STUDIES ON *CERCOSPORA ZEAE-MAYDIS*, THE CAUSE OF GREY LEAF SPOT OF MAIZE IN KWAZULU-NATAL

by

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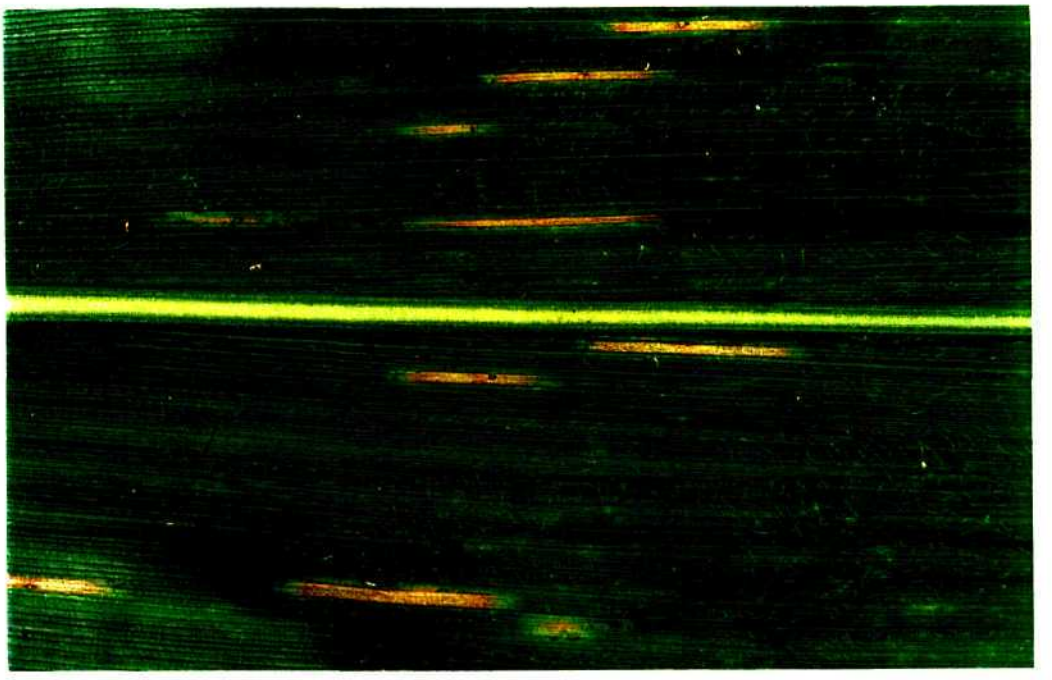
FRONTISPIECE - GREY LEAF SPOT ON MAIZE



Early, characteristic rectangular lesions symptomatic of grey leaf spot on maize

Lesions coalesce, resulting in severe leaf blighting and reduced photosynthetic area, with concomitant loss in carbohydrate production and grain yields

ABSTRACT

In 1983, Latterell and Rossi described grey leaf spot (GLS) of maize (*Cercospora zeae-maydis* Tehon and Daniels) as "a disease on the move". This pathogen has more than lived up to its reputation. It is estimated to be spreading at a rate of 80-160 km each year, and is recognized as one of the most grain yield-limiting diseases of maize world-wide . The occurrence of the pathogen in the Province of KwaZulu-Natal (KZN), Republic of South Africa (RSA), in 1988, was its first official report from the African Continent. It has since become pandemic, causing grain yield losses of up to 60%. It has spread to other provinces in RSA as well as other African countries, namely Cameroon, Kenya, Malawi, Mozambique, Nigeria, Swaziland, Tanzania, Uganda, Zaire, Zambia and Zimbabwe. It has also been reported to occur in Brazil, China, Columbia, Costa Rica, Mexico, Peru, Trinidad, and Venezuela.

The use of soil macro- and micronutrients in the management of fungal plant pathogens is widely documented in the literature. Specific nutrients are known to increase or decrease disease resistance in plants. However, each host-pathogen interaction must be considered on an individual disease basis, together with environmental and soil variables. Although few diseases can be eliminated by a corrective fertilizer regime, the severity of a disease can be reduced by specific nutrients, particularly when used in conjunction with other cultural practices. However, the economic implications, and not grain yield alone, of different control measures should be considered; i.e., farmers must compare the expected added gross margin ha $^{-1}$ (added income minus added costs) with the potential variability in expected added gross margin ha $^{-1}$ (upper and lower limits) of each treatment when deciding on which fertilizer applications and/or fungicide treatments to use.

Literature reviews were undertaken on both GLS and the use of soil nutrients to control fungal plant pathogens to provide the necessary background technical information in order to conduct research under local conditions, and to assist in interpretation of results of experiments.

Nutrient trials to control GLS were conducted at two sites in KZN, i.e., Cedara (1995/96, 1996/97 and 1997/98) and Ahrens (1995/96). Research at Cedara showed that with increased applications of nitrogen (N) at 0, 60 and 120 kg N ha^{-1}, and potassium (K) at 0, 25, 50 and 150 kg K ha^{-1}, leaf blighting occurred earlier, and final percentage leaf blighting and the standardized area under disease progress curve were higher. The Ahrens trial also showed that with increased applications of N (0, 60, 120 and 180 kg N ha^{-1}) and K (0, 50, 100 and 150 kg K ha^{-1}), there were also increases in final percentage leaf blighting. Increasing phosphorus levels of 0, 30, 60 and 120 kg P ha^{-1} did not have any effect on final percentage leaf blighting.

The application of systemic fungicides to GLS-susceptible maize was highly effective in controlling GLS and increasing grain yields substantially with increased N and K applications. In the non-fungicide treated plots, grain yields did not increase with increased applications of K in all three years of the trial. This was probably because grain yield response, which should have occurred at higher K applications, was reduced by increased GLS severity. Similarly, grain yields did not increase significantly with N application in 2 of the 3 years of the trial.

At Cedara, non-fungicide treated maize produced a financial loss of - R165 and - R 48 with 25 and 50 kg K ha^{-1}, respectively, relative to 0 kg K ha^{-1}. However, increasing N applications resulted in increasing grain yields, and added gross margins of R 714 ha^{-1} and R536 ha^{-1} with applications of 60 and 120 kg N ha^{-1}, respectively. The drop in added gross margin at 120 kg N ha^{-1} was probably because of increased GLS levels at higher fertiliser rates, resulting in reduced grain yields. In fungicide treated maize, added gross margin relative to 0 kg K ha^{-1} increased from R 851 to R 1212 ha^{-1}. However, there was a loss of - R 133 ha^{-1} in added gross margin relative to 0 kg N ha^{-1} at 60 kg N ha^{-1}, as increased grain yields did not offset the added cost of N fertilizer and fungicide applications. At 120 kg N ha^{-1} added gross margin relative to N0 was R423 ha^{-1}. Highest grain yields and gross margins in fungicide treated maize were obtained with 120 kg N ha^{-1} and 150 kg K ha^{-1}, as expected. However, in non-fungicide treated maize, highest grain yields and gross margins were obtained using

60 kg N ha $^{-1}$ and 50 kg K ha $^{-1}$. This was because of higher GLS severity at the higher N and K application rates.

Yields of wheat grown in soils with residual fertilizers after non-fungicide treated maize were higher (4.2 t ha $^{-1}$) compared to yields (3.6 t ha^{-1}) grown on residual fertilizers after maize that had been sprayed to control GLS. This was probably as a result of GLS reducing the photosynthetic area of maize leaves, causing premature death with a concomitant reduced uptake of nutrients by roots. This resulted in higher residual levels of fertilizers in soils where fungicide applications were not used to control GLS on maize compared to soils planted with maize where GLS was controlled through the application of fungicides.

In KZN there are approximately 350,000 small-scale farmers. The same diseases that affect commercial agricultural production also affect the small-scale farmer, the major difference being in the methods of disease control employed. At the commercial level, most farmers rely on the use of agro-chemicals, which are often not available to the small-scale farmer due to the relatively high cost of agro-chemicals, application methods, and the non-availability of products in the rural areas. The level of illiteracy of the small-scale farmer may also inhibit the use of agro-chemicals.

In many African countries, the per capita consumption of maize may be as high as 100 kg per year. Production of cereals in Africa has fallen in the past 25 years. This, together with yield reductions of maize caused by GLS, is likely to contribute to an even greater food deficit in many African countries. At present, low soil fertility and pH levels are a problem among small-scale farmers both in the RSA and other parts of Africa. In the RSA, government policy is to increase maize production by small-scale farmers through improved agronomic methods, including increased fertilizer application. Appropriate and affordable rotations and other improved agronomic practices need to be developed and promoted to ensure food security and sustainable systems for small-scale farmers.

The results from the nutrient trials presented in this thesis have practical applications for the small-scale farmer who does not have the option of controlling GLS through the use of agrochemicals. The small-scale farmer will be able to attain a maximum gross margin from his maize crop by applying 60 kg N ha $^{-1}$ and 50 kg K ha $^{-1}$, if no fungicides are applied. However, comparative analyses of manure showed that a small-scale farmer would have to apply 1-3 tonnes of manure in order to achieve similar nutrient levels - a procedure that would be impractical.

Comparative financial analyses of aerial and knapsack fungicide applications showed that it would be uneconomical for the small-scale farmer to apply fungicides using a knapsack sprayer. A simple spreadsheet has been created to help farmers make the best choice of N (0, 60 or 120 kg N ha $^{-1}$) and K (0, 25, 50 or 150 kg K ha^{-1}) and the number of fungicide application (O, 1, 2 or 3). This will eliminate the guesswork needed for farmers to maximize gross margins, based on a specific amount of money available.

The resistance expressed by different hybrids on conidial germination of *C. zeae-maydis* at varying temperatures, desiccation periods and interrupted dew periods was investigated using the susceptible ZS 206 and the less susceptible SC 625 maize cultivars. Germination of conidia was maximized at 28°C on both cultivars by 48 hr with ZS 206 showing 100% germination, in contrast to only 63% germination in SC 625. As the number of days (1-5) of desiccation increased following inoculation, germination decreased from 100 to 47% in ZS 206 and from 62 to 0% in SC 625, respectively. The observation that *C. zeae-maydis* is able to tolerate unfavourable conditions and resume germ tube growth when favourable conditions return was confirmed in interrupted dew period studies. There was no change in percentage germination after 48 hrs., when plants were subjected to interrupted dew periods of 2-36 hrs, following a 6 hr period at 95-100% RH at 28 °C in a dew chamber. However, germination was lower (64%) on SC 625 than ZS 206 (90%). The wider range of temperature conditions favourable for conidial germination of ZS 206, and the fact that it was less affected by desiccation and interrupted dew periods than SC 625, could account for the different susceptibility

levels of these two hybrids to GLS.

Peak daily conidial catches were found to be between 1200 and 1400 hrs when temperatures and vapour pressure deficits were highest and leaf wetness lowest. Multiple regression analyses identified high evaporation over a 24 hr period, low temperatures over a 48 hr period and wind over a 72 hr period as the weather variables most strongly associated with high conidial releases. Rain, high vapour pressure deficit values and temperatures between 20-30 °C with leaf wetness over a 72-day period, together with prolonged high evaporation over a 48 hr period were identified as limiting factors in conidial release. These results indicate that temperatures (< 20 °C) and moisture 24-48 hrs prior to release is required for production of conidia. However, dry air and leaf surfaces are required for conidia to break off conidiophores at the point of attachment, i.e., a hygroscopic process is involved in release of conidia in *C. zeae-maydis*.

In general, the process of conidiogenesis in *C. zeae-maydis* is similar to that observed on *C. beticola*. Successive formation of conidia on the same conidiophore are in accord with previous observations on *C. zeae-maydis*. Conidial measurements are also similar to other taxonomic descriptions of *C. zeae-maydis*. Hyphae aggregate in the substomatal cavity and give rise to fascicles of 1-2 septate conidiophore initials which emerge through the stoma. A single, aseptate conidium develops from the conidiogenous cell of the conidiophore initial. Extension growth of the conidiogenous cell from the base and one side of the terminal conidium, leads to the lateral displacement of the conidium on the conidiophore. After conidial secession, the conidiophore continues to grow, producing a second conidium from the conidiogenous cell at the apex of the extended conidiophore. This sympodial and successive proliferation of the fertile conidiogenous cell results in the formation of a characteristic 1-3 geniculate, occasionally 4, conidiophore, bearing a single conidium at each apex.

This body of research has added information that was previously missing in the life-cycle of *C. zeae- maydis*. However, this additional information has, in turn, led to other yet unanswered questions which need to be addressed in the future, particularly under southern African conditions. A thorough knowledge and understanding of the epidemiology of this pathogen can result in more effective control strategies with increased yields for both commercial and small-scale farmers in KZN.

DECLARATION

I, Patricia May Caldwell, declare that the research reported in this thesis, except where otherwise indicated, is my own original research. This thesis has not been submitted for any degree or examination at any other university.

Patricia May Caldwell

FOREWORD

The field research presented in this thesis was conducted at Cedara Agricultural Development Institute, Pietermaritzburg, and at Ahrens, near Greytown, KwaZulu-Natal, Republic of South Africa (RSA). All laboratory and electron microscopy studies were conducted at the University of Natal, Pietermaritzburg, RSA.

Since the first report of economic losses in South Africa by *Cercospora zeae-maydis,* the causal organism of grey leaf spot (GLS) on maize, in the 1990 and 1991 maize growing season, research has been carried out to find solutions to what has become a serious grain yield-reducing pathogen of maize in the country. Initial research in RSA was by Ward and Nowell, on the response of commercial hybrids to the pathogen, and to establish effective systemic fungicide treatments for controlling GLS. Their work established a framework for the research presented in this thesis.

There are more than a million small -scale subsistence farmers in South Africa, whose farms are usually only 1-4 ha with maize yields as low as 0.82 tonnes ha^{-1}, barely sufficient to meet family food needs. Most of the work is carried out by women and children as males often seek work in urban industries to supplement family incomes. Maize accounts for as much as 70% of their food production, but surpluses are rare. This, together with the lack of the sophisticated market infrastructure of large-scale commercial farmers, inhibits the sale of grain to supplement family incomes. The use of fungicides to maintain such low potential yields is therefore cost-prohibitive.

This method of maize production is common throughout the African continent. The impact of GLS on food production and security of these small-scale farmers could be devastating, especially because plant pathologists, expertise and resources are in short supply.

Large-scale commercial farmers can use a holistic approach to manage GLS, provided maize production remains profitable. Resistant hybrids, crop rotations, tillage practices and the use of foliar-applied fungicides remain the most popular management for commercial farmers. On the other hand, small-scale farmers often have limited resources. Open pollinated varieties with high levels of resistance remain the main option for these farmers, but their development is a slow process in developing countries.

Observations in RSA in the early 1990s indicated that GLS severity increased with increasing levels of N and that maize grown in soils deficient in K were less infected by *C. zeae-maydis*. Most small-scale farmers grow maize under low fertility conditions both in the RSA and the rest of Africa. The maize crop of these farmers may not be at such a great risk to GLS. However, the progressive and productive small - scale farmers applying manure or fertilizers to increase maize yields will be at greater risk from GLS.

As there is a paucity of information on the effect of soil nutrients on the development and severity of GLS in maize, particularly in Africa, the need for research on the reduction of GLS by the manipulation of inorganic fertilizers, was apparent.

The approach to this first investigation of different nutrient regimes on GLS of maize in KZN was to :

i) Review available literature on the effects of inorganic fertilizers for the control of fungal plant pathogens

ii) Investigate the effects of N, P and K on the development and severity of GLS related to grain yield in fungicide and non-fungicide treated maize

iii) Evaluate the economic effects of using N and K fertilizers to control GLS in fungicide and non-fungicide treated maize

iv) Determine the effect on yield of wheat grown during the winter months on residual levels of fertilizers after maize treated and non-treated with fungicides for the control of GLS.

In addition to the research described above, the following studies on *C. zeae-maydis* were conducted to add to the understanding of this pathogen both internationally and to southern Africa in particular :

i) determination of the effect of germination of conidia on a susceptible and more resistant hybrid at varying temperatures, desiccation and interrupted dew periods

ii) evaluation of the effect of a range of relationship of environmental factors on the incidence of airborne spores

iii) light, scanning and transmission electron microscopy studies on conidiogenesis

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To my husband, Robert,
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for their support, encouragement
and understanding
during my years of study

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GENERAL INTRODUCTION

Maize (*Zea mays* L.) is the most important cereal crop in the Republic of South Africa (RSA) (Anonymous, 1989). The area planted to maize accounts for 25-29% of the arable land usage or 3.9 million ha, which is over a third, of all crops cultivated in the country.

Maize is primarily produced in the Highveld, although smaller production regions occur throughout the summer rainfall region. White-grained maize forms the staple diet of millions of South Africans, particularly in the lower income groups, and is largely produced in the drier, western regions of the country. Total human consumption of white maize in RSA is approximately six million tonnes per annum (Anonymous, 1999). Yellow-grained maize is predominantly produced for animal consumption in the eastern maize production regions of the country. Provincial maize production in RSA for 1996/97 and 1997/98 is shown in Table 1. Table 2 lists data on production, consumption and related statistics of maize in RSA in 1996/97 and 1997/98.

In the 1970s and early 1980s leaf diseases, stalk rots, common smut and head smut were the most important diseases in maize production in the RSA. These problems have since been alleviated by the breeding of resistant hybrids. In the late 1980s *Stenocarpella maydis* (Berk.) Sutton emerged as a disease of considerable economic importance to the maize industry, being most intense on yellow-grained hybrids, with losses estimated at R200 million in 1986/87 alone (Anonymous, 1986). By the late 1980s and early 1990s significant progress had been made by managing this disease through the use of resistant hybrids and crop rotation. It was at this time that the occurrence of grey leaf spot (GLS), caused by *Cercospora zeae-maydis* Tehon and Daniels, was first officially reported in the Midlands of KwaZulu-Natal, RSA.

Table 1. Provincial commercial maize production in the Republic of South Africa for 1996/97 and 1997/98 (Anonymous, 1999)

PROVINCE	Production 1 000 t	
	1996/97	1997/98
Western Cape	24	5
Northern Cape	182	173
Eastern Cape	44	34
Free State	3374	2494
KwaZulu-Natal	367	264
North-West	3392	2240
Northern Province	69	48
Mpumalanga	1755	1460
Gauteng	375	364
TOTAL	9582	7082

Table 2. Maize production, consumption and related statistics for 1996/97 and 1997/98 marketing seasons in the Republic of South Africa (Anonymous, 1999)

ITEM	1996/97	1997/98
Total production (1000 t)	10 136	7 574
Human consumption (1000 t)	2 912	2 513
Total consumption (1000 t)	6 738	6 842
Exports (1000 t)	2 658	1 270
Area planted ('000 ha)	4 457	3 521
Price index	98.5	94
Gross value (R 1000)	6 000 866	4 387 585

Grey leaf spot in the United States

Grey leaf spot was first identified from specimens collected by Tehon and Daniels in 1924 in Alexander county, Illinois in the United States of America (USA) (Tehon and Daniels, 1925). Since the 1970s, GLS has increased in prevalence and severity in the maize-producing areas of the mid-Atlantic and south-eastern areas of the USA (Leonard, 1974; Roane *et al.,* 1974; Latterell and Rossi, 1983; Ayers *et al.,* 1985). The earlier appearance of the pathogen and the increase in distribution and severity were associated with maize monoculture (Latterell and Rossi, 1983; Ayers *et al.*, 1985; Thorson and Martinson,1993) and an increase in conservation tillage that increased infected maize residues on the soil surface.

Grey leaf spot of maize in Africa

Grey leaf spot was first observed in Southern, Central and West Africa in the late 1980s and early 1990s, and is considered a major threat to production in most maize regions of Africa. The disease has spread rapidly in Africa and is present in Cameroon, Ethiopia, Kenya, Malawi, Mozambique, Nigeria, RSA, Swaziland, Tanzania, Uganda, Zaire, Zambia and Zimbabwe (Nowell, 1997) (Fig. 1). The rapid increase in the geographic distribution of GLS on the African continent could have serious implications for food security and nutrition of African nations as maize forms the staple diet of the majority of the indigenous population in Africa (CIMMYT, 1990).

In 1990 to 1991, GLS epidemics in RSA were localized in KwaZulu-Natal. The pathogen has since spread into the neighbouring provinces of Eastern Cape, Free State, Gauteng, Mpumalanga and the Northern Province (Nowell, 1997; Ward and Nowell, 1998). Figure 2 shows the probable distribution of GLS in Africa.

Worldwide distribution of grey leaf spot of maize

Chupp (1953) identified Brazil, Colombia, Peru and Trinidad as countries where GLS occurred. The disease has also been reported in Costa Rica, Mexico, Venezuela (Boothroyd, 1964; Latterell and Rossi, 1983) and is a disease of economic importance in China (Coates and White, 1998). Figure 3 shows the worldwide distribution of GLS in 1996.

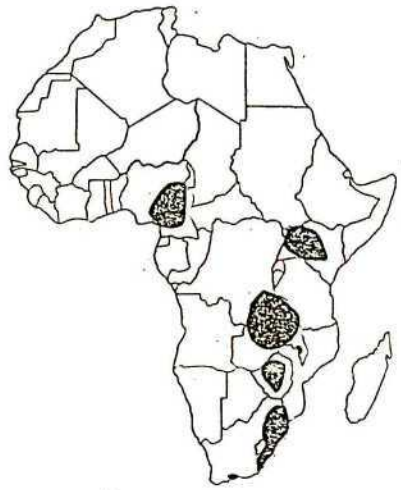

Fig. 1. Present distribution of grey leaf spot in Africa (after Nowell, 1997)

Fig. 2. Probable future distribution of grey leaf spot in Africa (after Nowell, 1997)

Fig. 3. Worldwide distribution of grey leaf spot in early 1996 (after Nowell, 1997)

The pathogen

Cercospora zeae-maydis is a polycyclic, facultative pathogen (Chupp, 1953; Stromberg and Donahue, 1986) and is known to infect only maize (Stromberg and Donahue, 1986). The pathogen overwinters only in infected maize residues (Beckman and Payne, 1982; Latterell and Rossi, 1983). Shurtleff (1980) suggests that sorghum may also be a host. However, this has not been confirmed nor is it widely accepted.

It is speculated that *C. zeae-maydis* could be seedborne given that many *Cercospora* spp. use this mode of transmission and overwintering (Chupp, 1953). The anamorph of *C. zeae-maydis* was originally described by Tehon and Daniels (1925) but later research has shown some variation from the original description (Chupp, 1953; Kingsland, 1963; Latterell and Rossi, 1983). Latterell and Rossi (1983) identified the teleomorph of *C. zeae-maydis* as a species of *Mycosphaerella* on overwintering field specimens but this finding has been disputed by a number of researchers. Reports of *C. sorghi* being a causal agent of GLS have not been substantiated (Mulder and Holiday, 1974). There have been no subsequent reports of the teleomorph, and because of the rarity of its occurrence, it is not regarded as a significant source of inoculum.

Epidemiology and environmental conditions influencing disease development

An ethograph of *C. zeae-maydis* is shown in Fig 4. In spring, conidia are produced from infested maize and are carried by wind to infect newly planted maize during moist periods (Beckman and Payne, 1982; Latterell and Rossi, 1983; Payne and Waldron, 1983; Stromberg and Donahue, 1986). Symptoms are first observed on the lower leaves as small, tan spots (about 1-3 mm long) that are rectangular to irregular in shape. Nowell (1997) noted that air-borne conidia may land on and infect the top of the maize canopy under ideal environmental conditions. The absence of suitable environmental conditions in the early season is the reason for the initial slow development of the disease (Payne and Waldron, 1983).

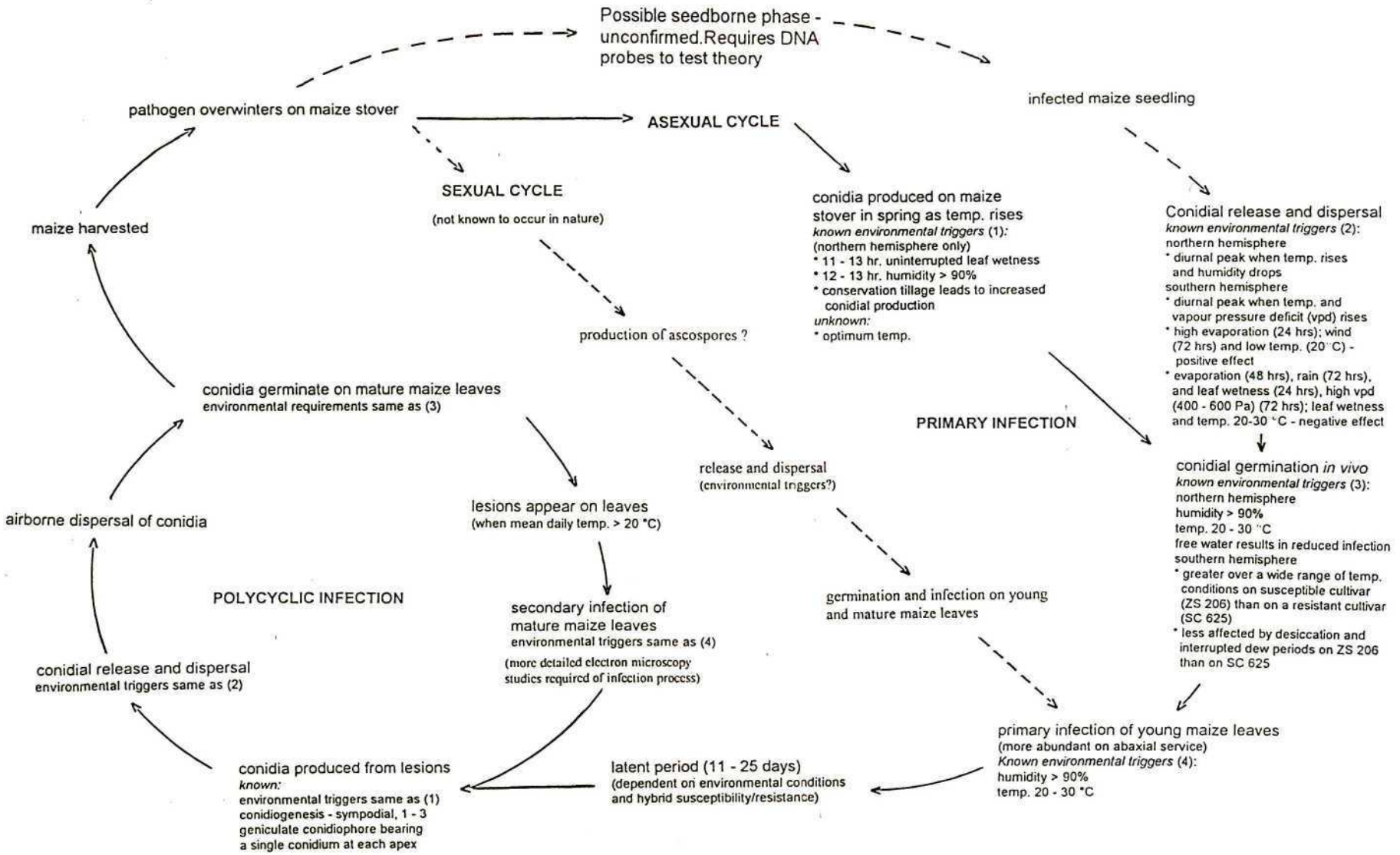

Fig. 4. Ethograph of *Cercospora zeae-maydis*

Grey leaf spot is described as a highly weather-dependent pathogen, requiring high relative humidity (> 90-95%) and cool cloudy conditions, with mists that extend the dew period (Latterell and Rossi, 1983; Anderson, 1995). Temperatures of 22-30°C are considered optimum for spore germination (Beckman and Payne, 1982; Rupe *et al.*, 1982). Rupe *et al.* (1982) found conidia require at least six hours of continuous leaf wetness at temperatures 18-25°C for germination.

In the presence of free water on the leaf surface, stomatal tropism is reduced, appressorial formation is rare and there is no penetration of the host tissue (Beckman and Payne, 1982; Thorson and Martinson, 1993). Although a continuous period of high humidity is required during germination, this is not a necessary requirement for infection (Thorson, 1989). Unlike many other maize pathogens, *C. zeae-maydis* is able to survive adverse conditions once the infection process has begun (Latterell and Rossi, 1983). If environmental conditions are unfavourable, the germ tube may become "dormant", but will resume growth on the return of favourable conditions.

Several germ tubes, one from each conidial cell, may emerge from each conidium (Latterell and Rossi, 1983). Germ tubes have a positive tropism toward stomata under high relative humidity (Beckman and Payne, 1982). A single conidium with germ tubes usually produces 2-5 appressoria over different stomata. However, only one infection peg develops from a single appressorium 6-7 days after inoculation (Beckman and Payne, 1982). Penetration only occurs from appressoria over stomata. Unlike Beckman and Payne (1982), Gwinn *et al.* (1987) found that stomatal penetration increased with plant age and that there were small differences between genotypes.

An infection hypha usually develops a slightly enlarged, generally one-celled vesicle, immediately after penetration. A robust primary hypha with septa grows from the vesicle until it encounters parenchyma or mesophyll tissue (Beckman and Payne, 1982).

Internal colonisation is confined to the air spaces and inter-cellular spaces within the parenchyma tissue of the mesophyll, with hyphal growth delimited by sclerenchyma tissue surrounding the major veins, resulting in the characteristic long, narrow leaf lesions running parallel to the main veins. Fungal stromata, which are formed in substomatal cavities, in the necrotic tissue, give rise to numerous conidiophores and conidia.

The production of conidia usually commences 1-3 days after the lesion becomes necrotic. Sporulating lesions assume a greyish cast, hence the name grey leaf spot (Latterell and Rossi, 1983; Ayers *et al.,* 1985). Chlorosis and subsequent necrosis of the cells is considered to be associated with the production of cercosporin. This toxin acts in the plant as a photosensitising agent that sensitizes and kills plant cells when they are exposed to visible light (Daub, 1982; Daub and Hangarter, 1983; Lipps and Pratt, 1987). Tissue from older maize is less sensitive to cercosporin. Genotypic differences have not been observed (Gwinn *et al.,* 1987).

Early signs of infection and colonisation are pin-point sized, yellow-flecked halos which are easily observed when the leaf is held to light. These elongate to form narrow leaf lesion initials 12 days after inoculation. Characteristic mature lesions show after 14-21 days (Beckman and Payne, 1982; Ringer and Grybauskas, 1995). Mature lesions are grey-tan in colour and are distinctly rectangular in shape (5-70 mm long by 2-4 mm wide). The latent period for GLS varies from 14-28 days, which is long in comparison to other foliar pathogens, depending on the environmental conditions and susceptibility of maize hybrids (Ringer and Grybauskas, 1995). Lesion size, number, and type can vary greatly among maize lines.

Primary infections usually develop on the lower maize leaves and when lesions mature, conidia are produced that serve as inoculum to infect upper leaves. As more lesions form, individual lesions coalesce, resulting in severe leaf blighting (Stromberg and Donahue, 1986; Ward and Nowell, 1997). When leaf blighting by GLS is initiated early,

leaves are blighted significantly during grain fill and stalk deterioration and increased lodging result (Roane, *et al.*, 1974; Latterell and Rossi, 1983; Stromberg and Donahue, 1986). When there is a greater demand for carbohydrates from stalks and root tissue by developing kernels as a result of decreased photosynthesis in diseased leaves, maize plants are predisposed to stem and root-rotting fungi, which leads to increased lodging (Dodd, 1980a and 1980b). Severe lodging can adversely affect mechanical harvesting and results in further grain loss due to a reduction in harvestable grain yield.

Reported grain yield loss from maize fields by GLS vary widely in the USA and range from 50-100% (Lipps and Pratt, 1987; Jenco, 1995). However, grain yield losses usually vary from 0-30 % (Hilty *et al.*, 1979; Latterell and Rossi, 1983; Ayers *et al.*, 1985; Donahue *et al.*, 1991; Lipps and Pratt; 1991; Wegulo; 1994; Jenco, 1995). In RSA, grain yield losses range from 0-60%, with losses usually between 30-40% in areas where GLS is endemic (Ward, 1996; Nowell, 1997).

Management of grey leaf spot

Management strategies to reduce the rate of disease development are aimed at maintaining the plant, especially the upper canopy above the ear, in a healthy condition until physiological maturity. The upper 8-9 leaves of the maize plant contribute 75-90% of the photosynthate required by ears during grain fill (Allison and Watson, 1966). For maximum grain yields to be achieved, these leaves must be healthy because grain yield is a function of photosynthesis, and is related to a healthy leaf area and its duration after flowering (Eik and Hanway, 1966).

Chemical control

Research in the USA to determine the efficacy of fungicides and their economic feasibility in controlling GLS were variable (Hilty *et al.*, 1979; Ayers *et al.*, 1985, Smith, 1989; Lipps and Pratt, 1991; Carter, 1992; Carter and Stromberg, 1992a and 1992b; Riviera-Canales, 1993; Martinson *et al.*, 1994; Wegulo 1994; Martinson and Munkvold, 1995; Wegulo *et al.*, 1997).

Wegulo (1994) and Wegulo *et al.* (1997) suggested several factors play a role in fungicide control of GLS in maize crops. These include correct timing of fungicide applications, number of sprays, prevailing climatic conditions, efficacy of the fungicide group and the level of host resistance. In RSA, Ward *et al.* (1997a) found grain yield response was not necessarily the best parameter to justify spraying and showed that the decision to apply fungicides should be based on the expected added income which should exceed the added costs of fungicide treatments. Fungicides belonging to the benzimidazole and triazole chemical groups provide good control of *C. zeae-maydis.* Combinations of these two groups have been registered for use in RSA and have been widely adopted by commercial maize producers in this country (Ward, 1996; Ward *et al.*, 1997c; Nowell, 1997). The timing of application of systemic fungicides is critical. The most effective time to commence treatments is prior to the start of the logistic phase of the epidemic (Ward *et al.*, 1997c).

Rotational cropping

Several studies have shown that even a single year of crop rotation can significantly reduce the initial level of *C. zeae-maydis* inoculum (Stromberg and Donahue, 1986). As *C. zeae-maydis* does not survive longer than two years in maize stover, crop rotation has been recommended as a control measure or an alternative to ploughing (Latterell and Rossi, 1983; Stromberg and Donahue, 1986; Spink and Lipps, 1987; Huff *et al.*, 1988, Ward *et al.*, 1993). Although rotations to other crops are likely to have significant agronomic benefits (Palti, 1981), crop rotation is not economically attractive

to producers when alternative rotation crops are likely to produce a lower income. Furthermore, the highly efficient windborne nature of dissemination of the pathogen makes it is unlikely that maximum benefits will be obtained from a rotation system as maize grown in rotation may still be at risk as a result of wind-blown inoculum originating from infested maize debris in the area.

Tillage practices

Maize debris from the previous season is the only source of inoculum for subsequent maize crops (Hilty *et al.*, 1979; Beckman and Payne, 1982; Stromberg and Donahue, 1986; Payne *et al.*, 1987, White *et al.*, 1996). The increased use of conservation tillage practices in RSA and USA, has been associated with the increase in incidence and severity of GLS. However, trials in the USA and RSA indicate that tillage is of little value in controlling the disease in areas where GLS is endemic and weather conditions are favourable (Payne *et al.*, 1987; Smith, 1989; Ward *et al.,* 1997d). Rather, the abundance of external inoculum and the distance for dissemination of inoculum from adjacent fields are more likely to affect GLS epidemics. The benefits from improved moisture conservation, the economic and environmental benefits of conservation tillage are unlikely to be abandoned in favour of conventional tillage practices for the control of GLS (White *et al.*, 1996).

Maturity group and planting dates

In contrast to the findings by Hilty *et al.* (1979) and Beckman and Payne (1982), Rupe *et al.* (1982) suggested that plant age is important in GLS development. In general, the period of the season with the highest rainfall will result in the highest incidence of GLS. Therefore, planting to avoid this peak infection period will be beneficial, provided grain yield potential and reliable grain yields are not compromised. Ward *et al.* (1997b) confirmed that short-season hybrids planted early in the season are less affected by GLS, as they may reach physiological maturity before significant foliar blighting and loss occur (Stromberg and Donahue, 1986).

In contrast, long-season hybrids, adapted to a longer growing season, are at greater risk from GLS as they are subjected to longer periods of blighting during a greater portion of the grain-fill period (Stromberg and Donahue, 1986).

Plant density

Beckman and Payne (1982), Payne and Waldron (1983), and Ayers *et al.* (1985) found that GLS severity was higher in high plant populations. They suggested that this was because of increased relative humidity microclimates which favoured development of the pathogen. This was in contrast to Smith (1989), de Nazareno *et al.* (1991) and de Nazareno *et al.* (1993a and 1993b) who proposed that less GLS occurred under high plant densities because of the "shielding effects" from spore interception in the denser canopies compared to more open, lower density maize stands as found in small-scale farming.

Host resistance and tolerance

In general, white-grained hybrids have higher levels of resistance to GLS than yellow-grained hybrids, owing to different genetic backgrounds (Nowell, 1997). However, in both types of grain, both resistant and susceptible germplasm has been found. Fortunately, approximately half of the maize grown in the RSA is white-grained.

Resistance and susceptibility are the two exremes of a continuous scale. Disease tolerance is defined as a relative measure of the yield response of two or more genotypes under equal levels of GLS (Nutter, *et al.*,1993). These definitions of resistance, susceptibility and tolerance have been used throughout this thesis.

To date, most resistance to GLS has been quantitative, with a few exceptions such as those noted by Gevers *et al.* (1994). Recent studies have shown some high grain-yielding hybrids have good levels of resistance to GLS (Ayers *et al.*, 1985; Roane and Donahue, 1986; Stromberg and Donahue, 1986; Lipps and Pratt, 1989; Coates and

White, 1994; Gevers and Lake, 1994; Perkins *et al.*, 1995, Ward, 1996; Nowell, 1997). Although host resistance is the most cost effective and cost-efficient means for managing GLS (Lipps and Pratt, 1989; Graham *et al.*, 1993; Coates and White, 1998), commercial hybrids are not currently available in the USA or RSA with adequate resistance to completely avoid grain yield loss due to GLS (Stromberg and Donahue, 1986; Perkins *et al.*, 1995; Nowell, 1997; Ward *et al.*, 1997d, Coates and White, 1998). Although some maize hybrids can produce higher yields than other hybrids with similar levels of GLS severity (Ward *et al.*, 1999). Under the definition of tolerance by Nutter *et al.* (1993), these hybrids can be defined as tolerant to GLS.

In contrast to the USA, a high frequency of quantitative resistance to GLS has been found in commercial hybrids in the RSA (Ward *et al.*, 1993; Nowell, 1997; Ward and Nowell, 1997). In addition to quantitative resistance, a single gene conferring qualitative resistance to GLS has been identified in a South African inbred (Thompson *et al.*, 1987; Gevers and Lake, 1994).

A number of breeding programmes have directed considerable effort toward discovering resistant or tolerant germplasm. Quantitative trait loci (QTL) with additive gene action (Thompson *et al.*, 1987; Bubeck *at al.*, 1993; Saghai Maroof *et al.*, 1996; Young, 1996) or dominant genes with major effects (Elwinger *et al.*, 1990; Gevers *et al.*,1994) have been implicated in expression of resistance to GLS. Quantitative resistance to GLS has been found to impact on lesion size, latent period and sporulation (Freppon *et al.*, 1996).

Many commercial farmers still prefer to plant higher yielding, susceptible, hybrids rather than hybrids with effective quantitative resistance (Ward *et al.*, 1999). This has necessitated the use of fungicides to effectively and economically manage GLS epidemics in the RSA.

Lambert and White (1997), as part of a recurrent selection programme designed to improve grain yield, showed that some hybrids, and their crosses, show multiple disease resistance. Wang *et al.*, (1998) has shown that in the USA, two pathogenic species of GLS exist with unknown abilities to evolve new pathotypes.

Soil fertility

The literature reflects limited and contradictory findings on the effect of fertility on the incidence and severity of GLS. Smith (1989) found increased levels of GLS in response to increased nitrogen (N) levels. However, Carrera and Grybauskas (1992) found increasing levels of N had no effect on GLS. Smith (1989) found potassium (K) had little effect on GLS but this may have been due to the relatively high levels of soil K at the trial site. Phosphorus was also found to have little effect on GLS severity (Smith, 1989).

Burning

Burning GLS infested maize debris may be effective in reducing inoculum. However, as *C. zeae-maydis* is a windborne pathogen, an external inoculum source is adequate to cause a GLS epidemic. In addition, the negative aspects, i.e., reduced organic matter of the soil that allows water run-off and erosion during rainfall, far outweigh the potential benefits of using burning to control GLS inoculum levels (Ward and Nowell, 1998).

Silage

Inoculum carry-over may also be reduced by harvesting maize for silage because most of the foliage is removed before GLS becomes epidemic. The effect of this on GLS severity the following season will be similar to practicing rotation and, or, ploughing the field. However, this has not been quantified (Ward and Nowell, 1998).

Irrigation

Overhead irrigation, particularly the use of centre pivots, can significantly increase the rate of GLS development (Ward *et al.*, 1993; Nowell, 1997). Ward (1996) suggested the judicious timing of irrigation applications, aimed at avoiding any increase in the leaf wetness period. No research has been undertaken in this field.

Large-scale commercial farmers compared with small-scale farmers in RSA

Approximately 55,000 commercial farmers occupy approximately 3,9 million ha of farmland, producing 4-9 million metric tonnes of maize grain annually (Anonymous, 1999). Farm incomes are stabilized by a sophisticated market infrastructure.

Where small-scale farmers are buying hybrid seed, the lack of resistant cultivars will remain a problem in the immediate future. However, where open-pollinated varieties are bing used, in particular by farmers who save seed from one season to the next, then 2-4 cycles of mass selection, and especially reciprocal recurrent selection, using random polycrosses, would develop a high level of GLS resistance in the population (Robinson, 1976).

Management of GLS is holistic and varied but vital for the continued economic production of maize. At present the most commonly used forms of GLS control are resistant hybrids, crop rotation, tillage practices and the use of foliar-applied fungicides.

In contrast, there are more than a million small-scale, subsistence farmers in the RSA, with maize accounting for 70% of their food production. Their farms are usually in the range of 1-4 ha, producing maize yields of 0.82 tonnes ha $^{-1}$, i.e., enough to feed a family but with no surplus for sale to supplement the family income. With these low yields, fungicide control of GLS remains cost-prohibitive. The only option available to these farmers is the use of hybrids resistant to GLS (Ward *et al.*, 1999).

However, breeding resistant hybrids is typically a slow process. These farmers are often women and children, as males seek urban employment to supplement income. Illiteracy, limited or no resources and insecure land rights under a system of communal land tenure are also major problems (Ward *et al.*, 1999).

These production methods and problems are common for small-scale farmers throughout the African continent, making fungicide control of GLS a non-viable option. However, South African researchers have observed that low soil fertility reduces GLS severity. As low soil fertility is common among small-scale maize growers in Africa, GLS may not be a big yield reducing factor. However, progressive small-scale farmers who apply manure or fertilizers to increase maize yields may experience greater yield reductions by GLS.

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CHAPTER 1

EFFECT OF SOIL NUTRITION ON FUNGAL DISEASES OF SELECTED CROPS

LITERATURE REVIEW

1.1 Introduction

The beneficial effects of reducing the incidence and severity of plant pathogen diseases by the manipulation of inorganic macro- and micronutrients are widely recognised (Huber, 1976; Huber, 1981; Graham, 1983; Huber and Dorich, 1988). The interaction of fertiliser practices and plant diseases is therefore of considerable importance in the field of agriculture.

The advent of readily available inorganic fertilizers for agriculture has served to supplement the limited supply of nutrients in the soil, especially macronutrients, in order to increase yield, nutritional quality and aesthetic appearances of crops. They have also brought about the effective control of many diseases, the effect of nitrogen (N) and phosphorus (P) on the decline of take-all (*Gaeumannomyces graminis* var. *tritici* [Sacc.] von Arx and Olivier) on wheat (*Triticum aestivum* L.) being particularly notable (Engelhard, 1989).

Nutrient elements function as an integral component of cells, substrates, enzymes, electron carriers, activators, inhibitors or regulators of metabolism. Each individual element is part of an intricate system of delicately balanced and interdependent reactions which influence pathogenicity (Huber, 1980a and 1980b; Marschner, 1985; Huber and Dorich, 1988; Huber and Wilhelm, 1988). This physiological interaction and substitution of nutrients with each other in metabolic processes makes it difficult to identify the role of a single nutrient affecting disease. A deficiency or excess of one element greatly influences the activity of others in the metabolic network and is expressed as symptoms in the plant. Many primary and secondary symptoms

associated with pathological problems in plants are similar to those expressed by nutrient deficiencies and toxic symptoms. This often makes it difficult to clearly distinguish between parasitic and non-parasitic symptoms (Huber, 1976).

Most metabolic and physiological mechanisms involved in host-pathogen interactions are not clearly understood (Huber, 1981). However, impressive progress in recent years, particularly in the field of macronutrients, has led to a better understanding of the uptake and function of these nutrients and the effects of fertilizers in reducing disease severity. Although a disease is seldom eliminated by a corrective fertilizer regime, the severity of the disease can be reduced by a given quantity and form of fertilizer applied to a crop. This can be achieved in a number of different ways, e.g., by altering the soil environment of soil-borne pathogens, maximizing the inherent resistance of plants by changing thickness of cell walls and cuticles, or by increasing the rate of plant growth, enabling seedlings to escape infection in their most susceptible stage (Huber, 1980b).

The presence of an element in the soil does not necessarily guarantee its availability for plant growth. Nutrient availability is dependent on the abundance of the element, its form and solubility, presence of competing or toxic elements, the assimilative capacity of the plant, as well as the interaction of environmental factors such as pH, moisture and temperature (Tisdale *et al.*, 1993). Microbial associations can also influence the availability of soil nutrients for uptake by plants; e.g., an N deficiency may be induced during the microbial decomposition of carbonaceous residues in soil (Huber, 1980a).

In contrast, microbial activity frequently prevents deficiency diseases caused through nutrient deficiencies; e.g., the symbiotic relationship involving N fixation by root nodule bacteria *Rhizobia* spp. on the roots of many leguminous plants provides N for the plant in return for plant-produced carbohydrates. Micro-organisms forming mycorrhizae may increase absorption of N, P and potassium (K) by plants. Many nutrients, e.g., N, sulphur (S) and P, are made available from the soil to the plant through microbial activity that change their form, solubility or the absorptive capacity of the root. Therefore, the soil environment in the rhizosphere is especially important as this is the

region of greatest nutrient uptake (Huber, 1980b).

Disease management options through macro- and micronutrient amendments is well documented in the literature. However, it is not possible to generalise the effects of any particular nutrient for all host-pathogen combinations. The influence of host and pathogen, as well as environment and any other variables must, therefore, be considered on an individual disease basis (Colhoun, 1973; Huber, 1981; Graham; 1983).

1.2 Elements required in plant nutrition

Correct plant nutrition can reduce levels of disease severity. One of the primary effects of pathogens is to disrupt the mineral nutrition of the plant; e.g., leaf spots and blights cause metabolic deficiencies and disruptive distribution of nutrients while root rots and damping off cause immobilization, solubilization, absorption and distribution effects. Therefore, an understanding of the mineral nutrition of plants is of fundamental importance before it can be effectively utilized for disease control (Huber, 1976).

Mineral nutrients have specific and essential functions in plant metabolism. A nutrient is said to be deficient when its concentration is low enough to limit yield and results in distinct deficiency symptoms (Graham and Webb, 1991). In contrast, nutrients applied in excess of sufficiency for plant growth may be toxic, causing stunted growth and even death.

Critical ranges of nutrients vary from species to species of plants but it is generally accepted as the level below which a yield response to added nutrients occurs. Excessive or toxic concentrations of nutrients can occur when they are present in concentrations high enough to reduce plant growth and yield.

Sixteen elements are considered essential to plant growth. Carbon, hydrogen and oxygen are the most abundant elements in plants; however, they are not considered mineral nutrients (Tisdale *et al.*, 1993). The 13 remaining elements are classified as

macronutrients and micronutrients depending on their relative abundance in plants. Where possible the most commonly used application forms of each element used in the RSA have been included.

1.2.1 Macronutrients

Nitrogen, P, K, calcium (Ca), S and magnesium (Mg) are classed as macronutrients. Their characteristics are outlined in Tables 1- 6, respectively.

1.2.2 Micronutrients

Micronutrients are often referred to as minor elements as their concentrations, when compared to macronutrients, are very small. However, micronutrients are no less important than macronutrients and their deficiencies or toxicities can reduce yields similar to macronutrient deficiencies or toxicities.

The characteristics of the micronutrients iron (Fe), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), manganese (Mn), chlorine (Cl), sodium (Na), silicon (Si), cobalt (Co), vanadium (V) and nickel (Ni) are listed in Tables 7-15, respectively.

