crosses. Therefore the high level of root rot susceptibility in these crosses is an indication that the use of these crosses will cause an increase in root discolouration in F1-hybrids.

The crosses (Table 3.5.2.2) showed significant differences for specific combining ability effects for plant length. The cross B14 X MO17 (20.90) had the highest specific combining ability effect and its effect was significantly higher than 26 of the other crosses. The crosses B37 X MO17 (14.34) and B37 X MO17 (9.58) and B37 X P28 (9.18) had the second, third and fourth largest specific combining ability effects for plant length. The effects of these four crosses exceeded the effects of 12 other crosses significantly.

The two crosses with the highest specific combining ability effects for root volume were B14 X MO17 and B37 X P28 (13.14). Their specific combining ability effects exceeded those of four other crosses significantly. It indicated that the parents involved in these two crosses carry specific genes which will enhance root volume when they are combined. The crosses B37 X I137TN (-8.65) and B37 X E739 (-7.88) had the lowest combining

ability effects for root volume indicating weaker root development in these two crosses.

Significant differences existed between the specific combining abilities of the crosses for effective root volume. The crosses with the highest specific effects were B37 X P28 (11.07), B14 X E739 (10.96) followed by B37 X MO17 (8.92), B14 X E739 (7.71) and B37 X B73 (7.36). The results indicate that the parents involved in these crosses also carried specific genes, which can enhance root rot resistance when they are combined into one hybrid. The crosses with the lowest specific effects for root efficiency were B37 X I137TN (-7.45), B37 X E739 (-728), MP706 X P28 (-6.87) and MO17 X P28 (-5.37). It can be assumed that these crosses might also show a tendency to be less tolerant to root rot.

Significant differences with regard to their specific effects for yield were observed between crosses (Table 3.5.2.2). The crosses I137TN X MP706 (1.58), B14 X MO17 (1.16) and B37 X P28 (1.06) had the highest specific combining ability effects for yield. The specific combining ability effect of cross I137TN X MP706 for yield is significantly higher than 20 of the other crosses. The specific combining ability effects for yield of combinations B14 X MP706 (-0.99), B73 X MP706 (-0.72) and MO17 X MP706 (-0.58) were negative and very low.

Table 3.5.2.2. Specific combining abilities of the different crosses for root discolouration, plant length, root volume, effective root volume and yield

Entry	Cross	RRD	PL	RV	ERV	Yield
1	B14XB37	-0.42	-1.67	3.52	3.74	0.64
2	B14XB73	-0.07	-3.27	0.64	0.37	0.10
3	B14XE739	-0.01	7.69	7.87	7.72	0.85
4	B14XI137TN	-0.53	3.65	2.47	1.76	0.33
5	B14XMO17	3.29	20.90	14.18	10.97	1.16
6	B14XMP706	1.16	3.77	-2.69	-2.20	-0.99
7	B14XP28	-1.19	-2.94	0.75	0.74	-0.32
8	B37XB73	-5.42	0.35	5.56	7.37	-0.08
9	B37XE739	-0.19	-3.85	-7.88	-7.28	-0.43
10	B37XI137TN	0.12	-2.90	-1.78	-2.07	0.01
11	B37XMO17	1.10	14.35	0.10	0.14	-0.14
12	B37XMP706	0.81	5.73	7.22	6.47	0.54
13	B37XP28	0.29	9.19	13.50	11.07	0.50
14	B73XE739	3.83	2.04	-0.92	-2.66	0.18
15	B73XI137TN	2.64	2.00	-8.65	-7.45	-0.01
16	B73XMO17	-0.38	9.58	10.89	8.93	0.60
17	B73XMP706	-1.01	-1.04	3.35	2.93	-0.72
18	B73XP28	2.31	0.08	5.79	4.37	1.06
19	E739XI137TN	0.20	5.63	-4.76	-4.43	0.91
20	E739XMO17	-3.48	4.04	4.79	5.62	0.86
21	E739XMP706	-1.94	2.25	-3.26	-1.55	0.44
22	E739XP28	-1.30	-10.63	-3.65	-2.62	0.12
23	I137TNXMO17	-0.51	-16.83	-6.11	-4.43	-1.03
24	I137TNXMP706	-1.13	9.21	5.85	5.32	-0.85
25	I137TNXP28	0.02	4.17	7.62	6.76	1.58
26	MO17XMP706	1.85	-3.04	0.39	-0.14	-0.58
27	MO17XP28	-1.67	4.42	-6.01	-5.37	0.44
28	MP706XP28	3.70	-0.54	-8.55	-6.87	0.47
	LSD(p=0.05)	8.11	8.93	9.13	7.88	0.74

3.5.3. General and specific combining ability ratio's (GCA:SCA ratio's)

The mean squares for general and specific combining ability effects and the GCA:SCA ratio's for root discolouration, plant length, root volume, effective root volume and yield are given in Table 3.5.3.

The GCA:SCA ratio's for root discolouration indicated that the additive effect was twice as large as the effect due to dominance and interaction. These results indicated that there were a fair amount of additive genes involved in the expression of this characteristic.

The GCA:SCA ratio's for plant length (1.6:1), root volume (1.8:1), and effective root volume (1.8:1) showed that the additive effect exceeded the effects due to dominance and interaction effects.

For yield the GCA:SCA ratio's were close to one indicating that the additive and dominance effects were of equal importance.

Table 3.5.3. Mean squares of general and specific combining ability effects and GCA:SCA ratio's for root rot discolouration, plant length, root volume, effective root volume and yield

Character	GCA	SCA	GCA:SCA
RRD	19.76	9.75	2.02:1
PL	339.23	209.67	1.61:1
RV	280.57	151.89	1.84:1
ERV	213.40	115.48	1.84:1
Yield	1.31	2.20	0.60:1

RRD – root discolouration, PL – plant length, RV – root volume, ERV – effective root volume

3.5.4. *Genetic correlations (r_A)*

The genetic correlations (r_A) between the different characteristics are listed in Table 3.5.4.

Effective root volume was highly significantly correlated with root volume ($r_A=0.99$). Since root volume is one of the parameters used in the calculation of effective root volume, a relatively high correlation is expected between these two characters. Effective root volume was also significantly correlated with plant length ($r_A=0.72$), which meant that there was a relationship between the effective root volume made up by the root volume and plant length. This was confirmed by the significant positive correlation between root volume and plant length ($r_A=0.78$)

Root discolouration was positively but not significantly correlated with plant length, root volume and effective root volume. This could be explained by the overall low levels of root discolouration that occurred in the trial, indicating that the level of discolouration was too low to have any significant effect on these characteristics.

Yield was not significantly correlated with root discolouration, and it was negatively correlated with plant length, root volume and effective root volume. Therefore it shows that any increase in root discolouration may decrease yield.

Table 3.5.4. Genetic correlations between root rot discolouration, plant length root volume, root efficiency and yield

Character	RRD	PL	RV	ERV
RRD				
PL	0.47			
RV	0.33	0.78*		
ERV	0.29	0.72*	0.99**	
Yield	0.25	-0.15	-0.41	-0.453

** indicates the probability of highly significant differences

* indicates the probability of significant differences

3.5.5. Inheritance of root rot resistance

The broad and narrow sense heritabilities for root rot discolouration, plant length, root volume, effective root volume and yield are given in Table 3.5.5.

The values of the broad sense heritabilities were relatively high in comparison with the narrow sense heritabilities. These varied from $h^2=0.81$ for root discolouration to $h^2=0.93$ for root volume.

The results in Table 4.3.3.4 show that the narrow sense heritabilities for root rot discolouration ($h^2=0.51$), plant length ($h^2=0.62$) and effective root volume ($h^2=0.58$) were relatively high. These results indicate that a plant breeder can select effectively for a low root rot discolouration as well as for high effective root volume that will probably enhance rot root resistance in maize.

The narrow sense heritabilities for root volume ($h^2=0.37$) and yield ($h^2=0.30$) were relatively low. This could be explained by quantitative type of inheritance of these characters and the large effect of environmental variances.

Table 3.5.5. Inheritance of root rot discolouration, plant length, root volume, root efficiency and yield

Inheritance	Characters				
	RRD	PL	RV	ERV	Yield
h^2_b	0.81	0.92	0.94	0.91	0.93
h^2_n	0.51	0.62	0.37	0.58	0.30

h^2_b – broad sense inheritance, h^2_n– narrow sense heritance

3.5.6. Correlated response (C_R)

The correlated responses between root rot discolouration, plant length, root volume, effective root volume and yield are listed in Table 3.5.6.

The results indicate that selecting for root discolouration will not bring about major changes in root volume, effective root volume or yield. However, selecting for root discolouration will have a small effect on plant length (C_R=0.14). Yield was negatively effected by an increase in root discolouration.