Table 1. Characteristics of nitrogen (N) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT FORM	Available to plants through biological mineralization of complex soil organic matter and microbial fixation of atmospheric N which provides N initially in the ammoniacal or reduced form.
CONCENTRATION IN PLANTS	The fourth most abundant nutrient in plants
ABSORBTION FORM	Absorbed mainly as nitrate (NO_3^-) and ammonium (NH_4^+) ions. In moist, warm, well-aerated soils the NO_3^- form is dominant.
REDUCTION PATHWAY	Ammonium nitrogen (NH_4^+N) is oxidised to nitrate nitrogen (NO_3^-N) and results in the availability of several forms of N throughout plant growth. NO_3^- is reduced NO_2^- which in turn is reduced NH_3^+ before it can be used by plants.
USES	NH_3^+ is assimilated into numerous amino acids that are subsequently incorporated into proteins and nucleic acids, proteins providing the framework for chloroplasts, mitochondria and other structures in which most other biochemical reactions occur. N is an integral part of chlorophyll.
MOBILITY	NO_3^- is freely mobile in the soil solution and therefore susceptible to leaching and denitrification losses.
DEFICIENCY SYMPTOMS	The loss of protein N from chloroplasts in older leaves produces the yellowing (chlorosis) and stunted growth indicative of N deficiency. Chlorosis usually appears first on the lower leaves while the upper, young, active leaves remain green. Under severe N deficiency the lower leaves turn brown and die.
pH EFFECTS	Nitrification is greatly reduced in acidic soils. P and Mo solubility is enhanced with liming and may be reflected in increased N efficiency via nitrate reductase.
INTERACTION WITH OTHER NUTRIENTS	Interactions are common. Potassium increases NO_3^- - N uptake and promotes the synthesis of organic N substances. Phosphate and chloride, on the other hand, decrease uptake of NO_3^- - N but enhance uptake of NH_4^+ - N. Chloride reduces amino-acid and protein synthesis and promotes protein degradation. Mn is required for NO_3^- - N assimilation and its synthesis into protein.
SOILS IN KWA-ZULU-NATAL, RSA	Most common and most easily recognized deficiency symptoms in KwaZulu-Natal, SA. Since crop N requirements are markedly affected by factors such as natural reserves, texture, and the soil's propensity to waterlog, it is not possible, in KwaZulu-Natal as a whole, to link N needs directly to yield expectation. Nitrogen application is dependent on soil type and yield target.
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	2.4 - 2.9 %
MOST COMMONLY USED APPLICATION FORMS IN RSA	Anhydrous ammonia (NH_3); aqua ammonia (20 - 25 % N); ammonium nitrate (NH_4NO_3); ammonium sulphate $(NH_4)_2SO_4$; mono ammonium phosphate ($NH_4H_2PO_4$); and di-ammonium phosphate [$(NH_4)2HPO_4$]; ammonium chloride (NH_4Cl); urea (NH_2-CO-NH_2)
MOST COMMONLY USED APPLICATION FORMS IN USA	Anhydrous NH_3, aqua NH_3, ammonium nitrate (NH_4NO_3), ammonium nitrate-sulphate, ammonium sulphate $(NH_4)_2(SO_4)$, ammonium phosphate, ammonium chloride (NH_4Cl), ammonium bicarbonate (NH_4HCO_3) and urea

Table 2. Characteristics of phosphorus (P) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	Obtained from mineral or organic phosphate. Plant roots may exert a solvent action on soil particles through root exudates to bring more P into solution. The availability of soil P is primarily dependent on microbial activity in the rhizosphere or through mycorrhizae
CONCENTRATION IN PLANTS	Occurs in most plants in concentrations 0.1-0.4%
ABSORBTION FORM	Inorganic phosphate must be in the soluble form to serve as a plant nutrient
REDUCTION PATHWAY	The phosphate ion is not reduced to a lower oxidation state in the cell
USES	The most essential function of P in plants is in energy storage and transfer. Adenosine di- and tri- phosphates (ADP and ATP) act as "energy currency" within plants. ATP is the source of energy that powers practically every energy-requiring biological process in plants. P is part of many plant components and is essential for carbohydrate utilization, nucleic acid synthesis and energy relationships in the plant. Adequate supply of P promotes root growth cell division, seed development and a shortened vegetative period (particularly in grain crops), greater straw strength in cereals while the quality of certain fruits, forage, vegetables and grain crops is improved
MOBILITY	Highly mobile and when a deficiency occurs, it is translocated from older tissues to active meristematic regions
DEFICIENCY SYMPTOMS	P deficiency retards overall growth. In maize and some other grass species, P deficiency symptoms are expressed by purple discolourations of the leaf edges but striking foliar symptoms are seldom observed
pH EFFECTS	In acidic soils, P is readily available but physiological absorption is impaired. Absorption of $H_2PO_4^-$ is greatest at low pH values, whereas uptake of HPO_4^{2-} is greatest at higher values of soil pH
INTERACTION WITH OTHER NUTRIENTS	P and K together promote strong mechanical tissue. Phosphate decreases uptake of NO_3^- - N but enhances uptake of NH_4^+ - N
SOILS IN KWA-ZULU-NATAL, RSA	P does not build up as rapidly in highly weathered clay and clay loams due to fixation, and long-term requirements are therefore considerably higher than they are on sandy soils. A minimal addition of 40 mg P L^{-1} is considered optimal for crop production as 2-8 mg P L^{-1} are common in virgin soils
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	0.22-0.30
MOST COMMONLY USED APPLICATION FORMS IN RSA	Superphosphate (7-9.5 % P); double superphosphate (19-23 % P); ammonium phosphates (MAP - 12% N and 26 % P; DAP - 18% N and 20 % P); ammonium polyphosphate (30% P); potassium phosphate KH2PO4 (22% P and 29% K0 and K_2HPO_4 - 18% P and 45% K)
MOST COMMONLY USED APPLICATION FORMS IN USA	Rock phosphate, superphosphate, ammonium phosphate, ammonium polyphosphate, nitric phosphates, potassium phosphate, basic slag or bone meal

Table 3. Characteristics of potassium (K) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	The exchangeable and water soluble forms of K are most readily available for plant nutrition. K is exchanged from soil particles. The source of K may influence uptake of other nutrients through its accompanying anion
CONCENTRATION IN PLANTS	The K content of plants depends on the level of magnesium and calcium which are influenced by soil reaction. The concentration of K^+ in vegetative tissue usually ranges from 1-4 % on a dry matter basis; i.e., plant requirements for available K^+ are quite high
ABSORBTION FORM	The K^+ ion is actively taken up from the soil solution by plant roots
USES	Enzyme activation is regarded as the single most important function of K, with over 80 plant enzymes requiring K. It has a particularly important role in osmotic regulation and is involved in essentially all cellular functions including photosynthesis, phosphorylation, protein synthesis, translocation of sugars made during photosynthesis, water maintenance, reduction of nitrates and reproduction. K provides much of the osmotic "pull" that draws water into plant roots. The opening of stomata is brought about by an influx of K into the guard cells. K can affect the rate of transpiration and water uptake through regulation of stomatal opening. A balanced level of K induces thicker cell walls, accumulation of amino acids and production of new tissues
MOBILITY	Highly mobile and may be readily leached from the root profile or soil
DEFICIENCY SYMPTOMS	K deficiency greatly reduces crop yields. In fact, serious yield reductions can occur without the appearance of deficiency symptoms. Mobility results in visual deficiency symptoms usually first appearing on the lower/older leaves. Deficiency symptoms can also occur in young leaves at the top of high-yielding, fast maturing crops like cotton and wheat. It results in weakening of straw in grain crops, which causes lodging in small grains and stalk breakage in corn and sorghum. Typical K deficiency symptoms in alfalfa occur as white spots on the leaf edges, while in maize and other grasses, chlorosis and necrosis of the leaf edges are observed. Plants that are K deficient are less able to withstand water stress. Malfunctioning of stomata due to a deficiency of this nutrient has been related to lower rates of photosynthesis and less efficient use of water
INTERACTION WITH OTHER NUTRIENTS	K availability in soil is enhanced by Ca in neutral, but not acidic soils. The K to Ca balance affects the differential permeability of membranes. K increases NO_3^- - N uptake and promotes the synthesis of organic N substances
SOILS IN KWA-ZULU-NATAL, RSA	K deficiencies are common in the province. They are especially marked in areas where silage and hay are produced. In virgin soils, 10-30 mg L^{-1} is common. The accepted K norm for crop production is 100 mg L^{-1}.
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	1.5-1.9%
MOST COMMONLY USED APPLICATION FORMS IN RSA	KCl (50-52%K); K_2SO_4 (42-44% K and 17% S); K_2SO_4, $MgSO_4$; KNO_3; KPO_3, $K_4P_2O_7$, KH_2PO_4, K_2HPO_4, K_2C_o3, KHC_o3, KOH
MOST COMMONLY USED APPLICATION FORMS IN USA	Potassium chloride (KCl) or potassium sulphate (K_2SO_4), potassium magnesium phosphate (K_2SO_4, $MgSO_4$), potassium nitrate (KNO_3), potassium phosphate (KPO_3, $K_4P_2O_7$, KH_2PO_4, K_2HPO_4), potassium carbonate (K_2CO_3), potassium bicarbonate ($KHCO_3$) and potassium hydroxide (KOH), potassium thiosulphate ($K_2S_2O_3$) and potassium polysulfide (KS_x)

Table 4. Characteristics of calcium (Ca) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	Limestone
CONCENTRATION IN PLANTS	Ranges from 0.2-1.0%
ABSORBTION FORM	Absorbed as Ca_2^+
USES	Its functions are probably complimentary to those of K in maintaining cell organisation, hydration and membrane permeability. It is involved in mitosis, cell elongation, enzyme activation and regulation, carbohydrate movement, the neutralization of metabolic acids and the structure and permeability of cell membranes. It is a structural component of the middle lamellae of cell walls. Mature plants may have large Ca reserves while younger tissues are deficient.
MOBILITY	Relatively immobile and is not readily re-distributed within the plant
DEFICIENCY SYMPTOMS	Characterized by weak stems and limited root development. Manifests itself in the failure of the terminal buds of shoots and apical tips of roots to develop which causes plant growth to cease e.g. in maize. Lack of Ca_2^+ produces a general breakdown of membrane structure and function
pH EFFECTS	Acidic soils tend to be deficient in Ca. By decreasing soil acidity, calcium decreases toxicity of heavy metals, i.e., Al, B, Mn and others which are soluble at an acidic pH. Excess Ca is usually associated with alkaline soils and may induce deficiencies of Fe, Mn, Cu, B and Zn
INTERACTION WITH OTHER NUTRIENTS	Ca enhances uptake of NO_3 - N and therefore is inter-related with N metabolism. The presence of Ca_2^+ also provides some regulation of cation uptake i.e. K^+ uptake greatly exceeds Na^+ uptake in the presence of Ca_2^+. Ca interacts with P to reduce adverse effects of excessive P and other elements on the growth of some plants
SOILS IN KWA-ZULU-NATAL, RSA	Ca deficiencies have not yet been positively identified in the province and are unlikely to occur unless the soils are excessively acid. In virgin soils, Ca levels are very variable ranging from 100-500 mg L^{-1}
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	0.20-0.25%
MOST COMMONLY USED APPLICATION FORMS IN RSA	Not normally formulated into mixed fertilizers but is present as a component of other fertilizers, e.g., superphosphate (18-21% Ca), double superphosphate (12-14% Ca); primary sources are liming material, e.g. calcite, dolomite; gypsum ($CaSO_4.2H_2O$)
MOST COMMONLY USED APPLICATION FORMS IN USA	Calcium carbonate (calcite-$CaCO_3$), calcium magnesium carbonate (dolomite-$CaMg(CO_3)_2$), calcium hydroxide (hydrated lime), calcium sulphate (gypsum-$CaSO_4.2H_2O$) and calcium phosphate. One important function of calcium fertilizers is the neutralization of soil acidity.

Table 5. Characteristics of sulphur (S) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT FORM	Present in the soil in organic and inorganic formsyrite (FeS_2O) and Co (CoAsS)
CONCENTRATION IN PLANTS	Typical concentrations of S in plants range between 0.1-0.4%
ABSORBTION FORM	Usually absorbed by roots as the sulphate ion (SO_4) or enters the leaves as sulphur dioxide (SO_2) from the atmosphere. S is absorbed by plant roots almost exclusively as the sulphate ion SO_4^{2-}
REDUCTION PATHWAY	Reduced in the plant and is incorporated into amino acids, proteins, enzymes, vitamins, aromatic oils and ferredoxins
USES	Many important functions in plant growth and metabolism and is required for synthesis of S-containing amino acids e.g. cystine and methionine, which are essential components of proteins. Approximately 90% of the S found in plants is found in these amino acids. One of the main functions of S in proteins is the formation of disulphide bonds between polypeptide chains. Sulphur is needed for the synthesis of other metabolites including co-enzyme A, biotin, thiamine (vitamin B1) and glutathione. Although not a constituent, it is required for the synthesis of chlorophyll. Sulphur occurs in volatile compounds responsible for the characteristic taste and smell of plant; e.g., in the mustard and onion families. It also enhances oil formation in crops such as soyabeans and flax. Promotes root growth and nodulation in legumes.
MOBILITY	Immobile in plants and therefore deficiency symptoms occur first in younger plant parts; e.g., young leaves.
DEFICIENCY SYMPTOMS	Sulphur deficiency is rare in industrial countries because of adequate atmospheric levels of various sulphur oxides. S deficiency has a pronounced retarding effect on plant growth and is characterized by uniformly chlorotic, stunted, thin-stemmed and spindly plants. In many plants these symptoms resemble those of N deficiency
SOILS IN KWA-ZULU-NATAL, RSA	No soil calibration work has been conducted on this element in the province
MOST COMMONLY USED APPLICATION FORMS IN RSA	Elemental S, sulphur-bentonite; ammonium thiosulphate (12% N and 26% S); single superphosphate, K_2SO_4, $CaSO_4$
MOST COMMONLY USED APPLICATION FORMS IN USA	Applied as soluble sulphate of Ca (gypsum), Mg, K and Na

Table 6. Characteristics of magnesium (Mg) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	Exists in soil in water-soluble, exchangeable, fixed and primary mineral forms
CONCENTRATION IN PLANTS	Varies between 0.1 and 0.4%
ABSORBTION FORM	Mg^{2+}
USES	Plays a role in photosynthesis as it is a constituent of chlorophyll which usually accounts for about 15-20% of the total Mg^{2+} content of plants. It is also associated with rapid growth, mitosis, high protein levels, carbohydrate metabolism, and oxidation phosphorylation in physiologically young cells. Mg is also a structural component in ribosomes
MOBILITY	Translocated from mature to actively growing regions of the plant. Because of its mobility, it can be leached out of the soil
DEFICIENCY SYMPTOMS	Deficiency results in a proportion of protein N decrease while that of non-protein-N generally increases in plants. Its ready translocation from older to younger plant parts, deficiency symptoms often appear first on the lower leaves. In many plant species, deficiencies result in interveinal chlorosis of the leaf in which only one vein remains green while in more advanced stages, the leaf tissue becomes uniformly pale yellow, then brown and necrotic
pH EFFECTS	Acid soils tend to show deficiencies because of impaired absorption of this ion
INTERACTION WITH OTHER NUTRIENTS	High levels of P or Ca relative to Mg may inhibit uptake of this ion and vice-versa
SOILS IN KWA-ZULU-NATAL, RSA	Mg deficiencies are fairly common. They usually indicate high levels of acidity. A Mg level of 60 mg L^{-1} is regarded as critical for maize when deciding to use calcitic or dolomitic lime. Magnesium levels in virgin soils range from 30-300 mg L^{-1}
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	0.15-0.25%
MOST COMMONLY USED APPLICATION FORMS IN RSA	With the exception of potassium magnesium sulphate; few of the carriers of primary nutrients contain large amounts of Mg; $MgSO_4.7H_2O$ (epsomite). Primarily dolomitic lime and $MgSO_4$ used
MOST COMMONLY USED APPLICATION FORMS IN USA	Magnesium nitrate ($MgNO_3$), magnesium silicate (basic slag) and magnesium chloride ($MgCl_2$); dolomitic lime ($MgCO_3$ and $CaCO_3$)

Table 7. Characteristics of iron (Fe) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	Present in the soil in mineral, oxide, sulphide and organic complexes
CONCENTRATION IN PLANTS	Sufficiency range is normally between 50 and 250 ppm
ABSORBTION FORM	Absorbed as Fe^{2+}, Fe^{3+} and as organically complexed (chelated) Fe
USES	The ferrous forms of Fe are the most available for plant nutrition. Fe is an important part of the oxidation-reduction reactions in both plants and soils. It provides the potential for many enzymatic transformations, several of which are involved in chlorophyll synthesis. Fe in the plant occurs primarily in the form of porphrins (hemes). These are critical elements of terminal oxidation systems (electron transport) and other oxidative enzymes. Fe is also essential for chlorophyll synthesis and is intimate with the reactions of photosynthesis
MOBILITY	Intermediate mobility. The Fe^{2+} form is more mobile
DEFICIENCY SYMPTOMS	Most frequently seen in crops growing on calcareous or alkaline soils although some crops exhibit Fe deficiency on acid soils. When Fe is deficient, chlorophyll production is reduced resulting in the characteristic chlorosis symptoms of Fe stress. Deficiency symptoms show up first in young leaves of plants which develop inter-veinal chlorosis which progresses rapidly over the entire leaf. It does not appear to be translocated from older tissues to the tip meristems and as a result growth ceases. Acid soils where Mn is dissolved and blocks Fe uptake , are common in KwaZulu-Natal
pH EFFECTS	As soils become more alkaline, ferrous iron is oxidised to the ferric form which is not available for uptake and growth
INTERACTION WITH OTHER NUTRIENTS	Heavy metal excesses; e.g., Mn and Cu may also interfere with Fe absorption. Deficiencies of K, P or Ca may induce or enhance Fe deficiency by interfering with its translocation. A change in the K : Ca ratio greatly alters K and Fe nutrition. P may immobilize Fe as ferriphosphate in marginal soils; i.e., the apparent deficiency of Fe may not be due to a lack of Fe, but to its unavailability because of high pH or mineral imbalance. Balanced K increases the efficiency of Fe utilization in chlorophyll production
SOILS IN KWA-ZULU-NATAL, RSA	No deficiency symptoms have been recorded for maize
MOST COMMONLY USED APPLICATION FORMS IN RSA	Ferrous sulphate and chelated Fe most widely used
MOST COMMONLY USED APPLICATION FORMS IN USA	Iron sulphide ($FeSO_4$) and synthetic chelates

Fe toxicity in rice causes nutritional disorders when rice is grown on poorly drained or submerged soils. This is known as bronzing and is associated with Fe levels greater than 300 ppm in the leaf blade of rice at tillering.

Table 8. Characteristics of zinc (Zn) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT MATERIAL	Most Zn-bearing minerals in soil are readily weathered, and therefore the release of Zn is generally absorbed onto colloids or complexed by organic matter
CONCENTRATION IN PLANTS	Zn concentrations in plants vary from 25-150 ppm
ABSORBTION FORM	Plant roots absorb Zn as Zn^{2+}
USES	The most prominent physiological role known for Zn is its inter-relationship with auxin. It is therefore essential for cell elongation and growth, as well as being functional in respiration and enzyme regulation. It is the metal component of several dehydrogenases, peptides and other metallo-enzymes. It is involved in many enzymatic reactions and is important in the synthesis of tryptophan, a component of some proteins and a compound needed for the production of growth hormones (auxins) like indole-acetic acid (IAA)
MOBILITY	Intermediate mobility in the plant which accounts for the intensity of deficiency symptoms being more pronounced in young tissues
DEFICIENCY SYMPTOMS	Maize and beans are particularly sensitive to Zn deficiency as well as citrus and deciduous fruit trees; e.g., peach. Zn deficient plants can suffer from reduced growth hormone production resulting in short internodes and smaller than normal leaves. Addition of Zn to deficient plants greatly stimulates auxin synthesis. Large increases in amino acids are noted with Zn deficiency
SOILS IN KWA-ZULU-NATAL, RSA	Zn deficiencies far less frequent than 20 years ago due to the use of zincated fertilizer. Very little calibrated data is available. In virgin soils, Zn levels range from 1-3 mg L^{-1}
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	20 mg kg^{-1}
MOST COMMONLY USED APPLICATION FORMS IN RSA	Zinc sulphate, $Zn(OH)_2$, $ZnCO_3$; synthetic chelate, and natural organic complexes
MOST COMMONLY USED APPLICATION FORMS IN USA	Zinc sulphate ($ZnSO_4$), synthetic Zn chelates, ZnO

Table 9. Characteristics of copper (Cu) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT FORM	Copper sulfide is the most important primary source of this element in soil. Atmospheric sources may provide significant amounts of copper together with iron, zinc, manganese, boron and molybdenum as volatile compounds or in precipitation
CONCENTRATION IN PLANTS	Ranges from 5-20 ppm
ABSORBTION FORM	Absorbed as the cupric ion, $Cu2^{+}$
USES	Cu is unique in its involvement in enzymes and cannot be replaced by any other metal ion. It is involved in protein and carbohydrate synthesis and N fixation.
DEFICIENCY SYMPTOMS	Cu deficiencies have been reported in many plants but are most prevalent in crops growing in peat and muck soils. Alfalfa, wheat, barley, oats, lettuce, onions, carrots, spinach and table beets are crops most susceptible to Cu deficiency. Symptoms vary according to the crop. In maize the youngest leaves yellow first and become stunted. As the deficiency symptoms become more severe, the young leaves become pale and the older leaves die back. In the advanced stages, the dead tissue and tips and edges of the leaves result in a pattern similar to that of K deficiency. In many vegetable crops the leaves lack turgor and develop a bluish-green cast, become chlorotic, curl and flower production fails to take place
SOILS IN KWA-ZULU-NATAL, RSA	No deficiency symptoms have been recorded for maize
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	5 mg kg^{-1}
MOST COMMONLY USED APPLICATION FORMS IN RSA	$CuSO_4.5H_2O$; chelates of Cu and other micro-elements
MOST COMMONLY USED APPLICATION FORMS IN USA	Copper sulphate ($CuSO_4$), chelated copper oxide (CuO), copper hydroxide ($Cu(OH)_2$)

Table 10. Characteristics of boron (B) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

PARENT FORM	Various complexes containing B are present in the soil
CONCENTRATION IN PLANTS	B concentration generally varies between 6 and 18 ppm in monocotyledons and 20 and 60 ppm in dicotyledons
ABSORBTION FORM	Most of the B absorbed by plants is undissociated boric acid (H_3BO_3)
USES	Functional in translocation, cellular differentiation and development, carbohydrate metabolism, pollen germination and the uptake or translocation of calcium. Plants require B for a number of growth processes, especially new cell development in meristematic tissue, proper pollination and fruit or seed set, translocation of sugars, starches, N and P synthesis of amino acids and proteins; nodule formation in legumes and regulation of carbohydrate metabolism. It is essential in varying but usually small quantities for the growth of many important agricultural crops. B plays an essential role in the development and growth of new cells in the plant meristem
MOBILITY	Not readily translocated
DEFICIENCY and TOXICITY SYMPTOMS	B deficiency is the most widespread micronutrient deficiency. Crops requiring a high B requirement include asparagus, carrots, celery, lettuce, onions, sugar beets, sunflowers, and various brassicas. Low B-requiring crops include small grains, peas and beans. Since it is not readily translocated from older to actively growing tissues, the first visual deficiency symptom is cessation of terminal bud growth followed by the death of the young leaves. B deficiency symptoms often occur in the form of thickened, wilted or curled leaves and a discolouration, cracking or rotting fruit tuber roots. There is a relatively narrow range of concentration between deficiency and toxicity of boron. Toxicity may result in arid areas where sodium and calcium borates accumulate in surface soils or in acidic soils where it is more soluble
pH EFFECTS	Easily leached from acidic soils. High pH soil levels reduces plant uptake
SOILS IN KWA-ZULU-NATAL, RSA	Boron levels are commonly very low in virgin soils making it essential to add B for crop production
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	5 mg kg^{-1}
MOST COMMONLY USED APPLICATION FORMS IN RSA	Sodium tetraborate is the most commonly used B source
MOST COMMONLY USED APPLICATION FORMS IN USA	Sodium tetraborate $(NA_2B_4)_7.5H_20$ and borax

Table 11. Characteristics of molybdenum (Mo) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

CONCENTRATION IN PLANTS	Less than 1 ppm
ABSORBTION FORM	This is a non-metal anion absorbed as molybdate (MoO_4^{2-})
USES	The essential component of NO_3^- reductase which catalyses the conversion of NO_3^- to NO_2^-. Most of the Mo in plants is concentrated in this enzyme, which primarily occurs in chloroplasts in leaves. It is also a structural component of nitrogenase, the enzyme involved in N_2 fixation by root-nodule bacteria of leguminous crops, by some algae and by free-living N_2-fixing organisms; e.g., *Azotobacter*. Mo is also reported to have an essential role in Fe absorption and translocation in plants
MOBILITY	Intermediate
DEFICIENCY SYMPTOMS	Colour changes in foliage; lack of chlorophyll in leaves resulting in a paler green appearance
pH EFFECTS	In acid soils absorbtion is impaired
INTERACTION WITH OTHER NUTRIENTS	Mo requirement of plants is influenced by the form of organic N supplied to plants, with either $N0_2^-$ or NH_4^+ effectively lowering its need
SOILS IN KWA-ZULU-NATAL, RSA	Mo deficiencies occur on almost all soils in the province, unless Mo treated seed is used. Foliar sprays with Mo compounds are very effective in correcting deficiencies which do occur
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	0.2 mg kg^{-1}
MOST COMMONLY USED APPLICATION FORMS IN RSA	Mo solutions sprayed onto foliage or applied to seed
MOST COMMONLY USED APPLICATION FORMS IN USA	Ammonium molybdate $(NH_4)6Mo_70_{24}.2H_20$) and sodium molybdate ($Na_2MoO_4.2H_2O$)

Table 12. Characteristics of manganese (Mn) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

CONCENTRATION IN PLANTS	Ranges from 20-500 ppm
ABSORBTION FORM	Mn is absorbed by plants as Mn^{2+} as well as in molecular combinations with certain natural and synthetic complexing agents
USES	Mn is a constituent of only one known plant component, manganin, but it activates various enzymes involved in nitrate reduction, carbohydrate metabolism and respiration. It plays a direct and primary role in photosynthesis. Mn is a competitive inhibitor of iron absorption, translocation and binding at high concentrations. It is involved in photosynthesis and can substitute for Mg^{2+} in many of the phosphorylating and group transfer reactions. Although it is not specifically required, Mn is needed for maximal activity of many enzyme reactions in the citric acid cycle. In the majority of enzyme systems, Mg is as effective as Mn in promoting enzyme transformations. Mn influences auxin levels in plants and it seems that high concentrations of this micronutrient favours the breakdown of IAA
MOBILITY	Relatively immobile
DEFICIENCY SYMPTOMS	Usually show up first in the younger leaves. Wheat plants low in Mn are often more susceptible to root rot diseases. Plants are injured by excessive amounts of Mn
pH EFFECTS	May be toxic in acidic soils because of increased solubility. Mn toxicity has been found in very acid soils in the USA in cotton, tobacco, soya beans, tree fruits and canola/rapeseed. Upward adjustment of soil pH by liming readily corrects this problem. pH and oxidative-reduction conditions present, largely determine the availability of Mn. Soil pH values below 6 favour reduction and values above 6.5 favour oxidation to non-available states. Biological oxidation in the rhizosphere is generally responsible for immobilization at pH's of 6 to 7.9
INTERACTION WITH OTHER NUTRIENTS	Commonly found at toxic levels in acid soils which accounts for 60% of soils in the Republic of South Africa. Toxicity very common in soils in KwaZulu-Natal, often in conjunction with aluminium toxicity. Causes stunting and leaf burn on edges
SOILS IN KWA-ZULU-NATAL, RSA	No attempt has yet been made to establish the Mn requirement of maize for the province.
CRITICAL CONCENTRATIONS FOR MAIZE LEAVES SAMPLED AT SILKING	15 mg kg^{-1}
MOST COMMONLY USED APPLICATION FORMS IN RSA	$MnSO_4$
MOST COMMONLY USED APPLICATION FORMS IN USA	Manganese sulphate ($MnSO_4.4H_2O$), manganous oxide (MnO) and manganese chloride ($MnCl_2$)

Table 13. Characteristics of chlorine (Cl) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

ABSORBTION FORM	This is absorbed by plants as Cl^- both through roots and aerial parts
USES	Chlorine functions in oxygen evolution of photosystem II. However, wilting and amino acid accumulation in deficient plants may indicate an additional role in transpiration and amino-acid metabolism. It is an active osmotic agent. A high level of Cl nutrition will increase total leaf water potential and cell sap osmotic potential in wheat plants
MOBILITY	Highly mobile
DEFICIENCY SYMPTOMS	Deficiencies result in partial wilting and loss of leaf turgor. Chlorosis in younger leaves and an overall wilting of the plants are the two most common symptoms of Cl-deficiency. Excesses can be harmful and crops vary widely in their tolerance of this condition. It is the only element which has not been shown to be deficient in nature. However, excess chloride is very much a matter of concern in many areas
INTERACTION WITH OTHER NUTRIENTS	Decreases uptake of NO_3^--N and enhances the uptake of $NH4^+$-N. Also reduces amino acid and protein synthesis and promotes protein degradation
MOST COMMONLY USED APPLICATION FORMS IN RSA	Ammonium chloride (NH_4Cl), calcium chloride ($CaCl_2$), magnesium chloride ($MgCl_2$), potassium chloride (KCl) and sodium chloride (NaCl)
MOST COMMONLY USED APPLICATION FORMS IN USA	Ammonium chloride (NH_4Cl), calcium chloride ($CaCl_2$), magnesium chloride ($MgCl_2$), potassium chloride (KCl) and sodium chloride (NaCl)

Table 14. Characteristics of sodium (Na) as a plant fertilizer (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

ABSORBTION FORM	Na is absorbed by plants as Na^+
USES	Many plants that possess the C_4 dicarboxylic photosynthetic pathway require Na as an essential nutrient. Lack of Na will cause certain plant species to shift their C_2-fixation pathway from C_4 to C_3. Provision of adequate Na can restore these plants to their normal C_4 fixation cycle. Na has been demonstrated to improve the growth of celery, turnips and many other plants but has not been determined as "essential" for most of them. It may partially replace K and functions to lower osmotic pressure of certain halophytes
pH EFFECTS	High concentrations of Na found in "saline" soils are toxic to many plants
MOST COMMONLY USED APPLICATION FORM IN RSA	Sodium nitrate ($NaNO_3^-$)
MOST COMMONLY USED APPLICATION FORM IN USA	K fertilizers with various NaCl contents and sodium nitrate ($NaNO_3^-$)

Some of the effects ascribed to Na may also be due to Cl^- since the usual source of Na is NaCl.

Table 15. Characteristics of silicon (Si), cobalt (Co), vanadium (V) and nickel (Ni) as plant fertilizers (Raven *et al.*, 1976; Huber, 1981; Anonymous, 1993; Tisdale *et al.*, 1993)

SILICON (Si)	
ABSORBTION FORM	Si is absorbed by many plants as monosilicic acid $Si(OH)_4$. Since KCl is the most commonly used K fertilizer, it is possible that K and / or Cl components of this fertilizer enhance Si uptake and metabolism
USES	It contributes to the structure of cell walls. Many of the favourable effects of Si on plant growth, such as disease resistance, stalk strength and reductions in lodging are also attributable to K
MOST COMMONLY USED APPLICATION FORMS	Calcium silicate slag ($CaAl_2Si_2O_8$), calcium silicate ($CaSiO_3$) and sodium metasilicate ($NaSiO_3$)
COBALT (Co)	
USES	Essential for the formation of vitamin B_{12} required by micro-organisms fixing N_2. Other functions attributed to Co include leghaemoglobin metabolism and ribonucleotide reductase in *Rhizobium*. Improved growth, transpiration and photosynthesis have been observed with applications of Co in cotton, beans and mustard
MOST COMMONLY USED APPLICATION FORMS IN RSA	Cobalt sulphate
MOST COMMONLY USED APPLICATION FORMS IN USA	$CoSO_4$ and superphosphates with small amounts of $CoSO_4$
VANADIUM (V)	
USES	Low concentrations of V are beneficial for the growth of micro-organisms. There is no decisive evidence that V is essential for higher plants but it has been suggested that V may partially substitute for Mo in N_2-fixation by microorganisms; e.g., *Rhizobia*. Increases in growth attributable to V have been reported for asparagus, rice, lettuce, barley and maize
NICKEL (Ni)	
USES	High levels of Ni may induce Zn or Fe deficiency because of cation competition. Ni has been shown to have a beneficial role in legumes. It is possible that it is essential for certain types of N nutrition and certain plant families. More research is needed to fully understand the role of this micronutrient in plants

1.3 The role of nutrients in the control of fungal plant pathogens

One of the most rewarding approaches for successful reduction of diseases is proper selection and utilisation of micro- and macronutrients. Although the importance of adequate soil nutrition for reduction to disease is a vital principle and well documented in the literature, it is often ignored in practical agriculture (Huber, 1976; Huber, 1981; Graham, 1983; Huber and Dorich, 1988). Since virtually all commercially produced crops in the developed world are fertilized, it is important to manipulate fertilizer levels to achieve a profit maximizing point between yield and disease severity. This is a viable alternative or supplement with the use of fungicides and pesticides which usually only give partial disease control.

Mineral nutrients determine, to a large degree, changes in growth pattern, plant morphology and particularly chemical composition in plants which, in turn, determines yield. Its effect on disease is secondary to this objective. However, it is an interaction of factors that determines whether disease can be managed by soil nutrition, including factors such as host, environment, pathogen, and time. These and any other variables, must be considered when examining the effects of nutrients on disease. It is at present difficult to detect any clear pattern of the role of nutrients in decreasing or increasing diseases in plants. Each disease must be considered in relation to the environment in which the host and pathogen occur, and the availability of essential nutrients. The presence of other pathogens further complicates the use of fertilizers.

Specific issues need mention relating to specific nutrients and their interactions on fungal plant diseases.

1.3.1 Nitrogen (N)

Nitrogen affects the mechanical strength of cell walls and consequently the penetration of pathogens into cells. This element has been extensively studied in relation to host nutrition and disease severity for many years (Huber, 1981).

The general increased use of N to increase production is considered to increase the severity of diseases such as powdery mildews, rusts and fire blight, caused by pathogens that are adapted to exploit young succulent tissue (Huber, 1981). On the other hand, increased N levels may decrease diseases caused by pathogens that attack primarily mature or senescent tissue (Agrios, 1988). There are, however. many exceptions to such generalisations.

Nitrogen form and plant disease

Huber and Watson (1974) reviewed the effects of N form on diseases of numerous crops. Although a wide range of interactions of pathogens and their hosts are influenced by N, it is frequently the form of N (nitrate or ammonium) available to the host or pathogen that affects the increase or reduction of disease, rather than the amount of N applied (Robbins, 1937; Huber and Watson, 1974; Huber, 1980a and 1980b). For example, in maize the addition of the NO_3^- form of N causes an increase in *Stenocarpella maydis* causing stalk rot, while the NH_4^+ form of N results in a decrease in disease. This is because N is assimilated both as a cation (NH_4^+) and as an anion (NO_3^-). Unlike the positively charged ammonium ion, which is relatively stationary because of its adsorption to organic matter or clay particles, the negatively charged nitrate ion is freely mobile in the soil solution. Thus, leaching and denitrification primarily involve a loss of NO_3-N. Inhibition of nitrification can reduce N losses, increase utilization efficiency and establish a predominantly ammoniacal form of N available to plant uptake (Huber and Watson, 1974; Marschner, 1985).

An increase or a reduction in disease usually results from the influence of a specific form of N on metabolic pathways affecting growth, plant constituents or exudates rather than the direct effect of N itself. The inability of certain pathogens to use a specific form of N that reduces severity of diseases has been found in *Rhizopus* spp. of sweet potatoes (Robbins, 1937). A specific form of N may affect virulence of a pathogen without affecting growth or germination, especially with facultative saprophytes. In these cases, the inhibition of extracellular enzyme production could account for the

reduction in severity of many diseases characterised by enzymatic activity in the breakdown of cell walls before penetration; e.g., *Rhizoctonia solani* (Kűhn) and *Verticillium* wilt in cotton (Patil and Dimond, 1967).

Water, pH, interactions with other elements and temperature influence the uptake and utilization of specific forms of N by plants, pathogens and interacting micro-organisms. Host response or preference, crop sequence, residual N, N rate and stability, timing of N application, soil microflora or the pathogen complex present can profoundly affect the form of N predominating in the soil (Huber and Watson, 1974). The fact that a given form of N reduces one disease but favours another points to the need for detailed understanding of the consequences of manipulating soil nutrients to manage specific diseases (Huber, 1966; Huber and Watson, 1970 and 1974).

Unfortunately, much of the data concerning N on plant disease reported in the literature is difficult to interpret because many of the parameters discussed above are not published and for this reason have not been included in this literature survey.

Timing and application methods

The time of application of nitrogenous fertilizers may also have a pronounced effect on disease expression. Delayed application of N to winter wheat until spring frequently results in an early N deficiency and predisposition to take-all (*G. graminis* f. sp. *tritici*) and *Cercosporella* foot rot. Side-dressing nutrients to plants after emergence avoids predisposition to seedling diseases such as damping off caused by *Rhizoctonia* and *Pythium* spp. but may increase *Fusarium (Gibberella)* and other root rots due to mechanical damage to root systems or other plant parts (Huber, 1981).

1.3.2 Phosphorus (P)

The combination of P and K ensures the development of strong mechanical tissue by increasing the proportion of sclerenchyma tissue. Additions of these nutrients therefore

help reduce wheat stem rust (*Puccinia graminis* f. sp. *tritici* Erikss and Henn.) which only lives in collenchyma tissue (Huber, 1981).

Application of P, absorbed in the PO_4^{2-} form, is most beneficial in reducing seedling diseases and other fungal diseases where vigorous root development permits plants to escape disease or produce roots faster than those lost to the pathogen. By shortening the vegetative period, P reduces the infective period for rusts and other foliar pathogens which usually infect plants in the vegetative stages of growth. Phosphorus is especially beneficial in counteracting effects of high levels of N (Huber and Arny, 1985).

The effects of P on plant diseases have been reviewed by Usherwood (1980). However, like other nutrients, there is no definite pattern on the effect of P amendments on disease and each host-pathogen combination must be examined under each set of environmental conditions; e.g., P increases resistance to *Thielaviopsis* root rot of tobacco, take-all (*G. graminis* f. sp. *tritici*) of wheat, flag smut (*Urocystis tritici* Liro) of wheat, *Septoria* leaf spot of tomato, downy mildew (*Peronospora parasitica* [Pers.] Fr.) of cabbage, *Gibberella* spp. on maize roots and *Pythium* root rot on wheat. In contrast, P reduces resistance of lettuce to downy mildew *(Bremia lactuca* Reg.) and cereal powdery mildew (*Erysiphe graminis* D.C.) (Huber, 1981).

1.3.3 Potassium (K)

The relationship between available K in soil and plant disease severity has been observed for many years. In recent years it has become common practice to fertilize with K to reduce severity of many tomato diseases. Potassium deficiency may predispose maize to root rot and lodging because of an accumulation of Fe in nodal tissues of stalks that interfere with translocation of nutrients to the roots. The application of K fertilizers has the greatest value in reducing these diseases when used in conjunction with the more resistant varieties. However, inconsistent results are reported because this disease may be caused by several pathogens; e.g.,

Stenocarpella maydis Sutton, *Gibberella zeae* Schw., *Fusarium moniliforme* Sheldon, *Pythium* spp. and *Colletotrichum graminicola* Ces. Wils., each of which may respond differently to K fertilization. This issue has been reviewed by Huber and Arny (1985).

1.3.4 Calcium (Ca)

Calcium is absorbed as the Ca^{2+} ion, in the ionic state. Tissues of plants deficient in Ca have thin cell walls, large intercellular spaces, poorly defined middle lamellae and appear poorly organized. Calcium protects pectate from maceration by extracellular enzymes produced by pathogens, reduces soil acidity by neutralizing effects of some toxins and affects cell division where abnormal growth occurs. Calcium fertilization reduces colonization by *Sclerotium rolfsii* Sacc. in tomatoes but increases scab severity (*Streptomyces scabies* Thaxter) on potatoes, particularly when soils are limed (Huber, 1981).

1.3.5 Manganese (Mn)

Manganese toxicity is widespread in the RSA, reducing yields particularly in broadleaf plants and also plays an important role in disease susceptibility of plants. It is involved in photosynthesis (Graham and Rovira, 1984), as well as in the synthesis of lignin and phenols, thereby reducing the susceptibility of plants to attack by pathogens (Reis, *et al.,* 1982; Graham and Rovira, 1984) and may inhibit production of certain extra-cellular fungal enzymes (Graham, 1983).

Huber and Wilhelm (1988) reviewed the effects of Mn on plant diseases. Like other elements, there are conflicting reports in the literature regarding the role of Mn in host-pathogen interactions. In general, Mn increases resistance of plants to disease. Direct application of Mn as a foliar spray, seed treatment or soil amendment may provide adequate disease control in some situations. Modification of the soil environment to maintain availability of Mn may be required in other situations, e.g., cultural practices such as lowering soil pH, use of irrigation at critical periods of growth, inhibition of

such as lowering soil pH, use of irrigation at critical periods of growth, inhibition of nitrification and the use of NH_4^+-N all increase Mn solubility and, in turn, reduce severity of pathogens (Huber and Wilhelm, 1988).

1.3.6 Other micronutrients

Silicon strengthens cell walls and helps impede pathogen penetration. It increases resistance to blast (*Pyricularia oryzae*) of rice and powdery mildew (*E. graminis*) of wheat (Graham and Webb, 1991).

With the exception of Fe, the great majority of studies on micronutrients and disease resistance have shown that the addition of soil micronutrients has decreased the incidence of disease in crop plants, particularly over the deficiency range of the element concerned. With the exception of Fe, adequate micronutrient nutrition should be viewed as an essential component of crop management. Although disease remission is rare, micronutrient fertilization reduces many diseases to an acceptable level as well as providing an inexpensive, and in many cases, long-lasting control measure. This has been well documented by Graham and Webb (1991).

1.3.7 Nutrient interactions

In soil fertility studies, there are frequently positive and/or negative interactions between plant nutrients (Tisdale *et al.*, 1993). However, this factor has often been overlooked in soil fertility studies, even though they have considerable influence on plant growth.

An interaction takes place when the response of two or more inputs used in combination is unequal to the sum of their individual responses. There can also be circumstances where there is no interaction. Positive interactions result if two factors are limiting, or nearly so, then addition of one will have little effect on growth, whereas provision of both together will have a much greater influence. In negative interactions,

the two nutrients combined increase yields less than when they are applied separately. Drastically altered ratios of some nutrients may also induce excess uptake of toxic quantities of other elements. Changes in soil pH can also result in numerous nutrient interactions where one ion or nutrient interferes with, or competes with, the uptake and utilization of other nutrients by plants (Tisdale *et al.*, 1993).

Much has been reported in the literature on the interactions of N, P and K on disease. Some of the numerous examples from the literature are highlighted below.

Particular attention has been devoted to the nutrient balance and the N:K ratio. The ability of NO_3-N to reduce northern leaf blight (*Exserohilum turcicum* [Pass.] Leonard and Suggs) is nullified if potassium chloride (KCl), which inhibits nitrate uptake, is applied with NO_3-N, rather than potassium sulphate (K_2SO_4) which has little effect on nitrate uptake (Engelhard, 1989). Stalk rot, caused by *D. zeae, F. monilifera* and *G. zeae*, increases with increasing levels of NH_4^+ and NO_3-only when K levels are low (Nelson, 1963; Huber and Watson, 1974). Stalk rot is reduced with applications of KCl, ammonium sulphate or ammonium chloride while similar rates of potassium nitrate increase severity of this disease. The reduction of stalk rot with KCl appears to result from competitive inhibition of NO_3-N uptake by the chloride ion and is not dependent on K. High rates of NO_3-N may overcome the competitive inhibition imposed by chloride and explain why application of NO_3-N without chloride increases stalk rot, whereas application of chloride without N has little effect on disease (Nelson, 1963). Other stalk rot pathogens; e.g., *Fusarium* spp., are not affected as severely as *Stenocarpella*. Much more confusion generated in the literature could be avoided if the pathogen rather than the symptom was identified (Nelson, 1963; Huber and Watson, 1974). This is complicated in the situation where pathogen complexes attack plant roots, crowns and stems.

The K:Ca balance in the soil is thought to be related to the differential permeability of cell membranes which in turn has an effect on disease. The K:Ca balance is important for development of club root (*Plasmodiophora brassicae* Wor.) of cabbages, with the

disease diminishing as the levels of Ca increase in the soil (Gries *et al.*, 1944). In contrast, potato scab (*S. scabies*) increases as available potash or Ca in the soil increases. Tomato brown rot gummosis (*Phytophthora parasitica* Dast.) is also more severe when high K is associated with low Ca. Excess Ca reduces resistance of wheat to flag smut (*U. tritici*) but reduces susceptibility of wheat to rust (*Puccinia* spp.) and lowers the water requirement in rusted as well as rust-free plants (Weiss, 1924).

Boron affects the accumulation of Ca and interacts with Ca to influence resistance of tomatoes to *Fusarium* wilt. Both elements have an effect on the development and structure of cell walls (Huber, 1980b).

It is beyond the scope of this literature survey to cover the volumes of literature available on nutrient effects on fungal diseases of all crops. Instead, eleven crops are given listing the main diseases associated with them and the affects of various nutrients in increasing or decreasing disease severity. Nutrient effects on common fungal plant pathogens on wheat, maize, rice, cereals, potatoes, cabbage, beans, cotton, peas, citrus and tomatoes are given in Tables 16-26, respectively.

Table 16. Nutrient effects on fungal pathogens of wheat *(Triticum aestivum* L.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Na	Mn	Ca	Li	B	Zn	Cu	REFERENCES
			NO_3-N	NH_4-N												
WHEAT	*Erysiphe graminis* D.C.	powdery mildew	↓	↑	↑					↓	↓	↓				Huber, 1981; Huber and Wilhelm, 1988
	Pseudocercosporella herpotrichoides (Fron) Deighton	eye spot	↓	↑												Huber, 1981
	Fusarium graminearum Schw.	Crown rot												↓		Grewal *et al.*, 1996
	Fusarium roseum f. sp. *cerealis* Link. Fr	wilt	↓	↑												Huber and Watson, 1974
	Gaeumannomyces graminis f. sp. *tritici* Sacc. Von Arx and Olivier	take-all	↑	↓	↑↓	↑↓	↓↑	↑↓		↓			↓	↓	↑	Glynne, 1953; Schütte, 1964; Christensen and Brett, 1965; Syme, 1966; Smiley and Cook, 1973; Huber and Watson, 1974; Graham and Rovira, 1984; Huber and Wilhelm, 1988; Huber, 1989 ; Rengel *et al.*, 1993; Mccaybuis *et al.*, 1995
	Gibberella zeae Schw.	scab				↑										Huber, 1981
	Helminthosporium sativum Pammel, C.M. King and Bakke	root rot	↓			↓										Huber, 1981
	Puccinia graminis tritici Erikss and Henn	stem rust								↓	↓	↓	↓			Huber, 1981
	Puccinia recondita Rob. ex Desm. f. sp. *tritici* Eriks. and Henn	leaf rust							↓				↓	↑	↑	Huber, 1981
	Puccinia striiformis Westend	stripe rust	↑	↓									↓			Huber and Watson, 1974
	Rhizoctonia solani Kuehn	root rot	↓	↑										↓		Huber and Watson, 1974; Thongbai *et al.*, 1993; Wall *et al.*, 1994
	Urocystis tritici K Horn. = *Tuburcinia tritici* (K Horn.) Liro	flag smut						↑								Huber, 1981
	Ustilago tritici (Pers.) Rostr.	loose smut							↓				↓		↑	Huber, 1981

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 17. Nutrient effects on fungal pathogens of maize (*Zea mays* L.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Mg	Cl	REFERENCES
			NO_3-N	NH_4-N					
MAIZE	*Stenocarpella maydis* Sutton	stalk rot	↑	↓	↑	↓		↓	Warren *et al.*, 1975; Huber, 1981
	Cercospora zeae-maydis Tehon and Daniels	grey leaf spot	↑*						Smith, 1989
	Fusarium moniliforme Sheldon	stalk rot	↓	↑		↓			Huber, 1981
	Gibberella zeae Schw.	stalk rot	↑	↓	↓	↓		↓	Younts and Musgrave, 1958; Huber, 1981
	Exserohilum turcicum ([Pass.] Leonard and Suggs)	Northern leaf blight	↓	↑		↓		↓	Huber, 1981; Huber and Arny, 1985.
	Exserohilum maydis Nisikado and Miyake	Southern leaf blight					↑		Huber, 1981
	Pythium spp.	root rot	↑	↓					Huber, 1981

↑ represents an increase in disease with the addition of the nutrient ; ↓ represents a decrease in disease with the addition of the nutrient

*** NH_4-N was applied which was probably converted to NO_3-N as in the case of the Cedara trial reported in the following chapters of this thesis. It was therefore assumed that the nitrate form of N on GLS was investigated by Smith (1989)**

Table 18. Nutrient effects on fungal pathogens of rice (*Oryza sativa* L.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Mg	Mn	Si	Cu	Cl	REFERENCES
			NO_3-N	NH_4-N								
RICE	*Cercospora oryzae* Miyake	leaf spot				↓						Huber, 1981
	Cochliobolus miyabeanus (Ito and Kuribayashi) Drechs. ex Dastur	brown spot				↓			↓	↓		Huber, 1981; Graham and Webb, 1991
	Fusarium moniliforme Sheldon	root rot								↓		Huber, 1981
	Helminthosporium sigmoidum Pammel, C.M. King and Bakke = *Bipolaris sorokiniana* (Sacc.) Shoemaker	leaf spot				↓	↓	↓	↓			Huber and Wilhelm, 1988
	Helminthosporium oryzae Breda de Haan	brown spot				↓	↓	↓	↓			Huber, 1981; Huber and Wilhelm, 1988
	Leptosphaeria salvinii Cattaneo	stem rot				↓						Huber, 1981
	Ophiobolus miyabeanus Ito and Kuribayashi	brown spot			↓	↓					↓	Powelson and Jackson, 1978; Huber, 1981
	Pyricularia oryzae Cavara	blast	↑	↓		↓		↓	↓	↓		Huber, 1981; Mbodj *et al.*, 1987; Huber and Wilhelm, 1988; Graham and Webb, 1991
	Sclerotium oryzae Cattaneo	sclerotium disease				↓						Huber, 1981

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 19. Nutrient effects on fungal pathogens of cereals

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Mn	Si	B	Fe	Cu	Zn	REFERENCES
			NO_3-N	NH_4-N											
CEREALS	*Curvularia ramosa* (Bainier) Boedijn	root rot							↓			↓			Huber and Wilhelm, 1988
	Erysiphe graminis D.C.	powdery mildew				↓			↓	↓	↓				Huber, 1981; Huber and Wilhelm, 1988
	Fusarium culmorum (Wm.G.Sm.) Sacc.	root rot							↓			↓	↓	↓	Huber and Wilhelm, 1988
	Gaeumannomyces graminis f. sp. *tritici* (Sacc.) Von Arx and Olivier	take-all	↓	↑					↓						Huber and Wilhelm, 1988
	Helminthosporium sativum Pammel, C.M. King and Bakke	root rot							↓		↓	↓		↓	Huber, 1981; Huber and Wilhelm, 1988
	Ophiobolus graminis Von Arx and Olivier	take-all	↑	↓	↓										Huber and Wilhelm, 1988
	Puccinia graminis Erik and Henn.	stem rust			↓		↑	↑	↓	↑		↑			Huber and Watson, 1974; Huber, 1981
	Puccinia recondita Rob. ex Desm. f.sp. *tritici* Erik. and Henn.	leaf rust							↓						Huber and Watson, 1974
	Puccinia striiformis Westend	stripe rust				↓	↑	↑		↑		↑			Huber, 1981
	Pythium arrhenomanes Drechs.	browning root rot			↓										Huber, 1981
	Pythium spp.	root rot	↑												Huber, 1981
	Rhizoctonia solani Kuehn	root rot					↓		↓						Huber, 1981; Huber and Wilhelm, 1988

↑ represents an increase in disease with the addition of the nutrient ; ↓ represents a decrease in disease with the addition of the nutrient

Table 20. Nutrient effects on fungal pathogens of potatoes (*Solanum tuberosum* L.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Mn	Cu	Zn	Si	Ni	Co	REFERENCES
			NO_3-N	NH_4-N											
POTATOES	*Alternaria solani* Sorauer	early blight											↓	↓	Barclay *et al.*, 1973; Colhoun, 1973; Soltanpour and Harrison, 1974
	Fusarium spp.	stem end rot				↓									Huber, 1981
	Phytophthora infestans (Mont.) de Bary	late blight			↑	↓			↓	↓	↓		↓	↓	Colhoun, 1973; Huber, 1981; Huber and Wilhelm, 1988
	Rhizoctonia solani Kuehn	root and stem rot	↓	↑		↓	↓	↓	↓	↓	↓				Huber, 1981; Huber and Wilhelm, 1988
	Streptomyces scabies Thaxter	scab	↑	↓		↑	↑		↓			↓			Huber, 1981; Huber and Wilhelm, 1988
	Verticillium spp.	wilt	↑	↓					↓			↑			Huber and Watson, 1974; Huber and Wilhelm, 1988

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 21. Nutrient effects on fungal pathogens of cabbage (*Brassica olereacea* L.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Na	Mn	Carb-onate	B	REFERENCES
			NO_3-N	NH_4-N									
CABBAGE	*Fusarium oxysporum* f. sp. *conglutinans* Schlechtend.Fr.. f.sp. (Wollenw.) Snyder and Hansen	yellows	↓		↑	↓							Huber and Watson, 1974; Huber, 1981
	Peronospora parasitica (Pers.) Fr.	downy mildew			↓	↑							Huber, 1981
	Plasmodiophora brassicae Wor.	club root	↓		↑		↓	↓	↓	↓	↓	↓	Huber, 1981; Huber and Wilhelm, 1988

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 22. Nutrient effects on fungal pathogens of beans (*Phaseolus* spp.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Na	Si	Fe	B	REFERENCES
			NO_3-N	NH_4-N									
BROAD BEANS	*Botrytis fabae* Sardiña	leaf spot	↓	↑			↓						Huber and Watson, 1974; Huber, 1981
CASTOR BEANS	*Botrytis* spp.	leaf spot				↑	↓	↓					Huber, 1981
SOYA BEANS	*Rhizoctonia solani* Kuehn	root rot/damping off	↓	↑	↓		↓	↓		↓	↓		Huber and Watson, 1974; Huber, 1981
	Cercospora kikuchii (Matsumoto and Tomoyasu) Gardner	leaf blight				↓							Ito *et al.*, 1993
	Cercospora sojina K. Hara	frog-eye leaf spot	↑										Sharma *et al.*, 1996
	Phakopsora pachyrhizi Syd. and P. Syd.	rust	↑		↓	↑							Sharma *et al.*, 1996
BEANS - with no reference to type	*Fusarium solani* f. sp. *phaseoli* (Mart.) Sacc.	root rot	↓	↑								↓	Huber, 1981; Guerra and Anderson, 1985
	Rhizoctonia solani Kuehn	root rot/damping off	↓	↑		↑	↓	↓		↑			Huber, 1981
	Thielaviopis basicola (Berk. and Broome) Ferraris	root rot	↑	↓									Huber, 1981

↑ represents an increase in disease with the addition of the nutrient ; ↓ represents a decrease in disease with the addition of the nutrient

Table 23. Nutrient effects on fungal pathogens of cotton (*Gossypium* spp.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Mg	Na	Mn	Fe	Cu	B	REFERENCES
			NO_3-N	NH_4-N										
COTTON	*Fusarium oxysporium* f. sp. *vasinfectum* Schlechtend.:Fr f.sp. (Atk.) Synd. and Hans.	wilt	↓	↑	↓	↓	↑	↓		↓	↑			Huber and Watson, 1974; Huber, 1981; Huber and Wilhelm, 1988
	Rhizoctonia solani Kuehn	damping-off					↑	↓		↓				Huber, 1981; Huber and Wilhelm, 1988
	Verticillium albo-atrum Reinke and Berthold	wilt	↑	↓			↑	↓		↓		↓	↓	Huber, 1981; Savov, 1986; Huber and Wilhelm, 1988

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 24. Nutrient effects on fungal pathogens of peas (*Pisum* spp.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Zn	Cu	Al	B	REFERENCES
			NO_3-N	NH_4-N								
PEAS	*Aphanomyces cochlioides* Drechs.	root rot	↓	↑			↓	↓	↓	↓		Huber and Watson, 1974
	Aphanomyces euteiches Drechs.	root rot	↑	↓		↓	↓					Huber, 1981
	Pythium spp.	root rot	↑	↓								Huber, 1981
	Rhizoctonia solani Kuehn	root rot									↓	Kataria and Grover, 1987

↑ represents an increase in disease with the addition of the nutrient ; ↓ represents a decrease in disease with the addition of the nutrient

Table 25. Nutrient effects on fungal pathogens of citrus

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	REFERENCES
			NO_3-N	NH_4-N				
CITRUS	*Fusarium* spp.	root rot		↑				Huber and Watson, 1974
	Phytophthora citrophthora (R.E.Sm. and E.H. Sm.) Leonian	root rot	↓	↑	↑			Huber, 1981
	Phytophthora parasitica Dast.	brown rot gummosis				↑	↓	Huber, 1981
	Rhizoctonia solani Kuehn	root rot		↓				Huber, 1981
	Thielaviopis basicola (Berk. and Broome) Ferraris	root rot			↑			Huber, 1981

↑ represents an increase in disease with the addition of the nutrient; ↓ represents a decrease in disease with the addition of the nutrient

Table 26. Nutrient effects on fungal pathogens of tomatoes (*Lycopersicon esculentum* Mill.)

HOST	FUNGAL PATHOGEN	DISEASE	NITROGEN		P	K	Ca	Na	Mn	B	Zn	Cu	Mo	REFERENCES
			NO_3-N	NH_4-N										
TOMATOES	*Alternaria solani* Sorauer	early blight			↓									Huber, 1981
	Aphanomyces cochlioides Dresch.	root rot	↓	↑										Huber and Watson, 1974
	Fusarium oxysporum f. sp. *lycopersici* Schlechtend.:Fr. f.sp. (Sacc.) Snyder and Hansen	wilt	↓	↑	↑	↓	↓	↑	↓	↓				Huber, 1981; Huber and Wilhelm, 1988
	Phytophthora infestans (Mont.) de Bary	late blight									↓			Huber and Watson, 1980
	Sclerotium rolfsii Sacc.	Southern blight	↓	↑			↓							Huber, 1981; Huber and Watson, 1974
	Septoria sp.	leaf spot			↓									Huber, 1981
	Verticillium albo-atrum Reinke and Berthold	wilt	↑	↓					↓	↓		↓	↓	Huber and Watson, 1974; Dutta and Bremner, 1981; Huber and Wilhelm, 1988

↑ represents an increase in disease with the addition of the nutrient ; ↓ represents a decrease in disease with the addition of the nutrient

1.4 Management of fungal diseases with macro- and micronutrients

Much research has been done on the effects of nutrients on plant disease (Tables 16-26). However, lack of accurate soil tests, the form of elements used in the fertilizer treatments recorded (especially the use of nitrogenous compounds), soil type, pH, environmental conditions and appropriate statistical analyses causes confusion. Great caution should therefore be exercised when integrating such information into generalised pathogen management strategies. Tables 16-26 give some indication of the volumes of literature available regarding the effect of macro- and micro-nutrients on fungal plant diseases. The problem that faces plant pathologists is to correlate this valuable research into sound, integrated production systems, based on optimizing yields.

However, some successful programmes have been developed for management of plant diseases by the manipulation of macro- and micronutrients.

1.4.1 Management of take-all (*G. graminis* f. sp. *tritici*) of wheat

Few diseases respond as dramatically to soil nutrition as take-all (*G. graminis* f. sp. *tritici*) of wheat (Huber and Dorich, 1988). In fact, the response of cereals infected with take-all to specific nutrients is so pronounced as to provide effective levels of field control, when combined with other management or cultural practices (Glynne, 1953; Huber, 1976, Huber, 1989).

Of the thirteen principal nutrient elements required for plant growth, six (N, P, K, S, Mg and Cl) have been shown to reduce the incidence or severity of take-all, while two (Ca and K) are known to increase disease severity (Huber, 1989). However, the effects of these elements individually or as interactions are greatly influenced by environmental and cultural conditions.

Although various workers have shown that applications of N fertilizers reduce the severity of take-all (Huber *et al.*, 1968; Smiley and Cook, 1973), the form of N appears to be more important than the rate of N application in reducing take-all (Huber *et al.*,

1968). Nitrogen fertilizer treatments enhance plant vigour, resulting in the production of more roots and thereby offsetting the reduced root absorption of water and nutrients from the soil caused by root rot. Increased resistance of wheat to take-all is indicated by reduced infection and smaller lesions with NH_4-N than NO_3-N and is most pronounced when plants have a balanced nutrient supply containing NH_4-N (Engelhard, 1989).

1.4.2 Management of *Fusarium* wilts of vegetables and ornamentals

In soils deficient in P, organic matter or the NH_4 form of N and liming to increase the pH from 6.0 to 7.5, generally results in increased resistance of many crops to *Fusarium* wilt (Jones *et al.*, 1989).

1.4.3 Management of *Verticillium* wilt

The effect of fertility on resistance to *Verticillium* wilt is governed by the interaction of the host, pathogen and environment and is infinitely variable, making it impossible to give specific recommendations. In general, resistance to *Verticillium* wilt is enhanced when the nutrient added is in the deficiency range of availability and when levels of N promote good, but not luxurious growth, are used. NO_3-N appears to increase susceptibility to *Verticillium*, but the effect of NH_4 -N on host response varies with host species (Pennypacker, 1989).

1.4.4 Management of *Aspergillus flavus* in maize and peanuts

In sandy, Ca deficient soil, applications of Ca, together with other production practices, increase yield and quality and decrease damage of peanuts by *Aspergillus flavus* Link and, consequently, aflatoxin contamination (Wilson *et al.*, 1989).

1.5 Influence of nutrients on high and low sugar diseases

The hypothesis that sugar content of tissues influences disease reaction has received considerable attention since it was proposed by Holbert *et al.* (1935) and De Turk *et al.* (1937). While some researchers have concluded that the quantity of soluble carbohydrates in tissues is strongly associated with disease (Horsfall and Dimond, 1957; Lukens, 1970), others (Jain and Pelletier, 1958; Krog *et al.,* 1961; Daly, 1967) reached the opposite conclusion.

However, high and low sugar diseases are frequently referred to in the literature, have been reviewed by Vanderplank (1984) and deserve mention in relation to nutrient amendments to control fungal plant pathogens.

The theory of high and low sugar diseases classifies a plant pathogen according to nutrient status of the plant and organ that it attacks. Pathogens appear to attack plant organs that are high or low in sugars and are respectively referred to as high and low sugar pathogens (Dodd 1980a; 1980b).

The nutrient status of a crop during the different stages of growth from seed germination to seed formation varies in different plant organs; i.e., roots, stems, leaves and seeds. In crop species, the effects of mineral nutrient supply on yield response curves is often a reflection of source limitations imposed by either a deficiency or excessive supply of mineral nutrients during certain critical periods of plant development (Marschner, 1985).

Infection by some pathogens; e.g., rusts and powdery mildews, is favoured by high levels of endogenous sugars (high sugar diseases), whereas infections by other pathogens, e.g., leaf spots and stalk rots are heaviest when levels of sugar are low (Horsfall and Dimond, 1957).

To illustrate the relationship of fertilizers on high and low sugar diseases, maize is used as an example. Modern farmers plant high-yielding maize hybrids and fertilize heavily to obtain high yields and maximise gross margins. However, high potential yields are incompatible with high resistance to disease. Normally, about 20% of the grain weight comes from carbohydrate stored in the stalk. With high yielding hybrids, cobs (referred to as the sinks) set many more kernels, resulting in a greater demand for carbohydrates from photosynthetic areas (the source), the leaves. If the supply of sugar is insufficient to meet the needs of both grain development and maintenance of the vegetative parts of the plant, the grain formation is accompanied by a reduction in carbohydrates from the maize stalk. Stalk cells become depleted and tissues lose their metabolically dependent defence systems and are predisposed to stem rots (Dodd 1980a; 1980b). Similarly, plants with severe infection by leaf blights have a reduced photosynthetic area (source) and consequently a higher incidence of stalk rot, as carbohydrates are drained from the stalks to compensate for the lack of carbohydrates in the leaves in order to meet the demands of the developing kernels (sinks). These observations on the increased incidence of stalk rot with high yielding hybrids are in agreement with the work by Koehler (1960) who showed that maize hybrids known to be the most susceptible to stalk rot were the highest yielding.

On the other hand, if the total demand for carbohydrates is reduced because of a smaller sink, carbohydrates accumulate in the stalk, resulting in more resistance to stalk rot diseases. Hybrids resistant to the disease have a higher sugar content than susceptible hybrids when grown under recommended cultural practices (Mortimer and Ward, 1964). Several investigators (Holbert *et al.*, 1935; DeTurk, 1937; Dodd 1980a) have reported that resistance to stalk rot of corn caused by *S. maydis* or *G. zeae* is associated with high carbohydrate levels in the stalk. This may indicate that the ultimate in stalk rot resistance may be incompatible with the ultimate in grain yields if stalk rot resistance is achieved only by living cells (Dodd, 1980a). A number of high yielding hybrids have been released in recent years which solved this problem by having high stalk strength which avoids lodging even in the presence of stem diseases.

Stress, e.g., adverse environmental conditions, nutrient availability and high plant populations, which reduce photosynthesis, result in a carbohydrate drain from the stalk

and consequently invasion by low sugar pathogens. Carbohydrate levels must be maintained above a critical point in the plant to prevent infection occurring (Dodd, 1980a).

If fertilizer levels directly affect nutrient levels in plants, fertilization, especially with high levels of nitrogenous fertilizers, may help suppress low sugar fungal diseases. Fertilizers high in N and low in K are often associated with stalk rot. However, the role of these elements is not as clear as that of other plant stresses (Dodd, 1980a; 1980b).

1.6 Discussion

Controlling disease severity by altering host nutrition through the application of inorganic soil fertilizers, is an attractive alternative to chemical disease control especially as agricultural chemical prices continue to increase. The effect of nutrients on disease is an important management tool to improve production efficiency and crop quality, because crops are fertilized to promote maximum plant productivity, quality and yield. Although disease management through soil nutrition is probably indirect, its practical application through easily modified agricultural practices, facilitates its implementation. However, it will be most effective when it is integrated with other practices such as planting date, crop rotations, weed and pest control and the use of less susceptible or, where possible, resistant hybrids (Skeen, 1997).

The effect of soil nutrition on each host-pathogen combination must be determined experimentally and evaluated separately. However, in an economic productive system, a holistic view must be made. This further complicates the use of fertilizers to control diseases. The likelihood of accurate general trends is small and few conclusions can be made regarding even the same pathogen on different host plants. Each disease must be considered by itself in relation to the environment in which the host and pathogen are growing, the availability of essential nutrients and the complex of pathogens potentially present. Statements concerning the effects of any one factor on infection are relative and valid only under certain combinations with other factors, which must be specified.

Obvious nutrient deficiencies which limit yield or quality should be corrected and nutrient levels adjusted to avoid or reduce predisposition to disease where possible. It is equally counter-productive to starve the plant into an unproductive state in order to escape disease. Therefore, it is imperative that nutrient status, disease levels and yield are economically assessed. Other measures to control disease should be utilized if yields fall below an economically viable level (Huber and Dorich, 1988).

Generally it is not a simple factor that determines whether disease is controlled by soil nutrition, but the sum of many interacting factors of pathogen, host, environment and time (Huber and Dorich, 1988), the complexities of which have been highlighted in this literature survey. The greatest benefits from soil nutrition have been observed with partially resistant varieties. Here it is clearly seen that proper fertility improves their resistance or opportunity to escape the consequences of serious disease (Huber, 1981).

Statements concerning the effects of one factor on infection are relative and valid only under certain combinations with other factors, which must be specified. When occurrence of disease epidemics is forecast, it is, of course, necessary to consider the effects of interactions of environmental factors. It therefore follows that much of the published information concerning the effects of individual factors can be applied to field conditions only with extreme caution (Huber, 1981).

In the great majority of studies reported here, the addition of micronutrients has decreased the incidence of disease in crop plants. The response is greatest over the deficiency range for the element concerned, although further suppression of disease by supra-optimal rates of micronutrients has been reported in a number of cases. Iron appears to be the exception with either an increase or decrease in disease severity. Micronutrient amendments may reduce disease to an acceptable level where other cultural practices can be used to lower disease incidence still further. Adequate micronutrient nutrition should be viewed as an essential component of any crop protection programme, especially in light of the fact that micronutrients are required in small amounts, have long residual value and are the cheapest agricultural chemicals on the market (Graham and Webb, 1991).

One of the goals of sustainable agriculture is to reduce chemical inputs, such as pesticides and fertilizers, without decreasing product quality or gross margins. The long -term promise of increased economic gains through improved disease management practices offered by manipulation of nutrient amendments, provides incentives to agriculturalists to begin the transition process away from costly fungicide control programmes.

Frequent failure in the literature to report form or application rate and time of fertilizer application, proper soil analyses, base line fertility levels, statistical analysis or environmental conditions makes evaluation of divergent results difficult. Pot trials are equally difficult to assess relative to field conditions.

The financial analysis of fertilizer treatment may indicate that the treatment resulting in the highest yields and lowest disease levels are not always the most economical treatments. Agriculturalists should, therefore, consider the financial implications, especially the added income compared with the added costs of fungicide treatment. The optimal treatment chosen will depend on the individual farmer's risk-aversion preferences and capital availability.

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CHAPTER 2

Development and severity of grey leaf spot of maize grown under different nitrogen and potassium fertilizer regimes

Abstract

Management of soil nutrient levels can reduce the incidence and severity of plant diseases. This study determined the influence of nitrogen (N) and potassium (K) soil amendments on the development and severity of *Cercospora zeae-maydis* Tehon and Daniels, the causal organism of grey leaf spot (GLS) on maize (*Zea mays* L.). The effects of 0, 60 and 120 kg N ha^{-1} and 0, 25, 50 and 150 kg K ha^{-1} on the rate of disease progress depicted as days to 1, 5 and 10% leaf blighting, final disease severity, standardized area under disease progress curve and grain yield. These were investigated at Cedara (29°32'S, 30°17'E), Republic of South Africa, on a maize hybrid that is susceptible to grey leaf spot. The trial was a randomised 3X4X2 design, split for fungicide treatments, and replicated three times. With increased N and K applications, leaf blighting occurred earlier, and both the final percentage leaf blighting and the standardized area under disease progress curve were higher. In the fungicide treated maize, grain yields increased with increasing applications of N and K, as expected. In non-fungicide treated maize, grain yield increased with increasing applications of N, despite increased disease severity. This was in contrast to grain yields from non-fungicide treated maize with increased K application rates, which manifested only small increases in yield. This was probably because grain yield response, which should have occurred at higher K applications, was reduced by increased disease severity. The effect of N, phosphorus and K on GLS was investigated at Ahrens (29°2' S, 30° 4'E). Maize was grown in a 4X4X4 N, P, K factorial, in a randomised complete block design. No fungicides were applied. A single point disease assessment at physiological maturity, showed that final disease severity increased with increasing applications of N and K. Phosphorus had no significant effect on final percentage leaf blighting. These results have implications for small-scale farmers who are encouraged to fertilize for increased grain yields but may not have the resources to apply fungicide sprays to

control fungal diseases.

2.1 Introduction

Grey leaf spot (GLS), caused by *Cercospora zeae-maydis* Tehon and Daniels (1925), has become a significant problem in maize (*Zea mays* L.) production in some regions of the world over the past 25 years. The pathogen can cause grain yield losses of up to 79% in the United States but losses usually range from 0-30% (Hilty *et al.*, 1979; Latterell and Rossi, 1983; Ayers *et al.*, 1984; Stromberg and Donahue, 1986; Lipps and Pratt, 1989; Nutter *et al.*, 1995). Grey leaf spot was first reported in the Republic of South Africa (RSA) in KwaZulu-Natal (KZN) in 1988, and had become epidemic by 1992 (Ward *et al.,* 1993). Ward and Nowell (1997) reported that the disease has spread throughout the maize-growing areas of the Republic of South Africa (RSA), with grain yield reductions as high as 60 %. Gevers *et al.* (1990) forecast that this disease could assume greater importance than other maize diseases in RSA.

Grey leaf spot has also been reported in Cameroon, China, Kenya, Malawi, Mocambique, Nigeria, Swaziland, Tanzania, Uganda, Zaire, Zambia and Zimbabwe (Nowell, 1997; Ward and Nowell, 1997) and is considered to threaten maize production in southern Africa (Nowell, 1997).

Cercospora zeae-maydis does not survive beyond two seasons in infested debris (de Nazereno *et al.*, 1992). Tillage operations aimed at complete burial of debris have been demonstrated as a means of managing the disease (Payne and Waldron, 1983; Huff *et al.*, 1988; White *et al.*, 1996). As GLS is host-specific, rotations with crops such as soyabeans and cereals are an alternative to ploughing (Latterell and Rossi, 1983; Stromberg and Donahue, 1986; Huff *et al.*, 1988). However, very few South African maize farmers practice crop rotation (Farina and Channon, 1988).

Efforts to breed hybrids with improved resistance to GLS have increased dramatically in the 1990s. However, farmers still prefer planting higher yielding hybrids rather than lower yielding hybrids with effective quantitative resistance. This, together with

increasing quantities of infested maize crop residues each year, has necessitated the use of fungicides for continued economic production of maize.

Fertilizer usage is a prime determinant of maize grain yields and profitability, and is an aspect of production that can be manipulated by the farmer (Farina *et al.*, 1980). The beneficial effects of reducing the incidence and severity of plant diseases by manipulation of fertilizers are widely recognized (Trolldenier, 1969; Huber, 1976; Huber, 1981; Graham, 1983; Huber and Dorich, 1988).

Research on the effect of plant nutrition on the development of GLS has been limited and somewhat contradictory. Smith (1989) found increased levels of GLS in response to increased nitrogen (N) levels, whereas potassium (K) and phosphorus (P) had little or no significant effect on GLS development. This may have been due to high residual K and P levels on the trial sites. This underlines the importance of soil testing in research of this nature. In contrast, Carrera and Grybauskas (1992) found increasing levels of N to have no effect on GLS. Other diseases caused by *Cercospora* spp. appear to increase in severity with increased N fertilization but decrease in severity with increased K fertilization (Wang, 1966; Huber, 1981; Huber and Arny, 1985). Wang (1966) found that an increase in Sigatoka disease (caused by *Mycosphaerella musicola* Meredith) of banana (*Musa acuminata* Colla) was favoured by high applications of N. Studies on brown leaf spot (*Cercospora oryzae* Sutton and Pons) of rice (*Oryza sativa* Hochst. ex Steud) showed an increase in disease with increasing N and K rates (Huber, 1981; Groth and Brandon, 1985). Applications of fertilizers increase the incidence of other leaf diseases of maize, e.g., NH_4^+-N increases *Exserohilum turcicum* Leonard and Suggs (*Helminthosporium turcicum Pass.*) (Bogyo, 1955; Gorsline *et al.*, 1963; Karlen *et al.*, 1973; Huber, 1981) and Mg^{2+} increases *E. maydis* Nisikado and Miyake (*Cochliobolus heterostrophus* Drechs.) (Taylor, 1954; Huber, 1981).

Although a wide range of interactions of pathogens and their hosts are influenced by N, it is frequently the form of nitrogen (nitrate or ammonium) available to the host or pathogen that affects susceptibility or resistance rather than the amount of N applied. Reduced disease from altered host resistance generally results from the influence of a

specific form of nitrogen on metabolic pathways. The uptake of NH_4-N relative to NO_3-N has been shown to markedly reduce the incidence of some diseases. However, the use of nitrification inhibitors that increase the uptake of NH_4-N relative to NO_3-N is uneconomical in practice (Huber and Watson, 1974; Huber 1980a and b).

Literature on the effects of soil nutrition on GLS disease incidence in maize is limited. In particular, there is a paucity of information on the effect of soil nutrients on the development of GLS related to grain yield. Efficient fungicide control programmes have been developed for control of GLS in RSA, making it possible to study grain yield losses (Ward *et al.,* 1997). The objective of this study was to determine the effects of N, P and K soil nutrition on the incidence and severity of GLS, related to grain yield of maize with and without fungicide treatments in KZN, RSA.

2.2 Materials and methods

2.2.1 *Cedara trial*

Trial site

The trial was conducted at Cedara Agricultural Development Institute (CADI) (29°32'S, 30°17'E) during 1996/97 and 1997/98 on well-drained, deep sandy-clay loams of the Hutton form and Doveton series (MacVicar, 1991). Temperature and rainfall data were recorded by the weather station at CADI, located less than 1 km from the trial site. The trial site was previously planted to a grass ley, *Eragrostis curvula* (Schrad.) Nees.

Land preparation

Six weeks before planting, dolomitic lime (6.3 t ha $^{-1}$) was applied to reduce acid saturation to < 20% and incorporated into the soil to a depth of 200-250 mm. Before the trial commenced, soil samples were taken at 150 mm intervals to 900 mm (Table 1a).

Land preparation, involving mouldboard ploughing and discing, was carried out in September, 1996 and 1997. The trial was a randomised split plot design with whole plots being a factorial of three levels of N (0, 60 and 120 kg N ha^{-1}) and four levels of K (0, 25, 50 and 150 kg K ha^{-1}) with three replications. Whole plot size was 8 m x 6 m comprising 8 rows, 8 m long, spaced 750 mm apart. The sub-plots were either sprayed or non-sprayed fungicide treatments, i.e., there were 72 experimental units.

The levels of N and K applications ha^{-1} were chosen to cover those used by both small-scale and commercial farmers, as well as levels substantially higher, to test the hypothesis of the trial.

Detailed soil sampling was carried out in both seasons in which the trial was conducted. Twenty-one cores, 0-150 mm deep, were taken from each experimental unit three weeks before and three weeks after planting. A 1 m border of plants at the end and sides of each experimental unit was excluded for sampling purposes. Samples were mixed and air-dried before analysis for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminium (Al), zinc (Zn), acid saturation, and pH by the Cedara Fertilizer Advisory Service (Farina and Channon, 1988). These analyses were made to ensure that only soil K was affected by increased applications of K fertilizer.

Immediately before planting, fertilizers were applied by hand and incorporated by discing to a depth of approximately 100-150 mm. Soil base line fertility levels are shown in Table 1a. All plots in both seasons received 105 kg P ha^{-1} (as double superphosphate; 20% P), 50 kg S ha^{-1} (as calcium sulphate; 18% S) and 30 kg Zn ha^{-1} (as zinc sulphate; 23% Zn) as KwaZulu-Natal soils are deficient in S and Zn. Potassium treatments (as potassium chloride; 50% K) were applied at planting at 0, 25, 50 and 150 kg K ha^{-1}. Nitrogen treatments (as limestone ammonium nitrate; N as 14 % NH_4^+ and 14% NO_3^-) were 0, 60 and 120 kg $N^{-1}ha$. The 60 and 120 $kg^{-1}N$ ha treatments were split with 30 kg N ha^{-1} as a preplant application, and the remainder was applied as a topdressing when plants were 300 mm tall. During the summer months in the RSA, NH_4^+ is converted into NO_3^- within 10-14 days of N application (Miles, personal

communication)[1]. It was therefore assumed that the effect of the nitrate form of N on GLS was investigated.

The maize hybrid, ZS 206, was used because it is high grain-yielding and highly susceptible to GLS. It was hand-planted on 27 November, 1996 and 26 November, 1997. Two seeds per plant station were hand-planted. Approximately 30 days after planting (DAP), plants were hand-thinned to 44,000 plants ha $^{-1}$. A tank-mix of metolachlor (1.86 g a.i. ha $^{-1}$) plus atrazine / metolachlor / terbuthylazine (550 / 663 / 5 50 g a.i. ha $^{-1}$) was applied as a pre-emergent, overall treatment in 300 L water for the control of grasses and broadleaf weeds. Fenvalerate (28 g a.i. ha $^{-1}$) was included in the herbicide tank-mix for the control of cutworm. Carbofuran granules (2.7 kg a.i. ha $^{-1}$) were applied in the planting furrow for the control of soil insect pests.

Fungicide applications

In both seasons, a spraying programme commenced when GLS appeared on the basal 5-leaves: 68 and 69 DAP in 1996/97 and 1997/98, respectively. In both years a pre-mix combination of 188 g carbendazim and 94 g flusilazole ai ha $^{-1}$ was applied (Punch Xtra, Du Pont de Nemoirs and Coy) using a CO_2-pressurized backpack sprayer fitted with a vertically mounted sprayboom having three Whirlrain (WRW2-20°) nozzles, spaced 1 m apart. Full-cover sprays were applied to the centre two rows of each plot. Second and third spray treatments were applied 97 and 121 DAP in 1996/97 and 99 and 120 DAP in 1997/98.

Both active ingredients in the fungicide spray are systemic and curative and therefore eliminate both symptomatic and latent infections.

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[1] Dr N. Miles, Cedara Agricultural Development Institute, Private Bag X9059, Pietermaritzburg 3200 RSA

Table 1a. Cedara soil analyses (0-900 mm) of plots, after liming in 1996

Depth (mm)	Exchangeable cations					Acid Saturation (%)	pH (KCl)	P (mg kg^{-1})	C (g kg^{-1})	N[2] organic carbon (g kg^{-1})	C:N (g kg^{-1})	Particle size (mm)		
	Ca	Mg	K	Extr. Acid.	Total cations							clay <2 μm	silt 2-50 μm	sand 50-2000 μm
	----------		cmol$_c$kg^{-1}		----------							----------(g kg^{-1}) --------		
0-150	5.3	1.5	0.2	0.07	7.0	1	5.0	6	35	2.7	131	390	200	402
150-300	3.7	1	0.2	0.43	5.3	8	4.6	5	32	2.5	128	411	181	413
300-450	2.2	0.7	0	0.55	3.5	16	4.4	2	21	1.7	121	482	150	375
450- 600	1.8	0.7	0	0.28	2.8	10	4.6	1	15	1.2	124	504	122	376
600-750	1.2	0.8	0	0.13	2.2	6	4.7	1	11	1.1	102	503	121	374
750-900	0.8	0.8	0	0.14	1.7	8	4.8	1	9	0.9	101	486	132	392

[2] Organic carbon percentage, estimated by near-infra-red (NIRS) spectroscopy, is given. However, the NIR analyser is not calibrated for subsoils or for topsoils with high total cations or high sample densities. High sample densities were recorded in other soil tests in this paper, with the result that organic carbon percentages could not be calculated.

Disease assessments

Whole-plant standard area diagrams described by Ward *et al.* (1997) were used as a guide to estimate disease severity. Disease severity assessments were made regularly at 10-14 day intervals on eight plants in the centre of the two middle rows of each plot, from the first signs of disease, and continued until the crop was physiologically mature. In 1996/97 plots were assessed for GLS at 72, 91,107,125 and 146 DAP and in 1997/98 at 66, 85, 99, 125 and 146 DAP. In both seasons these data were used to calculate the area under disease progress curve (AUDPC) using a trapezoidal integration program (Berger, 1981). The AUDPC was standardized (SAUDPC) by dividing the AUDPC value by the duration of the epidemic to allow disease comparisons over seasons. Rate of disease progress was determined using Vanderplank's (1963) logistic equation:

$$X_1 = X_0 \cdot e^{rt} \cdot (1 - x)$$

where X_1 is the final disease; X_0 is initial disease; **e** is log e; **r** is the rate of disease progress; **t** is time and **(1 - x)** is the correction factor.

Leaf sampling

Leaves were sampled for chemical analysis. The leaf opposite and below the ear of each plant was collected in the centre two rows of each fungicide and non-fungicide treated plot at 50% anthesis. A 1 m border of plants was excluded from both ends of each row for sampling purposes. Leaf samples were oven-dried overnight at 75°C, milled to pass through a 1 mm screen and then analyzed. Nitrogen was analyzed by near infrared spectroscopy, and after dry-ashing, P was measured colorimetrically and K, calcium (Ca), magnesium (Mg), sodium (Na), Zn, copper (Cu) and manganese (Mn) by atomic absorption.

Harvesting

Maize was hand-harvested from 6 m of the centre two rows of each plot on 18 June, 1997 and 19 June, 1998. The ears of the harvested rows were weighed in the field. Sub-samples of five or six ears were weighed and shelled in the laboratory and the shelling percentage determined to calculate the shelled grain mass. Grain yields were expressed in tonnes ha^{-1}, adjusted to 12.5% grain moisture content.

Statistical analyses

Statistical analyses of trial data were conducted using analysis of variance (ANOVA) and mean separations were based on the LSD at the 5% level of probability using Genstat 5.2 (Anonymous, 1987). Linear and quadratic effects of N and K and their interaction with spray treatments were investigated in the ANOVA.

Disease severity data were transformed to fit the logisitic model described by Vanderplank (1963) and used to estimate the number of days between planting and 1% leaf blighting.

2.2.2 Ahrens trial [3]

Soil nutritional effects on the severity of GLS were monitored in 1995/96 in a field trial at Ahrens near Greytown (29°04' S, 30° 34'E) RSA, under natural rainfall in the 1995/96 maize cropping season. Weather data were collected from a weather station in Greytown, about 4 km from the trial site. An analysis of the soil profile is shown in Table 1b.

Trial site

The trial site was comprised of Balmoral clay (MacVicar, 1991), and was planted to maize for the previous 26 years. This trial was a single replicate with four levels each of N, P and K. It consisted of four blocks of 16 units with the NPK interaction partially confounded with blocks, i.e., there were 64 experimental units. The remaining degrees of freedom for the NPK interaction were used for residual. Each plot consisted of 6 rows, 12 m long, spaced 750 mm apart. The high grain-yielding cultivar, PAN 6242, moderately susceptible to GLS, was planted on 5 November, 1995. Two seeds per plant station were hand-planted. Approximately 30 DAP, plants were hand - thinned to 40,000 plants ha $^{-1}$. Fertilizer was applied at 0, 60, 120 and 180 kg N ha^{-1} (as limestone ammonium nitrate; 28%N), 0, 30, 60 and 120 kg P ha^{-1} (as double superphosphate; 19.6%P), and 0, 50, 100 and 150 kg K ha^{-1} (as KCl; 50% K). (Soil base line fertility levels are shown in Table 1b). Weed and pest control practices for the area were followed as described for the Cedara trial.

Disease assessments, leaf, soil and harvesting procedures

An assessment of GLS was made at physiological maturity (146 DAP). Leaf, soil and harvesting procedures were the same as those described for the Cedara trial except that 10 m of the centre four rows of each plot were used for leaf analyses and grain yield.

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[3] Trial conducted by Dr M.P.W. Farina, Agricultural Research Council, Grain Crops Research Institute, Private Bag X9059, Pietermaritzburg 3200

Statistical analyses

Statistical analysis of trial data were conducted using analysis of variance (ANOVA). Mean separations were based on the Fisher's LSD test for means separation at the 5% level of probability using Genstat 5.2 (Anonymous, 1987). As the trial was a single replicate design, the N : P : K interaction is used as error or residual.

Table 1b. Ahrens soil analyses (0 - 900 mm) of plots, after liming in 1995

Depth (mm)	Exchangeable cations					Acid Saturation (%)	pH (KCl)	P (mg kg^{-1})	C (g kg^{-1})	Particle size (mm)		
	Ca	Mg	K	Extr. Acid.	Total cations					clay <2 μm	silt 2-50 μm	sand 50-2000 μm
	----------		$cmol_c kg^{-1}$		----------					----------($g\ kg^{-1}$) ---------		
0-150	5.05	2.10	0.07	0.45	7.67	6	4.37	5.0	39	560	158	282
150-300	4.87	2.10	0.07	0.44	7.47	6	4.41	3.3	nd	630	100	270
300-450	2.87	1.30	0.06	1.24	5.46	23	4.24	1.6	nd	758	105	137
450- 600	2.18	0.78	0.05	1.56	4.58	34	4.20	0.6	nd	768	101	131
600-750	1.48	0.53	0.04	1.61	3.66	45	4.18	nd	nd	780	90	130
750-900	1.65	0.65	0.06	1.24	3.60	34	4.35	nd	nd	nd	nd	nd

nd = not detected

2.3 Results

2.3.1 *Cedara trial*

Climatic Data

Rainfall from October to April of 1996/97 and 1997/98 was 811 and 702 mm, respectively. Mean maximum temperatures over these months ranged from 22.4-26.0°C and from 20.7-25.9°C in 1996/97 and 1997/98, respectively. Mean minimum temperatures ranged from 11.9-15.3°C and from 10.4-16.2°C in 1996/97 and 1997/98, respectively. Heat units ranged from 162.0-319.3 and from 204.0-319.3 in 1996/97 and 1997/98, respectively (Table 2). Heavy rainfall in December, 1996 and January, 1997 impacted on the trial. All environmental factors were conducive for good grain yields. Both seasons were characterized by above average rainfall, well-distributed throughout the growing season. Mists were abundant in both seasons, especially during grain fill in January and February, favouring GLS development.

Table 2. Rainfall, temperature and heat unit data for Cedara Agricultural Development Institute for the maize-growing seasons of 1996/97 and 1997/98

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	TOTAL
Rainfall (mm)								
1996/97	92	82	125 [1]	214 [2]	63	103	132	811
1997/98	91	117	71	123	165	95	40	702
Monthly mean (50 years)	84	110	128	134	124	113	51	744
Mean max. temp. (°C)								
1996/97	23.1	23.9	26.0	24.8	25.0	23.5	22.4	
1997/98	20.7	21.5	24.8	25.2	25.9	24.5	23.1	
Monthly mean (50 years)	22.6	23.5	24.7	25.0	25.1	24.3	22.7	
Mean min. temp. (°C)								
1996/97	12.4	12.9	14.5	15.3	14.9	14.2	11.9	
1997/98	11.8	12.2	14.1	15.2	16.2	14.2	10.4	
Monthly mean (50 years)	10.7	12.3	13.7	14.8	14.8	13.6	10.6	
Heat units [3]								
1996/97	204.6	249.0	319.3	310.0	319.0	272.8	162.02	1836.7
1997/98	217.0	204.0	291.4	319.3	310.8	291.4	258.0	1891.9

[1] and [2] - very heavy rainfall with frequent thunderstorms that impacted on the trial in 1996/97

[3] Heat units = $\frac{Tx + Tn}{2}$ - base temperature of maize (10°C)

where Tx = mean daily maximum temperature for the month and Tn = mean daily minimum temperature for the month

Soil Test Data

Analyses of soil samples taken three weeks after fertilizing, confirmed that soil K levels increased in response to increasing K fertilizer application in 1996/97 and 1997/98 (Tables 3a and 3b).

Nitrogen and K fertilization did not significantly affect P, Ca, Mg, Al, Zn, pH and acid saturation (N. Miles, personal communication) and, for the purposes of this thesis, have not been included.

Table 3a. ANOVA table of soil potassium levels ($cmol_c\ kg^{-1}$) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	0.009	0.009	2.770	0.390	2.22	0.680
K	3	0.263	0.937	82.170	39.170	<0.001 ***	<0.001 ***
N.K	6	0.003	0.010	1.250	0.420	0.319	0.856
Residual 22							
Rep. N.K sprayed stratum							
Sprayed	1	0.000	0.004	0.020	0.340	0.887	0.563
N sprayed	2	0.002	0.007	0.660	0.600	0.526	0.556
K sprayed	3	0.000	0.002	0.130	0.200	0.939	0.897
N.K sprayed	6	0.003	0.014	0.890	1.200	0.519	0.338
Residual 24							
Total 71							

CV% 1996/97 23.4 %; 1997/98 = 29.4 %

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 3b. Table of means of soil potassium levels ($cmol_c\ kg^{-1}$) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
		0.263	0.235	0.226	0.391	0.363	0.353
$LSD_{(0.05)}$		NS			NS		

MAIN EFFECT - POTASSIUM		1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
		0.138	0.161	0.265	0.403	0.180	0.241	0.365	0.691
$LSD_{(0.05)}$		0.039				0.1069			

INTERACTION EFFECTS - NITROGEN : POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
	N0	0.142	0.173	0.282	0.457	0.174	0.248	0.438	0.706
	N60	0.131	0.154	0.272	0.386	0.197	0.233	0.365	0.656
	N120	0.142	0.156	0.240	0.367	0.169	0.242	0.291	0.712
	$LSD_{(0.05)}$	NS				NS			

All table figures refer to soil potassium levels ($cmol_c\ kg^{-1}$)

Leaf Analyses

Leaf analyses confirmed that leaf N and K levels increased with increased N (Tables 4a and 4b) and K fertilizer applications (Tables 5a and 5b) in both fungicide treated and non-fungicide treated plots. However, this was not always significant. There was no N : K interaction or differences in leaf N and K levels between fungicide treated and non-fungicide treated maize in either year of the trial. Other leaf nutrient levels were as expected for increased N and K fertilizer applications and have not been included for the purposes of this paper (Miles, personal communication).

Table 4a. ANOVA table of leaf nitrogen levels (%) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	1.775	6.7026	16.760	25.190	<0.001 ***	<0.001 ***
K	3	0.149	0.062	2.330	0.460	0.102	0.713
N.K	6	0.047	0.581	0.740	2.190	0.622	0.005
Residual 22							
Rep. N.K sprayed stratum							
Sprayed	1	0.027	0.010	0.260	0.040	0.617	0.489
N sprayed Linear ($P \leq 0.05$)	2	0.061	0.970	0.570	3.650	0.571	0.041 *
K sprayed	3	0.119	0.065	1.130	0.250	1.359	0.864
N.K sprayed	6	0.055	0.347	0.520	1.300	0.791	0.293
Residual 24 Total 71							

CV% 1996/97 = 9.9 %; 1997/98 = 16.3 %

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 4b. Table of means of leaf nitrogen content (%) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
Fungicide treated maize		2.66	2.94	3.13	2.81	3.27	3.44
Non-fungicide treated maize		2.59	3.07	3.18	2.34	3.33	3.77
$LSD_{(0.05)}$		NS			0.435 all comparisons		

MAIN EFFECT - POTASSIUM		1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize		3.06	3.01	2.71	2.84	3.14	3.28	3.16	3.10
Non-fungicide treated maize		3.02	2.86	2.92	2.98	3.14	3.19	3.03	3.24
$LSD_{(0.05)}$		NS				NS			
INTERACTION EFFECTS - NITROGEN : POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	3.00	2.83	2.28	2.51	3.03	3.47	2.34	2.38
	N60	2.95	3.01	2.82	2.97	3.08	2.94	3.66	3.93
	N120	3.22	3.20	3.04	3.04	3.31	3.45	3.48	3.52
Non- fungicide treated maize	N0	2.69	2.41	2.48	2.79	2.69	2.28	1.74	2.67
	N60	3.18	3.02	3.09	3.00	3.25	3.37	3.36	3.36
	N120	3.19	3.17	3.12	3.17	3.49	3.91	3.99	3.68
	$LSD_{(0.05)}$	NS				NS			

Table 5a. ANOVA table of leaf potassium content (%) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

STRATUM	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	6.154	0.192	5.680	4.050	0.010 *	0.03 *
K	3	1.805	5.233	1.670	110.360	0.203	<0.001 ***
N.K	6	1.305	0.0384	1.200	0.810	0.341	0.574
Residual 22							
Rep. N.K sprayed stratum							
Sprayed	1	1.138	0.0184	1.680	0.40	0.207	0.535
N sprayed	2	0.700	0.0853	1.030	1.840	0.371	0.181
K sprayed Quadratic (($P \leq 0.05$)	3	1.984	0.1490	2.930	3.210	0.054	0.041 *
N.K sprayed	6	1.060	0.0344	1.570	0.740	0.200	0.621
Residual 24 Total 71							

CV% 1996/97 =49.9 %; 1997/98 = 17.4 %

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 5b. Table of means of leaf potassium (%) content as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
Fungicide treated maize		1.85	1.55	1.17	1.32	1.3	1.14
Non-fungicide treated maize		2.35	1.94	1.03	1.35	1.13	1.19
$LSD_{(0.05)}$		NS			NS		

MAIN EFFECT - POTASSIUM		1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize		1.31	1.30	1.52	1.97	0.54	1.03	1.48	1.97
Non-fungicide treated maize		2.50	1.13	1.77	1.72	0.76	0.99	1.29	1.85
$LSD_{(0.05)}$		NS				0.2112 all comparisons; 0.2096 same K levels only			
INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	1.82	2.25	1.48	1.86	0.62	1.19	1.50	1.99
	N60	1.62	0.82	1.67	2.09	0.58	1.06	1.53	2.02
	N120	0.50	0.83	1.39	1.96	0.41	0.84	1.42	1.89
Non- fungicide treated maize	N0	3.95	0.98	2.53	1.95	0.69	1.21	1.51	2.00
	N60	2.82	1.47	1.43	2.05	0.70	0.93	1.19	1.70
	N120	0.73	0.89	1.36	1.15	0.90	0.83	1.16	1.87
	$LSD_{(0.05)}$	NS				NS			

All table figures refer to leaf potassium (%) levels

Earliness of leaf blighting

Grey leaf spot appeared earlier with increased applications of N and K at the 1, 5 and 10% level of leaf blighting in the non-fungicide treated maize in both years of the trial (Table 6a , 6b and 6c) (Fig. 1-6). Fungicide treated maize was not analysed for DAP to 1, 5 and 10% leaf blighting because final percentage leaf blighting was <10%, resulting in CV's too high for valid assessments.

Table 6a. ANOVA table of earliness (days after planting) of leaf blighting (1, 5 and 10%) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

	Degree of freedom	Mean square		F Value		P	
1% LEAF BLIGHTING	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
Nitrogen	2	347.58	925.03	12.68	19.74	<0.001 ***	<0.001 ***
Potassium	3	238.11	348.19	8.68	7.43	<0.001 ***	<0.001 **
Nitrogen : Potassium	6	8.36	14.99	0.30	0.32	0.928	0.920
5% LEAF BLIGHTING							
Nitrogen	2	218.69	1179.19	15.73	25.94	<0.001 ***	<0.001 ***
Potassium	3	208.69	245.29	15.02	5.39	<0.001 ***	0.006 **
Nitrogen : Potassium	6	5.03	49.79	0.36	1.10	0.895	0.396
10% LEAF BLIGHTING							
Nitrogen	2	164.58	1253.53	16.65	18.72	<0.001 ***	<0.001 ***
Potassium	3	198.99	295.59	20.13	4.41	<0.001 ***	0.014 **
Nitrogen : Potassium	6	5.77	94.68	0.58	1.41	0.740	0.254

CV%

1996/97 = 7.0 (1% leaf blighting); 4.1 (5% leaf blighting); 3.2 (10 % leaf blighting)

1997/98 = 10.5 (1% leaf blighting); 7.5 (5% leaf blighting); 8.2 (10 % leaf blighting)

NS = non-significant (P= > 0.05) ; * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 6b. Table of means of earliness (days after planting) of leaf blighting (1, 5 and 10%) in non-fungicide treated maize as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN Nitrogen (N) applied (kg ha $^{-1}$)	**1996/97**			**1997/98**		
% leaf blighting	**N0**	**N60**	**N120**	**N0**	**N60**	**N120**
1%	81	72	71	75	61	59
LSD $_{(0.05)}$	4.43			5.79		
5%	97	90	89	101	86	83
LSD $_{(0.05)}$	3.16			5.70		
10%	104	98	97	112	96	93
LSD $_{(0.05)}$	2.66			6.90		

MAIN EFFECTS - POTASSIUM Potassium (K) applied (kg ha^{-1})	**1996/97**				**1997/98**			
% leaf blighting	**K0**	**K25**	**K50**	**K150**	**K0**	**K25**	**K50**	**K150**
1%	81	76	73	69	73	66	59	61
LSD $_{(0.05)}$	5.12				6.70			
5%	97	95	91	86	96	91	90	83
LSD $_{(0.05)}$	3.64				6.60			
10%	104	103	99	93	105	102	102	92
LSD $_{(0.05)}$	3.07				8.00			

All table figures refer to days after planting (DAP)

Table 6c. Table of means of earliness (days after planting) of leaf blighting (1, 5 and 10%) in non-fungicide treated maize as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
% leaf blighting	Nitrogen (N) applied (kg ha^{-1})	K0	K25	K50	K150	K0	K25	K50	K150
1%	N0	87	81	82	73	83	77	69	72
	N60	79	74	69	67	67	64	58	56
	N120	77	72	69	66	70	58	52	56
5%	N0	101	99	98	90	104	102	108	91
	N60	96	92	88	85	91	88	83	80
	N120	94	92	87	83	91	84	78	78
10%	N0	107	107	105	97	114	112	123	99
	N60	103	100	97	93	102	98	94	88
	N120	102	100	95	90	100	96	89	87
$LSD_{(0.05)}$ for 1, 5 and 10%		NS				NS			

All table figures refer to days after planting (DAP)

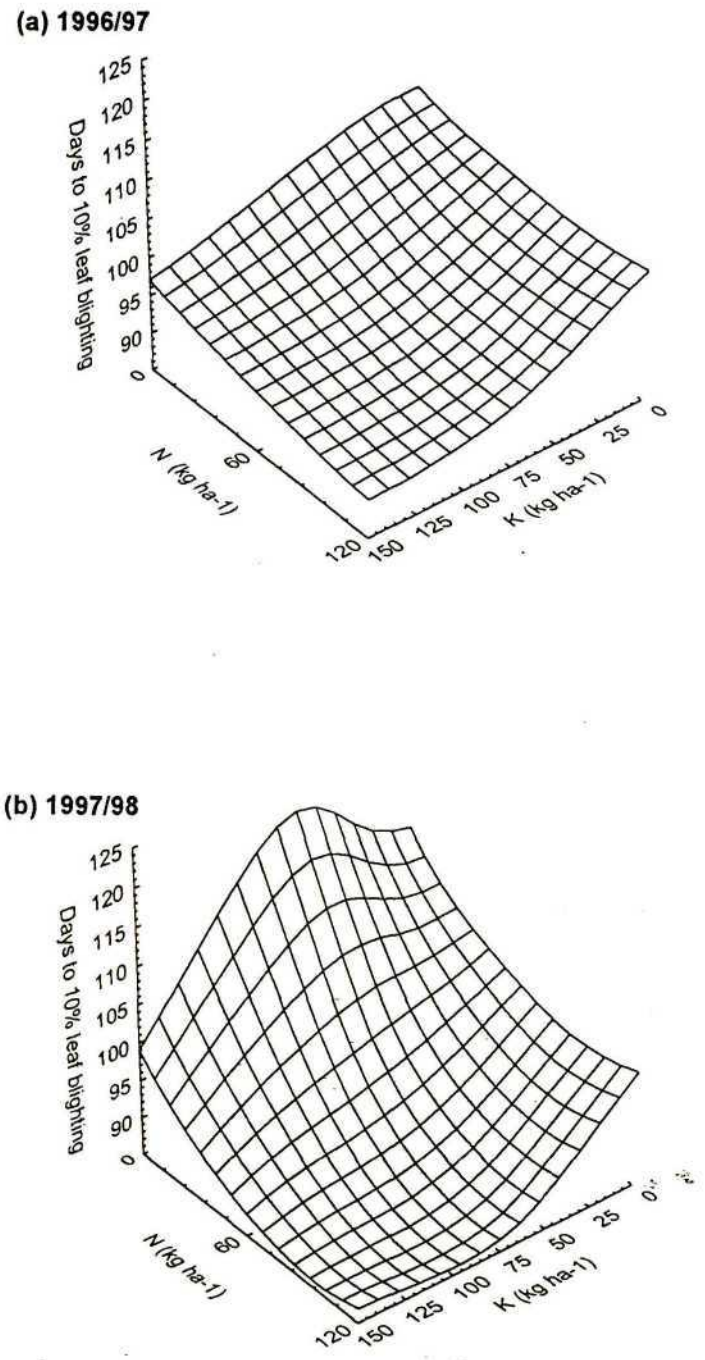


Fig. 1. Effect of nitrogen and potassium (kg ha^{-1}) on days to 10% leaf blighting in non-fungicide treated maize at Cedara (a. 1996/97; b. 1997/98)

Final percentage leaf blighting

In 1996/97, increased N and K applications had a significant increase on final percentage leaf blighting 146 DAP in non-fungicide treated maize. In 1997/98, increased levels of N and K significantly increased final percentage leaf blighting in both fungicide treated and non-fungicide treated maize (Table 7a and 7b; Fig. 2a and b). There was an N : K interaction in the fungicide treated plots in 1997/98. In 1996/97 and 1997/98, final percentage leaf blighting was higher in non-fungicide treated compared to fungicide treated maize (83% and 79%, respectively).