The correlated response between plant length and effective root volume was relatively high (C_R=0.25), indicating that root efficiency can be increased by at least 25% when indirect selection for plant length is applied to a maize population. The correlated response between plant length and root volume equalled 14%, indicating that selecting for taller plants will also cause an increase of 14% in root volume. The correlated response between yield and plant length (C_R=-0.04) was for all practical reasons non-existent.

The correlated response between root volume and effective root volume (C_R=0.21) is relatively high, indicating that an increase in effective root volume will enhance root rot volume by 21%. The correlated response between root volume and yield (C_R=-0.05) was very low and negative. The correlated response between effective root volume and yield is very low and negative. It indicated that an increase in effective root volume will not necessarily cause an increase in the yield. This could be explained by the fact that high yields are also a function of the genotypic yielding ability of the maize plant.

Table 3.5.6. Correlated response (C_R) between root rot discolouration, plant length root volume, root efficiency and yield

Characters	RRD	PL	RV	ERV
RRD				
PL	0.149			
RV	0.064	0.177		
ERV	0.085	0.258	0.214	
Yield	-0.038	-0.035	-0.046	-0.080

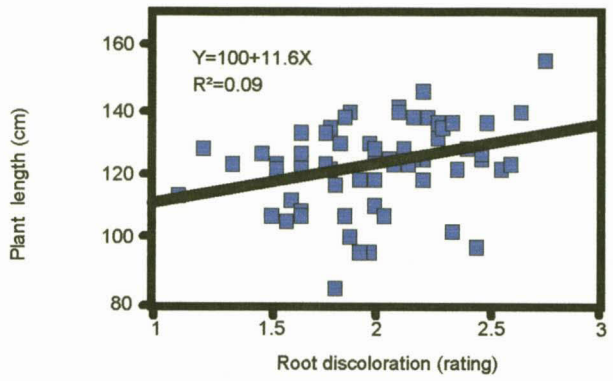

Figure 3.5.1. Relationship between root discoloration and length of maize plants evaluated in a diallel cross (Model 1).

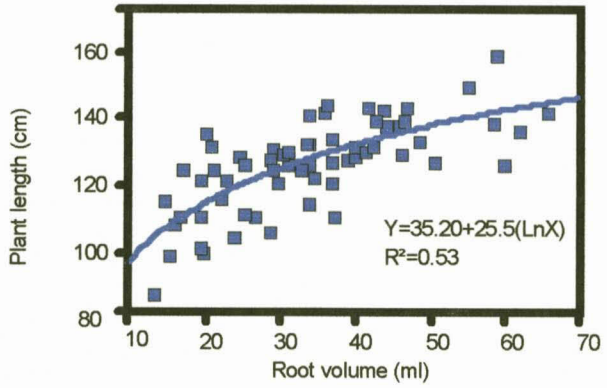

Figure 3.5.2. Relationship between root volume and length of maize plants evaluated in a diallel cross (Model 1).

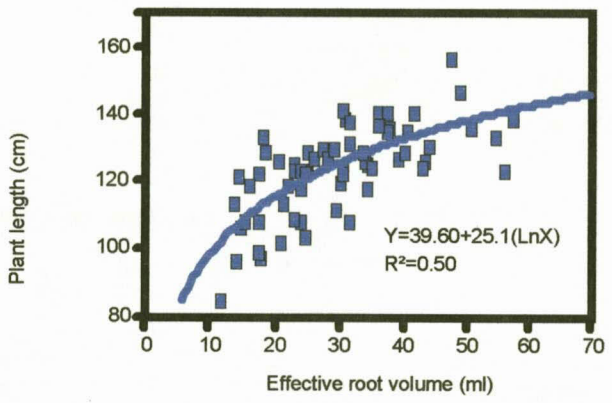

Figure 3.5.3. Relationship between effective root volume and length of maize plants evaluated in a diallel cross (Model 1).

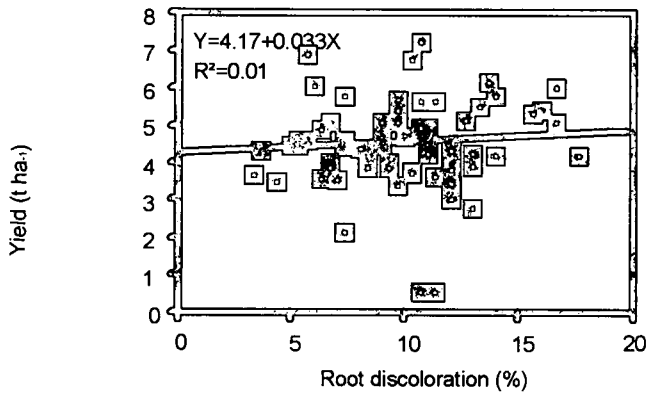

Figure 3.5.4. Relationship between root discolouration and yield of maize evaluated in a diallel cross (Model 1).

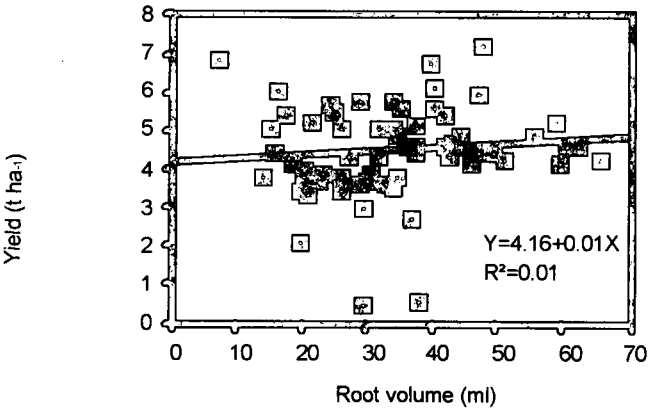

Figure 3.5.5. Relationship between root volume and yield of maize evaluated in a diallel cross (Model 1).

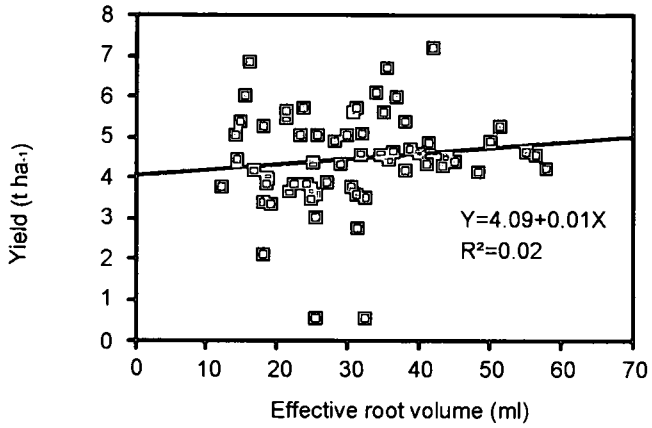

Figure 3.5.6. Relationship between effective root volume and yield of maize evaluated in a diallel cross (Model 1).

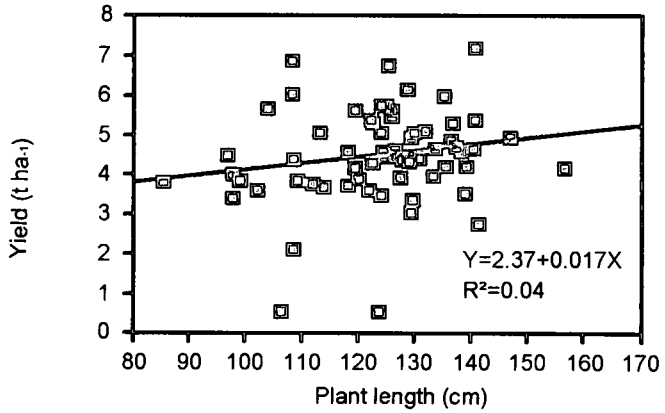

Figure 3.5.7. Relationship between plant length and yield of maize evaluated in a diallel cross (Model 1).

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CHAPTER 4

ASSESSMENT OF FIELD RESISTANCE TO ROOT ROT IN MAIZE HYBRIDS

ABSTRACT

Thirty four maize hybrids were planted at Bethlehem and Potchefstroom over three seasons from 1997 to 2000 at five environments to study the stability of resistance to root rot of maize over environments. A randomized block design with three replicates was used. Roots were recovered seven to eight weeks after planting, washed and visually assessed for root rot severity based on percentage root discolouration. Recovered root volume was determined using water displacement. Plant length at the time of assessment was measured from the crown to the tip of the uppermost fully extended leaf. The root rot x locality/season (environment) interaction was highly significant. Mean root rot severity in the hybrids ranged from 8.11% in PAN6479 to 24% in PAN6480. The locality/season x hybrid interaction was highly significant for root volume. The values ranged from 68.87 ml in PHB3442 to 113.32 ml in CRN3815. The yield x locality/season interaction was also highly significant. The mean yield of the hybrids over localities ranged from 4.14 t/ha for PAN6243 to 5.82 t/ha for PHB30h22. Additive main effects and multiplicative interaction analysis (AMMI) was used to identify those hybrids in which root rot, rot volume, plant length and yield were significantly influenced by environmental factors.