Table 7a. ANOVA table of final percentage leaf blighting (146 days after planting) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	230.460	442.014	7.770	29.560	0.003 **	<0.001 ****
K	3	402.380	634.115	13.560	42.400	<0.001 ***	<0.001 ****
N.K	6	31.520	10.417	1.060	0.700	0.414	0.655
Residual 22							
Rep. N.K sprayed stratum							
Sprayed Linear (P ≤ 0.05)	1	802.000	879.250	3072.890	1.220	<0.001 ***	<0.001 ***
N sprayed Linear (P ≤ 0.05)	2	144.070	121.181	5.480	17.670	0.011 **	<0.001 ***
K sprayed Linear (P ≤ 0.05)	3	355.060	162.587	13.500	23.710	<0.001 ***	<0.001 ***
N.K sprayed Linear (P ≤ 0.05)	6	33.100	17.361	1.260	2.530	0.313	0.048 *
Residual 24							
Total 71							

CV% 1996/97 =13.2%; 1997/98 = 6.2%

NS = non-significant (P > 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 7b. Table of means of final percentage leaf blighting (146 days after planting) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
Fungicide treated maize		4.67	5.46	5.96	5.62	8.54	9.58
Non-fungicide treated maize		66.25	73.75	77.08	68.75	78.75	81.04
$LSD_{(0.05)}$		4.47 all comparisons; 4.32 same N levels only			2.79 all comparisons; 2.21 same N levels only		

MAIN EFFECT - POTASSIUM		1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize		4.89	5.39	5.39	5.78	4.72	6.39	8.89	11.67
Non-fungicide treated maize		65.56	64.44	75.56	83.89	65.56	74.72	77.22	87.22
$LSD_{(0.05)}$		5.16 all comparisons; 6.76 same K levels only				3.22 all comparisons; 2.55 same K levels only			
INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	5.33	5.33	3.67	4.33	3.33	5.00	5.83	8.33
	N60	4.67	5.83	5.33	6.00	5.00	5.00	10.00	14.11
	N120	4.67	5.00	7.17	7.00	5.83	9.17	10.83	12.5
Non- fungicide treated maize	N0	60.00	53.33	71.67	80.00	60.00	66.67	66.67	81.67
	N60	65.00	73.33	75.00	81.67	66.67	80.00	80.00	88.33
	N120	71.67	66.67	80.00	90.00	70.00	77.50	85.00	91.67
	$LSD_{(0.05)}$	NS				5.58 all comparisons; 4.41 same N.K. level only			

All table figures refer to final percentage leaf blighting (146 DAP)

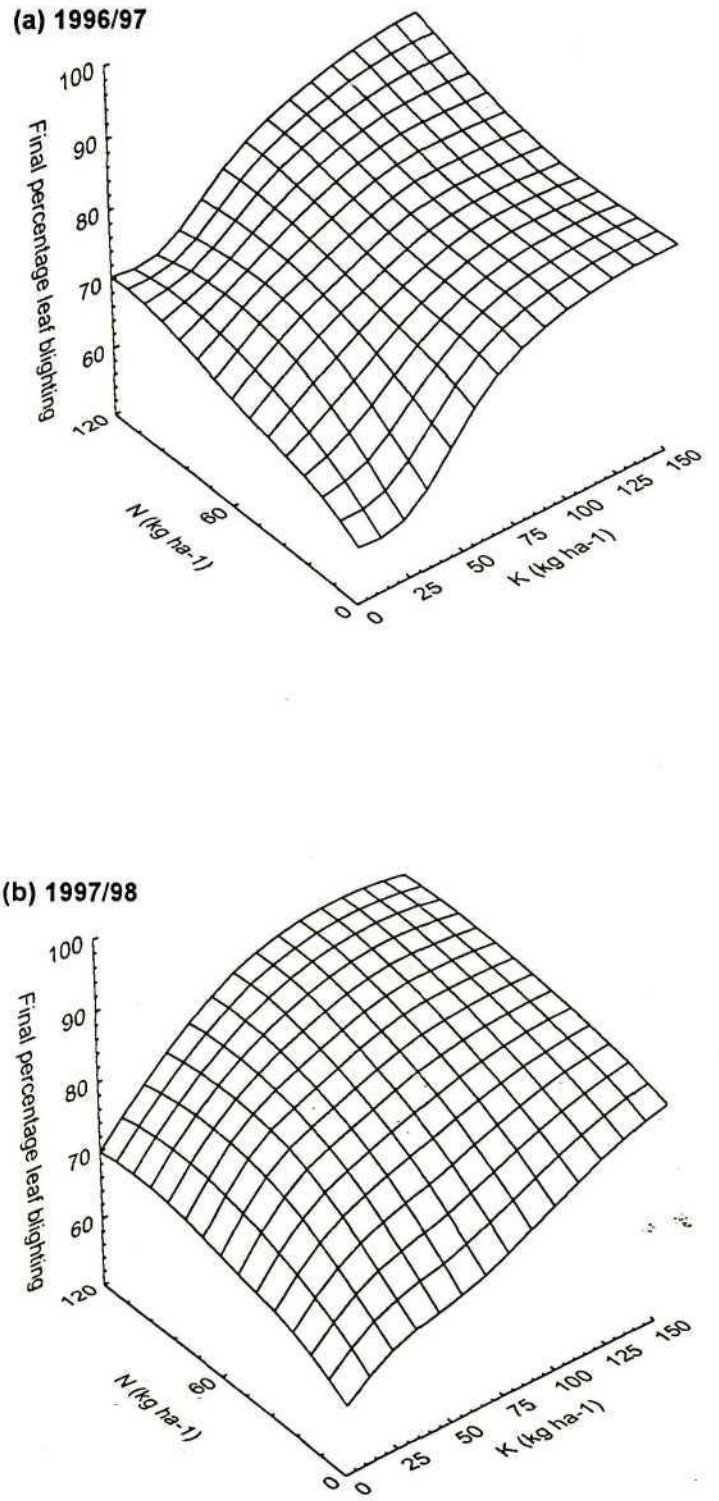


Fig. 2. Effect of nitrogen and potassium (kg ha^{-1}) on final percentage leaf blighting in non-fungicide treated maize at Cedara (a. 1996/97; b. 1997/98)

Rate of disease development

The rate of disease development was not always significant or consistent over the trial period (Tables 8a and 8b). There was no N : K interaction, except in the fungicide treated maize in 1997/98 . In both years of the trial the rate of disease development was faster in the non-fungicide than the fungicide treated maize.

Table 8a. ANOVA table of rate of disease development as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	0.002	0.000	5.820	0.730	0.009 **	0.493
K	3	0.001	0.000	4.930	2.650	0.009 **	0.074
N.K	6	0.000	0.000	0.460	2.400	0.829	0.062
Residual 22							
Rep. N.K sprayed stratum							
Sprayed Linear (P ≤ 0.05)	1	0.059	0.022	1092.280	199.640	<0.001 ***	<0.001 ***
N sprayed Linear (P ≤ 0.05)	2	0.000	0.000	0.030	3.540	0.969	0.045 *
K sprayed Linear (P ≤ 0.05)	3	0.003	0.000	5.280	0.430	0.006 **	0.736
N.K sprayed Linear (P ≤ 0.05)	6	0.000	0.001	0.700	4.920	0.650	0.002 **
Residual 24							
Total 71							

CV% 1996/97 = 10.4%; 1997/98 = 19.3 %

NS = non-significant (P > 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 8b. Table of means of rate of disease development (r) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98) (r = infection rate X 100 , calculated by regressing the logistic transformation on time)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
Fungicide treated maize		5.2	3.7	3.8	3.2	4.4	3.4
Non-fungicide treated maize		10.80	9.5	9.5	7.3	7	7.2
LSD $_{(0.05)}$		NS			0.0094 all comparisons; same N levels only		

MAIN EFFECT - POTASSIUM	1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})	K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	5.8	4.4	3.7	3.1	4.1	3.4	3.3	3.8
Non-fungicide treated maize	10.8	9.4	9.7	9.8	7.4	6.8	6.5	7.8
LSD $_{(0.05)}$	0.012 all comparisons; 0.007 same K levels only				NS			

INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	7.1	5.4	4.6	3.5	4.3	3.6	3.5	1.5
	N60	4.9	3.9	3.2	2.9	3.6	3.3	3.2	7.2
	N120	5.2	3.7	3.2	3	4.4	3.3	3.1	2.8
Non- fungicide treated maize	N0	12.4	9.7	10.9	10.2	7.7	7	6.1	8.5
	N60	10.1	9.7	8.9	9.2	6.8	7.1	6.5	7.2
	N120	10	8.9	9.4	9.9	7.8	6.4	6.9	7.6
	LSD $_{(0.05)}$	NS				0.0188 all comparisons; 0.0177 same N.K levels only			

Standardised area under disease progress curve (SAUDPC)

The SAUDPC increased with increasing applications of N and K in the fungicide treated and non-fungicide treated maize in both years of the trial, with the exception of the N treated plots in 1996/97 (Table 9a and 9b) (Fig.3a and b). The synergistic effect of the N : K interaction in both fungicide treated and non-fungicide treated maize resulted in even higher SAUDPC levels in 1997/98. The SAUDPC was significantly higher in the non-fungicide compared to the fungicide treated maize in both years of the trial.

Table 9a. ANOVA table of standardized area under disease progress curve (SAUDPC) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	297.050	327.400	6.780	145.610	0.002 **	<0.001 ***
K	3	357.050	204.920	12.860	91.140	0.004 **	<0.001 ***
N.K	6	31.7040	15.596	2.260	6.940	2.41	<0.001 ***
Residual 22							
Rep. N.K sprayed stratum							
Sprayed Linear ($P \leq 0.05$)	1	7870.710	8908.590	822.280	3340.790	<0.001 ***	<0.001 ***
N sprayed Linear ($P \leq 0.05$)	2	757.040	209.298	2.880	78.490	0.076	<0.001 ***
K sprayed Linear ($P \leq 0.05$)	3	696.050	133.465	10.910	50.050	<0.001 ***	<0.001 ***
N.K sprayed Linear ($P \leq 0.05$)	6	23.201	14.162	0.680	5.310	0.66	<0.001 ***
Residual 24 Total 71							

CV% 1996/97 =22.3%; 1997/98 =11.4 %

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 9b. Table of means of standardized area under disease progress curve (SAUDPC) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN		1996/97			1997/98		
Nitrogen (N) applied (kg ha $^{-1}$)		N0	N60	N120	N0	N60	N120
Fungicide treated maize		2.32	3.07	3.25	2.34	3.37	3.79
Non-fungicide treated maize		18.17	21.07	22.73	17.88	27.88	30.47
$LSD_{(0.05)}$		NS			1.324 all comparisons; 1.376 same N levels only		

MAIN EFFECT - POTASSIUM	1996/97				1997/98			
Potassium (K) applied (kg ha^{-1})	K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	2.53	2.93	2.91	3.14	2.47	2.87	3.24	4.07
Non-fungicide treated maize	18.09	16.81	21.33	26.38	21.47	21.23	24.71	34.23
$LSD_{(0.05)}$	1.791 all comparisons; 1.783 same K levels only				1.529 all comparisons; 1.589 same K levels only			

INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	2.18	2.81	1.89	2.37	1.79	2.38	1.97	3.22
	N60	2.83	3.36	2.91	3.2	2.84	2.73	3.59	4.29
	N120	2.58	2.61	3.94	3.86	2.78	3.5	4.17	4.7
Non- fungicide treated maize	N0	18.26	13.34	16.9	24.17	15.06	13.46	12.91	30.09
	N60	17.85	18.93	21.92	25.57	21.52	24.89	30.49	34.63
	N120	18.17	18.16	25.18	29.39	27.82	25.33	30.74	37.98
	$LSD_{(0.05)}$	NS				2.648 all comparisons; 2.752 same N.K. level only			

All table figures refer to SAUDPC levels

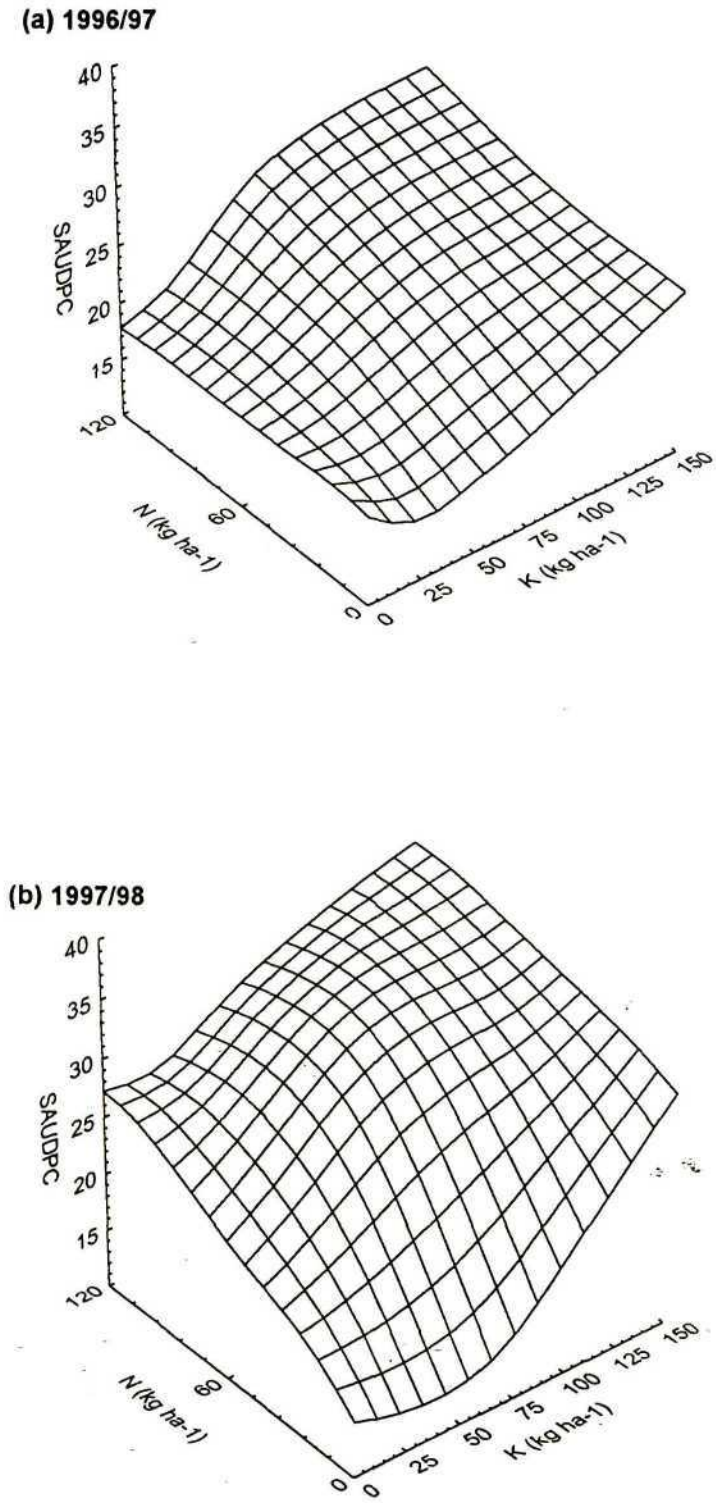


Fig. 3. Effect of nitrogen and potassium (kg ha^{-1}) on standardized area under disease progress curve (SAUDPC) on non-fungicide treated maize at Cedara (a. 1996/97; b. 1997/98)

Grain yield

Grain yields increased with increasing applications of N, in the fungicide treated maize in 1997/98. The lack of grain yield response to N in the fungicide treated maize in 1996/97, may have been due to the high rainfall in December, 1996 and January, 1997 (Table 2). Despite increased leaf blighting in the non-fungicide treated maize, grain yields increased with increasing applications of N in 1997/98. In the K treated plots, grain yields increased with increasing applications of K in fungicide treated but not in non-fungicide treated maize, in both years of the trial. There was no N : K interaction but a significantly higher grain yield in the fungicide treated compared to non-fungicide treated maize (Tables 10a and 10b) and (Fig. 4a, b, c and d). In both seasons of the trial, highest grain yields in fungicide treated maize were obtained from 120 kg N ha^{-1} and 150 kg K ha^{-1}, as expected. In non - fungicide treated maize, highest grain yields were achieved using 60 kg N ha^{-1} and 50 kg K ha^{-1}, as increased leaf blighting at 120 kg N ha^{-1} and 150 kg K ha^{-1} negated increased grain yields. In fungicide treated maize, increased levels of N with zero K applications, resulted in decreased grain yields as K became a limiting factor.

Table 10a. ANOVA table of maize grain yields (tonnes ha^{-1}) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

Stratum	Degree of freedom	Mean square		F value		Probability	
Rep. N.K. stratum	1996/97 and 1997/98	1996/97	1997/98	1996/97	1997/98	1996/97	1997/98
N	2	2.227	1.340	0.8	8.75	0.461	0.002 **
K	3	1.088	1.038	3.93	6.78	0.022 **	0.002 **
N.K	6	1.847	3.425	0.67	2.24	0.677	0.082
Residual 22							
Rep. N.K sprayed stratum							
Sprayed	1	9.667	1.756	90.35	139.35	<0.001 ***	<0.001 ***
N sprayed	2	4.909	3.819	0.26	3.03	0.774	0.003 **
K sprayed	3	1.047	5.699	5.54	4.52	0.006 **	0.013 *
N.K sprayed	6	2.368	2.961	1.25	2.35	0.320	0.068
Residual 21 (3)							

CV% 1996/97 = 16.8%; 1997/98 = 14.5 %
NS = non-significant (P > 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 10b. Table of means of maize grain yields (tonnes ha $^{-1}$) as affected by nitrogen and potassium fertilizer applications at Cedara (1996/97 and 1997/98)

MAIN EFFECT - NITROGEN	1996/97			1997/98		
	N0	N60	N120	N0	N60	N120
Fungicide treated maize	7.61	7.53	7.91	8.80	8.93	10.15
Non-fungicide treated maize	4.61	5.70	5.81	5.09	6.72	6.71
$LSD_{(0.05)}$	NS			1.01 all comparisons; 0.95 same N levels only		

MAIN EFFECT - POTASSIUM	1996/97				1997/98			
	K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	6.79	7.01	7.74	9.18	7.56	9.18	10.07	10.34
Non-fungicide treated maize	5.38	4.72	5.43	6.03	5.99	5.79	6.13	6.78
$LSD_{(0.05)}$	1.35 all comparisons; 1.15 same K levels only				1.16 all comparisons; 1.10 same K levels only			

INTERACTION EFFECTS - NITROGEN: POTASSIUM		1996/97				1997/98			
		Potassium (K) applied (kg ha^{-1})							
Nitrogen (N) applied (kg ha^{-1})		K0	K25	K50	K150	K0	K25	K50	K150
Fungicide treated maize	N0	7.58	6.42	6.62	8.85	8.18	8.87	8.91	9.25
	N60	6.64	6.82	7.74	8.9	7.97	8.73	9.81	9.23
	N120	6.15	7.78	8.86	9.47	6.52	9.95	11.74	12.41
Non- fungicide treated maize	N0	4.75	3.87	4.04	5.12	5.03	4.72	3.96	6.64
	N60	4.53	4.48	6.4	6.26	6.17	6.63	7.55	6.52
	N120	4.84	4.83	4.94	5.85	6.78	6.01	6.87	7.18
	$LSD_{(0.05)}$	NS				2.01 all comparisons; 1.91 same N.K levels only			

All table figures refer to grain yield (tonnes ha $^{-1}$)

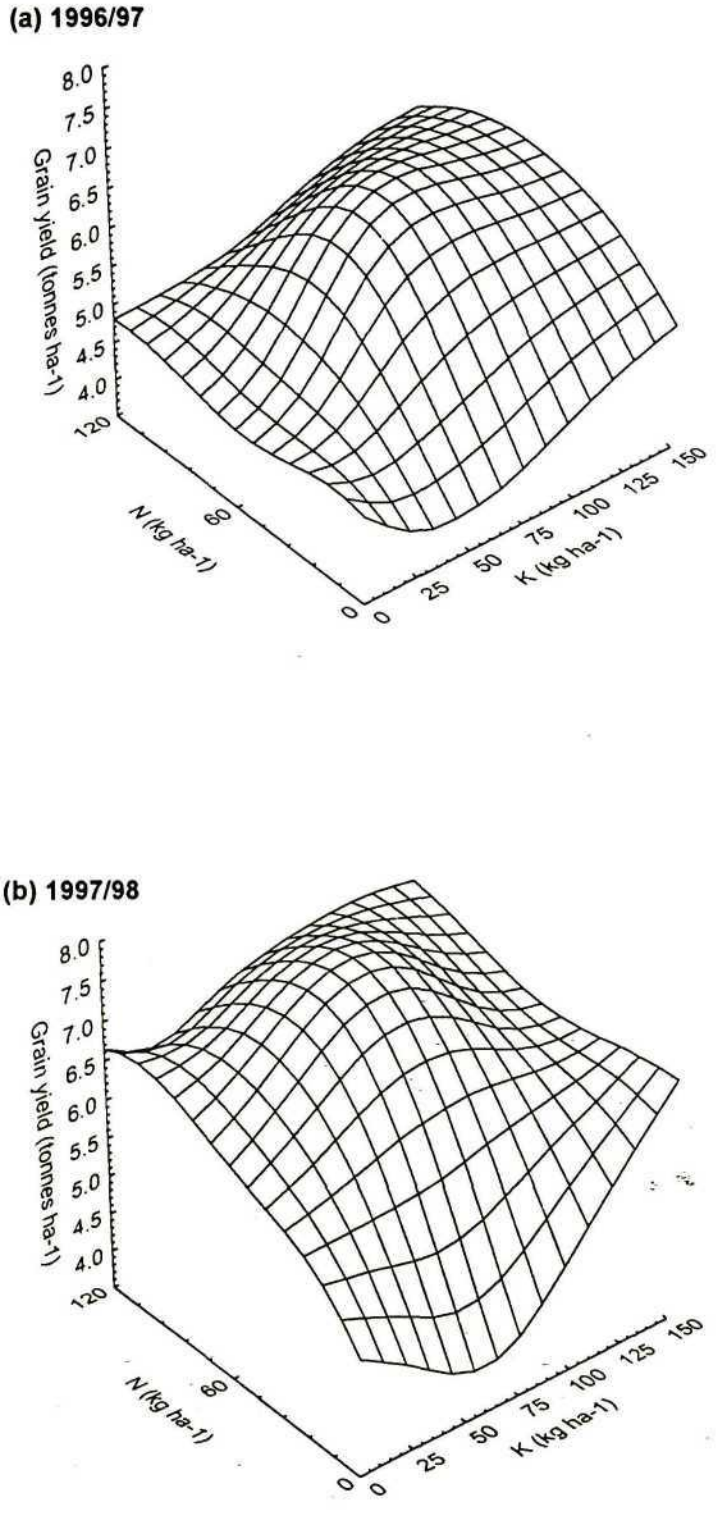
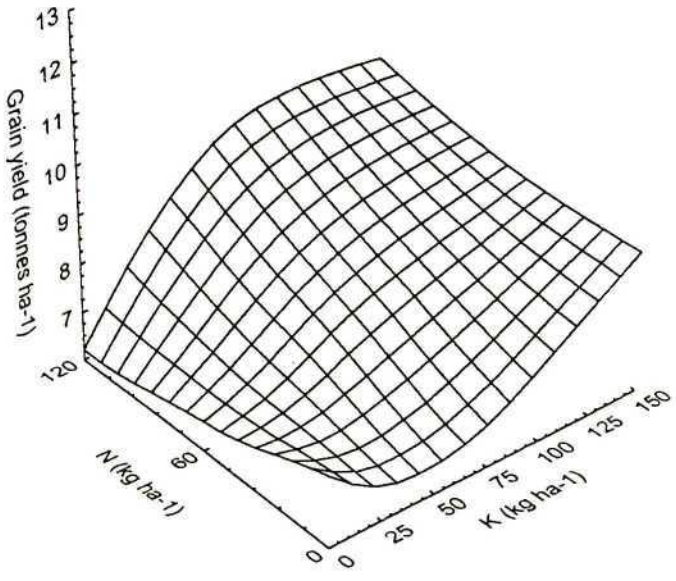


Fig. 4. Effect of nitrogen and potassium on grain yield (tonnes ha $^{-1}$) in non-fungicide treated maize at Cedara (a. 1996/97; b. 1997/98)

(c) 1996/97



(d) 1997/98

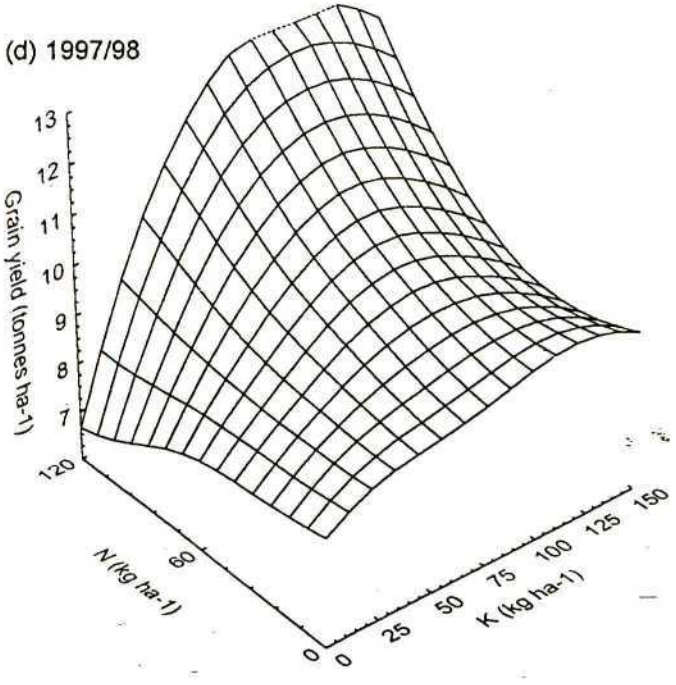


Fig. 4. Effect of nitrogen and potassium on grain yield (tonnes ha $^{-1}$) in fungicide treated maize at Cedara (c. 1996/97; d. 1997/98)

2.3.2 *Ahrens trial*

Climatic data

Temperature, rainfall and heat unit data for Ahrens are recorded in Table 11.

Table 11. Temperature, rainfall and heat unit data for Ahrens for the maize growing season of 1995/96.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	TOTAL
Rainfall (mm)	80.1	206.3	160.7	106.4	280.0	108.0	13.0	954.5
Mean max. temp.	24.5	24.2	23.8	25.4	25.1	24.2	21.7	
Mean min. temp. (°C)	12.4	14.1	14.1	16.7	16.0	13.6	10.5	
Heat units [1]	260.9	265.4	279.6	340.9	302.9	272.5	198.1	1920.3

[1] Heat units = $\frac{Tx + Tn}{2}$ - base temperature of maize (10°C)

where Tx = mean daily maximum temperature for the month and Tn = mean daily minimum temperature for the month.

Soil test data

Analyses of soil samples taken after fertilizing confirmed that P and K increased with increasing applications (Tables 12a, 12b and 12c, and Tables 13a, 13b and 13c, respectively). Nitrogen, P and K applications did not make any unexpected changes to other soil nutrient levels (Miles, personal communication).

Table 12a. ANOVA table of soil phosphorus (mg kg^{-1}) levels as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen	3	9.190	0.350	0.792
Phosphorus Linear ($P \leq 0.05$)	3	1966.190	74.120	< 0.001 ***
Potassium	3	60.330	2.270	0.106
Nitrogen : phosphorus	9	18.110	0.680	0.717
Nitrogen : potassium	9	51.60	1.950	0.093
Phosphorus : potassium	9	20.970	0.790	0.628
Residual 24 Total 63				
CV% = 37.7 NS = non-significant (P = > 0.05); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)				

Table 12b. Table of means of soil phosphorus levels (mg kg $^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	**N60**	**N120**	**N180**
	10.35	10.78	10.5	11.56
$LSD_{(0.05)}$	NS			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	3.40	5.96	12.96	20.87
$LSD_{(0.05)}$	2.66			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
	9.85	9.86	9.39	12.09
$LSD_{(0.05)}$	2.66			

All table figures refer to soil phosphorus levels (mg kg $^{-1}$)

Table 12c. Table of means of soil phosphorus (mg kg $^{-1}$) interactions as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTION	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	2.70	5.82	9.72	22.25
N60	3.92	5.4	10.73	16.98
N120	3.97	5.20	12.02	21.10
N180	2.47	5.92	17.08	19.80
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTION	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
N0	9.17	9.77	9.85	11.70
N60	10.20	8.82	10.55	7.45
N120	13.32	11.52	9.50	7.95
N180	10.97	11.32	6.27	16.7
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTION	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
P0	4.85	2.77	2.87	2.57
P30	7.50	4.75	4.65	5.45
P60	12.42	12.22	8.80	16.1
P120	18.90	21.70	19.85	19.67
$LSD_{(0.05)}$	NS			

All table figures refer to soil phosphorus levels (mg kg $^{-1}$)

Table 13a. ANOVA table of soil potassium ($cmol_c kg^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen	3	0.012	2.42	0.091
Phosphorus Linear ($P \leq 0.05$)	3	0.046	9.21	<0.001 ***
Potassium Linear ($P \leq 0.05$)	3	0.035	69.37	<0.001 ***
Nitrogen : phosphorus	9	0.009	1.82	0.116
Nitrogen : potassium	9	0.010688	2.14	0.066
Phosphorus : potassium Linear ($P \leq 0.05$)	9	0.017875	3.58	0.006 **
Residual 24 Total 63				

CV% = 25.1

NS = non-significant ($P = > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 13b. Table of means of soil potassium ($cmol_c kg^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	**N60**	**N120**	**N180**
	0.28	0.24	0.26	0.24
$LSD_{(0.05)}$	NS			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	0.30	0.26	0.24	0.21
$LSD_{(0.05)}$	0.036			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
	0.13	0.23	0.28	0.38
$LSD_{(0.05)}$	0.036			

All table figures refer to soil potassium ($cmol_c kg^{-1}$) levels

Table 13c. Table of means on soil potassium interactions levels ($cmol_c kg^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTION	Phosphorus (P) applied ($kg\ ha^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	0.30	0.23	0.27	0.25
N60	0.25	0.26	0.25	0.18
N120	0.33	0.22	0.24	0.23
N180	0.31	0.29	0.17	0.17
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTION	**Potassium (K) applied ($kg\ ha^{-1}$)**			
	K0	**K50**	**K100**	**K150**
N0	0.13	0.22	0.29	0.41
N60	0.10	0.21	0.31	0.33
N120	0.15	0.20	0.33	0.34
N180	0.12	0.28	0.22	0.32
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTION	**Potassium (K) applied ($kg\ ha^{-1}$)**			
	K0	**K50**	**K100**	**K150**
P0	0.13	0.24	0.39	0.43
P30	0.10	0.28	0.27	0.35
P60	0.15	0.20	0.29	0.28
P120	0.12	0.18	0.19	0.34
$LSD_{(0.05)}$	NS			

All table figures refer to soil potassium ($cmol_c kg^{-1}$) levels

Leaf analyses

Leaf analyses confirmed that with increasing applications of N, P and K there was an increased uptake of these nutrients (Tables 14a, 14b and 14c, Tables 15a, 15b and 15c, and Tables 16a, 16b and 16c, respectively). Increasing applications of N, P and K did not show any unexpected changes in nutrient uptake (Miles, personal communication).

Table 14a. ANOVA table of leaf nitrogen (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen Linear ($P \leq 0.05$)	3	2.734	73.770	<0.001***
Phosphorus	3	0.053	1.430	0.258
Potassium	3	0.045	1.230	0.322
Nitrogen : phosphorus	9	0.067	1.810	0.119
Nitrogen : potassium	9	0.038	1.030	0.445
Phosphorus : potassium	9	0.014	0.390	0.930
Residual 24 Total 63				

CV% = 6.5

NS = non-significant (P = > 0.05); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 14b. Table of means of leaf nitrogen (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	**N60**	**N120**	**N180**
	2.37	3.00	3.17	3.30
$LSD_{(0.05)}$	0.041			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	3.03	2.89	2.95	2.97
$LSD_{(0.05)}$	NS			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
	2.89	3.01	2.99	2.95
$LSD_{(0.05)}$	NS			

All table figures refer to leaf nitrogen (%) levels

Table 14c. Table of means of leaf nitrogen interactions (%) as affected by nitrogen, phosphorus and potassium applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTIONS	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	2.66	2.34	2.17	2.30
N60	3.01	2.97	2.99	3.02
N120	3.13	3.03	3.33	3.18
N180	3.32	3.22	3.30	3.37
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
N0	2.32	2.49	2.40	2.26
N60	2.97	2.97	2.94	3.10
N120	3.09	3.19	3.16	3.24
N180	3.16	3.38	3.47	3.20
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
P0	2.95	3.06	3.04	3.06
P30	2.85	2.94	2.91	2.85
P60	2.87	3.05	3.04	2.84
P120	2.76	2.98	2.96	3.05
$LSD_{(0.05)}$	NS			

All table figures refer to leaf nitrogen (%) levels

Table 15a. ANOVA table of leaf phosphorus (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen	3	0.002	2.910	0.055
Phosphorus Linear ($P \leq 0.05$)	3	0.014	17.310	<0.001***
Potassium	3	0.001	1.740	0.185
Nitrogen : phosphorus Linear ($P \leq 0.05$)	9	0.002	2.520	0.034*
Nitrogen : potassium	9	0.000	0.420	0.912
Phosphorus : potassium	9	0.001	0.890	0.552
Residual 24 Total 63				

CV% = 12.8

NS = non-significant (P = > 0.05); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 15b. Table of means of leaf phosphorus (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	**N60**	**N120**	**N180**
	0.21	0.23	0.24	0.24
$LSD_{(0.05)}$	NS			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	0.19	0.22	0.24	0.27
$LSD_{(0.05)}$	0.02			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
	0.24	0.23	0.22	0.23
$LSD_{(0.05)}$	NS			

All table figures refer to leaf phosphorus (%) levels

Table 15c. Table of means of leaf phosphorus interactions (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTIONS	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	0.18	0.21	0.21	0.25
N60	0.21	0.23	0.24	0.25
N120	0.23	0.21	0.24	0.28
N180	0.16	0.22	0.28	0.28
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
N0	0.22	0.21	0.21	0.21
N60	0.26	0.24	0.22	0.22
N120	0.25	0.24	0.24	0.23
N180	0.25	0.23	0.22	0.24
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
P0	0.20	0.21	0.16	0.16
P30	0.25	0.2	0.21	0.22
P60	0.25	0.23	0.23	0.25
P120	0.28	0.28	0.26	0.25
$LSD_{(0.05)}$	NS			

All table figures refer to leaf phosphorus (%) levels

Table 16a. ANOVA table of leaf potassium (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen Linear (P ≤ 0.05)	3	0.217	3.120	0.045*
Phosphorus] Linear (P ≤ 0.05)	3	0.632	9.070	< 0.001 ***
Potassium Linear (P ≤ 0.05)	3	4.989	71.600	< 0.001 ***
Nitrogen : phosphorus	9	0.150	2.150	0.065
Nitrogen : potassium	9	0.073	1.050	0.434
Phosphorus : potassium	9	0.083	1.200	0.342
Residual 24 Total 63				

CV% = 18.4

NS = non-significant (P = > 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 16b. Table of means of leaf potassium (%) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	**N60**	**N120**	**N180**
	1.61	1.41	1.35	1.37
$LSD_{(0.05)}$	NS			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	1.71	1.44	1.30	1.29
$LSD_{(0.05)}$	0.19			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K25**	**K50**	**K150**
	0.68	1.36	1.80	1.90
$LSD_{(0.05)}$	0.19			

All table figures refer to leaf potassium (%)

Table 16c. Table of means of leaf potassium (%) interactions as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTIONS	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	1.74	1.41	1.78	1.49
N60	1.54	1.56	1.31	1.25
N120	1.67	1.41	1.07	1.26
N180	1.90	1.40	1.04	1.14
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
N0	0.94	1.58	1.80	2.10
N60	0.49	1.37	1.93	1.88
N120	0.66	1.09	1.84	1.83
N180	0.62	1.38	1.66	1.81
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
P0	0.69	1.65	2.16	2.36
P30	0.65	1.47	1.78	1.89
P60	0.71	1.19	1.64	1.66
P120	0.66	1.12	1.64	1.71
$LSD_{(0.05)}$	NS			

All table figures refer to leaf potassium (%) levels

Final percentage leaf blighting (146 DAP)

Increased leaf blighting occurred with increased applications of N, P and K (Tables 17a, 17b and 17c) (Fig. 5a, 5b and 5c). However, P was found to have little ($P \leq 0.05$) effect on final percentage leaf blighting.

Table 17a. ANOVA table of final percentage leaf blighting (146 DAP) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen Linear ($P \leq 0.05$)	3	103.792	11.280	<0.001 ***
Phosphorus Linear ($P \leq 0.05$)	3	34.375	3.740	0.025 *
Potassium Linear ($P \leq 0.05$)	3	54.740	5.950	0.004 **
Nitrogen : phosphorus	9	9.292	1.010	0.460
Nitrogen : potassium	9	15.642	1.700	0.144
Phosphorus : potassium	9	7.740	0.840	0.587
Residual 24 Total 63				

CV% = 20.9

NS = non-significant (P = > 0.05); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 17b. Table of means of final percentage leaf blighting (146 DAP) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	**Nitrogen (N) applied (kg ha $^{-1}$)**			
	N0	**N60**	**N120**	**N180**
	3.31	6.94	7.00	9.50
$LSD_{(0.05)}$	2.21			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	**P30**	**P60**	**P120**
	4.56	6.87	7.56	7.75
$LSD_{(0.05)}$	2.21			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
	4.12	6.91	7.19	8.53
$LSD_{(0.05)}$	2.21			

All table figures refer to final % leaf blighting

Table 17c. Table of means of final percentage leaf blighting (146 DAP) interactions as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTION	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	**P30**	**P60**	**P120**
N0	1.37	3.75	4.00	4.12
N60	6.25	5.75	9.38	6.37
N120	3.00	7.12	7.50	10.38
N180	7.62	10.88	9.38	10.13
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTION	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
N0	3.37	4.12	2.50	3.25
N60	5.25	7.00	8.63	6.87
N120	3.75	6.50	7.50	10.25
N180	4.12	10.00	10.13	13.75
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTION	**Potassium (K) applied (kg ha^{-1})**			
	K0	**K50**	**K100**	**K150**
P0	4.50	3.00	4.62	6.12
P30	2.75	8.88	7.37	8.50
P60	5.00	7.50	7.75	10.00
P120	4.25	8.25	9.00	9.50
$LSD_{(0.05)}$	NS			

All table figures refer to final percentage leaf blighting

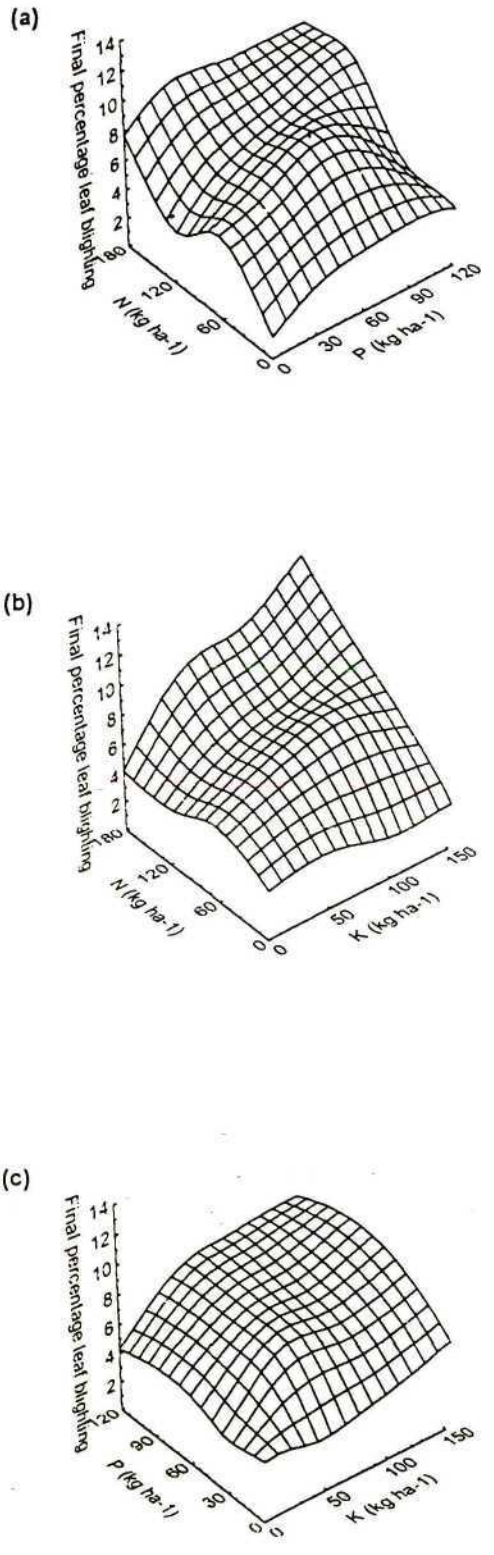


Fig. 5. Effect of nitrogen, phosphorus and potassium (kg ha^{-1}) on final percentage leaf blighting on non-fungicide treated maize at Ahrens (1995/96) (a. nitrogen and phosphorus; b. nitrogen and potassium; c. phosphorus and potassium)

Grain yield

Increases in N, P and K resulted in increased maize grain yields (Tables 18a, 18b and 18c) (Fig. 6a, 6b and 6c).

Table 18a. ANOVA table of grain yield (t ha $^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

Rep N.P.K stratum	Degree of freedom	Mean square	F Value	Probability
Nitrogen Linear (P ≤ 0.05)	3	5.257	5.570	0.005 **
Phosphorus Linear (P ≤ 0.05)	3	1.322	14.020	<0.001 ***
Potassium Linear (P ≤ 0.05)	3	1.201	12.730	<0.001 ***
Nitrogen : phosphorus	9	5.377	0.570	0.808
Nitrogen : potassium	9	1.261	1.340	0.270
Phosphorus : potassium	9	1.985	2.100	0.071
Residual 24 Total 63				

CV% = 26.2

NS = non-significant (P = > 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)

Table 18b. Table of means of grain yields (t ha $^{-1}$) as affected by nitrogen, phosphorus and potassium fertilizer applications at Ahrens (1995/96)

MAIN EFFECT - NITROGEN	Nitrogen (N) applied (kg ha $^{-1}$)			
	N0	N60	N120	N180
	2.93	3.61	4.11	4.24
$LSD_{(0.05)}$	0.71			
MAIN EFFECT - PHOSPHORUS	**Phosphorus (P) applied (kg ha $^{-1}$)**			
	P0	P30	P60	P120
	2.43	3.75	4.36	4.53
$LSD_{(0.05)}$	0.71			
MAIN EFFECT - POTASSIUM	**Potassium (K) applied (kg ha^{-1})**			
	K0	K50	K100	K150
	2.42	4.13	4.14	4.37
$LSD_{(0.05)}$	0.71			

All figure tables refer to maize grain yields (t ha^{-1})

Table 18c. Table of means of grain yield (t ha $^{-1}$) interactions as affected by nitrogen, phosphorus and potassium interactions at Ahrens (1995/96)

NITROGEN : PHOSPHORUS INTERACTIONS	Phosphorus (P) applied (kg ha $^{-1}$)			
	P0	P30	P60	P120
N0	1.58	2.53	4.02	3.64
N60	2.66	3.80	4.16	3.88
N120	2.92	4.07	4.38	5.05
N180	2.68	4.24	4.49	5.32
$LSD_{(0.05)}$	NS			
NITROGEN : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	K50	K100	K150
N0	2.76	2.97	3.21	2.80
N60	1.88	3.86	40.60	4.71
N120	2.40	4.89	4.52	4.61
N180	2.64	4.57	4.50	5.02
$LSD_{(0.05)}$	NS			
PHOSPHORUS : POTASSIUM INTERACTIONS	**Potassium (K) applied (kg ha^{-1})**			
	K0	K50	K100	K150
P0	2.44	2.06	2.64	2.66
P30	1.54	4.77	4.40	3.94
P60	3.02	4.70	4.32	5.02
P120	2.69	4.76	4.92	5.52
$LSD_{(0.05)}$	NS			

All figure tables refer to maize grain yields (t ha^{-1})

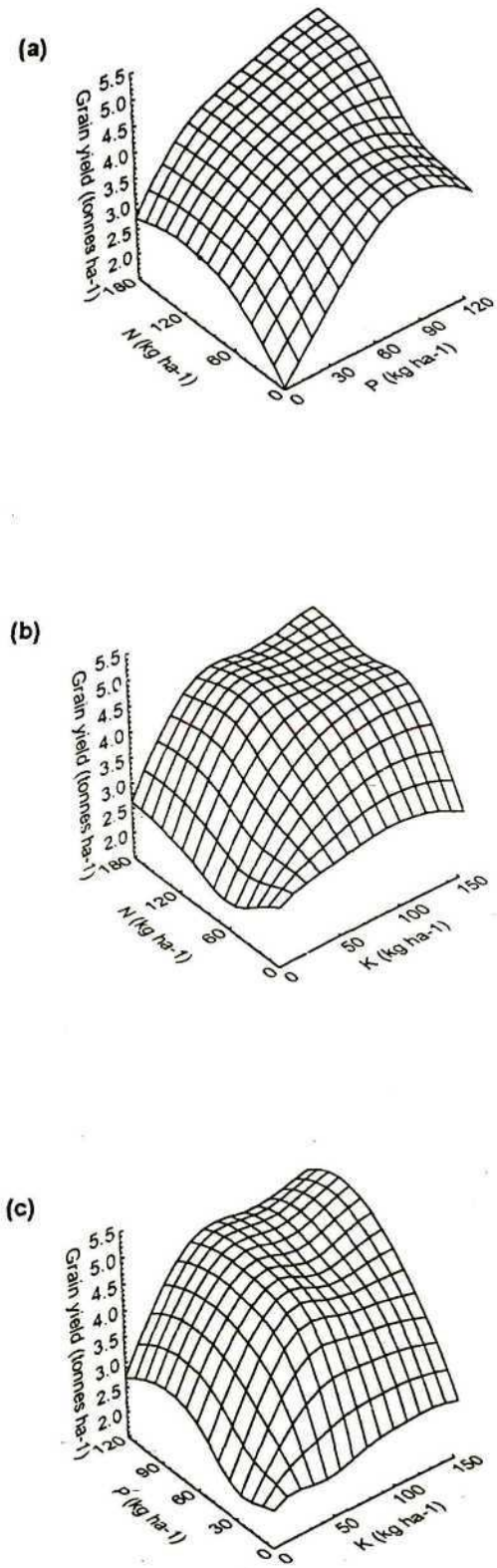


Fig. 6. Effect of nitrogen, phosphorus and potassium (kg ha^{-1}) on grain yield (tonnes ha^{-1}) of non-fungicide treated maize at Ahrens (1995/96) (a. nitrogen and phosphorus; b. nitrogen and potassium; c. phosphorus and potassium)

2.4 Discussion

Increased applications of N and K resulted in increased foliar N and K levels, and resulted in higher final percentage leaf blighting and SAUDPC levels in both the Cedara and Ahrens trials. Grey leaf spot was more severe on plants with a high nutritional status. These results also explain why this disease is not frequently observed among small-scale farmers growing maize on soils that are usually deficient in nutrients.These results are in support of observations by Nowell (1997) and are also in agreement with observations for certain other diseases caused by *Cercospora* spp. (Wang, 1966; Huber, 1981).

At Cedara, although the rate of disease development did not increase, GLS appeared earlier, final percentage leaf blighting was greater and the SAUDPC was higher as N and K applications increased in non-fungicide treated maize. Well fertilized maize is therefore at greater risk from GLS, because maize is subjected to leaf blighting over a longer period than maize with no, or very low, N and K applications.

The Ahrens trial confirmed that increased N and K applications result in increased final percentage leaf blighting. It also confirmed the findings of Smith (1989) that increased P applications have little effect on severity of leaf blighting by GLS (P was only significant at ≤ 0.05). However, it is important to note that this was a single observation and that PAN 6242 is a different hybrid to ZS 206 in terms of genotype, growth habit, root development, resistance to GLS (and other diseases), growing period and adaptability.

Several studies have shown a positive relationship between leaf N content and grain yield (Tyner, 1946; Bennett *et al.*, 1953; Amoruwa *et al.*, 1987) and a direct grain yield response to increased soil N applications (Shukla, 1972; Balko and Russell, 1980; Ulger *et al.*, 1987). This was reflected in increased grain yields with increasing N and K levels in the fungicide treated maize at Cedara. However, in the non-fungicide treated maize, the increased leaf blighting at the higher N and K levels explain why grain yields did not increase as expected with increased N and K applications.

In non-fungicide treated maize, there were significant increases in grain yield with increased N applications, despite increased leaf blighting. However, in the non-fungicide treated K maize, potential grain yields were not achieved as can be seen from the increased losses in grain yield between fungicide and non-fungicide treatments with increasing K rates. Grain yield losses increased from 1.4 -3.15 tonnes ha^{-1} in 1996/97 and from 1.57-3.56 tonnes ha^{-1} in 1997/98. This loss in grain yield between fungicide treated and non-fungicide treated maize was not reflected with increasing N levels, possibly because of the retention and build up of N on the clay soils of the trial site.

In the non-fungicide treated maize in the Ahrens trial, there was a significant increase in grain yield with increasing N, P and K applications. This was probably due to the fact that at zero and low application rates of N and K, the soil was more severely depleted of these nutrients from the long-term trial at Ahrens than at Cedara. In addition, levels of final percentage leaf blighting at 146 DAP were < 10%, which probably had little effect on grain yield with increasing N, P and K application rates.

In fungicide treated maize, highest grain yields were obtained using 120 kg N ha^{-1} and 150 kg K ha^{-1}, and in non-fungicide treated maize, 60 kg N ha^{-1} and 50 kg K ha^{-1}. Highest added gross margins (relative to minimum gross margins) were also obtained using these fertilizer applications (see Chapter 3).

Analysis of dry matter in pig, chicken, cattle (kraal), horse and sheep manure show that they contain 1-3% N and 0-3 % K (CADI -unpublished data). Therefore, a small-scale farmer would have to transport and apply 1-3 tonnes of manure to substitute for 60 kg inorganic N and 50 kg inorganic K ha^{-1}. This would be an impractical and uneconomical exercise.

In the absence of high N and K applications, the relative impact of GLS is minimized, e.g., in small-scale farming systems, maize may produce grain yields higher than expected as the plants reach physiological maturity without significant foliar blighting, and resultant grain yield losses.

Grain yield alone should not be used to justify the use of fertilizers for increased grain yields. Grain yield losses from increased GLS result in reduced grain yield potential. More important are the economic implications of the extra costs of added fertilizers and the grain yield related to disease.

The significant positive N:K interaction of SAUDPC in the fungicide treated and non-fungicide treated plots in 1997/98 illustrates the compounding influence of high levels of fertilization on the incidence of disease and the associated increase in grain yield loss between fungicide treated and non-fungicide treated maize.

These results have important implications for farmers. For commercial farmers who are financially able to spray for control of GLS, increased applications of N result in increased yields and gross margins. However, for small-scale farmers, who are financially unable to embark on costly fungicide control programmes, increased N fertilization results in increased GLS severity and consequent grain yield losses. Best yields and gross margins are obtained using 60 kg N ha^{-1} and 50 kg K ha^{-1}.

Maize is produced on millions of hectares in Southern Africa, much of which is subject to GLS incidence. Hybrids less susceptible to GLS, rotational cropping, cultural control methods and the use of fungicides to control GLS are economically viable for commercial farmers in RSA (Ward *et al.*,1993; Ward and Nowell, 1997). In the present economic climate for commercial farmers, the price-cost squeeze tends to reduce the profitability of maize production, and to increase the break-even yield level. A small yield loss for commercial farmers may result in reduced gross margins but could also determine whether maize production is economically viable. However, for the small - scale farmer, fungicide control may not be an option because they do not have access or finances to buy and maintain fungicide equipment, and often do not have the knowledge of the use of chemical sprays and maintenance of equipment. They will have to rely on using less susceptible hybrids, cultural control and rotational cropping as a small loss in yield could result in a family food shortage.

Cercospora zeae-maydis is considered to be a high sugar disease. This is possibly the reason why GLS is not considered to be a major problem where maize is grown in nutrient deficient soils in RSA. In poorly fertilized crops in Cameroon, Kenya, RSA and Zimbabwe, the severity of GLS was generally low and disease development was slow (Nowell, 1997).

Reducing nutrient levels has been suggested as a control measure for many diseases, but control at the cost of grain yield and gross margins is unacceptable. Increased N and K fertilization does increase the susceptibility of maize to GLS. This must be taken into account when encouraging the use of fertilizers for small-scale farmers to increase production if increased disease offsets the responses expected from increased fertilizer application. It also follows that the more progressive small-scale farmers who are able to fertilize their lands will have a greater problem with GLS, and will need to take precautions against disease to realise maximum grain yields and gross margins.

As it was important to ensure that the cultivars most susceptible to GLS, e.g., ZS 206, were affected by soil inorganic fertilizers, the results presented from this trial represent the worst case scenario. Future research needs to investigate the effects of N, P and K on maize hybrids grouped into the three categories of susceptibility to GLS, i.e., highly susceptible, moderately susceptible and resistant (Ward *et al.*, 1999). From this trial in the southern hemisphere and Smith's trial (1989) in the northern hemisphere, we propose that N and K will increase GLS blighting and that P will have little effect in other highly susceptible and moderately susceptible hybrids but that the magnitude of increased GLS will decrease with hybrids showing more resistance to GLS.