INTRODUCTION

Maize root rot is an important disease in South Africa and in other countries where maize is grown. The disease is ascribed to a number of fungi which inhabit the soil and occur as a maize root rot complex. The disease is becoming an increasingly important and limiting factor in maize production. Weather conditions, particularly rainfall has a large influence on yield. Rainfall in the South African maize producing areas is low and poorly distributed. Absence of rain during critical growth stages of the crop causes extended periods of plant stress. These stresses may predispose maize to root rot.

Growth and development of aerial parts of the maize plant have been extensively studied but relatively little attention has been given to soil borne diseases. The main reason is that the symptoms of root diseases are not always easily visible (Tarr, 1962). Yet the disease complex can cause growth reductions with concomitant yield losses or poor grain fill as well as reduce root efficiency and hence drought tolerance (McLaren, 1999). Lodging may also occur (Pappelis & BeMiller, 1984).

Successful cultivars need to have high yield performances across a wide range of environmental conditions. The basic cause for differences in yield or stability between genotypes is the occurrence of genotype x environment interactions. The aim of this study, therefore was to determine resistance to root rot in commercial maize hybrids and to quantify the stability of resistance over different environments.

4.1 SCREENING OF MAIZE HYBRIDS FOR ROOT ROT RESISTANCE AND GENOTYPE ENVIROMENT INTERACTION

Evaluation of resistance is aimed at quantifying the resistance of established genotypes and to facilitate the selection of genotypes with resistance. The skill with which disease resistance is measured and the selection that is practised determines, therefore the potential, which the hybrids may have (Personal Communication).

A number of authors have repeatedly called attention to the difficulty of evaluating root rot in the field (Mc Laren, 1987). This has been attributed to the laborious task of removing roots from the soil and the lack of suitable techniques to quantify root rot improvement (Zuber *et al.*, 1957). Some authors are concerned about visible symptom development while other are concerned about actual losses in yield and quality.

Under field conditions root development and root rot are difficult to separate when plants approach maturity (Chambers, 1986). Thompson (1972) quantified root rot by studying root clump. He found root clump to be significantly related to root lodging and regarded it an efficient and usefull criterion for studying root lodging and anchorage. Root pulling resistance is the force required to pull a plant vertically from the soil and has been used by a number of investigators to evaluate root rot (Koehler, 1960; Zuber *et al*, 1981). Measurements of root volume to select extensive root types was used by Zuber *et al*, (1957).

Various techniques have been reported in the literature, but these techniques either involve the use of heavy and sophisticated equipment or are labour intensive. Furthermore, most of these techniques are destructive (Chambers, 1987b). According to him root decay rating was correlated with plant yield

and is therefore an easy method of evaluation root rot and even selecting for maize root rot resistance. This method has been used by many breeders but few reports are found in the literature.

MATERIAL AND METHODS

Thirty four maize hybrids were planted in five trials at Bethlehem and Potchefstroom from 1997 to 2000. Hybrids were planted in single row plots, 15 m in length with 1.2 m inter row and 0.33 intra row spacings. The trials were planted according to a randomized block design with three replications each. Plots were fertilized with 300 kg 2:3:2 (22) prior to planting. Trials were conducted under dryland conditions and irrigated only when necessary. Weed and insect control were applied as required.

Seven to eight weeks after planting 10 plants were removed from each plot, endeavouring to recover as much of the root system as possible. Roots were washed free from soil and visually assessed for root rot severity based on percentage root discolouration. Recovered root volume was determined using the water displacement method. Plant length at the time of assessment was measured from the crown of the plant to the tip of the upper leaf. Effective root volume (ERV) was calculated with the following equation:

$$ERV = (((100 - \text{root rot severity})/100) * \text{root volume})$$

Yield was determined at maturity. Grain yield was calculated as shelled grain mass per plot adjusted to 12.5% grain moisture and converted to tons per hectare, according to the following formula:

$$GY = (Wt\ Kg / Np) * Pp * (100 - H\%) / 87.5\%) * 1t / 1000\ Kg$$

where: GY is grain yield in t/ha, Wt is grain mass in Kg, Np is final stand (number of harvested plants) , Pp is plant population (total number of

plants/hectare) calculated from plot size, H% is the percentage moisture taken after harvest and 87.5% is coefficient of moisture correction (100 – 12.5%). Data were analyzed according to the Multiplicative Interaction Model of AMMI. The statistical programme Agrobase (1998) was used to analyze the data.

RESULTS AND DISCUSSION

Analyses of variance for root discolouration, root volume, effective root volume and yield according to the best AMMI 4 fit are presented in Table 4.1. For root discolouration the mean squares were significant for environments, genotypes, genotypes x environment interactions as well as both principal components. For root volume only the environments and genotypes showed significant effects.

The environments, genotypes and main principle component showed significant differences for root volume. For yield the only exception was genotypes that showed no significant differences. The results indicated that genotype x environment interactions are very important with regard to root rot discolouration and yield.

The contribution of each source of variation was calculated by dividing their sum of squares by the total sum of squares. These percentages indicated the importance of each source of variation. For root discolouration the contribution of genotypes, environments and genotype x environment interaction were respectively 13.6, 40.0 and 18.0 percent. It indicated that the environment had by far the largest influence on root discolouration. This

result is in line with numerous reports of the influence of environmental, edaphic factors and production practices on root rot of cereals as well as in others crops. On maize these include water stress, temperature stress, nutrient stress, crop rotation, soil acidity, herbicides and tillage (Schoenewiess, 1975) and it is evident that these and other factors have a greater effect on root discolouration and yield than genetic effects.

The percentages of genotype, environment and genotype x environment effects were respectively 15.0, 16.6 and 14.4 percent for root discolouration, 13.0, 16.4 and 16.7 percent for root volume 2.5, 68.3 and 8.8 percent for yield.

To summarize, it is clear that for root discolouration and yield the environment had the largest effect. The genotypic variability for root volume and effective root volume is sufficient to improve these characteristics genetically.

Table 4.1. Analysis of variance for 34 maize genotypes evaluated over five environments at Bethlehem and Potchefstroom from 1997-2000

		Root discolouration			Root volume			Effective root volume			Yield		
Source	df	SS	MS	Prob	SS	MS	Prob	SS	MS	Prob	SS	MS	prob
Total	509	535			383			3841			0.330		
Enviroments	4	214	535	0.002**	63	0.30	0.011*	6289	1572	0.003**	0.220	0.568	0.000**
Genotypes	33	72	22	0.000**	57	0.20	0.000**	4977	150	0.000**	0.084	0.002	0.261
G X E	132	96	0.07	0.000**	55	0.04	0.960	6417	0.48	0.912	0.293	0.002	0.086*
IPCA 1	36	52	0.14	0.000**	38	0.11	0.001	3552	0.98	0.012*	0.127	0.003	0.001**
IPCA 2	34	34	0.10	0.000**	12	0.36	0.919	161	0.47	0.787	0.092	0.002	0.044*
Residual	330	120	0.04		179	0.54		1967	0.59		0.604	0.001	

** P=0.01

* P=0.05

Root rot discolouration

The mean root rot severities associated with environments and hybrids are presented in Table 4.2. The hybrids differed significantly with PAN6479 the most resistant genotype with a root rot severity of 8.11% and PAN6480 the most susceptible with a root rot severity of 24.10%.

The genotype x environment interaction effects on root rot, although significant, are relatively low (18%). The AMMI 4 model indicated that IPCA 1 explained in excess of 54.23% of the genotype x environment interactions sum of squares, while IPCA 2 accounted for 36.11% of the interaction. IPCA 3 (7.24%) and IPCA 4 (2.41%) effects are of relatively minor magnitude (Table 4.3).

Biplots of environments and hybrids for root rot severity are presented in Figure 4.1. Biplots for environments indicated that root rot infection were relatively low at Bethlehem 1997/98, Bethlehem 1998/99 and Potchefstroom 1997/98 (quadrants I and III). At Potchefstroom 1998/99 and Bethlehem 1999/2000 in particular the infection rates were much higher (quadrants II and IV). Analyses of the mean temperatures and total rainfall during the vegetative growth period as well as temperature and rainfall distributions do not correlate with root rot severities reiterating the complexities of the environmental interactions.

Figure 4.1a confirms the relatively low genotype x environment interaction effect on root rot severity and most hybrids lay within the IPCA 1 range of −1 to 1, indicating that most entries gave stable root rot reactions over the environments tested. The deviations from this range indicated that the hybrids CRN3604, PAN6480 and SNK2266 were particularly susceptible and unstable under increasing root rot infection (quadrants II and IV). The hybrids which showed the most unstable root rot reactions were PAN6043,

PAN6364, PAN6480, PAN6243, CRN3815, CRN3604, NS9100, SNK2721, and SNK2266 and could be regarded as environmentally unstable genotypes with regard to root rot severity.