It is noted that in this trial, the primary effect of fungicides was to control GLS. There may have been secondary effects from fungicide applications, e.g., control of other maize pathogens and other physiological effects, e.g., hormonal effects. In addition,

root morphology of different hybrids, the effect of fungicides on root and stalk health relative to nutrient uptake, translocation and utilization may prevent general organic soil fertilizer recommendations to be made. However, this research does provide a framework for further investigation into the effects of soil organic and inorganic nutrients on GLS and other foliar fungal pathogens of maize.

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CHAPTER 3

Effect of fertilizers and grey leaf spot on the financial returns of maize in South Africa

Abstract

Increased nitrogen (N) and potassium (K) fertilizer applications increase the susceptibility of maize to grey leaf spot (GLS), caused by *Cercospora zeae-maydis,* Tehon and Daniels, resulting in increased grain yield losses. Commercial farmers, fertilizing for maximum grain yields, must also apply a fungicide spray programme to realize maximum grain yields and gross margins from increased fertilizer applications and costs. On the other hand, small-scale farmers, financially unable to fertilize for maximum grain yields, will experience smaller grain yield losses at lower fertilizer rates because of lower disease severity. However, for the small-scale farmer, a small loss in grain yield could result in hunger or even starvation. Grain yield alone should not be used to justify the use of fertilizers. More important are the financial implications of the extra costs of added fertilizers, and grain yield as affected by disease. The financial analysis in this paper was based on the 1997 average operating costs of 17 dryland maize farmers in the Winterton and Karkloof areas of KwaZulu-Natal, Republic of South Africa, where fungicides were used to control GLS [1]. These costs were used in the analysis of data generated from trials at Cedara in 1997/98 to determine whether reduced N and K applications were more effective for controlling GLS infections than a fungicide control programme. Where the effects of several different levels of N and K were analysed independently of each other, highest gross margins in fungicide treated maize were obtained using 120 kg N ha $^{-1}$ and 50 kg K ha $^{-1}$. In non-fungicide treated maize, highest gross margins were obtained using 60 kg N ha $^{-1}$ and 150 kg K ha $^{-1}$. Where the effects of several different levels of N and K were analysed together, highest gross margins in fungicide treated maize were obtained using 120 kg N ha $^{-1}$

[1]Exchange rate - R6.08 = $1 (on 24 / 1 / 2000)

and 150 kg K ha $^{-1}$. In contrast, for non-fungicide treated maize, highest gross margins were obtained using 60 kg N ha $^{-1}$ and 50 kg K ha $^{-1}$, because of increased leaf blighting from GLS at the higher N and K application rates.

3.1 · Introduction

Many maize pathogens, including fungi, bacteria and viruses, are present in the Republic of South Africa (RSA) (Gorter, 1977). Most occur every season but are seldom of economic significance. Grey leaf spot (GLS), caused by *Cercospora zeae-maydis* Tehon and Daniels, 1925, however, has resulted in significant economic losses in commercial maize production since 1992 and has emerged as a major threat to a large part of the South African maize industry.

In recent years there have been economically important epidemics of GLS in the RSA which have adversely affected grain yields of harvested maize *(Zea mays* L.). The disease first appeared in the Midlands of KwaZulu-Natal (KZN) in the 1988/89 growing season. From this initial focus, it has spread to neighbouring provinces, as well as neighbouring countries (Kenya, Malawi, Mozambique, Nigeria, Swaziland, Uganda, Zambia and Zimbabwe) (Nowell, 1997).

Efforts to increase resistance to GLS in maize has escalated dramatically over the past decade. However, farmers still prefer to plant the higher yielding cultivars and apply fungicides rather than use hybrids with effective quantitative resistance as they result in the highest economic return (Ward *et al.*, 1999).

The use of macronutrients in the management of fungal plant pathogens is widely documented in the literature (Trolldenier, 1969; Huber and Watson, 1974; Huber, 1976, 1980a, 1980b,1981; Graham, 1983; Huber and Arny, 1985; Huber and Dorich, 1988).

Specific nutrients have been shown to increase or decrease the incidence of diseases in plants. However, each host-pathogen interaction must be considered on an individual disease basis, together with environmental and soil variables (Huber, 1981,

Huber and Dorich, 1988). Although it is seldom that a disease can be eliminated by a corrective fertilizer regime, the severity of a disease can be reduced by specific nutrients. Applications of fertilizers have been shown to affect the severity of other leaf diseases of maize such as *Exserohilum turcicum* Leonard and Suggs (Bogyo, 1955; Gorsline *et al.*, 1963; Karlen *et al.*, 1973), and *Cochliobolus heterostrophus* Drechsler (Taylor, 1954).

The purpose of this study was to evaluate the influence of different levels of N and K on grain yield in order to establish gross margins in fungicide treated and non-fungicide treated maize. The model was created to reflect the financial returns and kinds of interactions of various inputs based on fertility of a particular maize hybrid in a single year at a particular location with particular soil types.

3.2 Materials and methods

Trial site

The trial was carried out at Cedara Agricultural Development Institute (29°32'S, 30°17'E; altitude 1070 m) for three seasons (1995/96, 1996/97 and 1997/98) on well-drained, deep sandy-clay loams of the Hutton form and Doveton series (MacVicar, 1991). The trial site was previously planted to *Eragrostis curvula* (Schrad.) Nees. The results from the 1997/98 season were used as an example to calculate the financial returns of the trial, because soil analyses showed that the soils at the trial site had stabilized after three years. The mean rainfall and temperature for this growing season were 702 mm and 18.9 °C, respectively. The trial was a randomised 3X4X2 design with three levels of N and four levels of K. Each treatment was replicated three times. Gross plot size was 8 m x 6 m comprising 8 rows, 8 m long, spaced 750 mm apart. Plots were split for fungicide treatments.

Land preparation and fertilizer applications

Dolomitic lime, at a rate of 6.3 t ha $^{-1}$, was applied to reduce acid saturation to < 20% and disced to a depth of 200-250 mm six weeks before planting. Immediately prior to planting, fertilizers were applied by hand and incorporated by discing to a depth of approximately 100-150 mm. All plots received 105 kg P ha^{-1} (as double superphosphate; 20% P), 50 kg S ha^{-1} (as calcium sulphate; 18% S) and 30 kg Zn ha $^{-1}$ (as zinc sulphate; 23% Zn) as KZN soils are deficient in S and Zn. Potassium (as potassium chloride; 50% K) treatments were applied at planting at zero, 25, 50 and 150 kg K ha^{-1}. Nitrogen (as limestone ammonium nitrate with N as 14% NH_4^+ and 14% NO_3^-) treatments were zero, 60 and 120 kg N ha^{-1}. The 60 and 120 kg N ha^{-1} treatments received 30 kg N ha $^{-1}$ as a preplant application, and the remainder was applied as a topdressing when plants were 300 mm tall. In South African soils, NH_4^+ is converted to NO_3^- within 10 to 14 days of application during the summer months (Miles, personal communication)[2]. It was therefore assumed that this trial evaluated the effect of the nitrate form of N on GLS development.

Planting procedure

A maize cultivar, ZS 206, was used because it is high grain yielding but highly susceptible to GLS. It was hand-planted on 26 November, 1997. Two seeds per plant station were hand-planted. Approximately 30 days after planting (DAP), plants were hand-thinned to 44 000 plants ha^{-1}. A tank-mix of metolachlor (1.86 g a.i. ha^{-1}) plus atrazine / metolachlor / terbuthylazine (550 / 663 / 5 50 g a.i. ha $^{-1}$) was applied as a pre - emergent, overall treatment in 300 L water for the control of grasses and broadleaf weeds. Fenvalerate (28 g a.i. ha $^{-1}$) was included in the herbicide tank - mix for the control of cutworm. Carbofuran granules (2.7 kg a.i. ha $^{-1}$) were applied in the planting furrow for the control of soil insect pests.

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[2] Dr N. Miles, Cedara Agricultural Development Institute, Private Bag X9059, Pietermaritzburg 3200

Fungicide applications

A spraying programme commenced when GLS appeared on the basal 5-leaves, 69 DAP. A pre-mix combination of 188 g carbendazim and 94 g flusilazole ai ha^{-1} was applied (Punch Xtra, Du Pont de Nemoirs and Coy) using a CO_2-pressurized back pack sprayer fitted with a vertically mounted sprayboom having three Whirlrain (WRW2-20°) nozzles, spaced one meter apart. Full-cover sprays were applied to the central two rows of each fungicide treated plot. Second and third spray treatments were applied 99 and 120 DAP.

Disease assessments

Whole-plant standard area diagrams described by Ward *et al.,* (1997c), were used to estimate percent disease severity of the central plants in the two centre rows of each plot 66, 85, 99, 125 and 146 DAP. These data were used to calculate the area under disease progress curve (AUDPC), which is a quantitative summary of the disease epidemic and is calculated using a trapezoidal integration program (Berger, 1981).

Harvesting procedure

Maize was harvested on 19 June. A 1 m border of plants was excluded from both ends of each row for sampling purposes. Only ears in the central two, 6 m rows were harvested and weighed in the field. Sub-samples of five or six ears were weighed and shelled in the laboratory and the shelling percentage determined to calculate the shelled grain mass. Grain yields were expressed in tonnes ha^{-1}, at 12.5% grain moisture.

Statistical analysis

Final percentage leaf blighting, area under disease progress curve and grain yields were processed by analysis of variance (ANOVA). Fischer's least significant differences were based on the 5% level of probability. The analysis was conducted using Genstat 5.2 (Anonymous, 1987).

Economic analysis

Commercial farmers

Economic analyses were based on the average operating costs from a survey of 17 representative dryland maize farms in the Winterton and Karkloof areas of KwaZulu-Natal in 1996/97. Selection of farms was based on the presence of GLS and the use of fungicides for control during the 1997/98 season.

Costs of machinery and labour (for land preparation, initial fertilizer applications, planting, insecticide and herbicide applications) seed, fertilizers (P, Zn and S) and agro-chemicals that were common to all treatments were regarded as fixed costs. Interest, depreciation, fuel, repairs and insurance were included in machinery costs. Additional costs of varying N and K application rates, N topdressing applications, fungicide spray applications and harvesting of increased grain yields resulting from varying fertilizer regimes, were defined as variable costs. The unit price of N (urea) kg $^{-1}$ and K (KCl) kg $^{-1}$ was R 2.97 and R 2.07, respectively. Machinery and labour costs for N topdressing applications was R 11 ha^{-1}. Costs of fungicides were estimated at R 85 and R 50 ha^{-1} for agro-chemicals and aerial application, respectively. Harvesting costs were calculated using machinery and labour costs of R 35.68 ha $^{-1}$. An estimated maize price of R 600 ton $^{-1}$ was used to estimate the value of increased grain yields from implementing N and K applications.

The economic benefits of N and K soil applications for the control of GLS are based on a modification of the equation used by Ward *et al.* (1997a) to estimate the economic benefits of fertilizer treatments of maize for the control of GLS compared to fungicide applications.

Gross margins of grain yields obtained from N, K and N.K interactions were calculated as follows :

Gross margin from fungicide treated grain yields (Ps):

$$Ps = (Ys \times R) - (H + F + A + S)$$

where Ys, the grain yield from the fungicide treated maize, is multiplied by the maize price per ton (R), less the costs of harvesting (H), fertilizer and application (F), N topdressing application (A), and three spraying operations (S).

Gross margin from non-fungicide treated grain yields (Pu):

$$Pu = (Yu \times R) - (H + F + A)$$

where Yu, the grain yield of the non-fungicide treated maize is multiplied by the maize price per ton (R), less the costs of harvesting (H), fertilizer and application (F), and N topdressing application (A).

Ninety five percentage confidence limits were calculated in order to establish upper and lower confidence limits; i.e.,

$$t_{21\,(3)\ (P = 0.05)} \times \text{standard error of deviation}$$

95% confidence limit (N) = 2.08 x 0.341
= 0.7

95% confidence limit (K) = 2.08 x 0.394
= 0.8

95% confidence limit (N.K) = 2.08 x 0.682
= 1.4

Small-scale farmers

The situation for small-scale farmers using a knapsack sprayer is difficult to estimate with confidence. Input costs include fixed costs such as the cost of a knapsack sprayer plus boom (R800) and fungicide (R85 ha^{-1} $application^{-1}$). If the initial cost of the spray equipment is shared between 4 small-scale farmers, then the cost is reduced to R200 per annum. Annual depreciation on the equipment will be R200 per annum over 4 years i.e. R 50 per annum. The variables affecting the costs are so undefined that they cannot be calculated usefully, e.g., the life expectancy of the sprayer which will, in turn, be determined by the size of the area to be sprayed; the ability of the farmer to access capital; his/her ability to pay back the interest on the loan; the availability or transport of clean water to apply with the fungicide; the transport cost of fungicides and the opportunity cost (value) of the farmer's time.

3.3 Results

Weather conditions were warm and moist with heavy dews and mists during January and February, favouring GLS development. Rainfall was well-distributed throughout the maize growing months of 1997/98. Only a summary of results necessary for economic analysis is presented below.

Final percentage leaf blighting

Final percentage leaf blighting increased with increasing N and K applications in both the fungicide treated and non-fungicide treated plots at 146 DAP. In fungicide treated plots, increasing N applications resulted in increased final disease severity levels from 5.6% in non-fertilized N plots compared to 9.6% in 120 kg N ha^{-1} plots. Similarly, final disease severity was lower (4.7%) in non-fertilized K plots compared to 11.7% in 150 kg K ha^{-1} plots (Table 1a and 1b).

In non-fungicide treated plots, final disease severity was lower (68.8%) in non-fertilized N plots than the 60 and 120 kg N ha^{-1} treatments (78.8% and 81.0%, respectively). With increasing K applications, final disease severity also increased significantly, from 65.6% in non-fertilized K plots to 87.2% in 150 kg K ha^{-1} plots (Table 1a and 1b).

Table 1a. ANOVA table of final percentage leaf blighting (146 days after planting) as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

Stratum	Degree of freedom	Mean square	F value	Probability
Rep. N.K. stratum				
N	2	442.014	29.560	<0.001 ***
K	3	634.115	42.400	<0.001***
N.K	6	10.417	0.700	0.655
Residual 22				
Rep. N.K sprayed stratum				
Sprayed Linear ($P \leq 0.05$)	1	83879.250	1.220	<0.001 ***
N sprayed Linear ($P \leq 0.05$)	2	121.181	17.670	<0.001 ***
K sprayed Linear ($P \leq 0.05$)	3	162.587	23.710	<0.001 ***
N.K sprayed Linear ($P \leq 0.05$)	6	17.361	2.53	0.048 *
Residual 24				
Total 71				

CV% 1996/97 =13.2%; 1997/98 = 6.2%

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 1b. Table of means of final percentage leaf blighting (146 days after planting) as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

MAIN EFFECT - NITROGEN		1997/98			
Nitrogen (N) applied (kg ha $^{-1}$)		**N0**	**N60**	**N120**	
Fungicide treated maize		5.62	8.54	9.58	
Non-fungicide treated maize		68.75	78.75	81.04	
LSD $_{(0.05)}$		2.79 all comparisons; 2.21 same N level only			
MAIN EFFECT - POTASSIUM		**1997/98**			
Potassium (K) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize		4.72	6.39	8.89	11.67
Non-fungicide treated maize		65.56	74.72	77.22	87.22
LSD $_{(0.05)}$		3.22 all comparisons; 2.55 same K levels only			
INTERACTION EFFECTS - NITROGEN: POTASSIUM		**1997/98**			
		Potassium (K) applied (kg ha $^{-1}$)			
Nitrogen (N) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize	N0	3.33	5.00	5.83	8.33
	N60	5.00	5.00	10.00	14.11
	N120	5.83	9.17	10.83	12.50
Non- fungicide treated maize	N0	60.00	66.67	66.67	81.67
	N60	66.67	80.00	80.00	88.33
	N120	70.00	77.50	85.00	91.67
	LSD $_{(0.05)}$	5.58 all comparisons; 4.41 same N.K. level only			

All table figures refer to final percentage leaf blighting (146 DAP)

Area under disease progress curve

Nitrogen and K had a significant effect on AUDPC in fungicide treated and non-fungicide treated plots (Table 2a and 2b). In the fungicide treated plots, AUDPC levels increased from 187.2 to 302.8 with increasing N applications and from 197.5 to 325.7 in the non-treated to 150 kg K ha $^{-1}$ plots, respectively. In non-fungicide treated maize there was an increase in AUDPC from 1430.6 to 2437.3 from the non-fertilized to the 120 kg N ha $^{-1}$ plots, respectively. Similarly, in the K treated plots the AUDPC also increased significantly from 1717.3 to 2738.8 kg K ha $^{-1}$ in the non-treated to 150 kg K ha^{-1}, respectively.

Table 2a. ANOVA table of area under disease progress curve as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

Stratum	Degree of freedom	Mean square	F value	Probability
Rep. N.K. stratum	1997/98	1997/98	1997/98	1997/98
N	2	2.095	122.730	<0.001 ***
K	3	1.311	76.800	<0.001 ***
N.K	6	9.981	5.850	<0.001 ***
Residual 22				
Rep. N.K sprayed stratum				
Sprayed Linear ($P \leq 0.05$)	1	5.70107	3340.79	<0.001 ***
N sprayed Linear ($P \leq 0.05$)	2	1.34006	78.49	<0.001 ***
K sprayed Linear ($P \leq 0.05$)	3	8.54205	50.05	<0.001 ***
N.K sprayed Linear ($P \leq 0.05$)	6	9.06404	5.31	0.001 **
Residual 24 Total 71				

CV% 1997/98 = 11.4 %

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 2b. Table of means of area under disease progress curve as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

MAIN EFFECT - NITROGEN		1997/98			
Nitrogen (N) applied (kg ha $^{-1}$)		**N0**	**N60**	**N120**	
Fungicide treated maize		187.2	269.2	302.8	
Non-fungicide treated maize		1430.6	2230.6	2437.3	
$LSD_{(0.05)}$		110.1 all comparisons			
MAIN EFFECT - POTASSIUM		**1997/98**			
Potassium (K) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize		197.5	229.8	259.5	325.7
Non-fungicide treated maize		1717.3	1698.2	1977	2738.8
$LSD_{(0.05)}$		127.1 all comparisons			
INTERACTION EFFECTS - NITROGEN: POTASSIUM		**1997/98**			
		Potassium (K) applied (kg ha $^{-1}$)			
Nitrogen (N) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize	N0	142.9	190.6	157.4	257.8
	N60	227.6	218.8	287.5	343.1
	N120	222	279.8	333.5	376
Non- fungicide treated maize	N0	1205.1	1077.1	1032.7	2407.5
	N60	1721.7	1991.4	2438.9	2770.3
	N120	2225.2	2026.2	2459.5	3038.4
	$LSD_{(0.05)}$	220.1 all comparisons			

All table figures refer to area under disease progress curve (AUDPC)

Grain yield

Grain yields were higher in fungicide treated than in non-fungicide treated maize (Table 3a and 3b). Grain yield increased significantly with increasing N applications in both fungicide treated and non-fungicide treated maize. In fungicide treated maize, grain yield increased with increasing rates of N application, from 8.8 to 10.2 t ha $^{-1}$ and from 7.6 to 10.3 t ha $^{-1}$ in non-fertilized to 150 kg K ha $^{-1}$ plots. In non-fungicide treated maize, increases in N applications resulted in a significant increase in grain yield, from 5.1 to 6.7 t ha $^{-1}$ in non-fertilized compared to 120 kg N ha $^{-1}$ plots. In the K treated plots, grain yields increased , although not significantly, with increasing applications of K, from 6.0 to 6.8 t ha $^{-1}$.

The N.K. interaction means of grain yields are shown in Table 3b. Highest grain yields in fungicide treated maize were achieved using 120 kg N ha $^{-1}$ and 150 K ha $^{-1}$, as expected. In non-fungicide treated maize, highest grain yields were obtained using 60 kg N ha $^{-1}$ and 50 kg K ha $^{-1}$. This was probably because of the increased leaf blighting caused by *C. zeae-maydis* at 120 kg N ha $^{-1}$ and 150 kg K ha $^{-1}$.

Nutrients limited yield at the lower end of the nutrient application levels. This confirms our hypothesis that at lower nutrient levels, GLS levels are lower than at higher fertilization application levels.

Table 3a. ANOVA table of grain yield as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

Stratum	Degree of freedom	Mean square	F value	Probability
Rep. N.K. stratum	1997/98	1997/98	1997/98	1997/98
N	2	1.340	8.750	0.002 **
K	3	1.028	6.780	0.002 **
N.K	6	3.425	2.240	0.082
Residual 22				
Rep. N.K sprayed stratum				
Sprayed Linear ($P \leq 0.05$)	1	1.7756	139.35	<0.001 ***
N sprayed Linear ($P \leq 0.05$)	2	3.81906	3.03	0.003 **
K sprayed Linear ($P \leq 0.05$)	3	5.69906	5.42	0.013 *
N.K sprayed	6	2.96106	2.35	0.068
Residual 21 (3) Total 71				

CV% 1997/98 = 14.5%

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Table 3b. Table of means of grain yield as affected by nitrogen and potassium fertilizer applications at Cedara (1997/98)

MAIN EFFECT - NITROGEN		1997/98			
Nitrogen (N) applied (kg ha $^{-1}$)		**N0**	**N60**	**N120**	
Fungicide treated maize		8.8	8.9	10.2	
Non-fungicide treated maize		5.1	6.7	6.7	
LSD $_{(0.05)}$		1.0 all comparisons; 1.0 same N levels only			
MAIN EFFECT - POTASSIUM		**1997/98**			
Potassium (K) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize		7.6	9.2	10.1	10.3
Non-fungicide treated maize		6	5.8	6.1	6.8
LSD $_{(0.05)}$		1.2 all comparisons; 1.1 same K level only			
INTERACTION EFFECTS - NITROGEN: POTASSIUM		**1997/98**			
		Potassium (K) applied (t ha $^{-1}$)			
Nitrogen (N) applied (kg ha^{-1})		**K0**	**K25**	**K50**	**K150**
Fungicide treated maize	N0	8.2	8.9	8.9	9.3
	N60	8.0	8.7	9.8	9.2
	N120	6.5	10.0	11.7	12.4
Non- fungicide treated maize	N0	5.0	4.7	4.0	6.6
	N60	6.2	6.6	7.6	6.5
	N120	6.8	6.1	6.9	7.2
	LSD $_{(0.05)}$	2.0 all comparisons; 1.9 same N.K level only			

All table figures refer to grain yield (t ha $^{-1}$)

Economic analysis

Gross margins as affected by nitrogen or by potassium applications

Gross margin (Ps) from grain yields of fungicide treated maize increased from R4561 to R4984 ha $^{-1}$ from the 0 to 120 kg N ha^{-1} plots. With increased K applications (0-150 kg K ha $^{-1}$), there was an increase in gross margin from R3884 to R5096 ha^{-1} (Table 4).

There was a similar increase in gross margin (Pu) in the non-fungicide treated plots with increases from R2878 to R3414 in the non-fertilized to 120 kg N ha^{-1} plots (Table 5). This increase was also reflected in the K treated plots with gross margins of R3386 to R3526 ha $^{-1}$ in the 0 to 150 kg K ha $^{-1}$ plots.

Added gross margins as affected by nitrogen or by potassium applications

Added gross margins (Ps_r) in fungicide treated maize resulted in a loss of - R133 and a gain of R423 ha $^{-1}$ in the 60 and 120 kg N ha $^{-1}$ plots, and an increase from R851 to R1212 in the 25 to 150 kg K ha $^{-1}$ plots (Table 6). Added gross margins (Pu_r) in the non-fungicide treated plots was R714 ha $^{-1}$ and R536 ha $^{-1}$ with 60 kg N ha $^{-1}$ and 120 kg N ha $^{-1}$. Added gross margins (Pu_r) showed a financial loss of - R165 ha $^{-1}$ and - R48 ha $^{-1}$ in the 25 and 50 kg K ha $^{-1}$ plots (Table 6). However, in the 150 kg K ha $^{-1}$ plots, Pu_r was R140 ha $^{-1}$.

Table 4. Economic analysis of effects of nitrogen or potassium soil applications on grain yield of fungicide treated maize at Cedara in 1997/98

	Grain yield (Ys) (t ha^{-1})			Total revenue [1] (R) (R t^{-1})			Harvesting costs [2] (H) (R t^{-1})			Cost of fertilizer (F) (R ha^{-1})	Cost of N topdressing application (A) (R ha^{-1})	Spraying [3] costs (S) (R ha^{-1})	Gross margin (Ps)[4] (R ha^{-1})		
N applied (kg ha^{-1})	Actual	Lower limit	Upper limit	Actual	Lower limit	Upper limit	Actual	Lower limit	Upper limit				Actual	Lower limit	Upper limit
0	8.8	8.1	9.5	5280	4860	5700	314	289	339	0	0	405	4561	4166	4956
60	8.9	8.2	9.6	5340	4920	5760	318	293	343	178	11	405	4428	4033	4823
120	10.2	9.5	10.9	6120	5700	6540	364	339	389	356	11	405	4984	4589	5379
LSD $_{(0.05)}$	1.01														
K applied (kg ha^{-1})															
0	7.6	6.8	8.4	4560	4080	5040	271	243	300	0	0	405	3884	3432	4335
25	9.2	8.4	10	5520	5040	6000	328	300	357	52	0	405	4735	4283	5186
50	10.1	9.3	10.9	6060	5580	6540	360	332	389	104	0	405	5191	4739	5642
150	10.3	9.5	11.1	6180	5700	6660	368	339	396	311	0	405	5096	4645	5548
LSD $_{(0.05)}$	1.16														

[1] Total revenue = grain yield (t ha^{-1}) X R 600 t^{-1} ; [2] Harvesting costs = R35.68 ha^{-1}; [3] Costs based on three spays; [4] Gross margin (Ps) = (Ys X R) - (H + F + A +S) where Ys = grain yield from sprayed maize; R = maize price per ton; H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application; S = cost of three spraying operations

Table 5. Economic analysis of effects of nitrogen or potassium soil applications on grain yield of non-fungicide treated maize at Cedara in 1997/98.

	Grain yield (Yu) (t ha $^{-1}$)			Total revenue [1] (R) (R t $^{-1}$)			Harvesting costs [2] (H) (R t $^{-1}$)			Cost of fertilizer (A) (R ha $^{-1}$)	Cost of N topdressing application (A) (R ha $^{-1}$)	Gross margin (Pu)[3] (R ha $^{-1}$)		
N applied (kg ha $^{-1}$)	Actual	Lower limit	Upper limit	Actual	Lower limit	Upper limit	Actual	Lower limit	Upper limit			Actual	Lower limit	Upper limit
0	5.1	4.4	5.8	3060	2640	3480	182	157	207	0	0	2878	2483	3273
60	6.7	6	7.4	4020	3600	4440	239	214	264	178	11	3592	3197	3987
120	6.7	6	7.4	4020	3600	4440	239	214	264	356	11	3414	3019	3809
LSD $_{(0.05)}$	1.01													
K applied (kg ha $^{-1}$)														
0	6	5.2	6.8	3600	3120	4080	214	186	243	0	0	3386	2934	3837
25	5.8	5	6.6	3480	3000	3690	207	178	235	52	0	3221	2770	3673
50	6.1	5.3	6.9	3660	3180	4140	218	189	246	104	0	3338	2887	3790
150	6.8	6	7.6	4080	3600	4560	243	214	271	311	0	3526	3075	3978
LSD $_{(0.05)}$	1.16													

[1] Total revenue = grain yield (t ha^{-1}) X R 600 t $^{-1}$; [2]Harvesting costs = R35.68 ha; [3] Gross margin (Pu) = (Yu x R) - (H + F + A) where Yu =grain yield from non -sprayed price per ton; H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application

Table 6. Gross margins and added gross margins from increased nitrogen or potassium applications and fungicide sprays at Cedara in 1997/98.

	Gross margin (Ps) from grain yield of fungicide treated maize (R ha^{-1})			Added gross margins (Ps_r)[1] from grain yield of fungicide treated maize relative to N0 and K0 (R ha^{-1})			Gross margin (Pu) from grain yield of non-fungicide treated maize (R ha^{-1})			Added gross margins (Pu_r)[2] from grain yield of non-fungicide treated maize relative to N0 and K0 (R ha^{-1})		
Fertilizer application	**Actual**	**Lower limit**	**Upper limit**	**Actual**	**Lower limit**	**Upper limit**	**Actual**	**Lower limit**	**Upper limit**	**Actual**	**Lower limit**	**Upper limit**
N applied (kg ha^{-1})												
0	4561	4166	4956	-	-	-	2878	2483	3273	-	-	-
60	4428	4033	4823	**- 133**	**- 133**	**- 133**	3592	3197	3987	714	714	714
120	4984	4589	5379	423	423	423	3414	3019	3809	536	536	536
K applied (kg ha^{-1})												
0	3884	3432	4335	-	-	-	3386	2934	3837	-	-	-
25	4735	4283	5186	851	852	851	3221	2770	3673	**- 165**	**- 164**	**- 164**
50	5191	4739	5642	1307	1307	1307	3338	2887	3790	**- 48**	**- 47**	**- 47**
150	5096	4645	5548	1212	1213	1213	3526	3075	3978	140	141	141

(1) Added gross margins (Ps_r) was calculated from the gain in gross margin (of fungicide treated maize) at different N and K fertilizer applications compared to non-fertilized plots

(2) Added gross margins (Pu_r) was calculated from the gain in gross margin (of non-fungicide treated maize) at different N and K fertilizer applications compared to non-fertilized plots

Gross margins as affected by combinations of nitrogen and potassium applications

Grain yields from N.K interactions (actual, upper and lower limits) are recorded in Table 7. Total revenue of fungicide treated (Ys X R) and non-fungicide treated maize (Yu x R) is recorded in Table 8. Total costs for fungicide treated maize (H + F + A + S) and non-fungicide treated maize (H + F + A) are recorded in Table 9. Gross margins for fungicide treated and non-fungicide treated maize are shown in Table 10 and Fig.1.

In fungicide treated maize, highest gross margins for N.K interaction means were obtained from 120 kg N ha^{-1} and 150 kg K ha^{-1}, as expected. In non-fungicide treated maize, highest gross margins were obtained from the highest grain yields, i.e., 60 kg N ha^{-1} and 50 kg K ha^{-1}.

Added gross margins as affected by combinations of nitrogen and potassium applications

A summary of fertilizer and spraying recommendations with gross margins is shown in Table 11. Highest gross margin resulted from applying 120 kg N ha^{-1} and 150 kg K ha^{-1} with three sprays of fungicides. There was a loss in added gross margins with various combinations of N and K with and without fungicide applications, e.g., a loss of - R708 ha^{-1} using zero N and 50 kg K ha^{-1} with no fungicide applications (Table 11). With an added cost of R826 using 120 kg N ha^{-1} and no K with three fungicide applications, added gross margins was only R68 ha^{-1} due to the limiting effect of K resulting in very low grain yields, despite the use of fungicides to control GLS.

Table 7. Table of actual, upper and lower limits of maize grain yields (t ha $^{-1}$) as affected by nitrogen and potassium interactions at Cedara (1997/98)

Fungicide treated maize	Fertilizer added	Grain yield (t ha $^{-1}$)			Fertilizer added	Grain yield (t ha $^{-1}$)			Fertilizer added	Grain yield (t ha $^{-1}$)			Fertilizer added	Grain yield (t ha $^{-1}$)		
		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit
	N0 K0	8.2	6.8	9.6	N0 K25	8.9	7.5	10.3	N0 K50	8.9	7.5	10.3	N0 K150	9.3	7.9	10.7
	N60 K0	8.0	6.6	9.4	N60 K25	8.7	7.3	10.1	N60 K50	9.8	8.4	11.2	N60 K150	9.2	7.9	10.6
	N120 K0	6.5	5.1	7.9	N120 K25	10	8.6	11.4	N120 K50	11.7	10.3	12.3	N120 K150	12.4	11.0	13.8
Non-fungicide treated maize	**Fertilizer added**	**Grain yield (t ha^{-1})**			**Fertilizer added**	**Grain yield (t ha $^{-1}$)**			**Fertilizer added**	**Grain yield (t ha $^{-1}$)**			**Fertilizer added**	**Grain yield (t ha $^{-1}$)**		
	N0 K0	5.0	3.6	6.4	N0 K25	4.7	3.3	6.1	N0 K50	4.0	2.6	5.4	N0 K150	6.6	5.2	8.0
	N60 K0	6.2	4.8	7.6	N60 K25	6.6	5.2	8.0	N60 K50	7.6	6.2	9	N60 K150	6.5	5.1	7.9
	N120 K0	6.8	5.4	8.2	N120 K25	6.0	4.6	7.4	N120 K50	6.9	5.5	8.3	N120 K150	7.2	5.8	8.6

All table figures refer to grain yield (t ha $^{-1}$)

Table 8. Economic analysis of interaction effects of nitrogen and potassium soil applications on total revenue of fungicide treated and non-fungicide treated maize at Cedara (1997/98)

Fungicide treated maize	Fertilizer added	Total revenue (R ha $^{-1}$)			Fertilizer added	Total revenue (R ha $^{-1}$)			Fertilizer added	Total revenue (R ha $^{-1}$)			Fertilizer added	Total revenue (R ha $^{-1}$)		
		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit
	N0 K0	4908	4068	5748	N0 K25	5322	4482	6162	N0 K50	5346	4506	6186	N0 K150	5550	4710	6390
	N60 K0	4782	3942	5622	N60 K25	5238	4398	6078	N60 K50	5886	5046	6726	N60 K150	5538	4698	6378
	N120 K0	3912	3072	4752	N120 K25	5970	5130	6810	N120 K50	7044	6204	7884	N120 K150	7446	6606	8286
Non-fungicide treated maize	**Fertilizer added**	**Total revenue (R ha^{-1})**			**Fertilizer added**	**Total revenue (R ha $^{-1}$)**			**Fertilizer added**	**Total revenue (R ha $^{-1}$)**			**Fertilizer added**	**Total revenue (R ha $^{-1}$)**		
	N0 K0	3018	2178	3858	N0 K25	2832	1992	3672	N0 K50	2376	1536	3216	N0 K150	3984	3144	4824
	N60 K0	3702	2862	4542	N60 K25	3978	3138	4818	N60 K50	4530	3690	5730	N60 K150	3912	3072	4752
	N120 K0	4068	4908	3228	N120 K25	3606	2766	4446	N120 K50	4122	3282	4962	N120 K150	4308	3468	5148

All table figures refer to total revenue (R ha $^{-1}$), i .e., Y x R where Y = grain yield (t ha $^{-1}$) and R = estimated price of maize (R600 t $^{-1}$)

Table 9. Economic analysis of interaction effects of nitrogen and potassium soil applications on costs (harvesting + fertilizer and application + nitrogen topdressing) in fungicide treated and non-fungicide treated maize at Cedara (1997/98)

	Fertilizer added	Total costs [1] (R ha $^{-1}$)			Fertilizer added	Total costs [1] (R ha $^{-1}$)			Fertilizer added	Total costs [1] (R ha $^{-1}$)			Fertilizer added	Total costs [1] (R ha $^{-1}$)		
Fungicide treated maize		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit
	N0 K0	697	647	747	N0 K25	773	724	823	N0 K50	827	777	877	N0 K150	1046	996	1096
	N60 K0	878	828	928	N60 K25	957	908	1007	N60 K50	1048	998	1098	N60 K150	1234	1184	1284
	N120 K0	1005	955	1055	N120 K25	1179	1129	1229	N120 K50	1295	1245	1345	N120 K150	1526	1476	1576
Non-fungicide treated maize	**Fertilizer added**	**Total costs [2] (R ha $^{-1}$)**			**Fertilizer added**	**Total costs [2] (R ha $^{-1}$)**			**Fertilizer added**	**Total costs [2] (R ha $^{-1}$)**			**Fertilizer added**	**Total costs [2] (R ha $^{-1}$)**		
	N0 K0	179	130	229	N0 K25	220	170	270	N0 K50	245	195	295	N0 K150	548	498	598
	N60 K0	409	359	459	N60 K25	478	428	528	N60 K50	562	512	612	N60 K150	733	683	783
	N120 K0	609	559	659	N120 K25	633	583	683	N120 K50	716	666	766	N120 K150	934	884	984

[1] Total costs = H + F + A + S; [2] Total costs = H + F + A where H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application ; S = cost of three spraying operations

Table 10. Gross margin analyses of interaction effects of nitrogen and potassium soil applications on grain yield of fungicide treated and non-fungicide treated maize at Cedara (1997/98)

	Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})			Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})			Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})			Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})		
Fungicide treated maize		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit		Actual	Lower limit	Upper limit
	N0 K0	4211	3421	5001	N0 K25	4549	3758	5339	N0 K50	4519	3729	5309	N0 K150	4504	3714	5294
	N60 K0	3904	3114	4694	N60 K25	4281	3490	5071	N60 K50	4838	4048	5628	N60 K150	4304	3514	5094
	N120 K0	2907	2117	3697	N120 K25	4791	4001	5581	N120 K50	5749	4959	6539	N120 K150	5920	5130	6710
Non-fungicide treated maize	**Fertilizer added**	**Gross margin (Pu) [2] (R ha^{-1})**			**Fertilizer added**	**Gross margin (Pu) [2] (R ha^{-1})**			**Fertilizer added**	**Gross margin (Pu) [2] (R ha^{-1})**			**Fertilizer added**	**Gross margin (Pu) [2] (R ha^{-1})**		
	N0 K0	2839	2048	3629	N0 K25	2612	1822	3402	N0 K50	2131	1341	2921	N0 K150	3436	2646	4226
	N60 K0	3293	2503	4083	N60 K25	3500	2710	4290	N60 K50	3968	3187	5118	N60 K150	3179	2389	3696
	N120 K0	3459	4349	2569	N120 K25	2973	2183	3763	N120 K50	3406	2616	4196	N120 K150	3374	2584	4164

[1] Gross margin (Ps) = (Ys x R) - (H + F + A + S) [2] Gross margin P u = (Yu x R) - (H + F + A) where H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application ; S = cost of three spraying operations

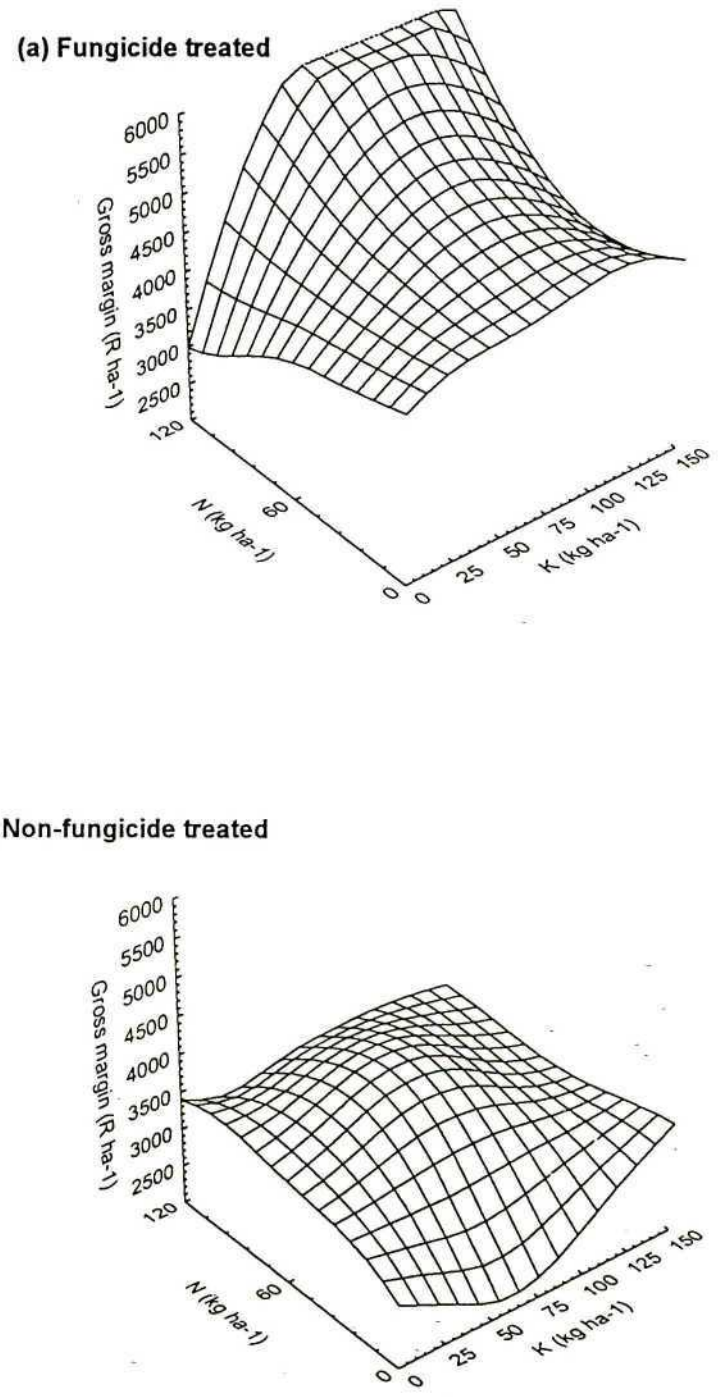


Fig. 1. Effect of nitrogen and potassium (kg ha^{-1}) on gross margin (R ha^{-1}) on fungicide and non-fungicide treated maize at Cedara (1997/98)

Table 11. Fertilizer (nitrogen and potassium) and fungicide recommendations showing gross margins and added gross margins for commercial farmers

Variable costs [1] (R ha^{-1})	Added costs relative to minimum variable costs [2] (R ha^{-1})	Fertilizer application (kg ha^{-1})	Fungicide applications (x3)	Gross margin (R ha^{-1})	Added gross margins relative to minimum gross margin [3] (R ha^{-1})
179	0	N0K0	NO	2839	0
220	41	N0K25	NO	2612	**-227**
245	66	N0K50	NO	2131	**-708**
409	230	N60K0	NO	3293	454
478	299	N60K25	NO	3500	661
548	369	N0K150	NO	3436	597
562	383	N60K50	NO	3968	1129
609	430	N120K0	NO	3459	620
633	454	N120K25	NO	2973	134
697	518	N0K0	YES	4211	1372
716	537	N120K50	NO	3406	567
733	554	N60K150	NO	3179	340
773	594	N0K25	YES	4549	1710
827	648	N0K50	YES	4519	1680
878	699	N60K0	YES	3904	1065
934	755	N120K150	NO	3374	535
957	778	N60K25	YES	4281	1442
1005	826	N120K0	YES	2907	68
1046	867	N0K150	YES	4504	1665
1048	869	N60K50	YES	4838	1999
1179	1000	N120K25	YES	4791	–1952
1234	1055	N60K150	YES	4304	1465
1295	1116	N120K50	YES	5749	2910
1526	1347	N120K150	YES	5920	3081

(1) Variable costs = H + F + A + S where H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application ;
S = cost of three spraying operations (where applicable)

(2) Variable costs minus minimum variable cost

(3) Gross margin minus minimum gross margin

3.4 Discussion

Maize farmers in KZN produce the highest and most consistent grain yields in RSA under dryland conditions as a result of the relatively high rainfall in the province. However, financial returns from investments in fertilizer and spray treatments must exceed the cost of treatments. In recent years there have been many changes in the South African maize industry, the most notable being that producer prices are no longer determined on the basis of production costs but on supply and demand. High costs of production have increased the risk of producing maize. To reduce the risk, input costs have to be minimized, with more emphasis on higher grain yields through correct fertilizer usage, and disease and pest control practices.

When making decisions about fertilizer application rates the number of fungicide applications, farmers usually make intelligent guesses based on intuitive integrations of a spectrum of contributing factors, especially costs of seed, agronomic practices, fertilizers, fungicides, and expected outcomes (grain yields and maize prices). This study analyses N and K input costs and grain yield responses with and without fungicide sprays, in an endeavour to provide concrete data for this decision-making process by farmers aiming to maximise their gross margins, based on a worst case scenario of GLS susceptibility using a highly susceptible maize hybrid, ZS 206.

Based on the history of GLS in a particular bioclimatic area, gross margins from increased grain yields following fertilizer and fungicide applications must compensate for added costs. If no spraying operations are planned, then increased fertilizer applications of N and K will result in lower grain yields and lower gross margins because of increased GLS blighting. For example, with an added cost of R 518 ha^{-1}, resulting from three fungicide applications but with no N or K applications, there was a gross margin of R4211 ha^{-1} and an added gross margin of R1372 ha^{-1}. In contrast,

with an added cost of R554, using 60 kg N ha $^{-1}$ and 150 kg K ha $^{-1}$ but with no fungicide applications, added gross margin was only R 340 ha $^{-1}$ (Table 11).

Yields from increased N and K applications in fungicide treated maize showed a typical linear response with increased grain yield expressed in increased gross margin. This is in accordance with findings by Ward *et al.* (1997b), who showed that the use of fungicides in commercial maize production in RSA, i.e., where farmers fertilize for maximum yields, was economical at existing input costs.

The economic analysis using the N:K interaction means showed that for farmers applying fungicides to control GLS, i.e., commercial farmers, highest grain yields and gross margins were obtained using 120 kg N ha $^{-1}$ and 150 kg K ha^{-1} . In contrast, where fungicides are not used to control GLS, i.e., small-scale farmers, highest grain yields and gross margins were obtained using only 60 kg N ha $^{-1}$ and 50 kg K ha^{-1} , because of the higher severity of GLS at higher N and K application rates.

Ward *et al.* (1997a), working on fixed costs of R1095.92 ha $^{-1}$ and variable costs of R144.12 ha $^{-1}$ based on the average operating costs of 18 representative dryland maize farmers in the Winterton and Karkloof areas of KZN, showed that the time and frequency of fungicide treatments determines added gross margin. Maize was fertilized for an 8-tonne yield, i.e., 120 kg N ha^{-1} and 150 kg K ha^{-1}. In the dry season of 1992/93, GLS severity was less than in the 1993/94 season, when normal, well-distributed rains occurred. The gain in yield due to fungicide treatment in the drier season was lower than that in the wetter season. Consequently, the added gain in yield from three fungicide applications was not high enough to compensate for the additional costs of the extra spray operations over the single spray treatment. However, in the wet season of 1993/94, three fungicide applications resulted in relatively high grain yields and the highest added gross margin compared to single and double sprays.

Ward (personal communication)[3] also demonstrated that commercial hybrids can be evaluated and grouped into susceptible, moderately susceptible and resistant hybrids based on grain yield response to frequency of fungicide applications (Table 12). Hybrid, time of planting, row spacings, in-row spacings, plant population and N and K fertilizer applications were the same as those used in the trial on which this economic analysis was based. Single, two-spray and three-spray fungicide applications were applied with a non-sprayed control. Using grain yield data from Ward's trial, gross margins and added gross margins were calculated. There was a linear grain yield response to fungicide treatments and maximum grain yields were only achieved using three applications. Highest gross margin and added gross margins were also achieved using three fungicide applications.

[3] Dr J.M.J. Ward, Cedara Agricultural Development Institute, Private Bag X9059, Pietermaritzburg 3200.

Table 12. Gross margin and added gross margins from maize grain yields related to the frequency of fungicide applications (Ward, personal communication)

No. of fungicide applications	Grain yield (tonnes ha $^{-1}$)	Variable costs [1] (R ha $^{-1}$)	Added costs relative to minimum variable costs [2] (R ha $^{-1}$)	Gross margin (R ha $^{-1}$)	Added gross margins relative to minimum gross margin [3] (R ha $^{-1}$)
0	4.9	864	0	2076	0
1	8.2	1117	253	3803	1727
2	9.5	1298	434	4402	2326
3	11.6	1508	644	5452	3376

(1) Variable costs = H + F + A + S where H = harvesting costs; F = fertilizer and application costs; A = cost of N topdressing application ; S = cost of one, two or three fungicide applications (where applicable)

(2) Variable costs minus minimum variable costs

(3) Gross margin minus minimum gross margin

3.4.1 Comparison of spraying costs for commercial and small-scale farmers

Commercial farmers

Where GLS is a problem, commercial farmers usually use aerial applications of fungicides to control the pathogen. The costs ha $^{-1}$ of three applications of fungicides applied aerially are shown in Table 13.

Table 13. Annual cost ha $^{-1}$ of three fungicide applications to control grey leaf spot of maize using aerial application of fungicides

Symbol	Cost identification	Annual cost ha $^{-1}$ (Rands)	Assumption
a.	*Aerial application*	150	*Cost of applying fungicides using an aerial application* is about R 50 application $^{-1}$ ha^{-1} , i.e. R 50 X 3 = R 150. This cost is relatively low as the commercial farmer can spread this expense over a large area.
b.	Fungicide for 3 applications (ha^{-1})	255	R 85 ha^{-1} application^{-1}
c.	Simple interest on loan of R 405	69	Interest taken at 17% on a loan of R 405 i.e. three aerial applications and cost of fungicides
d.	Opportunity cost (value) of farmer's time to supervise aerial application	150	This cost was taken at R100 hr $^{-1}$ but will depend the farmer's earning capabilities. The farmer's time for supervising three aerial applications has been costed out at 1/2 hr for each fungicide application ha^{-1}, i.e. 1.5 hrs for 3 applications
e.	**TOTAL COSTS**	**624**	

i.e. the total cost for a commercial farmer using aerial application to spray three applications of fungicide to control GLS on maize :

$$a + b + c + d = e$$

i.e. R150 + R255 + R69 + R150 = R624

Small-scale farmers

The annual cost of applying fungicides ha $^{-1}$ using a knapsack sprayer, are presented in Table 14. It was assumed that one knapsack sprayer is bought between four small-scale farmers, that the farmer hired labour and that there was no charge for transporting water and fungicides.

Table 14. Annual cost (R ha^{-1}) of three fungicide applications to control grey leaf spot of maize using a knapsack sprayer

Symbol	Cost identification	Annual cost ha $^{-1}$ (Rands)	Assumption
a.	Sprayer plus boom	50	Cost of sprayer plus boom is R 800 shared by 4 farmers, i.e., R 200 per farmer. Annual depreciation on the knapsack sprayer will be R 200 per annum over 4 years, i.e., R 50 per annum
b.	3 fungicide applications (ha^{-1})	255	R 85 ha^{-1} application^{-1} applied by the farmer himself
c.	Simple interest on loan of R455	91	Interest rate of 20%. Note: presently interest to small-scale farmers is charged at 3-5% more than prime or top rate to commercial farmers
d.	Opportunity cost (value) of farmer's time	480	This cost was taken at R 40 hr $^{-1}$ but would depend the farmer's earning capabilities. The farmer's time was costed out at 4 hr application^{-1} ha $^{-1}$, i.e., 12 hrs for 3 applications
e.	**TOTAL COSTS**	**876**	

namely, the total cost for a small-scale farmer using a knapsack sprayer to spray three applications of fungicide to control GLS on maize :

$$a + b + c + d = e$$

$$R50 + R255 + R91 + R480 = R\ 876$$

If a small-scale farmer controls GLS by spraying with a knapsack sprayer, and if he plants the same hybrids as a commercial farmer, he would be able to achieve the same grain yield ha^{-1} as a commercial farmer. However, based on the calculations and assumptions above, knapsack spraying is R252 ha^{-1} more costly than aerial application of fungicides used in commercial farming. Commercial farmers also have a higher earning capacity and interest is charged at a lower interest rate. This makes it more costly and less economical for a small-scale farmer to control GLS using a knapsack sprayer.

Costs for both the commercial and small-scale farmer will vary annually depending on the price of fertilizers and fungicides. For example, the price of limestone ammonium nitrate (LAN), the most commonly used N fertilizer in KZN for the 1999/2000 maize season, has a unit price of N = R 3.60. The unit price of N based on the 1997/98 season costs, used in the economic analysis of this research, was based on R 2.97. Urea can also be used as an N fertilizer, but is far less popular in KZN, and has a unit price of N = R 2.99. Similarly, KCl (50% K) is the most popular K fertilizer used and in 1999/2000 has a unit price of K = R 3.60, compared to the unit price of K = R 2.07 in the 1997/98 season used in the economic analysis recorded. Potassium nitrate KNO_3 (38% K; 13% N), a less commonly used inorganic K source in KZN, had a unit price of K = R 2.60 in the 1999/2000 maize season.

Fungicide applications in the 1997/98 season were based on R 85 and R 50 ha^{-1} for agrochemicals costs (Punch Xtra, Du Pont de Nemoirs and Coy) and aerial application, respectively. These figures have increased to R 110 and R 72 ha^{-1} for the same fungicide and application rates, respectively, in the 1999/2000 maize season. In addition, new fungicides to control GLS are on the market, i.e., Eria (125 g carbendazim and 625 g difenoconazole, Novartis) and is presently also being used in fungicide applications for the control of GLS at a similar cost of R 110 ha^{-1}.

Aerial application rates, interest rates and opportunity costs of the farmer's time may also increase. Similarly, for the small-scale farmer, knapsack and boom purchasing costs, interest rates and opportunity costs of time may also show annual changes.

3.4.2 Short- and long-term variables

Maize price tonne^{-1}, harvesting costs, fertilizer and fungicide costs and applications, harvesting costs as well as interest rates on loans can be referred to as short-term variables. Other factors, e.g., tillage operations, amount of lime required to achieve an acid saturation of <8%, phosphorus requirement of 60 kg P ha^{-1}, soil types, bioclimatic area, environmental factors, yield potential and susceptibility/resistance to GLS of the maize hybrid chosen, also play an important role in determining yield, and consequently financial return of a maize crop. These can be referred to as fixed and long-term variables (Fig. 2).

If finances, or financial loans are not a constraint, a farmer can fertilize, and apply fungicides to control GLS, ensuring maximum return on his investment. In contrast, a farmer might only have enough money to purchase enough seed for the season. Between these two extremes are many short-term variable choices, e.g., how much N and K to apply at planting and how many times to spray in a season. A farmer must make the right decisions at the beginning of the season and budget for, optimally, three fungicide applications to ensure adequate control of GLS, should it become epidemic.

Using short-term variables, i.e., N and K fertilizers plus fungicide applications, that directly impact on grain yield, a simple model has been drawn up to provide answers to a farmer's dilemma of how to obtain maximum return on the money he is able to spend on these short-term variables. At present, the optimum combinations of N and K fertilizers, with or without fungicide applications, are not possible to compute intuitively.

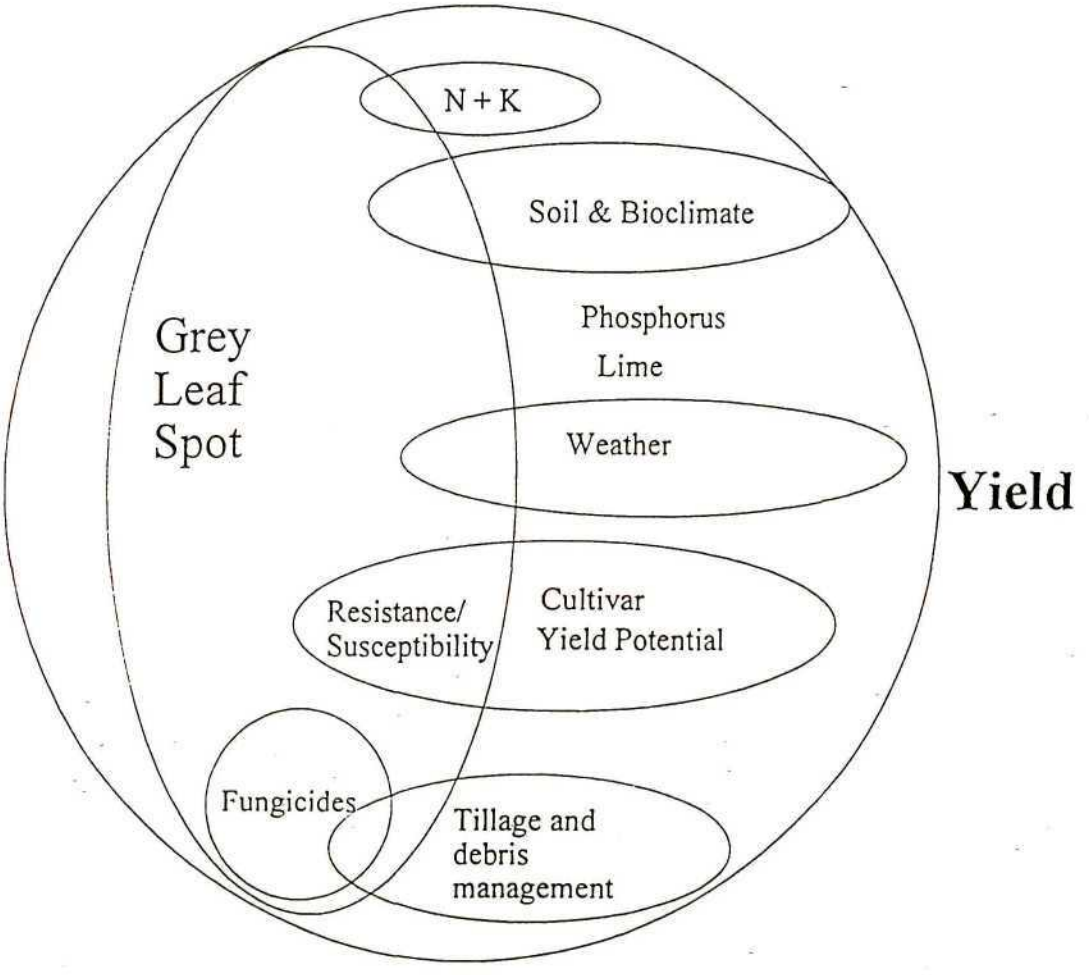
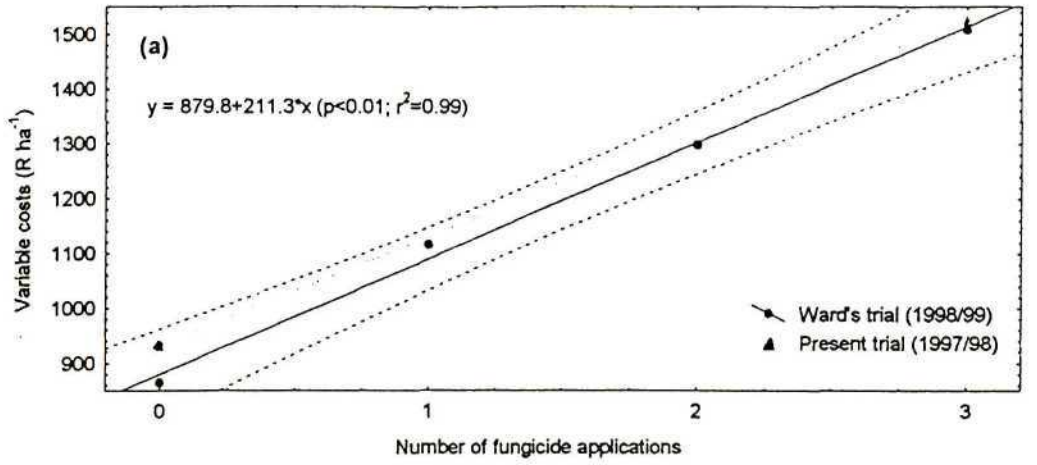


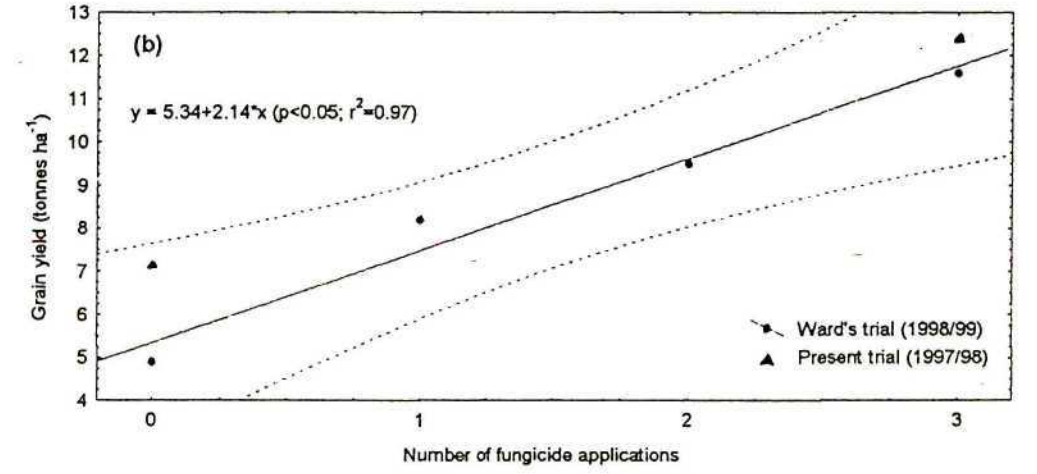
Fig. 2. Some fixed and long-term variables affecting maize yields

The model presented calculates yield and gross margin as a function of different levels of soil N and K application (kg ha^{-1}) with 0, 1, 2 and 3 fungicide applications, for a range of different financial inputs to ensure the best return on investment.

Table 15 uses the gross margin analyses of the interaction effects of N and K soil applications with three or no fungicide applications on results obtained in this trial (Table 10). Based on the finding of Ward *et al.,* (1997c), that there was a linear response to 0, 1, 2 and 3 fungicide sprays, a linear regression of the findings of the yield response to 0 and 3 fungicide applications at the different fertilizer levels was drawn up and the responses to 1 and 2 fungicide applications estimated from this.

In order to obtain yield and gross margin figures for 1 and 2 sprays, the results from the trial by Ward (1998/99) using the same maize hybrid (ZS 206) and fertilizer application (120 kg N ha^{-1} and 150 kg K ha^{-1}) (Table 13), have been extrapolated. Standardized AUDPC figures for Ward's 1998/99 trial were 6 % and 47 % for fungicide treated (three sprays) and non-fungicide treated maize, respectively, For the 1997/98 trial used in the economic analysis of this research, SAUDPC values were 5 % and 38 % for fungicide treated (three sprays) and non-fungicide treated maize, respectively. This would account for the lower yields recorded in Ward's 1998/99 trial in both fungicide and non-fungicide treated maize. Figure 3a, b and c shows the relationship between Ward's 1998/99 trial and the 1997/98 trial used in this economic analysis.





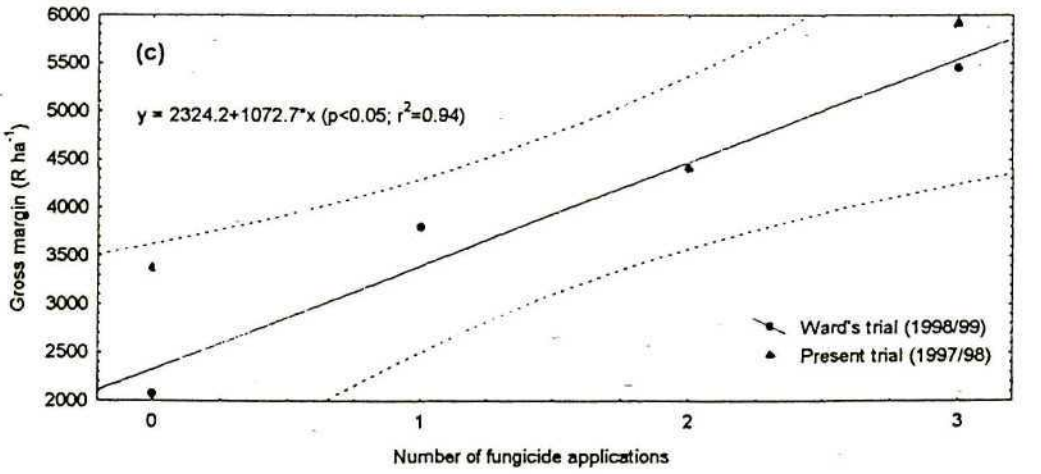


Fig. 3. Regression analysis of (a) variable costs (R ha^{-1}), (b) grain yields (tonnes ha^{-1}) and (c) gross margins (R ha^{-1}) of present research (1997/98) and the1998/99 trial by Ward *et al.* (1999) at Cedara using the maize hybrid RS 625 and 120 kg N ha^{-1} and 150 kg K ha^{-1}. Confidence limits (95%) are shown.

Table 15. Gross margins of short-term variables calculated from the 1997/98 maize fertility trial, combined with data from Ward's 1998/99 maize trial (Ward, personal communication) at Cedara using the maize cultivar ZS 206

Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})				Fertilizer added	Gross margin (Ps) [1] (R ha^{-1})				Fertilizer added		Gross margin (Ps) [1] (R ha^{-1})			Fertilizer added		Gross margin (Ps) [1] (R ha^{-1})		
(kg ha^{-1})	0 sprays	1 spray	2 sprays	3 sprays	(kg ha^{-1})	0 sprays	1 spray	2 sprays	3 sprays	(kg ha^{-1})`	0 sprays	1 spray	2 sprays	3 sprays	(kg ha^{-1})	0 sprays	1 spray	2 sprays	3 sprays
N0	*179*[1]	*340*	*510*	*697*	N0	*220*	*400*	*580*	*733*	N0	*245*	*340*	*630*	*827*	N0	*548*	*740*	*860*	*1046*
K0	5.0[2]	6.0	7.1	8.2	K25	4.7	6.1	7.3	8.9	K50	4.0	5.9	7.4	8.9	K150	6.6	7.6	8.4	9.3
	2839[3]	**3300**	**3750**	**4211**		**2612**	**3250**	**3900**	**4549**		**2131**	**2900**	**3750**	**4519**		**3436**	**3800**	**4420**	**4504**
N60	*409*	*560*	*720*	*878*	N60	*478*	*630*	*790*	*957*	N60	*562*	*720*	*860*	*1048*	N60	*733*	*880*	*1060*	*1234*
K0	6.2	6.8	7.4	8.0	K25	6.6	7.4	8.1	8.7	K50	7.6	8.4	9.1	9.8	K150	6.5	7.5	8.3	9.2
	3293	**3600**	**3800**	**3904**		**3500**	**3750**	**4000**	**4281**		**3968**	**4200**	**4500**	**4838**		**3179**	**3400**	**3800**	**4304**
N120	*609*	*740*	*870*	*1005*	N120	*633*	*760*	*880*	*1179*	N120	*716*	*820*	*920*	*1295*	N120	*934*	*1110*	*1300*	*1526*
K0	6.8	6.7	6.6	6.5	K25	6.0	7.5	8.6	10.0	K50	6.9	8.4	10.0	11.7	K150	7.2	8.5	10.4	12.4
	3459	**3250**	**3100**	**2907**		**2973**	**3650**	**4150**	**4791**		**3406**	**3950**	**4800**	**5749**		**3374**	**4050**	**5000**	**5920**

[1] Numbers in italics represent short-term variable costs, i.e. H + F + N + S $_{(0, 1, 2 \text{ or } 3)}$ (R ha $^{-1}$); [2] numbers in normal type represent yield (t ha^{-1}) ; [3] numbers in bold type represent gross margins (R ha^{-1})

From the data presented in Table 15 a model has been created to help farmers make the best choice of N and K fertilizer applications, and the best number of fungicide applications to ensure maximum return on investment of short-term maize production variables.

As the current maize price, yield and consequently harvesting costs for a particular season are unknown at the time of planting, a farmer will have to extrapolate from previous year's figures based on the maize hybrid to be used. The figures chosen to determine the best treatment will depend on the risk the farmer is prepared to take for the coming season with its unknown rainfall and other weather variables.

This model is simple. However, it will enable farmers to utilize capital to its maximum benefit by identifying the optimum combinations of N and K and number of fungicide applications, if any, to achieve maximum gross margins with different hybrids. It serves as a foundation for a bigger and more global model that will be formulated and tested by a successor in this field. In order for the bigger model to have a more global scale, it must incorporate :

a. Yield potential of different hybrids
b. Hybrid resistance/susceptibility to GLS
c. Yield potential and soil type of geographic zone / bioclimatic area
d. Plant populations and spacings
e. Hybrid response to variations in N, P, K levels.

The equation used in the model is :

$$P_t(T,n) = [Y_t(T,n) \cdot CP_t] - [H_t(T) + F_t(T) + A_t(T) + S_t(n)]$$

where,

$P_t(T,n)$ = **P**rofit (R ha^{-1}) for crop at a given fertilizer **T**reatment, **t**ime and **n**umber of fungicide applications

$Y_t(T,n)$ = **Y**ield (kg ha^{-1}) for crop at a given fertilizer **T**reatment and **n**umber of fungicide applications, and is given in Table 1

Cp_t = **C**urrent maize **P**rice (R ha^{-1})

$H_t(T)$ = **H**arvesting costs (R ha^{-1}) for a given **T**reatment at a given **t**ime, and is shown in Table 2

$F_t(T)$ = **F**ertilizer and application costs (R ha^{-1}) for a given **T**reatment at a given **t**ime, and is shown in Table 2

$A_t(T)$ = cost of N topdressing **A**pplication (R ha^{-1}), for a given **T**reatment at a given **t**ime, shown in Table 2

$S_t(n)$ = cost of **S**praying fungicide (R ha^{-1}), for **n** number of applications at a given time and is shown in Table 3

Table 16. **Y**ield (kg ha^{-1}) for **S**prayed crop at a given fertilizer **T**reatment and **n**umber of fungicide applications

FERTILIZER TREATMENT	NUMBER OF FUNGICIDE APPLICATIONS			
	0	1	2	3
N0K0				
N0K25				
NOK50 etc.....				

Table 2. Costs for aspects of each treatment (R ha^{-1})

FERTILIZER TREATMENT	COSTS (R ha^{-1})		
	HARVESTING	FERTILIZER & APPLICATION	N TOPDRESSING
N0K0			
N0K25			
N0K50 etc.....			

Table 3. Cost (R ha^{-1}) **n**umber of fungicide applications

	NUMBER OF FUNGICIDE APPLICATIONS			
	0	1	2	3
COST				

$$BT_t = MAX \quad [P_t (T,n)]$$

T= N0K0, N0K25, N0K50 etc.

where-

BT_t = **B**est **T**reatment at a particular **t**ime

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CHAPTER 4

Yield increases of wheat grown on residual fertilizers after grey leaf spot diseased maize

Abstract

Grey leaf spot (GLS) of maize (*Zea mays* L.), caused by *Cercospora zeae-maydis* Tehon and Daniels (1925) has risen from relative obscurity in the late 1980s to a major threat to economical production of maize in many areas of the Republic of South Africa (RSA). Maize trials to investigate the effects of nitrogen and potassium soil amendments on the severity and incidence of grey leaf spot relative to grain yield were commenced at Cedara (29°32'S, 30°17'E), RSA in 1995/96. The trial design was a randomised complete block, 3 N X 4 K factorial replicated three times. Plots were split for fungicide treatments. Grain yields from fungicide treated maize were 8.3 t ha^{-1} compared to 4.2 t ha^{-1} from non- fungicide treated maize. Results after the first year of the study showed that the soils were highly fertile. In an effort to reduce nutrients before the continuation of the trial in 1996/97, wheat *(Triticum aestivum* L. var. SST 38) was grown under irrigation on residual fertilizers during the winter months. Wheat grown in soils with residual fertilizers from non-fungicide treated maize yielded 4.2 t ha^{-1}, as silage, compared to wheat yields of 3.6 t ha^{-1} on soils where fungicide treatments were applied to maize to control GLS. The higher yield response of wheat grown on residual fertilizers in soils where maize was not sprayed was attributed to the hypothesis that the pathogen reduces the photosynthetic area of maize leaves, causing premature death with concomitant reduced uptake of nutrients by roots. This results in higher residual levels of fertilizers in soils where fungicide applications are not used to control GLS on maize, compared to soils planted with maize where GLS is controlled with fungicide applications. Implications of this may have far reaching implications for farmers whose maize crops are blighted by GLS. Planting a winter crop on residual fertility could compensate for losses incurred from reduced grain yields of maize blighted by GLS, and reduce acidifying effects and nitrogen build up which leads to increased GLS.

4.1 Introduction

Grey leaf spot (GLS) of maize (*Zea mays* L.), caused by *Cercospora zeae-maydis* Tehon and Daniels (1925), is recognised as one of the most significant grain yield-limiting diseases of maize world-wide (Lipps *et al.*, 1998; Ward and Nowell, 1998). It is estimated that GLS is spreading at a rate of 80-160 km each year (Garst Seeds, 1996). The occurrence of the pathogen in the province of KwaZulu-Natal (KZN), RSA in 1988 was the first official report from Africa (Nowell, 1997). It has caused grain yield losses of up to 60% in this region. The pathogen has since been detected in a number of African countries, including Cameroon, Kenya, Malawi, Mozambique, Swaziland, Tanzania, Uganda, Zaire, Zambia and Zimbabwe (Nowell, 1997; Ward and Nowell, 1998).

The diagnostic features of GLS are the distinct rectangular lesions along major veins caused by cercosporin, a non-host-specific toxin produced by several species of the genus *Cercospora* (Daub, 1982; Blaney, *et al.*,1988). Cercosporin is extremely toxic to plant cells, acting as a photosensitizing agent that sensitizes and kills plant cells when they are exposed to visible light (Daub, 1982; Daub and Hangarter, 1983; Lipps, 1987). With the decreased photosynthetic area in diseased leaves, there is a reduction in photosynthesis and consequently a reduction in carbohydrate metabolism in leaves and subsequent loss in grain yield. This could lead to a decrease in uptake of nutrients by the roots, leaving increased residual fertilizers in the soil, relative to soils where maize is not infected with *C. zeae-maydis*. If this does occur, then the following crop, whatever it is, needs a lower application level of fertilizer to account for the higher levels of residual fertilizer, especially as soil analyses would not detect the raised nitrogen levels present.

The findings presented in this paper were part of a series of trials to investigate the effects of nitrogen (N) and potassium (K) on the development and severity of GLS and the resulting economic implications. Although GLS increased with increasing applications of N and K, in the first year (1995/96) of the three-year

trial, the results were not significant. It was felt that this lack of response could have been due to high residual levels of fertilizers because a pasture ley of *Eragrostis curvula* (Schrad.) Nees had previously been planted on the site, together with the high fertility levels of organic soils in the Midlands of KwaZulu-Natal.

No information is available on the yields of crops grown on residual fertilizers after maize which had been blighted by GLS. The aim of this study was to investigate yield response of wheat, as silage, grown on soils after a maize crop severely blighted by GLS. At the same time, it was hoped that soil N and K levels would be reduced before continuing the maize trial in 1996/97.

4.2 Materials and methods

4.2.1 *Maize trial*

Trial site

The trial was carried out at Cedara Agricultural Development Institute (CADI) (29°32'S, 30°17'E; altitude 1070 m) on well-drained, deep sandy-clay loams of the Hutton form and Doveton series (MacVicar, 1991). The trial site had been previously planted to *Eragrostis curvula* (Schrad.) Nees.

Six weeks before planting, dolomitic lime (6.3 t ha $^{-1}$) was applied to reduce acid saturation to < 20% and disced to a depth of 200-250 mm. Land preparation, involving mouldboard ploughing and discing, was carried out in September, 1995. The trial was a randomized factorial design split for fungicide treatments. Three levels of N (0, 60 and 120 kg N ha $^{-1}$) and four levels of K (0, 25, 50 and 150 kg

K ha^{-1}) were applied. Gross plot size was 8 m x 6 m comprising 8 rows, 8 m long, spaced 750 mm apart.

Soil sampling and fertilizer application

Twenty one cores (0 -150 mm deep) were taken from each plot three weeks before and three weeks after planting and fertilizing the maize trial. A 1 m border of plants at the end and sides of each plot was excluded for sampling purposes. Samples were mixed and air-dried before analysis for phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), aluminium (Al), zinc (Zn), acid saturation, and pH by the Cedara Fertilizer Advisory Service (Farina and Channon, 1988) (Table 1).

Immediately before planting, fertilizers were applied by hand and incorporated by discing to a depth of approximately 100-150 mm. All plots in both seasons received 105 kg P ha^{-1} (as double superphosphate; 20% P), 50 kg S ha^{-1} (as calcium sulphate; 18% S) and 30 kg Zn ha^{-1} (as zinc sulphate; 23% Zn) as KZN soils are deficient in S and Zn. Potassium treatments (as potassium chloride; 50% K) were applied at planting at 0, 25, 50 and 150 kg K ha^{-1}. Nitrogen treatments (as limestone ammonium nitrate; with N as 14 % NH_4^+ and 14% NO_3^-) were 0, 60 and 120 kg N ha^{-1}. The 60 and 120 kg N ha^{-1} treatments were split with 30 kg N ha^{-1} as a preplant application, and the remainder was applied as a topdressing when plants were 300 mm tall. Ammonium nitrate is converted into nitrate within 10-14 days after application in summer in RSA (Miles, personal communication)[1]. It was, therefore, assumed that the effect of the nitrate form of N on GLS was investigated in the trial.

[1]Dr N. Miles, Cedara Agricultural Development Institute, Private Bag, X9059, Pietermaritzburg, 3200 RSA

Planting procedure

A maize cultivar, ZS 206, was used because it is both high grain-yielding and susceptible to GLS. Maize was hand-planted on 22 November, 1995 with two seeds per plant station. Approximately 30 days after planting (DAP), plants were hand-thinned to 44,000 plants ha^{-1}. A tank-mix of metolachlor (1.86 g a.i. ha^{-1}) plus atrazine / metolachlor / terbuthylazine (550 / 663 / 550 g a.i. ha^{-1}) was applied as a pre-emergent, overall treatment in 300 L water for the control of grasses and broadleaf weeds. Fenvalerate (28 g a.i. ha^{-1}) was included in the herbicide tank-mix for the control of cutworm. Carbofuran granules (2.7 kg a.i. ha^{-1}) were applied in the planting furrow for the control of soil insect pests.

Fungicide applications and disease assessments

Fungicide applications were made in accordance with frequency and timing of applications as described by Ward *et al.* (1997). Three full-cover sprays were applied to the centre two rows of each fungicide treated plot using a combination of 188 g carbendazim and 94 g flusilazole ai ha^{-1} (Punch Xtra, Du Pont de Nemoirs and Coy) during the course of the trial 61, 93 and 116 DAP.

Whole-plant standard area diagrams described by Ward *et al.* (1997) were used as a guide to estimate percent disease severity of the central plants in the two centre rows of each plot. These data were used to calculate the area under disease progress curve (AUDPC) using a trapezoidal integration program (Berger, 1981).

Leaf sampling

Leaf sampling for chemical analysis was carried out at 50% anthesis by collecting the leaf opposite and below the ear of each plant in the centre two rows of each fungicide and non-fungicide treated plot. A 1 m border of plants was excluded from both ends of each row for sampling purposes. The leaf samples were oven-

dried overnight at 75°C, milled to pass through a 1 mm screen and were then analyzed. Analysis of N was by near infra-red spectrophotometry, and after dry-ashing, P was measured colorimetrically and K, calcium (Ca), magnesium (Mg), sodium (Na), Zn, copper (Cu) and manganese (Mn) by atomic absorption.

Harvesting procedures

Net plot size for hand-harvesting was 6 m of the centre two rows of each plot in June, 1995. The dehusked ears of the harvested rows were weighed in the field. Sub-samples of five or six ears were weighed and shelled in the laboratory and the shelling percentage determined to calculate the shelled grain mass. Moisture content of a 250 g sample of shelled grain was determined and the grain yield, expressed in t ha^{-1}, was adjusted to 12.5% grain moisture content.

4.2.2 *Wheat trial*

After harvesting the maize trial, stalks were cut with a stalk chopper and raked to the side of the contour. Soils were cultivated to a depth of 10-15 cm prior to planting wheat (*Triticum aestivum* L. var. SST 38). A tank-mix of metolachlor (1.86 g a.i. ha^{-1}) plus atrazine / metolachlor / terbuthylazine (550 / 663 / 550 g a.i. ha^{-1}) was applied as a pre-emergent, overall treatment in 300 L water for the control of grasses and broadleaf weeds. Fenvalerate (28 g a.i. ha^{-1}) was included in the herbicide tank-mix for the control of cutworm. Carbofuran granules (2.7 kg a.i. ha^{-1}) were applied in the planting furrow for the control of soil insect pests.

Wheat was planted on 12 June, 1996 at a seeding rate of 200 kg ha^{-1} and irrigated throughout the winter months. Harvesting took place on 4 November before the wheat had formed fully-developed ears as sufficient time for soil sampling and seedbed preparation had to be made before the 1996/97 maize trial. Wheat was harvested by machine mowing the centre 1.4 m of each maize fungicide treated and non-fungicide treated plot. A 1m border of plants was excluded from both ends of each plot for sampling purposes. Harvested material was weighed in the

field (NPGW = net plot green weight) and a representative sample from each plot collected and weighed in the laboratory to record the net sample green weight (NSGW), then oven-dried at 75° C for 48h, and reweighed to record the net sample dry weight (NSDW) from which the dry matter yield of each plot was calculated.

Statistical analyses

Statistical analysis of leaf analyses, final percentage leaf blighting, AUDPC and yields of fungicide and non-fungicide treated maize, were conducted using analysis of variance (ANOVA) and mean separations were based on Fischer's LSD at the 1 and 5% level of probability using Genstat 5.2 (Anonymous, 1987).

4.3 Results

Increased N and K applications did not significantly affect leaf analyses, final percentage leaf blighting, AUDPC and yields of maize (as grain) and wheat (as silage). In addition, there were no N:K interactions. However, in all parameters measured, there was a significant difference between fungicide treated and non-fungicide treated plots. For these reasons, only the means of the trial of fungicide and non-fungicide treated maize are recorded for the purposes of this chapter.

Soil analyses

Analyses of soil nutrients were not split for fungicide treatments, as soil samples in the first year of the trial (1995/96) were taken before any fungicide applications commenced. Selected properties of soils at the trial site are shown in Table 1.

Table 1. Selected properties of soils (0-150 mm) after planting of 1995/96 maize trial prior to fungicide applications at Cedara.

Property	Level	CV (%)
Phosphorus (mg kg^{-1})	4.4	28.5
Potassium ($cmol_c kg^{-1}$)	0.3	17.2
Calcium ($cmol_c kg^{-1}$)	3.5	19.7
Magnesium ($cmol_c kg^{-1}$)	0.9	13.5
Aluminium ($cmol_c kg^{-1}$)	0.6	37.0
Zinc (mg L^{-1})	2.5	33.4
Acid saturation (%)	11.6	40.5
pH	4.5	2.2

Leaf analyses

Maize leaf nutrient analyses showed significant differences between fungicide and non-fungicide treated maize (Table 2). Calcium showed no change, and N, P, Mn, Mg and Na were all lower in the fungicide treated maize leaves. Potassium, Zn and Cu levels were lower in the non-fungicide treated than fungicide treated maize leaves.

Table 2. Leaf analysis of fungicide treated and non-fungicide treated maize leaves at Cedara (1995/96)

Element	Fungicide treated	Non-fungicide treated	% difference between non-fungicide and fungicide treated	F value	Probability	CV (%)
Nitrogen (%)	3.478	3.583	3	11.700	0.002 **	3.7
Phosphorus (%)	0.347	0.361	4	7.400	0.012 *	6.1
Potassium (%)	1.661	1.350	-19	43.160	< 0.001 ***	13.3
Calcium (%)	0.665	0.658	-1	0.390	0.538	6.8
Magnesium (%)	0.336	0.363	8	8.800	0.007 **	10.7
Sodium (%)	0.077	0.144	87	5.290	0.030 *	11.5
Zinc (mg kg^{-1})	21.560	19.030	-12	4.520	0.044 *	29.4
Copper (mg kg^{-1})	10.080	8.140	-25	28.490	< 0.001 ***	17.0
Manganese (mg kg^{-1})	50.750	55.250	9	10.870	0.003 **	17.0

NS = non-significant ($P > 0.05$); * = significant ($P \leq 0.05$);
** = highly significant ($P \leq 0.01$) ; *** = very highly significant ($P \leq 0.001$)

Final percentage leaf blighting and area under disease progress curve

Final percentage leaf blighting and AUDPC was significantly higher in non-fungicide treated compared to fungicide treated maize (Table 3).

Table 3. Final percentage leaf blighting and area under disease progress curve (AUDPC) in fungicide treated and non-fungicide treated maize at Cedara (1995/96)

	Fungicide treated	Non-fungicide treated	F value	Probability	CV (%)
Final percentage leaf blighting	53	93	213.350	< 0.001 ***	16
AUDPC	1120	3129	3102.640	< 0.001 ***	7.2

NS = non-significant (P > 0.05); * = significant (P ≤ 0.05);
** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)

Grain yields

Maize grain yields were significantly higher in fungicide treated compared to non-fungicide treated maize. In contrast, grain yields of wheat grown on the soils after non-fungicide treated maize were higher than those grown on the soils following fungicide treated maize (Table 4).

Table 4. Grain yields of fungicide treated and non-fungicide treated maize and yields of wheat, as silage, grown on soils following fungicide treated and non-fungicide treated maize at Cedara (1995/96)

Yield (t ha $^{-1}$)	Fungicide treated	Non-fungicide treated	% difference between non-fungicide and fungicide treated	F value	Probability	CV (%)
Maize (grain)	8.34	4.22	-51	496.65	< 0.001 ***	11.6
Wheat (silage)	3.61	4.15	15	7.04	0.014 *	12.3

NS = non-significant (P > 0.05); * = significant (P ≤ 0.05);
** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)

4.4 Discussion

In the absence of a reliable soil test for N, it is not possible to quantify reserves of N which exist in soils. However, increased yields of wheat grown on soils after maize severely blighted by GLS, indicated that there was a higher residual carry over of N and other nutrients compared to soils after a fungicide treated maize crop.

The acidifying effects from residual N-carryover after GLS-blighted maize in intensive cropping with high N-usage, leads to a build up of available soil Al and Mn. The toxic effects from excess Al result in a reduction of root growth which limits plants' ability to extract water and soil nutrients, with concomitant reduced grain yields (Farina *et al.*, 1993). High N levels also result in increased GLS as *C. zeae-maydis* is a high sugar disease (Nowell, 1997).

This has practical implications for small-scale farmers, who do not apply fungicide sprays, as well as commercial farmers who do not spray correctly to control GLS. Planting a winter crop to utilize residual fertilizers after a failed maize crop due to intense GLS blighting, would help to utilize residual N and prevent acidity build-up. This principle should be investigated for other crops to ascertain if this is a general principle.

Foliar leaf analyses of maize may not be a good indication of nutrient uptake because leaf samples are taken at the time of silking by which time final nutrient uptake is not yet complete; e.g., final uptake of N, P, Mg, Na and Mn is only completed at maturity (Anonymous, 1986). Furthermore, GLS is more severe from the time of tasselling to maturity. This could account for the unexpected higher foliar levels of N, P, Mg, Na and Mn in the non-fungicide treated maize leaves.

Lower foliar K levels were found in non-fungicide treated compared to fungicide treated maize. This could be due to the fact that increased leaf blighting resulted in reduced uptake of K. This was a true assessment of K uptake, as most soil K is taken up by silking (Anonymous, 1986).

Final disease severity and AUDPC were significantly higher in the non-fungicide compared to the fungicide treated maize which accounted for the lower grain yields in the non-fungicide treated maize plots. It is hypothesized that increased leaf blighting and loss of photosynthetic area resulted in reduced uptake of nutrients and higher residual levels of soil nutrients, resulting in higher dry matter yields in the subsequent wheat trial. In contrast, the fungicide treated maize, with a lower AUDPC value, had a higher photosynthetic leaf area and utilized more soil nutrients for photosynthesis, resulting in lower residual levels of soil nutrients and consequent lower wheat yields compared to wheat grown on soils after GLS infected maize. These results support the hypothesis of higher residual nutrient levels in soils following a maize crop severely affected by GLS.

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CHAPTER 5

Maize hybrid resistance to conidial germination of *Cercospora zeae-maydis* at varying temperatures, desiccation and interrupted dew periods

Abstract

Conidial germination of *Cercospora zeae-maydis* was investigated on two maize cultivars, one resistant (SC 625) and one susceptible (ZS 206) in a dew chamber at 95-100 % relative humidity with 14 hrs light and 8 hrs darkness. Conidia were inoculated onto maize leaves and incubated at 19, 22, 25, 28, 31 and 33 °C. No germination was observed at 19 °C or 33 °C in either SC 625 and ZS 206. Maximum germination occurred at 28 °C by 48 hr for both cultivars (100% and 63 % for ZS 206 and SC 625, respectively). As the number of days (1-5) of desiccation increased following inoculation, germination decreased from 100 to 47% in ZS 206 and from 62 to 0% in SC 625. In interrupted dew period studies (2-36 hrs) following a 6 hr period at 95 -100 % RH at 28 °C in a dew chamber, there was no change in percentage germination after 48 hrs, but germination was higher (90%) on ZS 206 than on SC 625 (64%). The wider range of temperature conditions favourable for conidial germination and the fact that conidia were less affected by desiccation and interrupted dew periods on ZS 206 than SC 625, could account for the different susceptibility levels of these two hybrids to GLS. These results confirmed field trials which showed ZS 206 to be highly susceptible to GLS and requiring three fungicide sprays to achieve maximum grain yield. In contrast, SC 625 was found to be resistant/tolerant to GLS with no increase in grain yield following one, two or three fungicide sprays.

5.1 Introduction

Cercospora zeae-maydis Tehon and Daniels is the causal organism of grey leaf spot (GLS) on maize (*Zea mays* L.), a disease that under conditions of prolonged moderate temperatures (20-30°C) and high (90-95%) relative humidity (RH) can result in extensive leaf blighting and significant yield loss (Beckman and Payne, 1982; Rupe *et al.*, 1982; Thorson, 1989, Ward, 1996; Nowell, 1997).

A notable feature of conidial germination of *C. zeae-maydis* is its ability to survive adverse conditions once germination has commenced. Relative humidity does not have to be continuous for infection to occur as developing conidia can remain quiescent until favourable RH conditions re-occur (Beckman and Payne, 1982; Latterell and Rossi, 1983; Thorson and Martinson, 1993).

Minor changes of temperature and humidity occur in a microclimate resulting in fluctuations of RH between 95 and >100%. This takes RH through the dew point resulting in leaf wetness from dew deposited on the leaf surface. However, leaf wetness and RH have often been confused parameters in previous research work, particularly research on *C. zeae-maydis*. .

Rupe *et al.* (1982) conducted germination trials on *C. zeae-maydis* using agar plates, glass slides and cut leaves. They found that optimum conditions for germination were 9 hrs of continuous leaf wetness at temperatures of 18-25° C. Thorson (1989), using leaf discs and high RH levels (95-100%), found that a minimum of 6 hrs continuous leaf wetness was required for germination. Non-germinating conidia were unable to survive wetting and drying but germinating conidia survived short dry periods without adverse effects on germ tubes. No record of hybrid resistance/tolerance or susceptibility to GLS was recorded in this research.

Genetic resistance in maize to GLS is the most cost-effective option for managing GLS (Graham *et al.,* 1993, Coates and White, 1995). In contrast to the situation in the United States of America (USA), a high frequency of quantitative resistance to GLS has been found in commercial hybrids in the Republic of South Africa (RSA) (Ward *et al*, 1993; Ward *et al.*, 1996; Nowell, 1997). In addition to polygenic quantitative resistance, monogenic qualitative resistance to GLS has been found in one South African hybrid (Thompson *et al.,* 1987; Gevers *et al.,*1994). A number of breeding programmes have directed considerable effort toward discovering resistant or tolerant germ-plasm. Quantitative trait loci (QTL) with additive gene action (Thompson *et al.*, 1987; Bubeck *at al.*, 1993; Saghai Maroof *et al.*, 1996) or dominant genes with major effects (Elwinger *et al.*, 1990; Gevers *et al.*, 1994) have been shown to control resistance to GLS.

Stromberg and Donahue (1986) classified maize hybrids into three susceptibility groups to GLS. Work conducted at Cedara Agricultural Development Institute (CADI) (29°32'S, 30°17'E) confirmed that South African commercial hybrids can be grouped into highly susceptible, intermediate and resistant/tolerant to GLS (Ward *et al.,*1999). Resistant hybrids, e.g., SC 625 showed no yield response to 1, 2 or 3 fungicide treatments. Intermediate hybrids had yield responses to 1 and 2 fungicide sprays. Hybrids most susceptible to GLS, e.g., ZS 206, only achieved maximum grain yields following three sprays.

Survival of spores in different environmental conditions before penetrating the host is a key component in the life cycle of many fungal pathogens. No research on environmental effects on conidial germination of *C. zeae-maydis in vivo* or on maize hybrids with known varying susceptibility to GLS, has been reported. The aim of this research was to investigate conidial germination of *C. zeae-maydis* at varying temperatures, desiccation periods and interrupted dew periods in a dew chamber using the maize hybrid, ZS 206 (highly susceptible to GLS) and SC 625 (resistant/tolerant to GLS).

5.2 Materials and methods

Trials were carried out in a dew chamber with 14 hrs light and 12 hrs darkness at 95-100% RH monitored with a 7-day recording thermohydrograph. Five SC 625 and five ZS 206 plants, positioned equidistant from the sides of the dew chamber, were used in each set of experiments. Plants were rotated inside the dew chamber at the time of leaf sampling. During sampling procedures, temperature within the chamber dropped less than 2-3 °C and re-equilibrated within 5-10 minutes. All temperature measurements in the dew chamber were taken with a mercury thermometer. Dew was visible on leaves within 20 minutes of being placed in the chamber. Each experiment was repeated at least twice, and the differences between mean germination percentages analysed using Genstat 5.3 (Anonymous, 1995). The same procedures were used for each of the different environmental conditions investigated.

5.2.1 Inoculum and inoculation procedure

Conidia of *C. zeae-maydis* were freshly collected from diseased maize plants grown in the field at CADI during the maize growing seasons of 1997/98 and 1998/99. Maize seedlings of SC 625 and ZS 206 were grown singly in 15 cm-diameter pots to the 6 -7 leaf stage in a glasshouse at 23-25° C. Conidia were collected from lesions on leaves with a damp camel hair paint brush. A conidial suspension (approx. 5×10^{-4} conidia per millilitre) was painted onto the adaxial surface of the distal two-thirds of the fifth leaf of the maize seedlings. Inoculated leaves were air-dried for approximately one hour before plants were placed in the dew chamber.

5.2.2 Leaf sample observations for light microscopy

After the specified treatments, leaf samples from each of the five inoculated leaves, starting from the distal end of the leaf, were removed and fixed in FAA (900 ml of 70% alcohol : 50 ml formalin : 50 ml glacial acetic acid). A minimum of 24 hrs was allowed for clearing of the leaf tissue. Leaf samples were then stained with 0.01% trypan blue in 0.05% lactic acid overnight. The midrib was excised and the adaxial leaf surface

examined under a light microscope (100X). All germinating conidia (50 to 100) were counted, excluding those germinating in large clumps. The arbitrary criterion developed by Manners (1996) was applied, where a spore was considered germinated if the length of the germ tube exceeded the average length of the spore. Conidia adhered tightly to leaf surfaces. Less than 0.5% of the conidia washed off during fixation and were not included in germination assessments.

5.2.3 Influence of temperature on conidial germination

Maize leaves were inoculated and placed in a dew chamber at 19, 22, 25, 28, 31 and 33 °C. After 2, 4, 6, 8 10, 12, 24, 36 and 48 hrs post inoculation (hpi), 35 mm sections of leaf were removed from each inoculated leaf and the adaxial leaf surface examined for germination.

5.2.4 Influence of duration of desiccation on conidial germination

To determine the influence of desiccation on conidial germination, inoculated plants were maintained in a controlled environment chamber with 14hrs light and 10 hrs darkness at 25 °C and 40-50% RH for 1, 2, 3, 4 and 5 days after inoculation. Plants were then transferred to a dew chamber at 28 °C and 95-100% RH. Five ZS 206 and five SC 625 plants were kept in the dew chamber as controls. Leaf samples were taken after 2, 4, 6, 8, 10, 12, 24, 36 and 48 hrs after the desiccation period and examined for conidial germination.

5.2.5 Influence of interrupted dew period on conidial germination

Inoculated plants were placed in a dew chamber at 28 °C and 95-100% RH for 6 hours. After this time plants were transferred to a controlled environment chamber at 25 °C with 40-50% RH for 2, 6, 12, 24 and 36 hrs. Plants were then returned to the dew chamber at 28 °C and 95-100% RH. Five SC 206 and five ZS 625 plants were kept in the dew chamber as controls. Leaf samples were taken 48 hpi and germination percentages assessed as described above.

5.3 Results

5.3.1 *Influence of temperature on conidial germination*

Maximum conidial germination after 48 hrs for both cultivars occurred at 28 °C with 100 and 63 % germination on ZS 206 and SC 625, respectively (Table 1 to 8a and b; Fig. 1a-1d). Germ tubes of ZS 206 were initiated on leaf surfaces 2 hpi but only 8 hpi on SC 625. At 25 °C, germination on ZS 206 commenced 4 hpi in contrast to 24 hpi on SC 625. No conidial germination was observed at 19 °C or 33 °C on either cultivar. Conidial germination 48 hpi on ZS 206 was 3, 98, 100 and 39 % at 22, 25, 28 and 31 °C. Germination on SC 625 was significantly lower (0, 62, 63 and 3 %) at these same temperatures.

TABLE 1a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 4 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 4				
temperature	3	3.113	5.110	0.003 **
cultivar	1	9.113	14.970	< 0.001***
temp.cultivar	3	3.113	5.110	0.003 **
Residual (63)				
CV % = 71.7				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 1b. Table of means of percentage conidial germination at varying temperatures at 4 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	0.00	1.20
28	0.00	1.50
31	0.00	0.00
Cultivar mean	0.00	0.68
$LSD_{(0.05)}$ temperature	0.49	
$LSD_{(0.05)}$ cultivar	0.35	
$LSD_{(0.05)}$ temp.cultivar	0.70	

Table 2a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 6 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 6				
temperature	3	3990.713	861.78	<0.001 ***
cultivar	1	6426.113	1387.70	<0.001 ***
temp.cultivar	3	3990.713	861.78	<0.001 ***
Residual (63)				
CV % = 24.0				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 2b. Table of means of percentage conidial germination at varying temperatures at 6 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	0.00	12.30
28	0.00	59.40
31	0.00	0.00
Cultivar mean	0.00	17.92
$LSD_{(0.05)}$ temperature	1.36	
$LSD_{(0.05)}$ cultivar	0.96	
$LSD_{(0.05)}$ temp.cultivar	1.92	

Table 3a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 8 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 8				
temperature	3	6330.150	906.98	<0.001 ***
cultivar	1	10351.250	1483.12	<0.001 ***
temp.cultivar	3	3810.950	546.03	<0.001 ***
Residual (63)				
CV % = 19.2 * = significant (P ≤ 0.05); ** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 3b. Table of means of percentage conidial germination at varying temperatures at 8 hours post inoculation (hpi)

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	0.00	35.10
28	9.40	65.30
31	0.00	0.00
Cultivar mean	2.35	25.10
$LSD_{(0.05)}$ temperature	1.67	
$LSD_{(0.05)}$ cultivar	1.18	
$LSD_{(0.05)}$ temp.cultivar	2.36	

Table 4a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 10 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 10				
temperature	3	10366.433	2289.92	<0.001 ***
cultivar	1	14098.050	3114.23	<0.001 ***
temp.cultivar	3	14176	4725.483	<0.001 ***
Residual (63)				
CV % = 11.4				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 4b. Table of means of percentage conidial germination at varying temperatures at 10 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	0.00	55.90
28	21.30	71.60
31	0.00	0.00
Cultivar mean	5.33	31.88
$LSD_{(0.05)}$ temperature	1.345	
$LSD_{(0.05)}$ cultivar	0.951	
$LSD_{(0.05)}$ temp.cultivar	1.901	

Table 5a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 12 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 12				
temperature	3	12648.800	2628.65	<0.001 ***
cultivar	1	17464.050	3629.34	<0.001 ***
temp.cultivar	3	5836.050	1212.84	<0.001 ***
Residual (63)				
CV % = 10.7				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 5b. Table of means of percentage conidial germination at varying temperatures at 12 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	0.00	61.20
28	22.90	79.90
31	0.00	0.00
Cultivar mean	5.73	35.28
$LSD_{(0.05)}$ temperature	1.39	
$LSD_{(0.05)}$ cultivar	0.98	
$LSD_{(0.05)}$ temp.cultivar	1.96	

Table 6a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 24 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 24				
temperature	3	29238.17	2124.70	<0.001 ***
cultivar	1	4410.45	320.50	<0.001 ***
temp.cultivar	3	997.95	72.52	<0.001 ***
Residual (63)				
CV % = 10.3				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 6b. Table of means of percentage conidial germination at varying temperatures at 24 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	0.00
25	55.10	73.70
28	57.20	89.90
31	2.40	10.50
Cultivar mean	28.67	43.53
$LSD_{(0.05)}$ temperature	2.34	
$LSD_{(0.05)}$ cultivar	1.66	
$LSD_{(0.05)}$ temp.cultivar	3.32	

Table 7a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 36 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 36				
temperature	3	30854.18	2366.46	<0.001 ***
cultivar	1	7840.80	6601.38	<0.001 ***
temp.cultivar	3	791.33	60.69	<0.001 ***
Residual (63)				
CV % = 9.0 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 7b. Table of means of percentage conidial germination at varying temperatures at 36 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	3.60
25	57.30	82.30
28	61.50	94.70
31	2.50	19.90
Cultivar mean	30.32	50.12
$LSD_{(0.05)}$ temperature	2.28	
$LSD_{(0.05)}$ cultivar	1.61	
$LSD_{(0.05)}$ temp.cultivar	3.22	

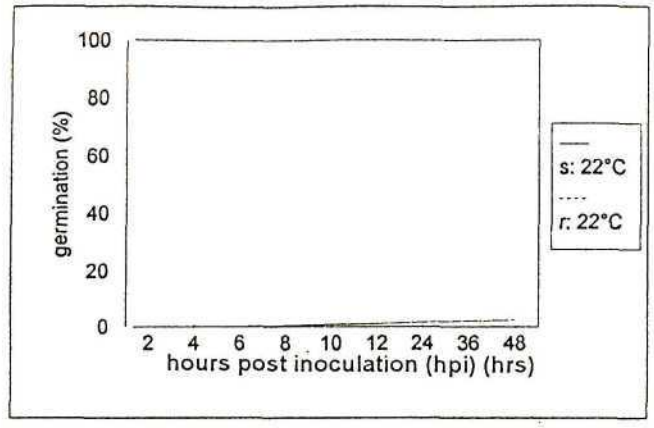
Table 8a. ANOVA table of effect of temperature on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivars 48 hrs post inoculation

	Degree of freedom	Mean square	F value	Probability
hours post inoculation = 48				
temperature	3	33207.446	4817.24	<0.001 ***
cultivar	1	15596.113	2262.45	<0.001 ***
temp.cultivar	3	1349.712	195.80	<0.001 ***
Residual (63)				
CV % = 5.7 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 8b. Table of means of percentage conidial germination at varying temperatures at 48 hours post inoculation

Temperature (°C)	% germination on SC 625	% germination on ZS 206
22	0.00	3.30
25	61.60	97.60
28	63.00	100.00
31	3.30	38.70
Cultivar mean	31.98	59.90
$LSD_{(0.05)}$ temperature	1.66	
$LSD_{(0.05)}$ cultivar	1.17	
$LSD_{(0.05)}$ temp.cultivar	2.35	

(a)



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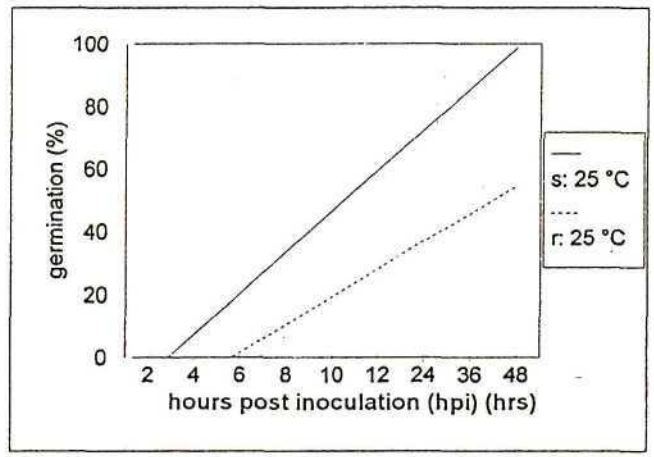

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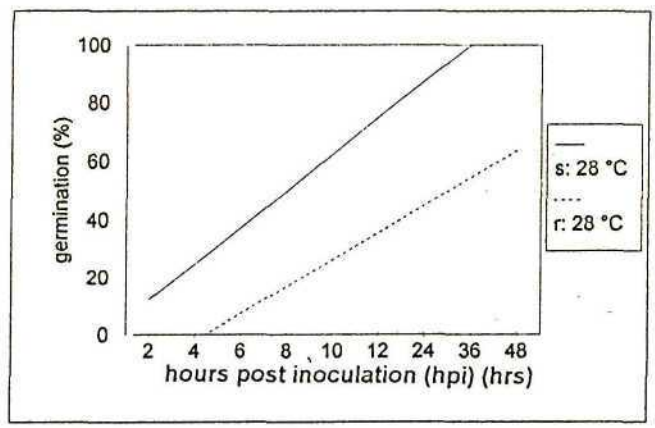

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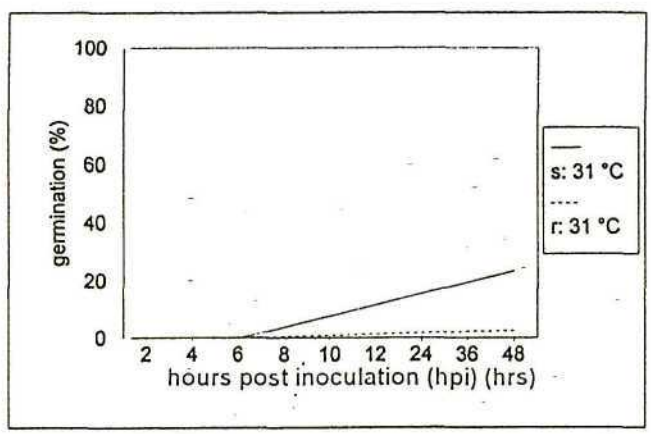

Fig. 1. Effect of temperature on conidial germination of *Cercospora zeae-maydis* on susceptible (s) and resistant (r) maize cultivars at (a) 22 °C; (b) 25 °C; (c) 28 °C; (d) 31 °C

5.3.2 Influence of desiccation on conidial germination

After one day's desiccation, germination after 48 hpi was the same as when plants were incubated at 28 °C and 95-100% RH immediately after inoculation (Tables 9-15a and b; Fig. 2a-f). However, there was a marked decrease in germination with increasing days of desiccation. On ZS 206, conidial germination decreased from 100 to 92, 63, 61, 53 and 46 % and on SC 625 from 63 to 62, 58, 38, and 0 % after 0 to 5 days' desiccation. Non-germinating conidia did not take up the stain well and started disintegrating after 3 days.