Since IPCA 2 also plays a significant role in the genotype x environment interactions (36.11%), IPCA 2 scores were plotted against IPCA 1 scores for the further determination of stability of the hybrids (Figure. 4.1b). The results indicated that the hybrids PAN6480, PAN6568, PAN6242, PAN6479, PAN6243, CRN3524, SNK2682 and SNK2147 were very unstable considering a second principle component and that the stability of their reactions with regard to root pathogens needs to be questioned.

Root volume

The mean root volumes of the hybrids for five environments are presented in Table 4.1. These fell in the range of between 68.87 ml for PHB3442 and 113.32 ml for CRN3815. Higher root volumes were generally associated with the trials planted at Bethlehem 1999/2000, Bethlehem 1998/99, Potchefstroom 1997/98 and Bethlehem 1997/98. The environments were particularly associated with wet conditions. The trial at Potchefstroom 1999/99 was associated with a reduced root volume. Root volumes of the hybrids PAN6364, PAN6568, PAN6242, SNK2721, SNK2401, SNK2682, SNK2782, and CRN3524 responded positively to the favourable conditions as experienced at Potchefstroom 1997/98 and Bethlehem 1998/99 in quadrants II and IV (Fig. 4.2a).

AMMI 4 model indicated that IPCA1 and IPCA 2 for root volume explained 69.39% and 22.59% of the total genotype x environment interaction sum of squares respectively. IPCA 3 explained only 7.07% and IPCA 4, 0.96%. Figure 4.2b showed that when IPCA 2 scores were plotted against IPC1 scores the hybrids CRN3815, PAN6335, PAN6561 PHB3432, SNK2721

and SNK2147 which were stable for IPCA 1 scores were unstable for IPCA 2 scores.

Effective root volume

The mean effective root volumes of the hybrids are presented in Table 4.1. Effective root volume ranged from 61.76 ml in PAN6480 to 98.75ml in CRN3815. The two hybrids differed significantly from one another. Higher effective root volumes were associated with Bethlehem 1998/99, Potchefstroom 1997/98, Bethlehem 1997/98 and Bethlehem 1999/2000 (quadrants II and IV). However effective root volume for the hybrids PAN6568, PA6480, PAN6043, PAN6256, CRN1598, CRN3818, CRN3815, CRN3524, PHB30h22, SNK2472, SNK2626, SNK2147, SNK2401, SNK2682, SNK2721 and SNK2021 both positvely and negatively responded to environment and were generally unstable under favourable environmental conditions as indicated by Figure 4.3a.

IPCA 1 scores of effective root volume explained 55.35% of the total genotype x environment interaction sum of squares while IPCA 2 explained 25.13% of the total genotype x environment interaction sum of squares. IPCA 3 and IPCA 4 accounted for 14.92% and 4.60% of the genotype x environment interaction, respectively. Interactions IPCA1 and IPCA 2 scores indicate that hybrids SNK2147, CRN3414, SNK2782, CRN3852, NS9100, PAN6335, PAN6332 and PAN6479 were very stable for IPCA 1 scores but unstable for IPCA 2 scores. It indicated that IPCA 2 scores played a significant role when the genotype x environment interactions were plotting against IPCA 1 scores to determine the stability of effective root volume.

Plant length

The mean plant length of hybrids are presented in Table 4.1. An AMMI analysis of variance was not done for plant length due to missing data for two of the environments.

A simple linear regression analysis was done to study the relationship between effective root volume as dependent variable and plant length and yield as independent variables. It was done for the three remaining environments where plant length data were collected. Effective root volume was poorly correlated with plant length at the Bethlehem 1999/2000 and Potchefstroom 1998/99 (R^2= 0.01) environments. A similar relationship was recorded between effective root volume and yield at Bethlehem 1999/2000 (R^2= 0.03).

Effective root volume was highly correlated with plant length at Bethlehem 1998/99 (R^2= 0.71). A relatively high correlation was also recorded between effective root volume and yield at Bethlehem 1998/99 (r^2= 0.68) and Potchefstroom 98/99 (R^2= 0.73) environments (Figure 4.5a,4.5b). It indicates that a high effective root volume is a necessity for high yields.

Yield

The mean yields of the hybrids at the different environments are presented in Table 4.2. The yields of hybrids differed significantly from one another and ranged from 4.14 t/ha for PAN6243 to 5.82 t/ha for PHB30h22.

The AMMI 4 model indicated that for yield the IPCA 1 explained 43.13% of the genotype x environment interaction sum of squares and IPCA 2 explained 31.52% of the genotype x environment interaction sum of squares.

IPCA 3 and IPCA 4 explained only 17.83% and 7.52% respectively. It indicates highly complex interactions which, require further investigation. Deviation from the means indicated that hybrids PHB3442, PHB30h22, CRN3604, CRN3524, CRN3414, CRN3760 PAN6335, PAN6479, and PAN6243 were very unstable for yield.

The biplots for environments indicates that the yield at Potchefstroom 1997/98 environment was relatively high, while the yields at Bethlehem 1997/98, Bethlehem 1998/99, Bethlehem 1999/2000 and Potchefstroom 1998/99 environments were relatively low. IPCA2 scores plotted against IPCA1 scores indicates that hybrids PAN6480, SNK2147, SNK2682, SNK2782, SNK2147 and SNK2778 were regarded as stable relative to IPCA 1 scores and were shown to be unstable relative to IPCA 2 scores (Figure 4.4c).

Despite discernable differences in adaptation over environments, it generally appears that some hybrids were specifically adapted to favourable conditions. Some were adapted to more unfavourable conditions and a few can be classified as hybrids which are well adapted to a wide range of environments. The study has clearly shown that the AMMI model can be used to summarise patterns and relationships of genotypes and environments successfully. It can also provide a valuable assessment of root rot discolouration in maize hybrids. For this reason it is recommended that this model can successfully be used to study genotype disease interactions in maize. It can also be used to identify superior disease resistant genotypes for commercial production.

Table 4.2. Mean root rot, root volume, root efficiency, plant length and yield of maize hybrids evaluated over five environments at Bethlehem and Potchefstroom for the period 1997-2000.

Entry	Hybrid	RRD	RV	ERV	PL	YIELD
1	CRN1598	13.15	72.24	65.71	191.33	4.49
2	CRN3414	17.71	83.06	63.87	199.94	5.10
3	CRN3524	20.73	88.09	69.00	192.67	5.05
4	CRN3604	16.05	97.76	82.70	218.61	5.47
5	CRN3760	18.43	80.89	67.20	197.83	5.81
6	CRN3815	13.03	113.32	98.75	224.67	5.11
7	CRN3818	12.50	84.04	74.18	213.50	4.95
8	CRN3852	14.13	92.49	80.59	220.28	5.34
9	CRN3891	12.77	91.42	80.78	223.39	5.08
10	NS9100	11.57	69.36	58.88	199.56	4.22
11	PAN6043	12.81	78.95	67.35	200.33	4.71
12	PAN6242	19.89	92.27	74.35	214.28	4.68
13	PAN6243	9.11	80.43	70.72	199.39	4.14
14	PAN6256	18.49	92.46	73.52	208.22	4.85
15	PAN6332	12.55	89.02	80.11	214.72	4.93
16	PAN6335	12.59	96.24	83.35	212.89	4.87
17	PAN6364	12.65	113.23	98.33	211.72	5.09
18	PAN6414	17.29	92.58	76.94	210.50	5.19
19	PAN6479	8.11	92.31	87.09	211.78	5.12
20	PAN6480	24.10	81.02	61.76	202.56	4.57
21	PAN6561	12.01	77.93	67.86	199.61	5.40
22	PAN6568	22.31	96.13	79.15	209.89	4.71
23	PHB30h22	19.83	82.37	67.64	202.17	5.82
24	PHB3442	17.75	68.87	55.39	191.67	4.47
25	SNK2021	17.82	75.57	61.90	189.89	4.35
26	SNK2147	10.63	101.77	90.41	221.08	4.49
27	SNK2266	17.96	95.67	74.79	215.11	4.92
28	SNK2401	17.84	96.50	76.67	207.44	5.29
29	SNK2472	12.27	78.95	72.89	202.61	5.22
30	SNK2626	13.25	80.53	68.85	195.28	4.95
31	SNK2682	10.83	97.43	78.74	215.00	5.14
32	SNK2721	14.29	92.10	78.79	209.89	4.70
33	SNK2778	17.72	91.93	77.21	223.33	5.54
34	SNK2782	13.65	97.99	80.50	208.72	4.54
	Grand mean	15.16	88.68	74.86	207.64	4.95
	CV	45.51	24.30	26.29	7.64	24.42
	LSD 0.05	7.85	29.80	27.89	21.59	1.60

Table 4.2. IPCA percentage explained by the total genotype x environment interaction sum of squares