Table 9a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 6 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 6				
days desiccation	5	2566.875	402.65	<0.001 ***
cultivar	1	2566.875	402.65	<0.001 ***
days desiccation. cultivar	5	2566.875	402.65	<0.001 ***
Residual (99)				
CV % = 54.6 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 9b. Table of means of percentage conidial germination after varying days of desiccation and 6 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	0.00	55.50
1	0.00	0.00
2	0.00	0.00
3	0.00	0.00
4	0.00	0.00
5	0.00	0.00
Cultivar mean	0.00	0.00
$LSD_{(0.05)}$ days desiccation	1.58	
$LSD_{(0.05)}$ cultivar	0.92	
$LSD_{(0.05)}$ days desiccation.cultivar	2.24	

Table 10a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 8 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 8				
days desiccation	5	3314.333	522.43	<0.001 ***
cultivar	1	11880.300	1872.65	<0.001 ***
days desiccation. cultivar	5	2624.760	413.73	<0.001 ***
Residual (99)				
CV % = 23.8 * = significant (P ≤ 0.05); ** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 10b. Table of means of percentage conidial germination at varying days of desiccation and 8 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	3.80	65.90
1	0.00	29.80
2	0.00	9.40
3	0.00	0.00
4	0.00	7.60
5	0.00	10.50
Cultivar mean	0.63	20.53
$LSD_{(0.05)}$ days desiccation	1.58	
$LSD_{(0.05)}$ cultivar	0.91	
$LSD_{(0.05)}$ days desiccation.cultivar	2.24	

Table 11a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 10 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 10				
days desiccation	5	4680.428	635071	<0.001 ***
cultivar	1	12060.075	1638.03	<0.001 ***
days desiccation. cultivar	5	1932.295	262.45	<0.001 ***
Residual (99)				
CV % = 17.48 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 11b. Table of means of percentage conidial germination at varying days of desiccation and 10 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	12.00	71.30
1	21.50	32.10
2	0.00	20.20
3	0.00	11.10
4	0.00	8.60
5	0.00	10.50
Cultivar mean	5.58	25.63
$LSD_{(0.05)}$ days desiccation	1.70	
$LSD_{(0.05)}$ cultivar	0.98	
$LSD_{(0.05)}$ days desiccation. cultivar	2.41	

Table 12a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 12 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 12				
days desiccation	5	7980.83	479.28	<0.001 ***
cultivar	1	12875.41	773.22	<0.001 ***
days desiccation. cultivar	5	1067.27	64.09	<0.001 ***
Residual (99)				
CV % = 20.7 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 12b. Table of means of percentage conidial germination at varying days of desiccation and 12 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	31.70	79.90
1	24.70	36.20
2	0.00	24.90
3	0.00	18.40
4	0.00	9.80
5	0.00	11.50
Cultivar mean	9.40	30.12
$LSD_{(0.05)}$ days desiccation	2.56	
$LSD_{(0.05)}$ cultivar	1.48	
$LSD_{(0.05)}$ days desiccation.cultivar	3.62	

Table 13a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 24 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 24				
days desiccation	5	14354.71	1072.52	<0.001 ***
cultivar	1	18476.01	1380.45	<0.001 ***
days desiccation. cultivar	5	1106.07	82.64	<0.001 ***
Residual (99)				
CV % = 9.1 * = significant (P ≤ 0.05); ** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 13b. Table of means of percentage conidial germination at varying days of desiccation and 24 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	58.50	90.40
1	55.60	64.80
2	50.40	61.40
3	2.90	52.10
4	0.00	27.30
5	0.00	20.30
Cultivar mean	27.90	52.72
$LSD_{(0.05)}$ days desiccation	2.30	
$LSD_{(0.05)}$ cultivar	1.33	
$LSD_{(0.05)}$ days desiccation. cultivar	3.25	

Table 14a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 36 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 36				
days desiccation	5	11300.02	739.12	<0.001 ***
cultivar	1	30912.30	2021.92	<0.001 ***
days desiccation. cultivar	5	1585.44	103.70	<0.001 ***
Residual (99)				
CV % = 8.1				
* = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 14b. Table of means of percentage conidial germination at varying days of desiccation and 36 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	59.10	94.30
1	62.40	78.60
2	56.50	61.60
3	14.30	56.40
4	0.00	52.00
5	0.00	42.00
Cultivar mean	32.05	64.15
$LSD_{(0.05)}$ days desiccation	2.45	
$LSD_{(0.05)}$ cultivar	1.42	
$LSD_{(0.05)}$ days desiccation. cultivar	3.47	

Table 15a. ANOVA table of effect of desiccation (days) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar and 48 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 48				
days desiccation	5	12134.11	905.74	<0.001 ***
cultivar	1	31882.80	2379.85	<0.001 ***
days desiccation. cultivar	5	1531.60	114.32	<0.001 ***
Residual (99)				
CV % = 6.9 * = significant (P ≤ 0.05); ** = highly significant (P ≤0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 15b. Table of means of percentage conidial germination at varying days of desiccation and 48 hrs after incubation at 28 °C

No. of days desiccation	% germination on SC 625	% germination on ZS 206
0	61.70	100.00
1	62.30	92.90
2	58.40	63.30
3	38.90	61.00
4	0.00	53.20
5	0.00	46.50
Cultivar mean	36.88	69.48
$LSD_{(0.05)}$ days desiccation	2.30	
$LSD_{(0.05)}$ cultivar	1.33	
$LSD_{(0.05)}$ days desiccation.cultivar	3.25	

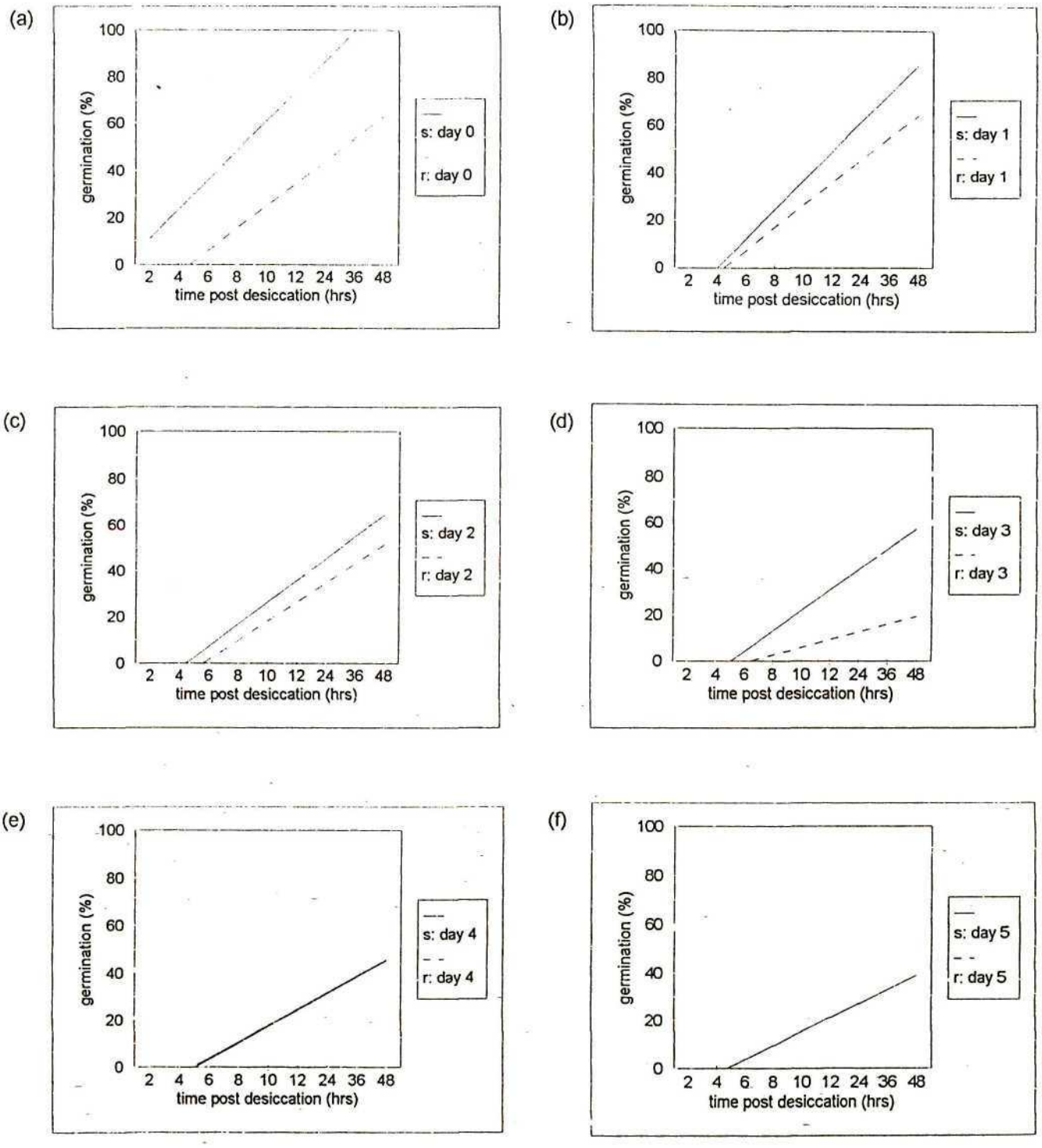

Fig. 2. Effect of desiccation on conidial germination of *Cercospora zeae-maydis* on resistant (r) and susceptible (s) maize cultivars at (a) day 0 - control; (b) day 1; (c) day 2; (d) day 3; (e) day 4; (f) day 5

5.3.3 Influence of interrupted dew period on conidial germination

No decrease in germination 48 hpi was observed in SC 625 and ZS 206 with interrupted dew periods of 2, 6, 12, 24 and 36 hrs following an initial incubation period of 6 hrs at 28 °C with 95-100% RH (Table 16a and b). Percentage germination at 48 hpi fluctuated between 91 and 96 % and between 63 and 65 % in ZS 206 and SC 625, respectively, with an interrupted dew period of 2-36 hrs.

Table 16a. ANOVA table of effect of an interrupted dew period (hrs) on conidial germination on a resistant (SC 625) and highly susceptible (ZS 206) maize cultivar 48 hrs after incubation at 28 °C

	Degree of freedom	Mean square	F value	Probability
hours after incubation at 28 °C = 48				
interrupted dew period	4	9.94	0.46	0.764
cultivar	1	21374.44	991.46	<0.001 ***
interrupted dew.cultivar	4	39.64	1.84	0.129
Residual (99)				
CV % = 5.9 NS = not significant (P ≥ 0.05); * = significant (P ≤ 0.05); ** = highly significant (P ≤ 0.01) ; *** = very highly significant (P ≤ 0.001)				

Table 16b. Table of means of percentage conidial germination at varying hours of interrupted dew periods and 48 hrs after incubation at 28 °C

No. of hrs of interrupted dew period	% germination on SC 625	% germination on ZS 206
0	63.00	100.00
2	62.50	96.10
6	63.80	93.90
12	63.70	91.20
24	65.10	91.40
36	64.40	93.10
Cultivar mean	63.90	93.14
$LSD_{(0.05)}$ interrupted dew period	NS	
$LSD_{(0.05)}$ cultivar	2.45	
$LSD_{(0.05)}$ interrupted dew period.cultivar	NS	

5.4 Discussion

Conidial germination was greater over a wider range of temperature conditions on the GLS susceptible cultivar, ZS 206 than on the resistant cultivar, SC 625. Furthermore, germination of conidia was less affected by desiccation and interrupted dew periods on ZS 206 than SC 625. This could account for the different susceptibility rates to GLS of these two maize cultivars as the resistance was clearly expressed before the conidia penetrated the host tissue of SC625. Further investigations are necessary to ascertain whether there is a pre-formed chemical on the leaf surface or a form of induced resistance, or perhaps a combination of the two. The implications of this form of resistance to GLS are that it would be rate-reducing in that it stops germination and reduces frequency of germ tube penetration. The significance of rate-reducing in the control of GLS has been recognized (Ward *et al.*, 1999b).

Our studies confirmed those of Rupe *et al.,* (1982) and Thorson (1989) that a minimum of 6 hrs leaf wetness is required for a significant proportion of conidia to germinate. Rupe *et al.* (1982) found that optimum temperature conditions for conidial germination were 18-25 °C while Beckman and Payne (1982) found that spores germinated after 24 hrs at 22-30 °C when plants were exposed to 12 hrs of mist. The conidial germination studies reported in this paper show that this variation in germination response to temperature was cultivar dependent.

A desiccation period of one day did not reduce germination in either SC 625 or ZS 206 but germination declined markedly after desiccation periods of 2-5 days. However, germination was significantly higher in ZS 206 than SC 625. In the field, low humidities (< 90%) of more than one day following conidial release and dispersal could have a marked adverse effect on pathogen infection of the host.

Studies showed that germinating conidia survive short dry periods without adverse effects on germination and germ tube elongation, provided conidia are initially exposed to a 6 hr (Thorson and Martinson, 1993) and 9 hr (Rupe *et al.*, 1982) incubation period at high RH. There has been confusion in the literature on *C. zeae-maydis* regarding high RH and leaf wetness. High RH (i.e., >95%) results in leaf wetness. It is leaf wetness

and not RH that determines conidial germination. Our results showed that following an initial 6 hrs of RH > 95% (i.e. RH >95% = leaf wetness) at 28 °C for both ZS 206 and SC 625, interrupted dew periods of up to 36 hrs did not reduce conidial germination after 48 hrs. Germination percentages for both cultivars were similar to those observed in uninterrupted dew period studies at similar temperatures (28 °C) and humidities (95-100%). Thus, periods of highly unfavourable conditions delay conidial germination, germ tube elongation and subsequently host penetration but do not limit infection. This confirms other reports that under unfavourable environmental conditions, germ tubes of *C. zeae-maydis* can remain quiescent until favourable conditions re-occur (Beckman and Payne, 1982; Latterell and Rossi, 1983; Thorson and Martinson, 1993). Germinating spores of other fungi in the genus *Cercospora* have also been found to have a considerable ability to tolerate severe desiccation, e.g., *Cercospora musae* (Zimm.) (Good and Zathureczky, 1967) and *C. beticola* Sacc. (Rathaiah, 1977). Alderman and Beute (1986) found that after a dry period, germ tubes of *C. arachidicola* Hori were able to resume growth at a rate similar to that under continuous dew.

Ward *et al.* (1999a) classified maize hybrids into disease severity groups based on area under disease progress curves and yield response. SC 625 was found to be in the group that is "resistant" to GLS because yield response remained the same in the non-sprayed control, as for one, two or three fungicide sprays. They recommended that fungicide applications are unnecessary to achieve high yields when planting SC 625. Our germination studies showed that a resistance mechanism is present on the leaf surface of this cultivar, reducing conidial germination, which could explain the lack of response to fungicide sprays. Failure of conidia to germinate on the leaves of SC 625 is probably attributable to physiological resistance factors produced by the leaf. Investigations of leaf morphology, longevity of spore life and nutrient requirements are required to establish the nature of factors which limit and enhance development of *C. zeae-maydis* in different cultivars.

In contrast, ZS 206 had a linear yield response to fungicide treatments in field trials and only achieved maximum grain yields following three sprays (Ward *et al.*, 1999a). It was classified as highly susceptible to GLS. This was confirmed in our trials as conidia on ZS 206 were able to germinate under a wider range of temperature conditions and increased periods of desiccation and interrupted dew periods.

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CHAPTER 6

Relationship of environmental factors to incidence of airborne conidia of *Cercospora zeae-maydis* of maize

Abstract

Weather variables, leaf blight and airborne conidia of *Cercospora zeae-maydis* (the causal organism of grey leaf spot (GLS) on maize) were monitored in maize fields using Burkard and Rotorod spore traps. Incidence of conidia showed marked daily periodicities, with a peak between 1200 and 1400 hrs when temperature and vapour pressure deficits (E_{def}) were highest and leaf wetness lowest. Multiple regression analyses identified high evaporation over a 24 hr period, low temperatures over a 48 hr period and wind over a 72 hr period as the weather variables most strongly associated with high conidial releases. Rain, high E_{def} values and temperatures between 20-30 °C with leaf wetness over a 72-hr period together with prolonged high evaporation over a 48 hr period were identified as limiting factors in conidial release. In order for conidia to form, moisture and temperatures < 20 °C with low evaporation must be present 48 hr before conidia are released. This may partly explain the relationship of weather variables over several days and airborne conidia. The results suggest that as the air surrounding each conidium dries due to a reduction in humidity and an increase in E_{def}, a fracture line develops between the conidium and the conidiophore. When wind blows over such a conidium, it breaks free and is dispersed. The fact that leaf wetness and rain resulted in low counts of airborne conidia, further confirmed that a hygroscopic process is involved in conidal release in *C. zeae-maydis*. The daily number of trapped conidia provides a valid estimate of daily inoculum pressure, enabling growers to establish more economical and effective control of GLS on maize.

6.1 Introduction

Grey leaf spot (GLS) caused by *Cercospora zeae-maydis* Tehon and Daniels, is recognized as one of the most significant yield-limiting diseases of maize worldwide (Nutter and Jenco, 1992; Ward and Nowell, 1998).

Grey leaf spot was first observed in KwaZulu-Natal, Republic of South Africa (RSA) in the late 1980s, but it was not an economically important disease to the maize industry at the time. However, several significant changes occurred in the early 1990s that set the stage for an epidemic. Since 1992, GLS has spread and reached epidemic proportions in many parts of the RSA, causing yield losses of up to 60% (Ward *et al.*, 1997).

Several aeromycological studies have been conducted in the genus *Cercospora* (Berger and Hanson, 1963; Lyle, 1964; Kaiser and Lukezic, 1965; Kaiser and Lukezic, 1966; Meredith, 1967; Sreeramulu, 1970; Berger, 1971; Smith and Crosby, 1973). Release of conidia of *C. musa* Zimm. is triggered by water but not by wind (Leach, 1946). Berger and Hanson (1963) suggested that conidial release of *C. zebrina* Pass. is brought about by wind or rainsplash, whereas conidia of *C. hayi* Calpouzos are removed by low initial wind velocities (Kaiser and Lukezic, 1966).

Rupe *et al.* (1982) found that conidial release of *C. zeae-maydis* reached a diurnal peak at 1400 hr at Quicksand, Kentucky and that more conidia were trapped on days with 12-13 hr of RH >90% and 11-13 hr of leaf wetness. Payne and Waldon (1983) investigated the seasonal patterns of conidial dispersal of *C. zeae-maydis* and found that although conidia were trapped at the beginning of the season, the characteristic GLS lesions did not appear until later in the season. They concluded that this was because the pathogen required high humidity (95-100%) and temperatures of 20-30° C for germination which were only present in the microclimate supplied later in the season once the canopy had formed. Payne *et al.* (1987) investigated the influence of different tillage systems on sporulation of *C. zeae-maydis* and found that fewer conidia were

trapped in conventionally tilled plots compared to conservation tillage areas. Jenco and Nutter (1992) investigated the diurnal and seasonal periodicities of *C. zeae-maydis*, using a Burkard volumetric spore trap to trap conidia in two experimental fields in Iowa in 1991 and 1992. Hourly conidial catches indicated a diurnal peak occurring between 1600 and 1800 hr at both locations. The total number of conidia trapped per day varied greatly within and among locations, during the season and over the two years of the study. Population growth models were used to transform cumulative conidial data and to obtain linear relationships between cumulative hours of relative humidity >/ 90% and cumulative numbers of conidia trapped. In both seasons, there was a strong relationship between cumulative seasonal conidial populations of *C. zeae-maydis* and cumulative hours of relative humidity >/90%, with r^2 ranging from 0.46 to 0.98%.

Conidia from debris and maize leaves is the main source of inoculum for epidemics of *C. zeae-maydis*. This is an important consideration for timing fungicide applications. However, airborne conidia of *C. zeae-maydis* has received little attention.

The aim of this study was designed to examine relationships of airborne conidia to diurnal patterns, disease development and weather variables and to ascertain if conidial release in the field can be predicted accurately from weather data. The use of weather variables to quantify GLS potential would ensure that fungicides for the control of GLS are applied only when justified. A prediction model is being developed for a fungicide spray programme based on the relationship of weather variables and conidial production, release, germination and infection of *C. zeae-maydis*. The implementation of such a model will maximize disease control with a minimum number of fungicide sprays, giving maximum yields, higher economic gains and reduced environmental impact.

6.2 Materials and methods

Conidia were trapped during the 1997/98 and 1998/99 maize growing seasons at the Cedara Agricultural Development Institute (29°32'S, 30°17'E), situated 15 km north of Pietermaritzburg at an altitude of 1070 m. The 1998/99 maize season was characterised by frequent thunderstorms with lightning, causing mechanical failure of the Rotorod spore trap and automatic weather station on several occasions. For these reasons, the results of the 1997/98 trial only are given.

Diurnal conidial release

The daily number of airborne conidia of *C. zeae-maydis* was estimated using a Burkard spore trap (Burkard Scientific Sales Ltd., Rickmansworth, Hertfordshire, England) sampling 19 ℓ air per minute from 15 February to 31 March, 1999. The spore trap was set up between dryland, non-fungicide treated maize (ZS 206) plots in a 1.5 m wide alleyway, with the orifice 75 cm above ground level. Conidia were trapped on slides coated with silicone grease. The slides were changed daily between 1700 hr and 1800 hr, divided into 24 hr divisions by drawing lines on the slides, and stained with lactophenol cotton blue overnight. The divisions (each division = 1 hr) were used during conidial counting using a compound microscope (X 400) to determine the beginning and end of each hour's conidial catches. The hourly number of conidia trapped was averaged for the 45-day period.

Seasonal conidial release

A Rotorod sampler (Model 92, Ted Brown Associates, 26338 Esperanza Drive, Los Altos Hills, CA 94022, USA) was set up in a dryland maize field 10 m from the edge of the plot in the 1997/98 and 1998/99 maize-growing seasons. The trap was placed 1 m above the ground and was adjusted to sample 10 ℓ of air per minute. Conidia were trapped over a 24 hr period (1700 to 16.59h) from 29 January to 31 March 1998 and from 6 February to 31 March, 1999. *Cercospora zeae-maydis* conidia counts were made from

two vaseline coated rotorods per exposure time (24 hrs). Rotorods were stained with lactophenol cotton blue overnight, counted with the aid of a microscope (X 400) and calculated as conidia per litre of air per 24 hrs.

Automatic weather station

An automatic weather station (Campbell Scientific Africa, Stellenbosch, RSA in 1998 and from Adcon Telemetry, Worcester, RSA in 1999) was positioned < 1 km from the Burkard spore trap in 1998 and 500 m from the Rotorod sampler in 1998 and 1999. Five leaf wetness sensors were exposed horizontally at three heights, i.e., 0.5, 1.0 and 1.5 m above the soil surface. The automatic weather station provided readings of maximum, minimum and mean temperature, relative humidity and leaf wetness every hour. These readings were averaged over the 24 hr period . Rainfall, sunshine hours, evaporation and wind speeds were collected from the Cedara weather station situated less than 1 km from the trial site (Appendix 1).

Vapour pressure deficit (E_{def}) (Pa) was used rather than percent relative humidity (RH) because (E_{def}) is less temperature-dependent than RH, and because RH is a parameter that cannot be averaged as a mean (Savage - personal communication)[1].

Disease assessments

To determine the seasonal progress of the GLS epidemic, whole-plant standard area diagrams described by Ward *et al.* (1997) were used as a guide to estimate disease severity. Disease severity assessments were made regularly at 10-14 day intervals on plants in the centre of the two middle rows of each plot, from the first signs of disease, and continued until the crop was physiologically mature. Plots were assessed for GLS at 89, 98, 109, 123, 136 and 150 days after planting (DAP). These data were used to

[1] M.J. Savage, Discipline of Agrometeorology, School of Applied Environmental Sciences,Univ. of Natal, Private Bag X01, Scottsville, 3209, Republic of South Africa.

calculate the area under disease progress curve (AUDPC) using a trapezoidal integration program (Berger, 1981).

Statistical analyses

Weather variables and airborne conidia were analysed by using stepwise multiple regression analysis (MRA) (Anonymous, 1993). Conidial count data were transformed to natural logarithms before they were analyzed so that the relationship with independent variables was linear and the variance was stabilized. Partial correlation coefficients from MRA, and prediction from these analyses, were improved when conidial counts and weather variables were analysed by using "days" which ran from 1700 on one day to 1659 hrs the following day rather than from 0001 to 2400 hrs on the same calendar day. This is probably because the rapid diurnal change in E_{def} and temperature occurred between 0900 and 1500 hrs. These environmental parameters were changing more slowly during other periods of time, and if the days were broken at midnight, parts of these periods of relatively constant low temperatures and E_{def}, and leaf wetness periods were placed into different days, so that continuity of these periods was lost. This may be particularly important where conidial catches on a given day depended on weather during the previous 2-3 days, as it does in *C. zeae-maydis*. Fifty variates were analyzed (Appendix 2).

The independent variables that did not contribute significantly to the percentage variance accounted for, were discarded. The variables that did contribute significantly were retained and used to predict conidial release. For interpreting data, a positive correlation of weather variables with conidial counts was considered to indicate that the variable was a favourable factor for conidial release. Conversely, when a correlation was negative, the variable was considered to be a limiting factor.

6.3 Results

Daily conidial release

The mean daily incidence of airborne conidia and trends in weather factors were determined for the sampling period. The mean was calculated for hourly numbers of conidia trapped, temperature, E_{def}, and leaf wetness for the 45-day sampling period (Fig.1). Number of conidia caught showed a strong diurnal periodicity, confirming previous reports (Rupe *et al.*, 1982). Conidia were only trapped during the day from 0600 to 1900 hr. Counts were highest between 1200 and 1400 hr, after which time there was a sudden drop in numbers. Few conidia were trapped in the early morning and late afternoon at low and constant E_{def}, temperature and leaf wetness. The increased number of conidia trapped daily coincided with conditions of decreasing leaf wetness and increasing E_{def} and temperature (Fig. 1).

Seasonal conidial release

Multiple regression analysis showed high evaporation over a 24 hr period, low temperatures over a 48 hr period and wind over a 72 hr period as the weather variables most strongly associated with high conidial releases. Rain, high E_{def} values and temperatures between 20-30 °C with leaf wetness over a 72 hr period together with prolonged high evaporation over a 48 hr period were identified as limiting factors in conidial release (Table 1).

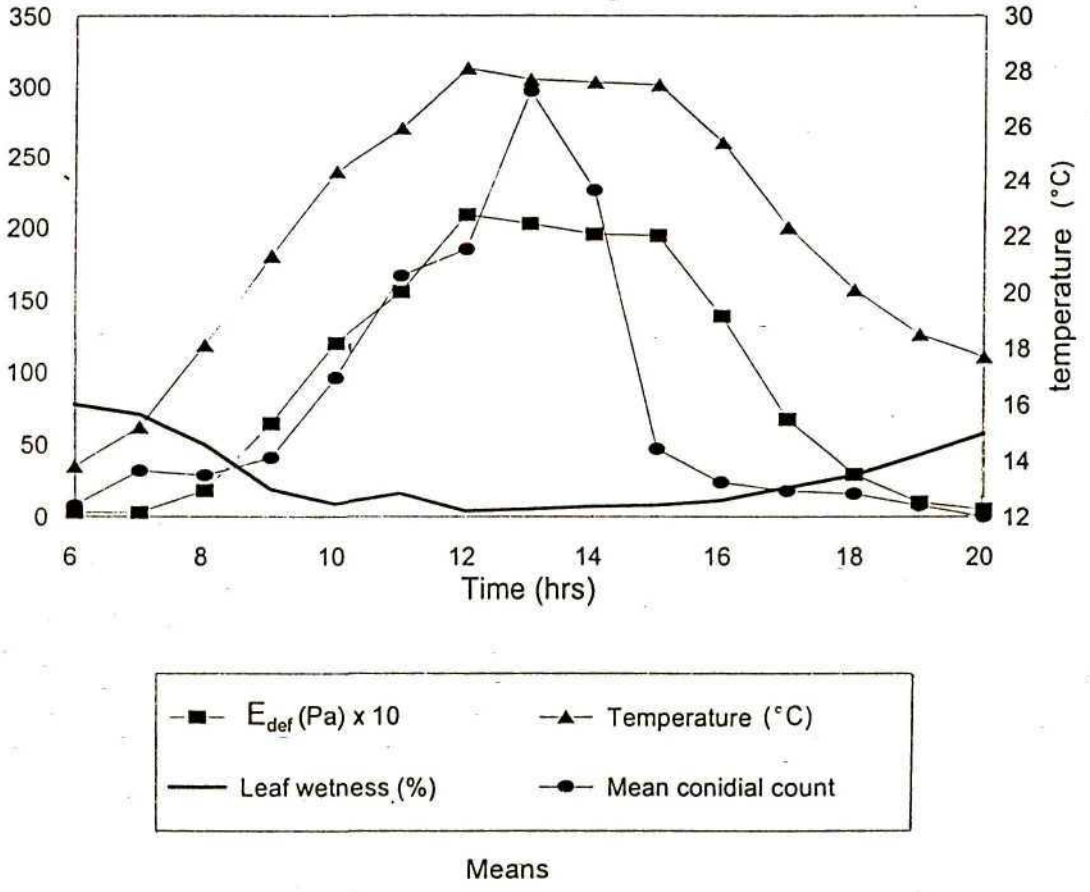

Fig. 1. Relationship of mean vapour pressure deficit (E_{def}) (Pa), temperature (°C) and leaf wetness (% of hour) to conidial release at Cedara (15 February to 31 March, 1999)

Table 1. Estimates of parameters of environmental factors affecting conidial release of *Cercospora zeae-maydis* at Cedara (1997/98)

Environmental factor	Estimate of partial regression co-efficient	Standard error	t (32)	Probability
Constant	3.93	3.70	1.06	0.297**
minimum temp. (48 hr period)	0.369	0.103	3.57	0.001**
wind (72 hr period)	0.000386	0.000147	2.63	0.013**
evaporation (24 hr period)	0.517	0.120	4.30	<.0.001**
evaporation (48 hr period)	- 0.659	0.203	-3.25	0.003**
rain (72 hr period)	- 0.0508	0.0138	-3.68	< 0.001**
leaf wetness (24 hr period)	0.1048	0.0328	3.20	0.003**
E_{def} (0-600 Pa) (72 hr period)	- 0.1184	0.0413	-2.87	0.007**
leaf wetness and temp. 20-30 °C (72 hr period)	- 0.0708	0.0220	-3.23	0.003**
* = significant ($P \leq 0.05$); ** = highly significant ($P \leq 0.01$) . **R^2 = 64.1**				

From Table 1 it is possible to draw up the following equation relating conidium release of *C. zeae-maydis,* to environmental variables :

$$\text{Log count of conidium release} = X_1 + X_2 + X_3 + X_4 + X_5 + X_6 + X_7 + X_8$$

where partial regression co-efficients were :

X_1 = 0.369 (minimum temperature over 48 hrs)

X_2 = 0.000386 (wind over 72 hrs)

X_3 = 0.517 (evaporation over 24 hrs)

X_4 = - 0.659 (evaporation over 48 hrs)

X_5 = - 0.1048 (leaf wetness 24 hrs)

X_6 = - 0.0508 (rain over 72 hrs)

X_7 = - 0.1184 (E_{def} of 0-600 Pa over 72 hrs)

X_8 = - 0 .0708 (leaf wetness and temp. of 20-30 °C over72 hrs)

Disease assessments

In 1997/98 GLS increased from 7-98 % from 89-151 DAP, with an AUDPC of 2936 (Table 2). Airborne conidia did not increase in number with increasing GLS blighting.

Table 2. Disease assessments and area under disease progress curve of ZS 206 at Cedara (1997/98) (after Ward *et al.*, 1997)

Rep.	Disease assessments (%)						AUDPC
	89 DAP(*)	98 DAP	109 DAP	123 DAP	136 DAP	151 DAP	
1	6	8	10	60	80	99	3030
2	8	9	10	55	75	95	2754
3	8	8	10	60	80	99	2911
4	8	8	10	65	85	99	3051
Mean	7	8.25	10	60	80	98	2937

(*) DAP = days after planting

6.4 Discussion

The results on the diurnal periodicity of *C. zeae-maydis* conidial release are, in general, in accordance with those of Rupe *et al.* (1982), showing that conidial release takes place during the day. Highest peaks at our location were found to be between 1200-1400 hrs when E_{def} was high and leaves were dry. The most plausible explanation for this is that the release mechanism for *C. zeae-maydis* conidia involves a hygroscopic process requiring dry air for conidia to break away from conidiophores at the point of attachment. The manner of conidial attachment to conidiophores (Chapter 7) confirms a hygroscopic response to drying air and release of conidia.

Periodicity of *Cercospora* conidia has been reported for several species, with peak catches during the daytime. However, there is at least one report (Pady *et al.*, 1962) where *Cercospora* conidia are present in the air during the day and night, with no definite peaks. Therefore, it is difficult to generalize about the diurnal periodicity of conidial dispersal in the genus *Cercospora*.

Abrupt increases in numbers of airborne conidia during the day coincided closely with an initial increase in E_{def} followed by a decrease after 1400 hrs. Conidial release ceased as soon as E_{def} returned to zero. Controlled environment studies on other fungi have indicated that conidial release is affected by increasing RH and not temperature changes (Leach, 1975). Although the effects of falling RH and rising temperature on conidial release cannot be distinguished in field experiments, the use of E_{def} and not RH is a useful variable, showing that high/increasing temperature is not important in conidial release. Furthermore, in the MRA, E_{def} but not RH, showed a positive correlation with conidial release. Light has been shown to trigger spore release in many fungi (Leach, 1975). However, sunshine hours were not shown to be significant in the MRA.

Multiple regression analysis is a useful tool for identifying weather variables most closely associated with release of significant numbers of conidia of *C. zeae-maydis*. Regression equations are empirical in that they predict from a limited number of

observed responses, and cannot be expected to allow for unexpected changes in weather patterns, cultural practices or other factors. Butt and Royle (1974) suggested that new generations of equations should be generated each year, or even more frequently, as there is always the danger of changing weather patterns or some new factors appearing, influencing the results.

Factors controlling spore release and dispersal condition daily periodicities of airborne conidia, but those affecting spore production may greatly influence the magnitude of daily peaks. Since weather factors appear to favour spore release and dispersal throughout the duration of the epidemic of *C. zeae-maydis*, the daily fluctuations in numbers could be attributed largely to factors conditioning conidial production. In deriving circumstantial evidence for relationships of conidial production to host and weather factors, it was assumed that most trapped conidia were produced during the few days immediately before trapping. In the present study, this was confirmed because conidial release and dispersal were highly correlated to several weather conditions 1-3 days before trapping.

Meredith (1967) worked on leaves of red beet and sugar beet (*Beta vulgaris* L.) colonised with *C. beticola*, and showed that wind was very effective in causing release of conidia. Movement and detachment of conidia were not observed when turgid conidia and conidiophores were contained in a damp petri dish. However, when leaves were subjected to sudden decreases in RH, i.e., increasing E_{def}, by transferring them from a damp petri dish to a drier atmosphere, conidiophores and conidia underwent violent hygroscopic movements and conidia were detached.

High daily evaporation promoted conidial release which further indicates that release of conidia from conidiophores is hygroscopic. However, high evaporation over a 48 hr period and a high E_{def} (0-600 Pa) over a 72 hr period had a negative effect on the number of conidia trapped. It appears that the changes in evaporation and E_{def} are more important than prolonged high periods of these environmental parameters to release conidia from conidiophores, due to their hygroscopic nature. High evaporation and high temperatures of 20-30°C appear to hamper conidial formation in the days prior to

release. It has been shown that most fungi sporulate best under low E_{def} conditions, although they can sporulate to some extent under a wide range of E_{def} (McLean and Sleeth, 1959; Ingold, 1971; Rotem *et al.*, 1978). The MRA also revealed that leaf wetness has a negative effect on conidial release, further confirming that dry conditions are necessary for conidia to be released.

The effect of rain, mist and dew on conidial release are confounded variables and difficult to assess independently in the field. Although rainfall can be eliminated from the MRA equation, its influence on temperature, leaf wetness and E_{def} still exist. Therefore, by measuring E_{def}, the effects of rainfall are still measured to some extent.

Wetness periods over several days may function collectively in influencing conidial production as conidiophores and conidia that fail to mature during a single wetness period may complete maturation during one or more successive wetness periods. Incomplete production or release of mature conidia during periods of dryness may partly explain the relationship of weather and airborne conidia over several days. Nelson and Tung (1973) showed that in *Exserohilum maydis* Leonard and Suggs, conidiophores may produce several crops of conidia during successive wetness periods.

The presence of rain over a 72 hr period has a negative influence on conidial release of *C. zeae-maydis*. Although rain provides the leaf wetness necessary for conidial germination and penetration, it hampers the drying out process required for removal of conidia from conidiophores. Possibly rain washes conidia off the leaf and are consequently not caught in the spore trap. This may account for the low number of conidia trapped on days following rain.

Optimal conditions for conidial germination, i.e., leaf wetness and temperatures of 20-30 °C were found to have a negative effect on conidial release. As minimum temperatures over a 2-day period were found to have a positive effect on conidial release in the MRA analyses, it is possible that optimum temperatures for conidial germination (20-30°C) as found by Beckman and Payne (1982) are unfavourable for conidial production and release. Rain and consequently, leaf wetness, appear to

interfere with the drying out process required for conidia to break away from conidiophores, resulting in low numbers of airborne conidia.

With two exceptions during the trial period, conidia were trapped every day, i.e., conidia were omnipresent to continue the presence of inoculum throughout the maize season. The lack of increase in airborne conidia with increasing AUDPC can be attributed to the fact that, although there is an increase in the number of blighted leaves as GLS progresses up the maize plant, only the upper blighted leaves release conidia at any time. This was confirmed while sampling maize leaves for electron microscopy studies of conidiogenesis of *C. zeae-maydis* (Chapter 7).

The daily and seasonal incidence of airborne conidia highlights the importance of applying fungicides before GLS reaches epidemic proportions. Inoculum that occurs early in epidemics is important in subsequent disease progress (Berger, 1977). Thus control of inoculum on maize leaves may be of critical importance for suppressing disease progress and maintaining effective disease control throughout the season. Protection is especially important after conditions found to promote abundant production, release and dispersal of *C. zeae-maydis* conidia. Careful interpretation of disease and weather relationships has the potential not only to improve the efficiency of disease control in integrated disease management systems, but may also optimise techniques to screen for disease resistance.

Favourable weather conditions could be used to calculate daily infection values (DIVs) which, in turn could be used to indicate the potential for sporulation. Weather stations established in strategic areas would be essential as weather figures depend on the availability of accurate and reliable weather data. Data from weather stations cannot accurately be extrapolated to fields throughout a wide area. In addition, inoculum levels vary between fields. However, DIVs would probably be most beneficial after the initiation of the first fungicide control programme which relies on visual assessments of disease in the field as microclimates can vary within and between fields. When conditions for GLS are marginal but inoculum is readily available, a low incidence of

successful infections can result in development of considerable disease. Therefore, it would be best to spray when conditions are best suited to high conidial release.

Any effort to relate epidemics to sporulation must be channelled through the subject of build up of inoculum (Ward *et al.*, 1998). Inoculum build up in the field is affected, in addition to weather, by the number of conidia produced by a given fungal species, dispersal of these conidia and their infectivity. However, interactions between these processes have not been studied sufficiently in *C. zeae-maydis* and are probably a basic phenomenon which could assist a more rational approach to control of GLS.

Studies concerning the aeromycology of *C. zeae-maydis* may provide valuable information regarding the biology of GLS and will assist in formulation of predictive models and new management strategies for this foliar disease of maize.

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Appendix 1. Temperature, relative humidity, vapour pressure deficit, wind, sunshine hours, rain and leaf wetness related to spore counts in the Cedara trial (6/2/1998-31/3/1998)

Day (Julian calendar)	Spore count	Evapo-ration (mm)	Max. Temp. (°C)	Min. Temp. (°C)	Mean Temp. (°C)	Max. RH (%)	Min. RH (%)	Mean RH (%)	Vapour pressure deficit (E_{def}) (Pa)	Wind (totaliser) (km)	Sunshine hours (hrs)	Rain (mm)	Leaf wetness (hrs)
37	128	4.5	34.08	18.47	24.90	97.4	57.40	83.8	640.34	13003	8.1	0.0	4.47
38	49	6.5	37.18	16.29	26.07	100.0	45.25	79.8	915.21	13005	11.4	0.0	10.68
39	21	7.0	31.16	20.15	23.42	97.0	63.69	86.9	595.87	05006	5.3	0.0	5.07
40	17	4.7	28.41	17.92	21.40	98.2	69.67	92.3	290.28	13005	2.3	0.2	11.11
41	17	3.3	20.78	15.10	17.42	99.0	88.00	96.0	101.16	13005	0.0	1.8	23.73
42	14	0.0	23.58	14.57	17.45	99.5	76.10	93.8	143.30	05006	0.3	2.5	18.54
43	196	2.5	31.86	15.12	21.22	100.0	60.80	88.3	398.17	13003	7.9	5.0	16.00
44	50	7.0	33.32	16.21	22.21	99.0	55.52	85.7	483.61	13003	9.0	16.5	12.06
45	5	6.0	33.44	13.57	22.37	99.7	51.12	84.2	618.39	0000	11.2	0.0	5.31
46	34	8.0	35.78	16.02	23.18	98.8	44.91	82.0	788.24	36005	9.6	0.0	8.21
47	5	8.0	20.20	12.01	16.43	99.7	92.40	97.3	123.23	05003	0.0	25.0	23.16
48	4	0.3	16.07	11.44	13.04	99.6	90.50	97.4	42.31	13006	0.0	25.8	23.92
49	40	0.3	19.84	11.79	14.76	99.3	81.00	94.7	94.54	09003	0.0	7.8	18.06
50	14	1.0	27.07	13.94	18.38	99.3	70.50	90.7	205.06	13006	1.2	3.0	16.58
51	26	2.2	28.71	16.21	20.14	99.2	65.79	91.1	295.76	18003	4.0	0.7	14.10
52	23	4.8	31.37	14.95	21.55	99.7	59.86	86.9	425.49	13005	9.2	15.8	15.32

53	22	5.5	28.70	15.25	20.89	99.5	70.80	90.4	360.62	05003	8.2	40.3	14.82
54	20	5.5	24.11	14.99	18.30	99.2	78.80	94.1	168.98	31008	0.7	0.5	13.26
55	25	2.0	24.97	15.03	18.30	99.5	76.10	92.7	174.73	09003	3.6	3.5	16.54
56	57	2.3	28.59	16.72	20.89	99.2	71.50	91.0	263.39	09003	7.4	0.8	14.39
57	630	4.0	30.54	14.86	21.22	99.6	62.38	88.1	393.69	09003	6.0	0.0	10.45
58	32	3.9	29.88	15.09	20.89	99.8	61.23	86.6	429.90	13005	4.9	1.4	7.65
59	64	3.5	29.47	16.03	20.01	99.8	65.04	91.6	282.34	13003	3.1	0.0	5.09
60	84	2.9	24.04	15.42	18.14	100.0	79.30	94.8	125.86	13005	1.8	1.4	11.68
61	26	2.2	26.47	13.86	17.60	100.0	70.30	92.0	176.21	13005	5.7	13.2	19.30
62	21	3.1	26.22	14.40	18.91	96.9	65.34	83.6	377.07	18008	7.4	4.6	2.21
63	18	3.0	29.42	10.91	20.00	100.0	64.27	86.5	449.26	05005	10.3	0.0	6.76
64	78	5.0	31.39	16.46	23.05	100.0	56.43	85.9	520.29	09003	9.6	0.0	4.07
65	224	5.0	33.54	14.58	23.31	100.0	42.86	79.0	761.28	09005	9.6	0.0	8.06
66	46	6.4	21.65	16.22	18.01	99.2	86.80	95.4	268.26	13006	0.1	2.9	12.29
67	2172	1.0	20.46	16.224	17.98	99.8	80.40	93.7	110.36	09006	0.0	2.0	19.80
68	16	1.0	27.23	11.48	19.01	99.5	59.03	82.0	474.43	09005	8.6	3.0	4.75
69	22	3.8	20.50	14.67	16.13	100.0	87.90	97.2	104.71	13006	0.5	0.3	16.60
70	773	0.9	33.61	12.31	21.90	100.0	30.65	76.2	729.37	05006	11.4	1.9	16.05
71	13	6.5	18.09	12.25	15.14	98.4	91.30	95.7	309.13	0000	0.0	0.0	11.14
72	52	1.0	18.43	11.88	14.12	100.0	75.10	93.2	136.49	05005	0.1	2.5	14.73
73	12	1.4	27.22	13.09	17.86	100.0	59.39	88.1	296.93	09005	5.4	0.4	16.45
74	15	3.0	29.18	11.04	17.66	100.0	58.53	87.3	416.18	05005	6.6	0.0	9.93
75	21	3.1	31.82	8.55	19.00	100.0	47.61	82.2	568.42	36005	10.4	3.1	16.40

76	29	4.7	33.88	15.33	25.41	97.7	38.94	66.3	698.21	13005	11.2	2.2	11.10
77	0	5.0	18.56	12.93	15.95	99.3	81.40	94.5	294.51	23005	0.0	0.3	6.68
78	48	2.5	27.05	12.66	16.75	100.0	55.45	89.9	231.45	09005	5.9	2.9	17.41
79	84	3.0	35.17	11.39	20.73	100.0	35.74	79.2	780.76	00000	11.1	0.0	8.51
80	113	5.5	31.85	11.26	20.71	100.0	54.12	84.4	561.84	09003	8.2	0.0	5.89
81	1225	4.0	30.81	14.92	21.25	100.0	55.68	87.4	516.01	09003	7.1	0.0	8.57
82	298	4.0	29.67	12.90	20.40	100.0	61.77	88.2	370.68	05003	6.6	3.5	16.70
83	845	3.2	32.87	13.20	20.41	100.0	49.67	84.4	566.77	09003	7.1	0.2	14.61
84	187	4.0	23.38	14.10	17.18	100.0	74.40	95.6	148.66	05003	1.2	3.5	20.69
85	75	2.0	21.05	15.31	17.14	100.0	84.20	96.2	81.18	18006	0.2	19.0	18.16
86	74	2.2	24.21	17.74	20.99	99.3	73.10	89.6	169.25	09005	0.2	20.7	15.52
87	151	3.0	29.32	13.77	20.40	100.0	56.60	85.9	414.10	13003	7.7	4.0	13.69
88	275	2.3	28.54	16.45	20.00	98.8	61.73	87.8	407.05	05003	6.9	3.5	7.34
89	87	4.4	31.89	13.61	20.84	100.0	42.08	80.1	617.97	13003	9.4	0.9	15.43
90	133	4.0	32.23	11.88	20.98	100.0	39.97	80.8	756.32	13005	10.0	0.0	7.53

Appendix 2. Variates analysed relating spore counts to environmental parameters

Number	Variate
1	leaf wetness (hrs) over 24 hrs
2	RH > 90% for 24 hrs
3	maximum temperature (°C) over 24 hrs
4	minimum temperature (°C) over 24 hrs
5	sum of hrs where leaf wetness >0 hrs and temperature <20° C > 30 °C
6	sum of hrs where leaf wetness > 0 °C and temperature < 20 °C > 30 °C
7	leaf wetness (hrs) over 48 hrs
8	leaf wetness (hrs) over 72 hrs
9	$RH_{\angle}$ 90% over 48 hrs
10	RH_{2} 90% over 72 hrs
11	maximum temperature (°C) within 48 hrs
12	maximum temperature (°C) within 72 hrs
13	minimum temperature (°C) within 48 hrs
14	minimum temperature (°C) within 72 hrs
15	number of hrs where temperature < 20 °C > 30 °C over 48 hrs
16	number of hrs where temperature < 20 °C > 30 °C over 72 hrs
17	hrs of favourable leaf wetness (> 6 hrs) and temperature (20-30°C) over 48 hrs
18	hrs of favourable leaf wetness (> 6 hrs) and temperature (20-30 °C) over 72 hrs
19	average wind speed (m sec $^{-1}$) over 24 hrs
20	wind speed (m sec $^{-1}$) at 20 00 hrs
21	wind speed (m sec $^{-1}$) at 8 00 hrs
22	wind speed (m sec $^{-1}$) at 14 00 hrs
23	average total wind (km) over 48 hrs
24	average total wind (km) over 72 hrs
25	wind speed (m sec $^{-1}$)
26	average wind speed (m sec $^{-1}$) over 48 hrs
27	average wind speed (m sec $^{-1}$) over 72 hrs
28	sunshine (hrs) over 24 hrs
29	total sunshine (hrs) over 48 hrs
30	total sunshine (hrs) over 72 hrs
31	evaporation (mm) over 24 hrs
32	average evaporation (mm) over 48 hrs
33	average evaporation (mm) over 72 hrs

34	rain (mm) over 24 hrs
35	total rain (mm) over 48 hrs
36	total rain (mm) over 72 hrs
37	vapour pressure deficit < 200 Pa over 24 hrs
38	vapour pressure deficit < 200 Pa over 48 hrs
39	vapour pressure deficit < 200 Pa over 72 hrs
40	vapour pressure deficit < 400 Pa over 24 hrs
41	vapour pressure deficit< 400 Pa over 48 hrs
42	vapour pressure deficit< 400 Pa over 72 hrs
43	vapour pressure deficit< 600 Pa over 24 hrs
44	vapour pressure deficit< 600 Pa over 48 hrs
45	vapour pressure deficit< 600 Pa over 72 hrs
46	average vapour pressure deficit over 24 hrs
47	RH > 95% for 24 hrs
48	RH > 95% for 48 hrs
49	RH > 95% for 72 hrs
50	Difference(°C) between max. and min. temp. (°C)

CHAPTER 7

LIGHT, SCANNING AND TRANSMISSION ELECTRON MICROSCOPY STUDIES ON THE CONIDIOGENESIS OF *CERCOSPORA ZEAE-MAYDIS* ON MAIZE

Abstract

Light, scanning and transmission electron microscopy were used to study conidiophore formation and conidiogenesis by *Cercospora zeae-maydis* Tehon and Daniels, the causal organism of grey leaf spot of the leaf tissue of its host, *Zea mays* L. Hyphae aggregate in the substomatal cavity and give rise to fascicles of 1-2 septate conidiophore initials which emerge through the stoma. A single, aseptate conidium develops from the conidiogenous cell of the conidiophore initial. As the conidium matures, septa are laid down. Extension growth of the conidiogenous cell terminally, leads to the lateral displacement of the conidium on the conidiophore. Schizolytic secession results in the secession of the conidium from the conidiogenous cell. On secession, a slightly everted geniscar, with a granular wall deposit, is left laterally on the parent conidiogenous cell. After conidial secession, the conidiophore continues to grow, producing a second conidium from the conidiogenous cell at the apex of the extended conidiophore. The second conidium, in turn, is also displaced to a lateral position as the conidiogenous cell continues to grow from beneath, displacing the second conidium laterally. This sympodial and successive proliferation of the fertile conidiogenous cell results in the formation of a characteristic 1-3, occasionally 4, geniculate conidiophore, bearing a single conidium at each apex.