	IPCA axis											
No	RRD			RV			ERV			YIELD		
	Eigen Value	% GXE explain	Cumul.	Eigen Value	% GXE explain	cumul	Eigen Value	% GXE explain	Cumul	Eigen value	% GXE explain	Cumul
1	1739.39	54.23	54.23	12773.33	69.39	69.39	11840.96	55.35	55.35	42.17	43.13	43.13
2	1158.17	36.11	90.35	4158.38	22.59	91.97	5375.93	25.13	80.48	30.82	31.52	74.65
3	232.29	7.24	97.59	1301.07	7.07	99.04	3192.53	14.92	95.40	17.43	17.83	92.48
4	77.34	2.41	100.00	176.34	0.96	100.00	983.34	4.60	100.00	7.35	7.52	100.00

Table 4.3 (a). IPCA 1 Axis of environment of 34 maize hybrids evaluated at Bethlehem and Potchefstroom

			RRD		RV		ERV		Yield	
No	Symbol	Envir.	Score	mean	score	mean	Score	mean	score	mean
1	A	ENV1	-1.97	6.73	-0.46	88.14	3.77	79.47	1.91	3.69
2	B	ENV2	1.97	12.94	6.11	91.19	-6.19	79.54	-1.59	9.13
3	C	ENV3	-3.07	10.74	-7.07	93.05	6.21	83.2	-0.44	3.93
4	D	ENV4	4.67	22.96	4.21	68.49	-4.19	52.86	-0.20	3.55
5	E	ENV5	-1.61	22.48	-2.78	102.50	0.39	79.31	0.32	4.46

Table 4.3 (b). IPCA 2 Axis of environment of 34 maize hybrids evaluated at Bethlehem and Potchefstroom

			RRD		RV		ERV		Yield	
No	simb.	Envir.	Score	mean	score	mean	Score	mean	score	mean
1	A	ENV1	-0.97	6.73	0.25	88.14	-4.90	79.47	1.07	3.69
2	B	ENV2	0.20	12.94	1.25	91.19	-1.90	79.54	0.91	9.13
3	C	ENV3	-3.10	10.74	4.22	93.05	0.41	83.2	0.16	3.93
4	D	ENV4	-0.88	3.00	0.92	68.5	-0.35	53	-0.31	3.55
5	E	ENV5	4.76	22.50	-6.64	102.5	6.73	79.31	-1.86	4.46

Table 4. 4. Mean and ranking of maize hybrids screened for root rot, root volume, root volume, effective root volume and yield in five trials at Bethlehem and Potchefstroom for the period 1997-2000

			RRD			RV			ERV			YIELD		
Entry	Cult.	Hybrid	Mean	IPCA 1	IPCA 2	Mean	IPCA 1	IPCA 2	Mean	IPCA1	IPCA 2	Mean	IPCA 1	IPCA 2
1	A	CRN1598	13.15	-0.73	-0.61	72.24	-1.61	-0.83	65.71	1.70	0.15	4.49	-0.07	-0.18
2	B	CRN3414	17.71	-1.00	0.50	83.06	-0.93	-0.65	63.87	-0.67	1.80	5.10	-0.67	-0.44
3	C	CRN3524	20.73	0.20	-0.02	88.09	1.90	-1.13	69.00	-1.91	-0.13	5.05	0.60	-0.11
4	D	CRN3604	16.05	1.63	0.02	97.76	-0.40	0.60	82.70	1.22	-0.01	5.47	0.98	0.38
5	E	CRN3760	18.43	-0.49	0.18	80.89	-1.60	-0.18	67.20	1.34	-0.72	5.81	-0.53	0.03
6	F	CRN3815	13.03	1.36	-0.25	113.3	0.27	3.61	98.75	1.40	-1.60	5.11	-0.04	0.01
7	G	CRN3818	12.50	-0.91	0.76	84.04	1.52	0.84	74.18	-1.25	-1.54	4.95	-0.19	0.08
8	H	CRN3852	14.13	0.45	-1.30	92.49	-0.76	-1.40	80.59	0.44	1.77	5.34	-0.14	-0.05
9	I	CRN3891	12.77	0.25	1.67	91.42	-0.53	-0.99	80.78	1.20	-0.85	5.08	0.28	-0.30
10	J	NS9100	11.57	-1.51	-0.08	69.36	-0.11	-0.91	58.88	-070	1.18	4.22	0.24	0.20
11	K	PAN6043	12.81	2.50	0.08	78.95	-0.20	-0.23	67.35	2.16	2.40	4.71	-0.28	-0.17
12	L	PAN6242	19.89	-0.25	0.52	92.27	-1.24	1.62	74.35	1.13	-010	4.68	0.15	0.40
13	M	PAN6243	9.11	-2.11	-0.21	80.43	-2.41	0.03	70.72	1.03	1.64	4.14	-0.74	0.55
14	N	PAN6256	18.49	-0.34	-0.44	92.46	0.64	-1.18	73.52	-1.40	0.90	4.85	0.25	0.41
15	O	PAN6332	12.55	0.23	0.68	89.02	0.86	0.48	80.11	-0.03	-1.66	4.93	0.33	0.02
16	P	PAN6335	12.59	-1.11	1.13	96.24	0.26	1.38	83.35	-0.37	-1.53	4.87	-0.49	0.41
17	Q	PAN6364	12.65	1.26	0.18	113.2	3.82	2.36	98.33	-2.00	-2.60	5.09	0.01	-0.48
18	R	PAN6414	17.29	0.03	0.38	92.58	0.15	-1.25	76.94	-0.05	-0.03	5.19	0.15	-0.15
19	S	PAN6479	8.11	-1.05	0.69	92.31	-0.84	0.49	87.09	1.12	-1.24	5.12	-0.74	0.30
20	T	PAN6480	24.10	2.12	0.10	81.02	-1.67	-2.54	61.76	1.90	1.42	4.57	-0.06	0.68
21	U	PAN6561	12.01	0.26	0.37	77.93	0.86	-2.09	67.86	-0.73	0.67	5.40	0.47	0.34
22	V	PAN6568	22.31	1.20	0.01	96.13	-3.40	1.48	79.15	3.71	-1.07	4.71	0.14	0.34
23	W	PHB30h22	19.83	0.93	-1.90	82.37	-1.60	1.07	67.64	1.60	-0.41	5.82	0.70	0.50
24	X	PHB3442	17.75	0.60	-2.50	68.87	1.04	1.29	55.39	-0.40	-0.41	4.47	0.79	-0.43
25	Y	SNK2021	17.82	0.70	0.09	75.57	3.90	-2.62	61.9	-3.21	-0.65	4.35	-0.07	-0.23
26	Z	SNK2147	10.63	-0.97	1.04	101.8	-0.17	1.30	90.41	0.11	-1.30	4.49	-0.30	0.56
27	!	SNK2147	17.96	-200	-2.96	95.67	-0.19	0.29	74.79	-2.12	2.22	4.92	0.13	-0.67
28	~	SNK2401	17.84	-0.63	0.40	96.5	2.70	0.94	76.67	-2.60	-0.95	5.29	0.47	-0.05
29	#	SNK2472	12.27	0.56	1.56	78.95	-3.10	0.58	72.89	3.80	-0.72	5.22	-0.45	-0.06
30	$	SNK2626	13.25	0.26	-1.06	80.53	1.40	-1.09	68.85	-1.31	0.90	4.95	-0.41	0.42
31	%	SNK2682	10.83	0.50	0.35	97.43	2.62	-0.85	78.74	-3.11	2.32	5.14	-0.32	-0.55
32	^	SNK2721	14.29	-1.74	0.71	92.1	2.98	1.23	78.79	-3.10	-2.30	4.70	-0.20	-0.11
33	&	SNK2778	17.72	0.40	0.70	91.93	-0.50	-0.64	77.21	1.08	-0.87	5.54	0.47	-0.60
34	(	SNK2782	13.65	-0.57	-0.80	97.99	-1.80	-0.99	80.5	0.12	3.35	4.54	-0.43	-1.02
		Grand mean	15.16			88.09			74.86			4.95		
		LSD 0.05		7.85			29.80			27.89			1.60	

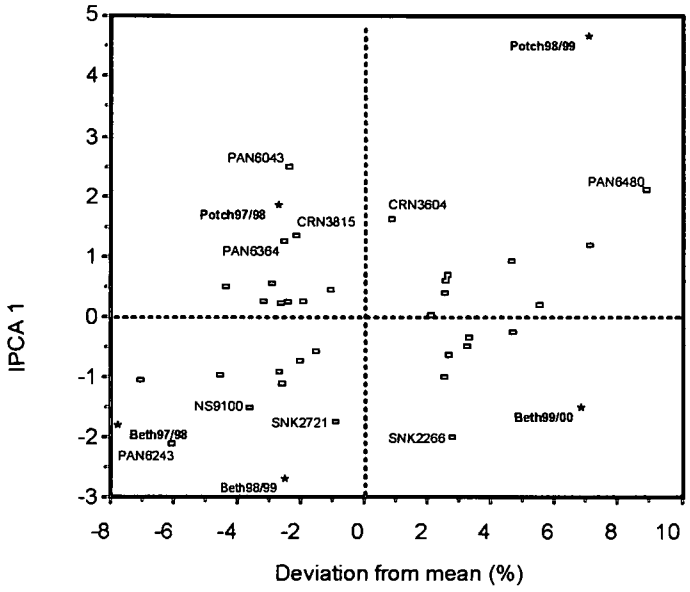

Figure 4.1a: AMMI biplot model 4 for root rot of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

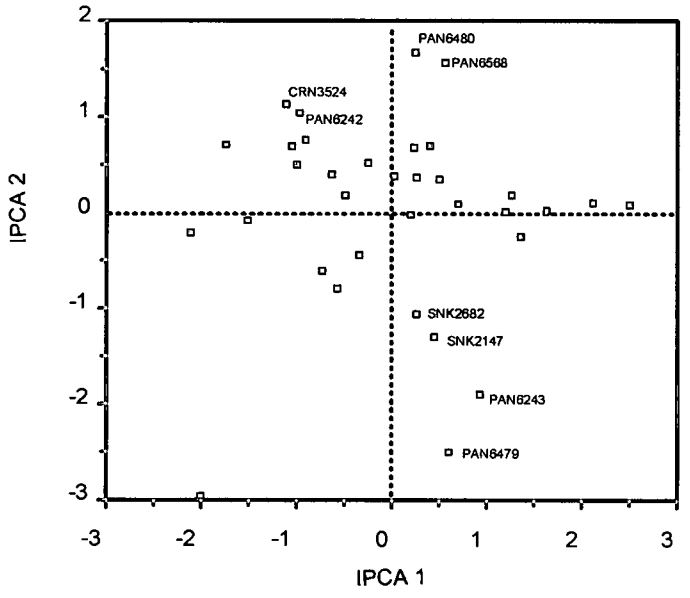

Figure 4.1b: Ploted IPCA 1 and IPCA 2 scores for root rot of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

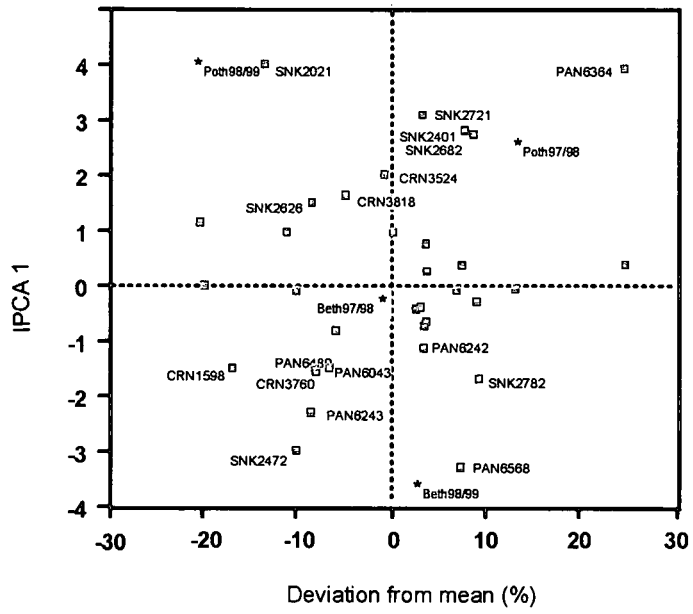

Figure 4.2a: AMMI biplot model 4 for root volume of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

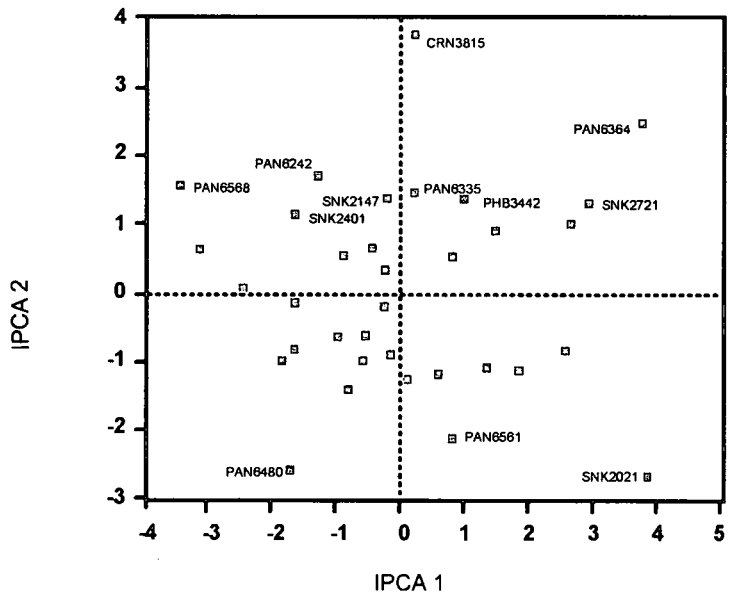

Figure 4.2b: Ploted IPCA1 and IPCA2 scores for root volume of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

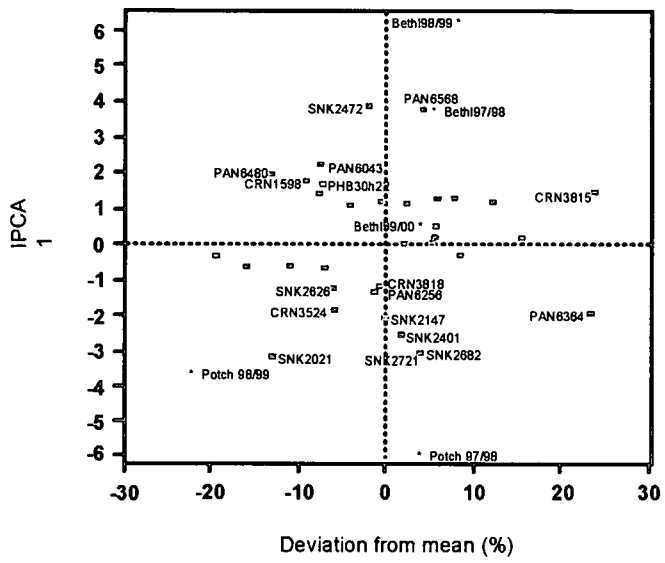

Figure 4.3a: AMMI biplot model 4 for effective root volume of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

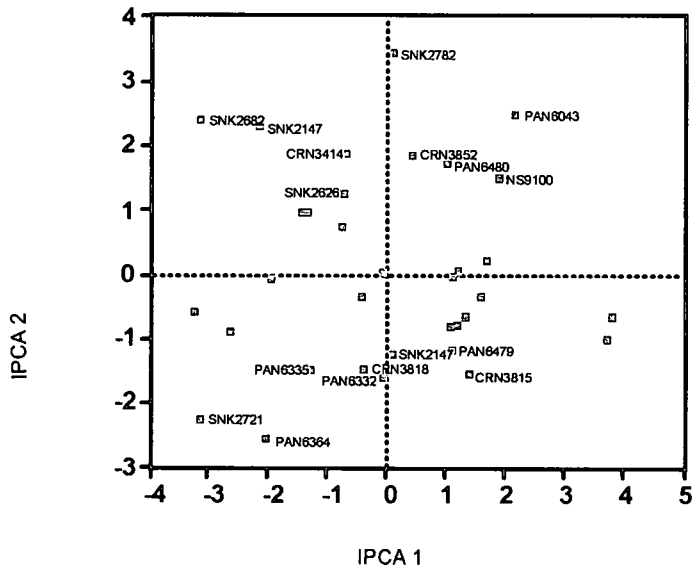

Figure 4.3b: Ploted IPCA1 and IPCA2 scores for effective root volume of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

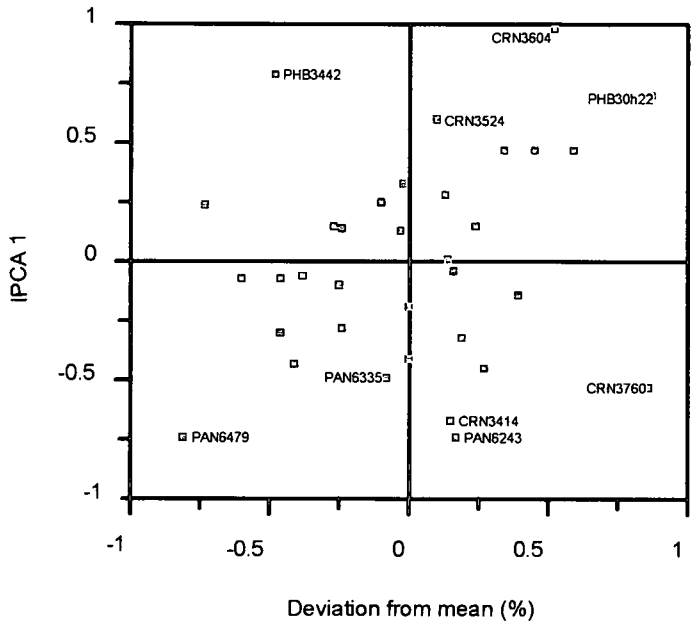

Figure 4.4b: AMMI biplot model 4 for yield over five environments at Bethlehem and Potchefstroom

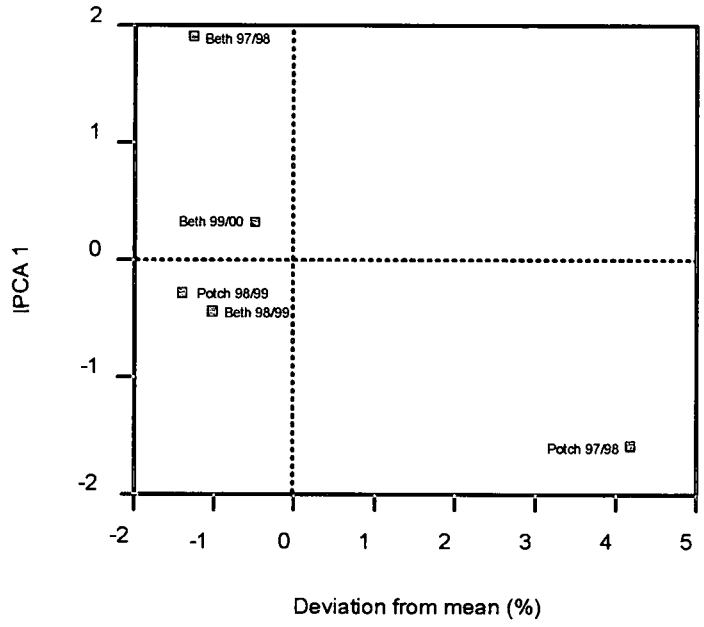

Figure 4.4b: AMMI biplot model 4 for yield over five environments at Bethlehem and Potchefstroom

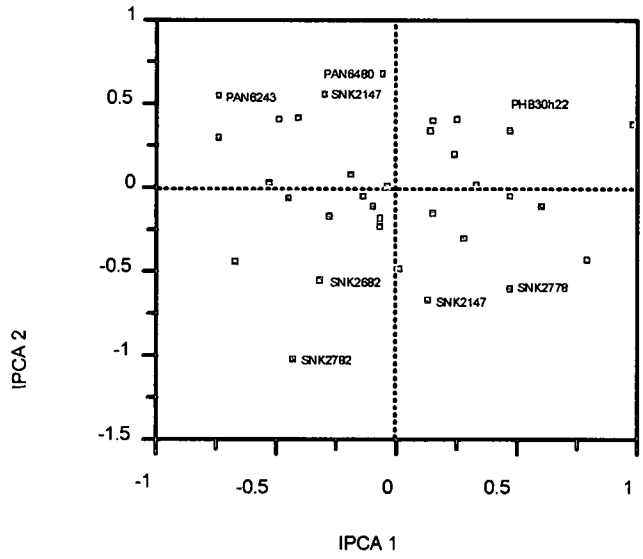

Figure 4.4c: Ploted IPCA1 and IPCA2 scores for yield of 34 maize hybrids over five environments at Bethlehem and Potchefstroom

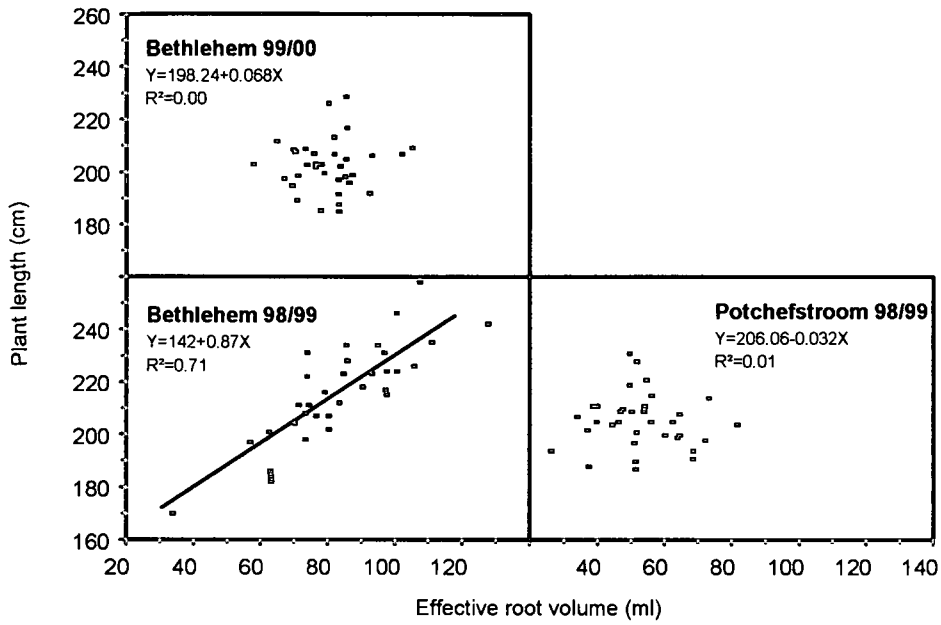

Figure 4.5a: Relationship between effective root volume and plant length in maize

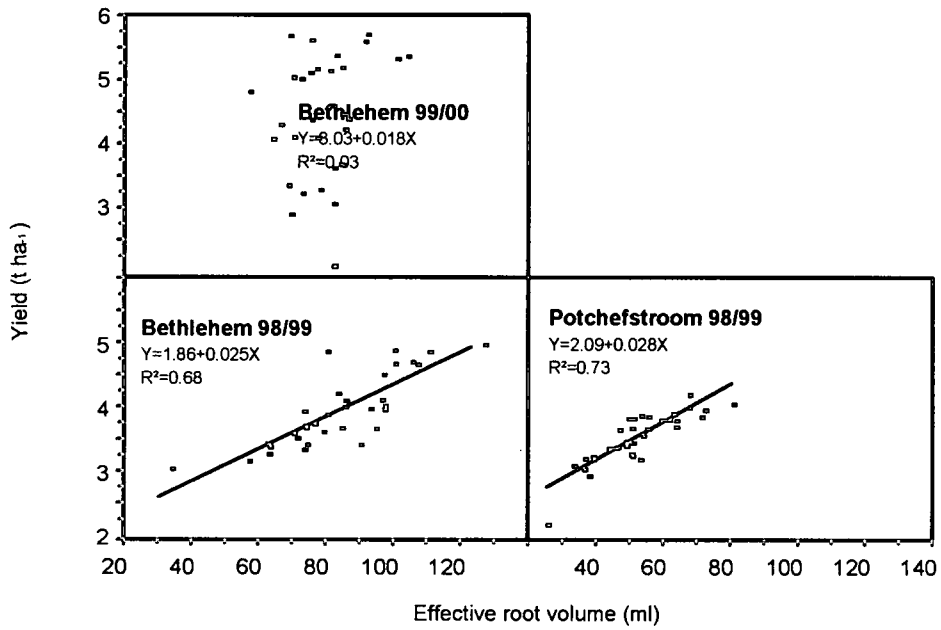

Figure 4.5b: Relationship between effective root volume and yield in maize

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SUMMARY

Root rot is an important disease of maize *(Zea mays* L.). Colonization of roots by fungi has been studied to a limited extent in field soils because of difficulty of visibility and quantification. Several fungal species are involved in maize root rot, occurring in a complex of causal fungi separated by time and space. Different fungal species occur throughout the season on and in the roots, making it difficult to determine the primary pathogens. In addition, fungi associated with roots differ between localities. Root rot therefore, requires study at more than one locality and the spectrum of fungi involved is to be determined (Chambers, 1987). According to him pathogenicity tests should include different plant growth stages. Mixtures of fungi should also be used, as well as different environmental stresses factors.

Although very little attention has been given to the study of root rots of maize, one of the major areas requiring urgent attention is the quantification of root rot of maize. The primary criteria used to measure root rot are root discolouration and root development. The use of these criteria is however, questionable since other factors may affect root discolouration and development. Furthermore, maize plants have a considerable ability to compensate for injury to root systems. A further complication is that general symptoms such as early senescence and lodging, only occur with extremely severe infection, or late in the season when the plants have reached physiological maturity. Normally the disease is characterized by an absence of distinct above ground symptoms, and subtle yield losses. A possibility also exists that fungal toxins may be involved in the root rot complex. Control of root rot has received limited attention. Interactions between practices and root rot incidence seem promising and need to be investigated with regard to developing a disease control system. The possibility of pesticides such as chlorpyrifos, which degrade to release a fungicidal component, should also be studied.

Breeding for resistance is a longterm control measure for root rot disease. Breeding for resistance to specific pathogens rather than to a complex of fungal species will ease control of genetic manipulation as well as enable the stability of resistance to be quantified particularly with regard to isolate differences or races.

The inheritance of resistance in maize is not stable and the fact that the resistance is quantitative rather than qualitative suggests that there are many genes involved. Resistance has also been associated with many different resistance mechanisms and factors.

In order to understand the principal aspects related to the root rot of maize, a literature survey concerning to the host range, host–pathogen interactions, control and economic importance of the disease was conducted. Furthermore, different methods of disease management are reviewed, with emphasis on genetic control.

To determine pathogenic variability and the heritance of resistance for root rot eight inbred lines were crossed and planted in a 8 x 8 full diallel (Model1) during the 1999/2000 season. The plants were infected with root rot isolate *Fusarium oxysporum*. Root rot discolouration, plant length, root volume, root efficiency and yield were measured. A diallel analysis was used to analyse the data and determine the combining abilities, genetic correlations, heritabilities and correlated response.

Significant differences in F 1-hybrids for root discolouration, plant length, root volume, effective root volume and yield were found. Effective root volume was highly significantly correlated with root volume and plant length and a similar correlation was recorded between root volume and plant length. Root rot discolouration was positively but not significantly correlated with plant length, root volume, effective root volume and yield.

Analyses of variance were done for GCA and SCA effects. Non-significant GCA and SCA effects existed for root rot discolouration. Highly significant GCA effects were found for plant length, root volume, effective root volume and high significant SCA effects existed for plant length and yield. Highly significant SCA effects were found for root volume and effective root volume.

Highly significant genetic correlations were found between root volume and effective root volume and between root volume and plant length. Genetic correlations between effective root volume and plant length were also significant. Yield was genetically negatively correlated with plant length, root volume and effective root volume and positively correlated with root rot discolouration.

To assess field resistance to root rot in maize, 34 hybrids were planted and evaluated over five environments at Bethlehem and Potchefstroom from 1997 to 2000. The Additive Multiplicative Interaction (AMMI) statistical model was used to describe genotype x environment (G X E) interactions. Highly significant G X E interactions were recorded for root discolouration and yield. No significant G X E interactions were found for root volume and effective root volume.

Additive main effects and multiplicative interaction (AMMI) model analysis clearly showed that different genotypes were identifiable with low potential environments predominating and other were identifiable with high potential environments predominating for root rot disease. The AMMI model can summarise patterns and relationships of genotypes and environments successfully, as well as provide a valuable prediction assessment of disease resistance.

In general, stability of root rot is very complex due to numerous fungal species associated with infection of maize roots. Breeding for resistance to specific

pathogens rather than to a complex of fungal species should ease control of genetic manipulations as well as enable the stability of resistance to be quantified particularly with regard to isolates and different races. This study will hopefully serve as an important source of information for future research or root rot resistance in maize.

OPSOMMING

Wortelvrot is 'n belangrike siekte by mielies (*Zea mays* L.). Weens probleme met sigbaarheid en kwantifisering, is kolonisering van wortels deur swamme min bestudeer. Verskeie swamspesies wat in 'n kompleks voorkom, is verantwoordelik vir wortelvrot. Hierdie patogene is in tyd en ruimte verspreid. Verskillende swamspesies kom deur die seisoen op en in wortels voor wat dit moeilik maak om die primêre patogene te bepaal. Swamme wat met wortels geassosieer is, verskil ook oor lokaliteite. Dus is dit belangrik dat wortelvrot by meer as een lokaliteit bestudeer word om die spektrum van swamme te bepaal. Volgens hom behoort patogenisiteitstoetse verskeie plant groeistadiums in te sluit. Mengsels van swamme en omgewingsstremmings behoort ook ingesluit te word.

Weens die feit dat wortelvrotstudies by mielies min aandag geniet het, bly een van die belangrikste studievelde dié van kwantifisering van wortelvrot. Die hoofkriteria om wortelvrot te meet is wortelverkleuring en wortelontwikkeling. Die gebruik van hierdie kriteria word bevraagteken aangesien verskeie ander faktore wortelverkleuring en ontwikkeling kan beïnvloed. Mielieplante het ook 'n aansienlike vermoë om te kompenseer vir wortelskade. Wortelvrotstudies word ook bemoeilik deurdat simptome, soos vroeë afsterwing en omval net by besondere strawwe besmettings of laat in die seisoen na fisiologiese rypheid, voorkom. Gewoonlik is duidelike bogrondse simptome afwesig en verliese is baie

subtiel. Dit is ook moontlik dat swamtoksiene by die wortelvrotkompleks betrokke is. Beheer van wortelvrot het min aandag geniet. Interaksies tussen produksiepraktyke en wortelvrot behoort ondersoek te word met die doel om beheerstelsels te ontwikkel. Die moontlikheid om insekdoders soos chlorpyrifos wat afbreek om 'n swamdoderkomponent vry te stel te gebruik behoort ook bestudeer te word.

Weerstandsteling is 'n langtermyn beheermaatreël vir wortelvrot. Deur vir weerstand teen spesifieke patogene te teel eerder as vir 'n kompleks, sal genetiese manipulasie vergemaklik word asook die bepaling van weerstandsstabiliteit teenoor spesifieke isolate of rasse.

Oorerwing van weerstand is nie vas nie en weens die feit dat weerstand kwantitatief eerder as kwalitatief is, dui aan dat heelwat gene betrokke is. Weerstand gaan ook gepaard met verskeie weerstandsmeganismes en faktore.

Om die hoofaspekte van wortelvrot te bepaal, is 'n literatuuroorsig uitgevoer oor gashere, gasheer-patogeen interaksies, beheer en die ekonomiese belangrikheid van die siekte. Aandag is ook gegee aan verskillende metodes van siektebestuur met die klem op genetiese beheer.

Agt ingeteelde lyne is onderling gekruis en in 'n 8x8 volledige diallel tydens die 1999/2000 seisoen geplant om patogeniese variasie en die oorerwing van

weerstand teen wortelvrot te bepaal. Plante is met *Fusarium oxysporum* besmet. Wortelverkleuring, plantlengte, wortelvolume, effektiewe wortelvolume en opbrengs is gemeet. Diallelanalise is gebruik om kombineervermoë, genetiese korrelasies, oorerwing en gekorreleerde reaksies te bepaal.

Betekenisvolle verskille in F1 basters is gevind vir wortelverkleuring, plantlengte, wortelvolume, effektiewe wortelvolume en opbrengs. Effektiewe wortelvolume was hoogs betekenisvol gekorreleerd met wortelvolume en plantlengte en 'n soortgelyke korrelasie is tussen wortelvolume en plantlengte verkry. Wortelverkleuring was positief maar nie betekenisvol met plantlengte, wortelvolume, effektiewe wortelvolume en opbrengs gekorreleerd nie.

Variasie-analieses is uitgevoer vir AKV en SKV. AKV en SKV effekte vir wortelverkleuring was nie betekenisvol nie. Hoogs betekenisvolle AKV effekte is vir plantlengte, wortelvolume en effektiewe wortelvolume gevind, en hoogs betekenisvolle SKV effekte het vir plantlengte en opbrengs voorgekom. Hoogs betekenisvolle SKV effekte is vir wortelvolume en effektiewe wortelvolume verkry.

Hoogs betekenisvolle genetiese korrelasies is verkry tussen wortelvolume en effektiewe wortelvolume en tussen wortelvolume en plantlengte. Genetiese korrelasies tussen effektiewe wortelvolume en plantlengte was ook betekenisvol.

Opbrengs is geneties negatief gekorreleerd met plantlengte, wortelvolume en effektiewe wortelvolume en positief gekorreleerd met wortelverkleuring.

Om veldweerstand teen wortelvrot by mielies te bepaal, is 34 basters vanaf 1997 tot 2000 oor vyf omgewings op Bethlehem en Potchefstroom geplant. Die "Additive Multiplicative Interaction" (AMMI) statistiese model is gebruik om genotipe x omgewing interaksies te bepaal. Hoogs betekenisvolle G x O interaksies is bepaal vir wortelverkleuring en opbrengs. G x O interaksies vir wortelvolume en effektiewe wortelvolume was nie betekenisvol nie.
ie "Additive main effects and multiplicative interaction (AMMI)" model het duidelik getoon dat verskeie genotipes aanpasbaarheid is vir lae siektepotensiaal omgewings *wat domineer* het, terwyl enkeles geidentifiseer is *wat meer aangepas is vir hoë wortelvrotpotensiaal omgewings*. Die AMMI model kan patrone en verhoudings tussen genotipes en omgewings dus suksesvol opsom asook 'n voorspelling voorsien van siekteweerstand.

In geheel is die stabiliteit van wortelvrot baie ingewikkeld as gevolg van die groot aantal swamspesies wat betrokke is by die besmetting van mieliewortels. Teling vir weerstand teen spesifieke patogene, eerder as 'n kompleks van swamspesies behoort genetiese manipulasies te vergemaklik asook die bepaling van die stabiliteit van weerstand soos deur isolate en rasse beïnvloed. Hierdie studie sal hopelik dien as 'n belangrike bron van inligting vir toekomstige navorsing oor wortelvrotweerstand by mielies.