7.1 Introduction

Grey leaf spot (GLS) caused by *Cercospora zeae-maydis* Tehon and Daniels, on maize (*Zea mays* L.) is an aggressive fungal pathogen that can severely damage maize foliage, reduce grain yield and increase the incidence of lodging (Lipps and Pratt, 1989; Nutter and Jenco, 1992; Ringer and Grybauskas, 1995; Ward and Nowell, 1997). It has become a major foliar disease of maize world-wide, causing substantial economic losses in areas where conditions are favourable for disease development (Lipps, 1987; Smith, 1989; Gevers and Lake, 1994; Jenco, 1995; Ringer and Grybauskas, 1995; Ward and Nowell, 1997). Since the mid-1970s, this disease has become increasingly important in the USA (Leonard, 1974; Roane *et al.*, 1974; Latterell and Rossi 1983; Smith, 1989). The disease was first observed in South Africa in KwaZulu-Natal in 1988. Since then it has spread to neighbouring provinces and countries in Africa (Ward and Nowell, 1997).

Variation in GLS severity among locations is most frequently attributed to environmental conditions and tillage practices. Roane (1950) recorded that the severity of GLS is often greater in the absence of other foliar diseases. This could account for the increase in GLS over the past few decades with the development of maize hybrids resistant to other foliar diseases.

Mature symptoms of GLS are characterized by typical brown to grey, long, narrow leaf lesions running parallel to the main leaf veins. The confinement of the fungal colonization by the major veins results in the characteristic rectangular necrotic GLS leaf lesions. Under favourable environmental conditions, the number of lesions increases rapidly and their coalescence is followed by the blighting of entire leaves.

In view of the absence of the sexual stage for fungi classified in the Deuteromycetes, investigations of developmental aspects of conidiophores, conidiogenous cells and conidia, correlated with existing morphological data of the fungi, are used in classification studies.

The taxonomy of *Cercospora* is based primarily on the dimensions and characteristics of the conidia (colour, length and width of base and tip) and conidiophores (length, width, fasciculation and geniculation) (Chupp, 1953). Conidial width is considered to be the most reliable taxonomic feature to distinguish between species and is a major characteristic used to distinguish *C. zeae-maydis* and *C. sorghi,* both pathogens on maize leaves. Characteristics of conidiophores are generally less reliable (Wang *et al.,* 1998). The number, length and diameter of conidiophores and the number of geniculations are influenced by temperature and moisture and are too variable to be taxonomically decisive (Wang *et al,* 1988). Authoritative descriptions of *C. zeae-maydis* differ in many characteristics of the conidia and conidiophores (Table 1).

For the majority of the Fungi Imperfecti, and particularly the genus *Cercospora* Fres., there have been few scanning (SEM) or transmission electron microscopy (TEM) studies. Pons *et al.* (1985) described the ultrastructure of conidiogenesis in *C. beticola* Sacc. and showed that some conidiophore initials develop enteroblastically while others develop holoblastically, conidia develop holoblastically and conidiogenous cell proliferation is enteroblastic. Yeh and Sinclair (1979) found that conidial ontogeny in *C. kikuchii* (Mats. and Tomoy.) M.W. Gardner is holoblastic. Besides a brief SEM study by Beckman and Payne (1982), there have been no electron microscopy studies of *C. zeae -maydis*. No work has been reported on conidiogenesis of the pathogen.

The objective of the present research was to describe conidiogenesis in *C. zeae-maydis* with the aid of light, SEM and TEM to determine morphological characteristics that could be used for taxonomic identification of *C. zeae-maydis.*

Table 1. Summary of the morphological descriptions of *C. zeae-maydis* (1925-1999) (after Nowell, 1997)

Conidium			Conidiophore		Author
Length (μm)	**Width (μm)**	**Shape**	**Colour**	**Description**	
50-85	5-9	hyaline, obclavate, 4-10 septa	olive-brown	single apical geniscar, 70-90 x 4 μm, 3-8 septa	Tehon and Daniels, 1925
30-90	5-9	hyaline, obclavate, 3-10 septa	olive-brown	occasionally 1-3 geniculate, 40-165 X 4-6 μm, 3-8 septa	Chupp, 1953
28-80	4-8	3-9 septa	brown	1-3 geniculate, 40-102 X 4 μm, sparingly septate	Kingsland, 1963
40-165	4-9	hyaline 6-12 septa	no reference	no reference	Shurtleff, 1980
70-180	5-6 base and 2-3 tip	hyaline, 4-10 septa	dark	geniculate	Latterell and Rossi, 1983
37-76 or 44-80	6-9 or 8-13	hyaline, obclavate, 3-7 septa	olivaceous	straight, unbranched, 3-5 septa, 1-2 geniculate, 129 x5 μm	Wang *et al.*, 1998
50-90	5-10 base and 3-5 tip	hyaline, 4-9 septa	brown	straight, unbranched, 1-2 septate, 1-3 and occasionally 4-geniculate	Caldwell, present data, 1999

7.2 Materials and methods

Selected pieces of maize leaves with lesions caused by *C. zeae-maydis* were collected from a maize hybrid (ZS 206), highly susceptible to GLS, grown in the field at Cedara Agricultural Development Institute (29°32'S, 30°17'E) in 1998 and 1999.

Light microscopy studies

Fascicles of conidiophores were removed from necrotic leaf tissue with a damp paint brush, mounted in a drop of distilled water and viewed with an Axiophot light microscope (Zeiss, Germany) at 100X magnification.

Scanning electron microscopy studies

Lesions on leaf samples were cut into approximately 3 mm x 3 mm and fixed in 3% glutaraldehyde in 0.05M sodium cacodylate buffer (pH 6.8-7.2) for 24 h. The samples were then washed twice in the buffer, post-fixed for two hours in 2% osmium tetroxide in buffer, and dehydrated in a graded ethanol series. The specimens were then critical-point dried with carbon dioxide as a transfusion fluid. Dried specimens were mounted on copper stubs previously coated with double-sided tape. The leaf-fracture method of Hughes and Rijkenberg (1985) was used to examine stromata in the substomatal spaces. All stubs were coated with gold-palladium in a Polaron Sputter Coater and viewed in a Hitachi S-570 scanning electron microscope operating at 8.0 or 10.0 kV.

Transmission electron microscopy studies

Lesions on leaves were cut into squares measuring approximately 3 mm x 3 mm and fixed for 24 hours in 3% glutaraldehyde in a 0.05 M sodium cacodylate buffer (pH 7.2), washed twice in that buffer, stained in 2% uranyl acetate for 45 min., followed by two further washes in 0.05 M sodium cacodylate buffer (pH 7.2) and post-fixed for 3 hours in 2% osmium tetroxide in the buffer at room temperature. Samples were dehydrated

in an ethanol series and embedded in Epon-Araldite resin. Ultrathin sections were cut using a diamond knife and collected on 200-or 300-mesh copper grids. Specimens were post-stained in lead citrate for 15 minutes, washed in double-distilled water and viewed with a Jeol 100 CX transmission electron microscope.

Fungal structures were measured directly from the micrographs.

7.3 Results

As host tissue becomes necrotic, hyphae grow toward the guard cell region of the substomatal cavity on both the ab - and adaxial leaf surfaces. Several hyphae aggregate and intertwine in the substomatal space to form a stroma that partially or completely fills the substomatal cavity (Fig. 1). The stroma is multicellular with the number of cells varying according to the size and maturity of the stroma. Some of the upper cells in the stroma become conidiophore mother cells which are usually closely packed, and of various shapes and sizes in the intercellular space beneath the host stoma (Fig. 2). An electron-opaque substance between the conidiophore mother cells is noticeable (Fig. 2).

Fascicles of 3-36 conidiophore initials, usually dense and compact, but sometimes loosely organized, emerge through the stoma from the substomatal stroma on the ab - and adaxial leaf surfaces without rupturing the guard cells (Fig. 3 and 4). Conidiophore initials develop to different lengths to accommodate the expansion of neighbouring conidiophore initials and conidiophores (Fig. 5). Conidiophore initials are brown, straight, unbranched, slender, and generally slightly tapered towards the apex (Fig. 5 and 6).

The conidiogenous cell extrudes a single, terminal conidium (Fig. 7 and 8). Before conidial secession, a large, lateral swelling appears on the conidiophore just below and to one side of the conidium, signalling the proliferation of the conidiogenous cell. The conidiogenous cell grows out from below and to one side of the first conidium (Fig. 9).

Such growth displaces the conidium to a 45° angle so that it becomes lateral in position before its secession (Fig. 9). Only a single conidium was seen attached to a conidiogenous cell at any one time. Conidial secession is schizolytic, resulting from the circumscissile break in the outer periclinal wall layer of the conidiogenous cell (Fig. 10).

Conidia are hyaline, thin-walled, obclavate, 50-90 μm long, 5-10 μm wide at the base and 3-5 μm at the tip (Fig. 11). Conidia are initially aseptate but at maturity, and before release, become 4-9 septate.

At secession, the outer, periclinal wall of the conidiogenous cell is ruptured and remains as a distinct broken hilum (Fig. 10). This results in the separation of the conidium from the conidiogenous cell. A granular wall deposit is usually laid down, with its boundary defined by the ring of the outer wall layer, resulting in the formation of a slightly thickened material to form an everted geniscar on both the half of the septum remaining on the conidiogenous locus and the half constituting the base of the conidium (Fig. 10 and 11).

The conidiophore continues to grow from below and to one side of the lateral geniscar formed by secession of the first conidium (Fig. 12). The conidiogenous locus on the extended conidiophore is apical in position and initiates a second conidium (Fig. 13). The conidiogenous cell again develops a protuberance and continues to extend laterally from below the second conidium, displacing it laterally before its secession. The conidiophore continues to grow, and a new conidiogenous cell at the apex produces a third conidium (Fig. 14).

The successive proliferations of the conidiogenous cells may occur on either side of the extended conidiophore but not necessarily from alternating sides (Fig. 15). Successive scars, all with a granular, everted appearance inside the ring of wall material left behind after secession of each conidium, occur at intervals along the conidiophore (Fig. 15). The continued proliferation of the conidiogenous cell and successive displacement of geniscars result in the typical geniculate appearance of the conidiophore (Fig. 16).

7.4 Discussion

Attempts to provide a functional classification of the anamorph-subdivision of conidial fungi have, in general, not been very successful. In Saccardo's (1886) classification scheme, taxonomic value was given to pigmentation, conidial shape and septation, and conidiophore arrangement. These characters often vary within a single species and consequently are of little taxonomic value. More recently, features of conidiogenesis have been incorporated into classifications, mainly for members of the anamorph class of the Hyphomycetes. A review of developmental and ultrastructural aspects of conidiogenesis has been presented by Cole and Samson (1979).

Sympodial proliferation of conidiogenous cells is characteristic of *Cercospora* and many other members of such anamorph genera, e.g., *Tritirachium* Limber, *Acrodontium* de Hogg, *Beauveria* Vuill., *Phaeoisaria* Höhnel and *Sympodiophora* Arnold (Pons *et al.*, 1985).

In general, the process of conidiogenesis in *C. zeae-maydis* is similar to that observed in *C. beticola* (Pons *et al.*, 1985). Successive formation of conidia on the same conidiophore are in accord with previous observations in *C. zeae-maydis* (Kingsland, 1963; Beckman and Payne, 1982; Latterell and Rossi, 1983). Conidial measurements are also similar to other taxonomic descriptions of *C. zeae-maydis* (Tehon and Daniels, 1925; Chupp, 1953; Kingsland, 1963; Wang *et al.*, 1998) (Table 1).

Tehon and Daniels (1925) recorded that a conidiophore bears a single, apical geniscar, suggesting that they are single-spored only. They reported that geniculation of the conidiophores was never observed and concluded that this was a rare feature in the genus *Cercospora*. Chupp (1953) reported that conidiophores were only occasionally 1-3 geniculate. However, Kingsland (1963) observed multi-geniculation of conidiophores, suggesting that 2-3 conidia are produced from each conidiophore. Our observations showed that conidiophores are usually 1-3 geniculate, and are consistent with the findings by Chupp (1953) and Kingsland (1963). Present research showed that

conidiophores can occasionally be 4-geniculate. We confirm the view of Chupp (1953) and Wang *et al.* (1998) that geniculation of conidiophores could be dependent on weather conditions and maturity. This could account for the varied observations by various researchers (Table 1). A variation in colour of conidiophores is also recorded by various researchers (Table 1). Lacy (personal communication)[1] confirmed that conidiophores of isolates from Cedara are brown compared to the olive-green colour found in isolates in Virginia, USA.

Distinctions between genera without a sexual stage often depend on minute differences in measurements and colour of conidia and conidiophores, as well as ultrastructural differences in the nature of the conidiogenous loci and the basal conidial scars (Deighton, 1976 and 1979; Thaung, 1984). It is probable that the inability to differentiate between these criteria in detail, particularly with light microscopy, has led to the lumping of many genera into the genus *Cercospora* (Carmichael *et al.,* 1980).

No one character is ever used to classify species within the genus *Cercospora* (Chupp, 1953). Conidial measurements and colour are the principal characteristics which separate *Cercospora* from other genera in the Deuteromycetes (Chupp, 1953). However, this has proved to be an unreliable morphological characteristic as measurements of conidiophores and conidia vary considerably. Taxonomic significance has been attributed to the characteristics of geniscars which possibly provide a more stable character in the Deuteromycetes (Cole and Samson, 1979).

The presence of a granular, everted geniscar on the conidiogenous cell after secession of conidia in *C. zeae-maydis* could be used as a criterion in the taxonomy of the genus *Cercospora.* Scanning and TEM studies in conidiogenesis of *C. beticola* showed granular wall material laid down on the outside of both the half of the septum remaining on the conidiogenous cell and the half constituting the base of the conidium (Pons *et al.,* 1985). Similar scars with granular wall deposits have been observed in *Cladosporium*

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Link, where Cole and Samson (1979) using SEM techniques, demonstrated granular material on the outer face of conspicuous scars left on conidiogenous cells. Such scars, and the material of which they are constructed, are quite different from those illustrated by similar techniques by Campbell (1970) in *Alternaria brassicicola* (Schw.) Wiltsh., by Reisinger (1969) in *Dendryphiella vinosa* (Berk. and Curt.) Reisinger, in *Drechslera sorokiniana* by Cole (1973) and in *Helminthosporium maydis* Nisikado, (a synonym of *Drechslera maydis* (Nisikado) Subram. and Jain) by Brotzman *et al.* (1975). The finding of granular deposits on the geniscar after secession of conidia in *C. zeae-maydis* will further confirm the differentiation of genera of *Cercospora* and *Cladosporium* from genera of *Alternaria, Dendryphiella* and *Drechslera* which have a ring of electron opaque material on the geniscars in the secondary layer of the conidiogenous cell wall.

Schizolytic secession of conidia involving a splitting of the delimiting septum so one half of the cross wall becomes the base of the seceding conidium and the other half remains at the apex of the conidiogenous cell, has been described for many Deuteromycetes (Cole and Samson, 1979). The additional granular wall material laid down on both the half of the septum remaining on the conidiogenous cell and the half constituting the base of the conidium, compliments observations on *C. beticola* by Pons *et al.* (1985). This phenomenon is not seen in many Deuteromycetes. It appears that additional wall material is laid down on the septum as conidia are maturing, as conspicuous scars are observed while conidia are still attached to conidiophores.

Certain developmental concepts initiated from light and SEM studies need to be substantiated by ultrastructural investigations in the Fungi Imperfecti. It has been suggested that the validity of the experimental classification of the Deuteromycetes largely depends on the ultrastructural investigations of wall relations. Therefore, it is essential to examine a large number of species in the Deuteromycetes representing the various modes of conidium and conidiogenous cell development.

Meredith (1967) working on *C. beticola,* showed that movements of conidiophores and detachment of conidia were not observed when turgid conidia and conidiophores were contained in a damp petri dish. However, conidiophores showed hygroscopic

movements and release of conidia in response to sudden increasing vapour pressure deficits (E_{def}), when infected leaves were transferred from the damp petri dish to the drier atmosphere. The geniscars on the conidiophores of *C. zeae-maydis* could be composed of hygroscopic material, which on drying out with an increase in E_{def} from drying air, could cause detachment of conidia and dispersal by air currents. This mechanism of spore release was supported by Pons *et al.* (1985). A similar mechanism of spore release has been proposed in conidial release of *C. asparagi* Sacc. (Cooperman, 1986).

Conidium release has been shown to correspond with increasing E_{def} for a number of fungi. Caldwell (Chapter 6) showed that in diurnal studies of spore release of *C. zeae-maydis* at Cedara, spore release increases with increasing E_{def}. At Cedara, maximum spore release takes place at between 12.00-14.00 hr, at the highest levels of E_{def} and temperature but at the lowest level of leaf wetness. It is possible that a hygroscopic response is involved in the release of conidia of *C. zeae-maydis* from dry leaf surfaces in dry air.

Very few conidia were seen attached to the conidiogenous mother cell both in SEM and TEM studies. The dehydration process in the graded ethanol series during preparation of specimens for both SEM and TEM studies could have caused conidia to secede. This further substantiates the view that geniscars are composed of hygroscopic material which, on desiccation, cause release of conidia.

This SEM study illustrates a number of developmental features concerning the way in which conidiophores originate and produce a succession of conidia in *C. zeae-maydis* that to date have only been described. The presence of granular geniscars on conidiogenous cells of *C. zeae-maydis*, together with further TEM studies of conidiogenesis to substantiate certain developmental features of *C. zeae-maydis*, could be particularly significant in taxonomic studies of the genus *Cercospora*.

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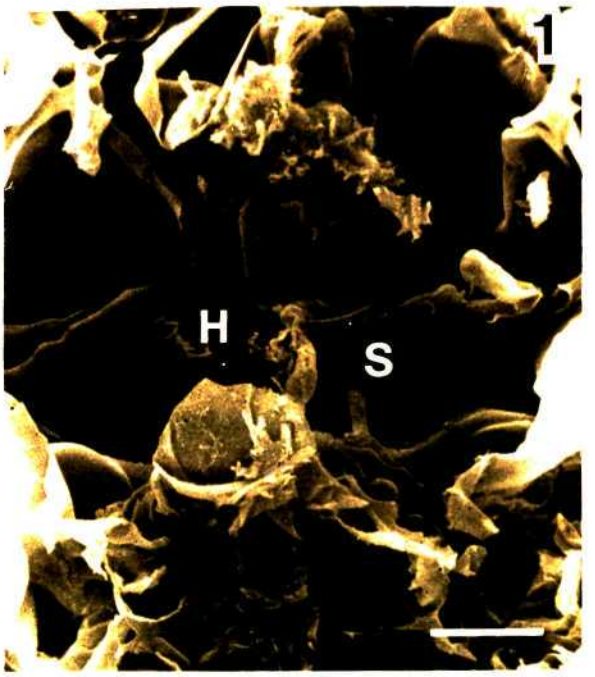
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H
S

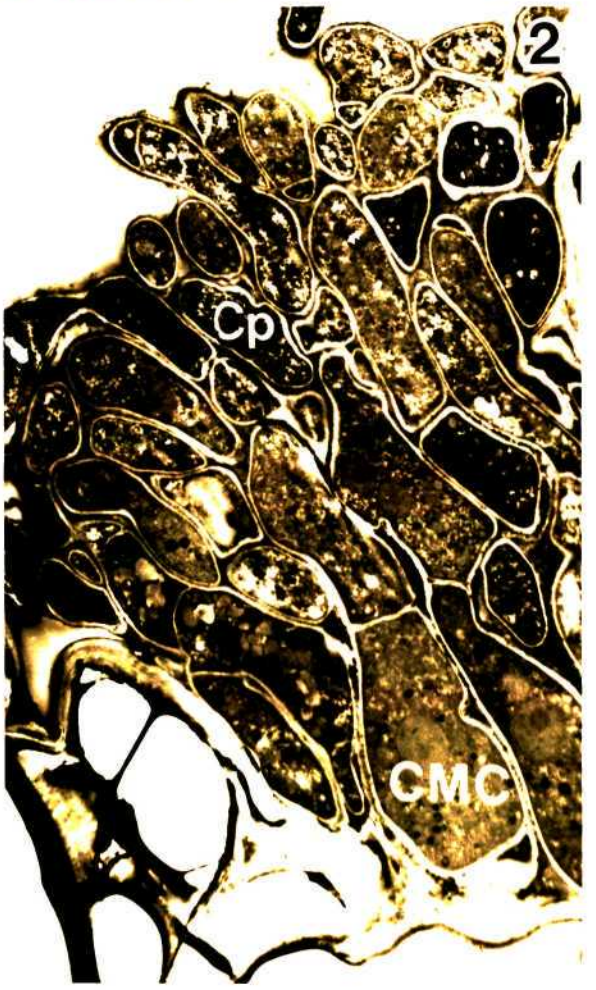

2
Cp
CMC

PLATE 2

Fig. 3. SEM of young conidiophores (Cp) emerging through a stoma (S) (Bar = 6 μm).

Fig. 4. SEM of conidiophores (Cp) emerging in small fascicles on the ab- and adaxial leaf surface from mature lesions (Bar = 60 μm).

Fig. 5. SEM of young, erect and unbranched conidiophores (Cp) of varying lengths emerging through a stoma (Bar = 6 μm).

Fig. 6. SEM of maize leaf surface showing conidiophores emerging through stomata (Bar = 0.15 mm).

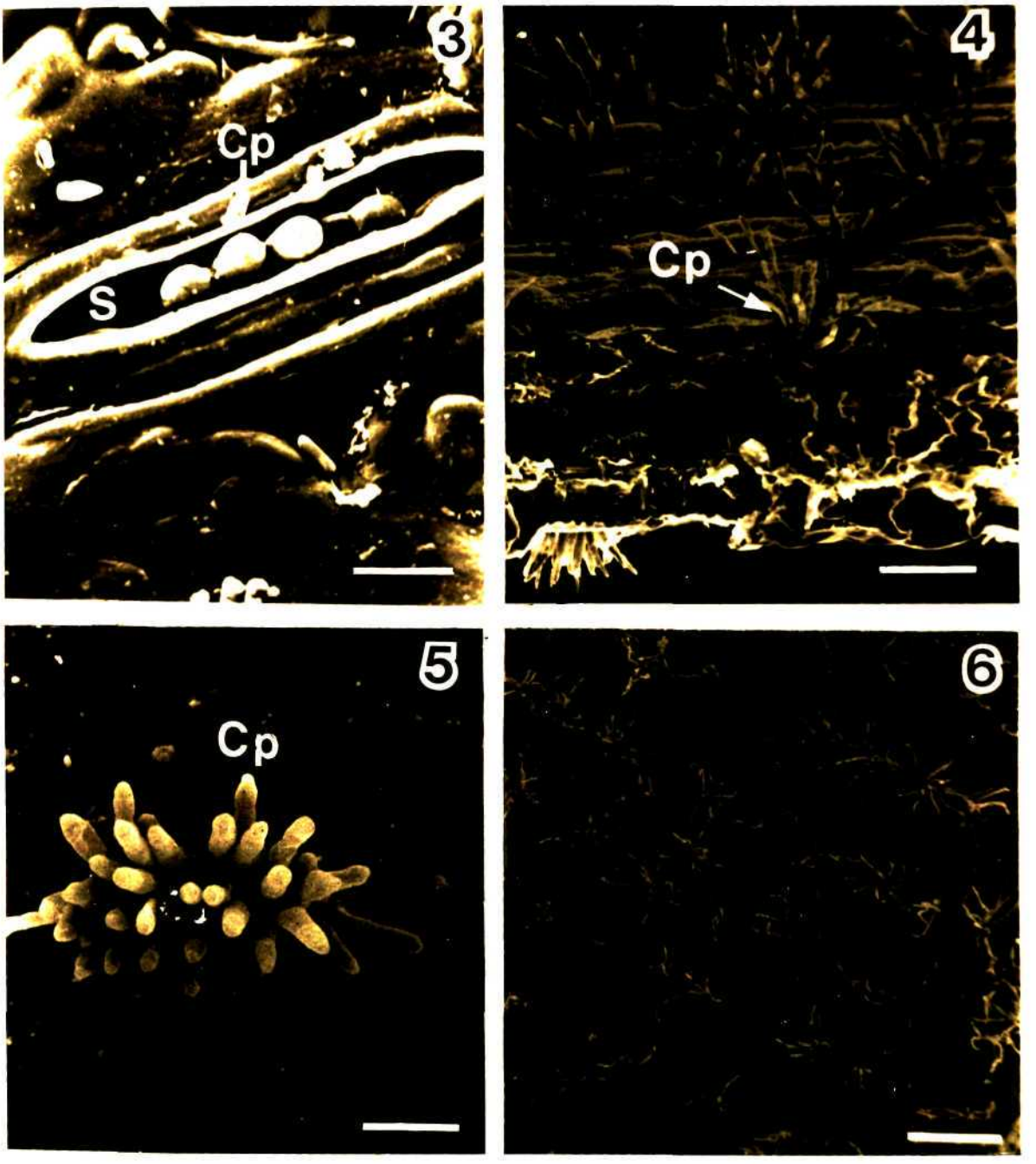

3
Cp
S
4
Cp
5
Cp
6

PLATE 3

Fig. 7. Each conidiophore (Cp) produces a single, terminal conidium (C) (Bar = 6 μm).

Fig. 8. A developing, young conidium (C) (Bar = 3 μm).

Fig. 9. The conidium (C) is borne singly and terminally but by the further growth of the conidiophore from the base and to one side of the first conidium it becomes lateral in position before secession (Bar = 9 μm).

Fig. 10. At secession of the conidium (C), a concentric ring of wall material is left on the conidiogenous cell. Note the conidiophore starting to grow from below and to one side of the conidium (Bar = 5 μm).

7
cp

8
c

9
c

10
c
cp

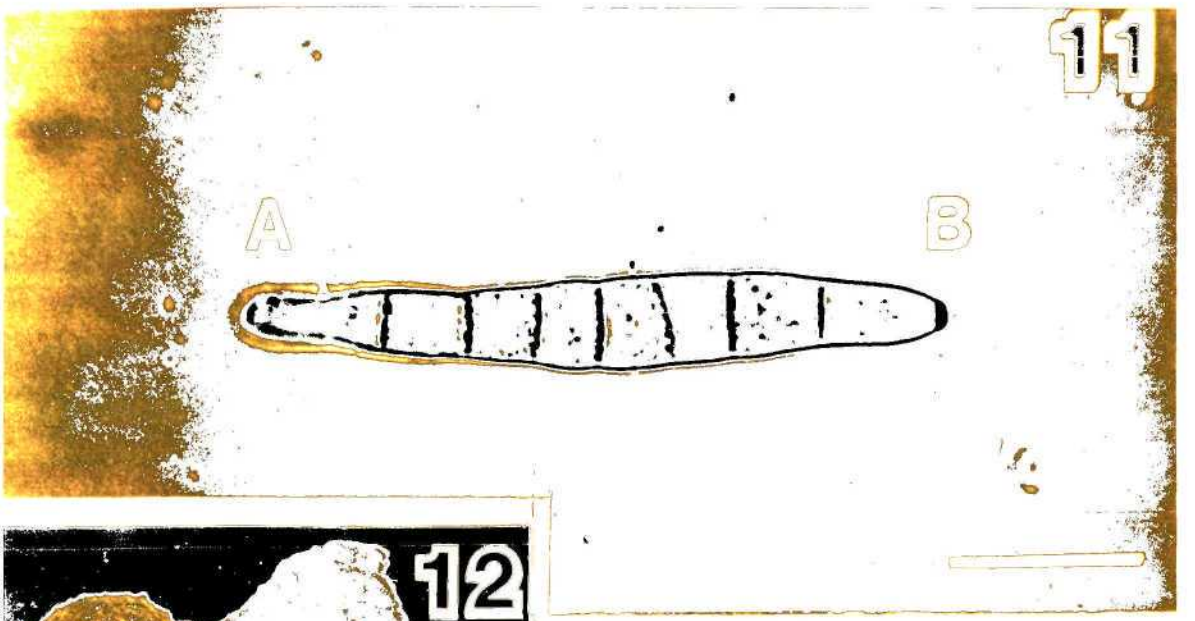
PLATE 4

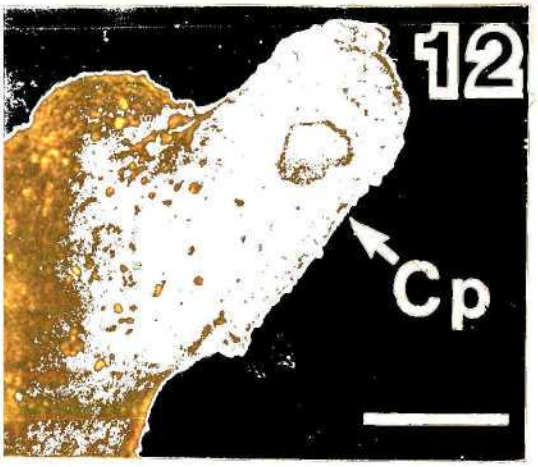
Fig. 11. The conidium is hyaline, septate and obclavate, with a subtruncate base (B) and slightly tapered towards the apex (A). The everted, granular scar where the conidium was attached to the conidiophore is visible at the basal end (Bar = 23 μm).

Fig. 12. The conidiophore (Cp) continues to grow from below and to one side of the lateral geniscar after secession of the first conidium (Bar = 1.5 μm).

Fig. 13. After secession of the first conidium, a concentric ring of wall material remains on the conidiophore (Cp). A granular deposit is laid down externally surrounded by the ring. The conidiophore differentiates a new growing point below and to one side of the conidial geniscar (Gs) of the first conidium, giving rise to a second conidium (C) at the newly formed apex (Bar = μm). A second conidium (C) is initiated at the terminal end of the extended conidiophore (Cp) (Bar = 4 μm).

Fig. 14. Development of the third conidium (C) on the extended conidiophore (Bar = 6 μm).


11
A
B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Cp


14
C

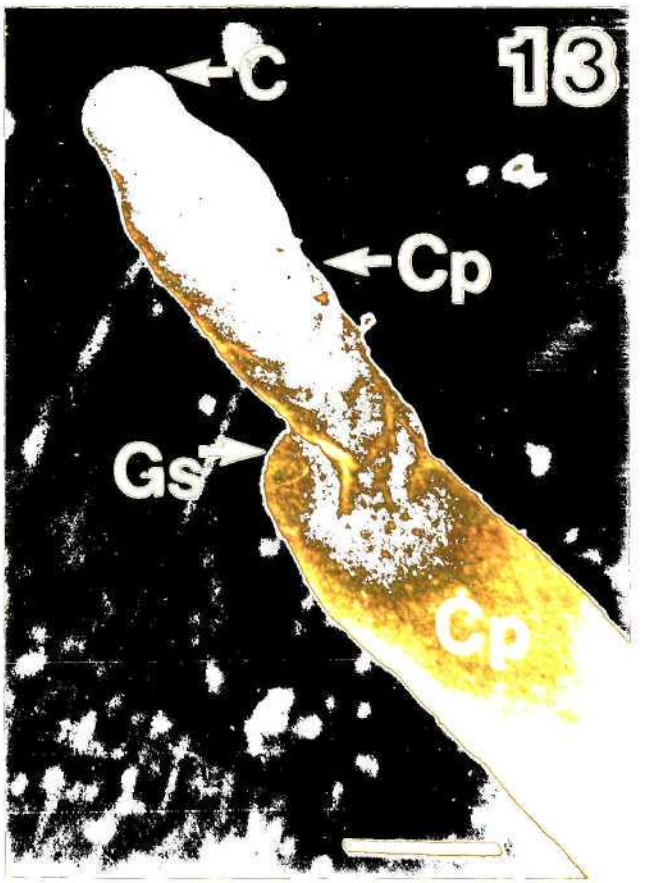
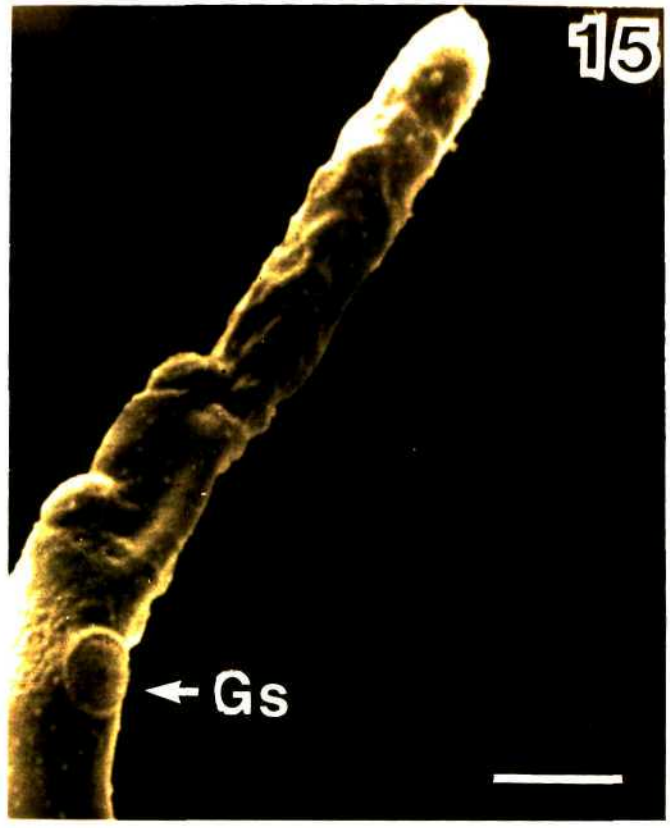

13
C
Cp
Gs
Cp

PLATE 5

Fig. 15. Slightly everted, granular geniscars (Gs) where conidia were attached occur on either side of the conidiophore (Bar = 4 μm).

Fig. 16. The successive displacement of geniscars by the sympodial growth of the conidiophore results in its characteristic geniculate appearance (Bar = 10 μm).


15
Gs


16

CHAPTER 8

THESIS OVERVIEW

8.1 Introduction

In the early part of the nineteenth century, potentially arable land was abundant. Whenever more food was required to meet the demands of a growing population and to substitute for cropland that had become unproductive due to nutrient depletion, more land was opened to cultivation. Today most of the opportunities for opening new agricultural land to cultivation have already been exploited. During the 20th century, agronomists and soil scientists have expanded and used their knowledge in genetics, plant breeding, plant pathology, plant physiology, entomology, agronomic practices and cereal technology, resulting in modest increases in yield per hectare during the 1900s.

In 1997, it was estimated that the world population was 5.8 billion of which 80% lived in developing countries where the population currently increases at about 1.9% per year. In the next 12 years, another billion people will be added to the global population if current growth rates continue in developing countries. Global food production is 5 billion tonnes per annum (Borlaug, 1997). An increase of the world population of 49% is predicted over the next 25 years (Skeen, 1997). As in the past, man will rely largely on plants, and especially cereals, to supply a large percentage of this increased food demand. The production of cereals in Africa has fallen in the past 25 years (CIMMYT, 1990). The rapid expansion of grey leaf spot (GLS) on the African continent in recent years has led to reductions in grain yield and quality. The impact of GLS in reducing maize yields will therefore add further to the widening food deficits, reduced food security and worsening nutrition in most African nations, particularly as maize is the major staple food for most rural populations of Africa, unless resistant hybrids are bred.

A greater use of irrigation and a 10-fold global increase in chemical fertilizer use has allowed world food production to increase more rapidly than global population. The number of undernourished people has decreased from 35 to 20% of the world's population and is predicted to decrease to 12% by 2010 (Borlaug, 1997).

Although the overall situation is improving, particularly due to the ongoing green revolution in Asia, large localized problems remain in countries in Asia and particularly Africa, where food production per person has declined. Growth in food production will have to continue to increase substantially, particularly in Africa, to meet the requirements of the population projected for 2030 (van der Graaff and Putter, 1998).

8.2 Crop losses from diseases, pests, and weeds

It is estimated that in the United States of America (USA) alone, in spite of the control measures practised, crops worth $9.1 billion were lost to diseases, $7.7 billion to pests and $6.2 billion to weeds (Agrios, 1997). Of the 878 million tonnes of food produced in developing countries in 1993, 200 million tonnes (23%) were lost to diseases. In comparison, only 59 million tonnes (6%) were lost to diseases of the 1,016 million tonnes of food produced in developed countries (Oerke *et al.*, 1994).

Crop protection is even more important in intensive agriculture, where increased fertilization, genetically uniform high-yielding cultivars, increased irrigation and other methods are used. Crop losses to diseases and pests not only affect national and world food supplies and economies but affect individual farmers even more, whether they grow the crop for direct consumption or for sale. Since operating costs for the production of crops remain the same in years of low or high disease incidence, pre- and post-harvest losses to disease and pests directly lower net returns.

8.3 Increased fertilizer use

Most of the increases in food production needed over the next several generations must be achieved through higher crop yields on land already under cultivation. Chemical fertilizers should be at the core of soil fertility restoration strategies to raise crop production (Borlaug and Dowswell, 1995). Their use should be a part of integrated nutrient management systems in which organic fertilizers should be included. The higher the level or build up of soil nutrients through organic matter, the less will be the amount of inorganic fertilizer required for a particular target yield of a crop.

Fertilization is necessary to supplement the natural supply of nutrients, to replace nutrients removed by cropping and weather losses, and to maintain or improve soil quality. However, despite the advent of cheap and plentiful chemical fertilizers, which has been one of the greatest agricultural achievements this century, sub-optimal levels of plant nutrients are the most common yield limiting factor in crops (Skeen, 1997). At present, fertilizer application to food crops in Sub-Saharan Africa (SSA) is the lowest in the world, probably no more than 5 kg ha^{-1} of nutrients. Unless fertilizer application is quadrupled in SSA, and combined with higher yielding varieties and improved crop management practices over the next 20 years, the food requirement of only three-quarters of its people will be met by the year 2020 (Borlaug, 1997).

Each decision to fertilize has an expected pay-off which can be defined as the net return to fertilizer use, or the value of the crop less the cost of fertilizer and application (Perrin, 1976.) The correct amount of fertilizer, for a specific set of conditions, will depend on the expected yield, the known prices of fertilizer and maize, the capital position of the farmer and the probable returns from alternative uses of his capital (Farina *et al.*, 1975). Pesek (1974) stated that fertilization is an economic activity based on biological and physical processes, so no choice is either correct or incorrect, provided it is within the rational economic limits for specified crop, soil, climate and price conditions.

A major component of soil fertility is the quantity of plant nutrients present in the soil, in particular, that portion of the total nutrient content that is readily accessible to plants. Yield is not only a function of added nutrients, but also of the nutrients released by the soil. There are a multitude of factors affecting the rate of release of soil nutrients. The more favourable the factors affecting this release, the more advantage crops can take of the soil nutrient supply (Eck, 1984). Balanced fertilization is vital since the value of one particular nutrient may be linked to the presence of adequate concentrations of other nutrients.

Kassier and Mallet (1966) point out that improved yields involve two sets of relationships. One set concerns physical production relationships, since the quantity and quality of a crop depend on soil, climate and agronomic skills of the producer. The second set of relationships are those economic principles governing production and resource allocation. As such, fertilizers are subject to these principles and compete for the capital the farmer has at his disposal. However, these decisions will be conditioned by the economic environment, and the preferences and expectations of the farmer. These are sound reasons for adjusting yield targets and hence reducing fertilizer inputs (Colwell, 1981).

8.4 Managing nutrition for disease control

Because crops are fertilized to promote maximum plant productivity, quality and efficiency, the effects of nutrients on disease is an important management consideration.

Plant nutrition, although frequently unrecognized, has always been an important component of disease control (Huber, 1966; Huber *et al.*, 1968; Trolldenier, 1969; Huber and Watson, 1970, 1974; Schoeneweiss, 1975; Huber, 1980a, 1980b, 1981; Graham, 1983; Huber and Arny, 1985; Huber and Dorich, 1988; Huber and Wilhelm, 1988). Agronomic practices such as crop rotation, crop sequence, irrigation, liming and pH adjustment help supply nutrients directly, or render them more or less readily available for plant uptake. These effects on disease are frequently through nutritional interactions as much as other factors.

The intricate relationship of plant pathogens with other micro-organisms, environmental factors and the host is dynamic and extremely complex. Nevertheless, knowledge of host nutrition in relation to disease development provides a basis for modifying agricultural practices to reduce disease severity.

The increased use and amounts of fertilizers, particularly nitrogen (N), for greater yields is generally considered to increase the severity of diseases, such as the high sugar pathogens, e.g., the powdery mildews, rusts and fire blight, pathogens that are adapted to young, succulent tissues. On the other hand, increased fertilization is considered to decrease diseases caused by low sugar pathogens, e.g., pathogens that attack primarily mature or senescent tissues (Agrios, 1997). In efforts to increase productivity through fertilization, nutrient effects on disease severity of plants to diseases must be taken into consideration.

Host response or preference, crop sequence, residual N, N rates and stability, and the timing of N applications can profoundly affect the form of N predominating in the soil (Huber and Watson, 1974). It is generally the form of N (nitrate or ammonium) available to the host or pathogen that affects disease severity or resistance rather than the amount of N (Huber and Watson, 1974). The fact that a given form of N reduces one disease but favours another, points to the need for detailed information of soil analyses, environmental factors and types of fertilizers used to control host-pathogen interactions. Unfortunately, many of these parameters are not reported in the literature, making it difficult to interpret results.

In the trial reported in this thesis, it was assumed that the effect of the nitrate form on N on GLS was investigated as NH_4^+ is converted into NO_3^- within 10-14 days in South African soils during the summer months. Maize takes up N primarily in the form of the NO_3^- ion (Miles, personal communication).[1]

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8.5 Soil nutrition and plant breeding

Most plant breeders and commercial growers discriminate between hybrids on the basis of their susceptibility to diseases. However, maize breeders are probably neglecting a potentially useful tool in the development of less susceptible genotypes, as insufficient attention is given to soil nutrition in maize-breeding programmes and performance testing of new hybrids at various nutritional levels.

8.6 Maize production, fertilization and disease incidence

Maize constitutes one of the major grain and fodder crops in the Republic of South Africa (RSA) (Anonymous, 1997). Extensive research has been conducted to find ways of improving the quality and quantity of yields. Rising fertilizer costs, and diseases related to soil nutrition make correct fertilization practices and advice to farmers, important aspects of maize production. Coupled with this are the economic risks associated with unpredictable climatic events and the debt-burden of maize producers.

The present economic climate in the RSA tends to reduce the profitability of maize production, and to increase the break-even yield level. Therefore, for maximum gross margins, it is important for farmers to utilize fertilizers correctly. Furthermore, fertilizer is one aspect of soil nutrition in maize production which can be manipulated by the farmer (Farina *et al.*, 1980).

The necessity of fertilization raises the problem of determining if increased fertilization increases or decreases disease levels. This will have consequences on the recommendations of fertilization rates. Much work has been published on the effects of N, phosphorus (P) and potassium (K) on a variety of plant diseases but little has been reported on the effects of soil nutrition on disease severity in maize. Fertilizer applications have been shown to affect the severity of fungal root and stalk rots in maize (Otto and Everett, 1956; Parker and Burrows, 1959; Thayer and Williams, 1960; Warren *et al.*,1975) and the severity of fungal leaf diseases caused by *Exserohilum turcicum*

([Pass.] Leonard and Suggs) (Bogyo, 1955; Gorsline *et al.*, 1963; Karlen *et al.*,1973) and *E. maydis* Nisikado and Miyake (Taylor, 1954).

During the 1970s and 1980s the most significant diseases of maize were leaf diseases, stalk rots, common smut and head smut. *Stenocarpella* emerged as a pathogen of major economic importance in RSA during the late 1980s, with estimated losses of around R200 million in 1986/87 (Nowell, 1997). Extensive research led to the establishment of effective control measures and the identification of resistant maize hybrids by the early 1990s (Rheeder, 1988; Gevers, 1989; Nowell, 1989a and 1989b; Rheeder *et al.*, 1989; Flett, 1990; Bensch and Flett, 1995; Hohls *et al.*, 1995).

Other pathogens, e.g., common rust *(Puccinia sorghi* Schw.) and northern leaf blight (*E. turcicum*) remain important diseases of maize. However, with the appearance of GLS in the Midlands of KwaZulu-Natal (KZN), RSA in 1988, attention in maize plant pathology turned to this new, threatening maize pathogen.

8.7 Grey leaf spot (*Cercospora zeae-maydis*)

Grey leaf spot caused by the fungus *Cercospora zeae-maydis,* was first identified on maize in southern Illinois in the USA by Tehon and Daniels (1925). It is now recognized as one of the most yield-limiting diseases of maize worldwide (Latterell and Rossi, 1983; Ward and Nowell, 1997b). It is estimated that GLS is increasing in distribution at a rate of 80-160 km each year in America (Ward *et al.,* 1999b). In Africa, GLS spread much faster than this and has become pandemic (Ward, 1996; Nowell, 1997). It is thought that the original source of *C. zeae-maydis* originated from infested maize residue accompanying maize imported from the USA during the drought years in the mid-1980s in the RSA (Ward, 1996). From its initial focus in KZN, the disease has spread throughout the maize-growing areas of RSA, with grain yield reductions as high as 60 % (Ward and Nowell, 1997b). Grey leaf spot has also been reported in Cameroon, China, Kenya, Malawi, Mozambique, Nigeria, Swaziland, Tanzania, Uganda, Zaire, Zambia and Zimbabwe (Nowell, 1997; Ward and Nowell, 1997b) and is considered to threaten maize production in southern Africa (Nowell, 1997).

The challenges facing the agricultural sector to control GLS in RSA are real. In this province, in commercial agriculture alone, the total cost per annum of losses caused through GLS is estimated at R50 million, with fungicide and aerial application costing almost R 5.8 million (Anonymous, 1997).

These are costs that the country can ill afford but just as important are the losses for small-scale and subsistence farmers whose basic food supply can be cut by as much as 60 % (Anonymous, 1997). Under such circumstances, starvation becomes a reality. South African plant pathologists should devise disease control strategies with an integrated approach that is economically sound and environmentally sustainable, as well as practical at all levels of production, both commercial and small-scale.

8.7.1 Implications of GLS for commercial and small-scale farmers

The RSA is part of a continent where the food situation is deteriorating - there are more undernourished people in the country today than 10 years ago (Skeen, 1997). Maize forms the staple diet of many of these people. Poverty is the major source of food insecurity and progress in poverty eradication is critical to improve access to food.

In the RSA there are approximately 55,000 commercial farms occupying approximately 3.9 million ha of farmland on which farmers produce 4-9 million metric tonnes of grain annually (Anonymous, 1997). In contrast there are more than a million small-scale farmers, with farms in the range of 1-4 ha with grain yields as low as 0.82 t ha $^{-1}$, which is barely sufficient to meet family needs (Ward *et al.*, 1999b). Many of these farmers are women and children, as males often have to leave the land in search of work in the cities.

While considerable research has been done in RSA on diseases of crops grown by commercial farmers, little attention has been paid to crop protection for small-scale farmers. A recent survey showed that the same diseases that affect commercial agricultural production also affect the small-scale farmer; the major difference being the methods of disease control employed (Adey *et al.*, 1998). At the economic level, most

commercial farmers rely on the use of agro-chemicals to control diseases. These are often not available to small-scale farmers, due to the relatively high costs of agro-chemicals, application methods, and the non-availability of products in rural areas. The level of illiteracy of the small-scale farmer may also play a role in inhibiting the appropriate use of agro-chemicals. However, in many other countries, illiterate farmers practice complex integrated pest management, often including the use of agrochemicals where no other option exists. It is possible that, in time, this will happen in the RSA.

Maize crops of small-scale farmers usually suffer from nutrient deficiencies due to the limited access to capital to fund fertilizer purchases and transport. Grey leaf spot, being a high sugar disease, will be more severe in healthy plants than plants that are stressed or have limiting growth factors (Nowell, 1997). Small-scale farmers, in general, should therefore, not have as severe GLS epidemics as farmers that have high fertilizer inputs and a healthy crop. Nowell (1997) while traveling through Cameroon, Kenya, RSA and Zimbabwe, observed that nutrient deficient maize crops showed less GLS blighting. In Africa, the small-scale farmer may be at lower risk from GLS as this pathogen is less likely to damage crops grown on soils with a lower nutritional status. However, grain production is lower with lower protein and carbohydrate values (Cedara Agricultural Development Institute - CADI - unpublished data)[2].

In a survey of community gardens conducted in KZN (Adey *et al.,* 1998), the major crop limiting factor was soil fertility. Most crops showed visible signs of nutrient deficiency. Even if cheaper sources of fertilizers existed and transport problems could be overcome to bring fertility levels up to those recommended for the various crops grown, costs would be well beyond the means of the communities.

In the present economic climate, the price-cost squeeze for the commercial farmer tends to reduce the profitability of maize production, and to increase the break-even yield level. Therefore a small loss in grain yield, e.g., 10% will result in reduced gross

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margins and may even result in maize production becoming uneconomical. However, for the small-scale farmer even a small reduction in yield could cause a major food shortage for a family whose main diet is maize. Integrated control using alternative cultural practices, resistant cultivars, insect repellants and biological control are more appropriate for these farmers. For the more progressive small-scale farmers, who can afford to fertilize their lands, GLS may become more important as a grain yield limiting factor.

Small-scale farmers often practice intercropping of a variety of crop species, and in particular, legumes. Higher N levels, resulting from N-fixing legumes putting N into the soil, could result in better fertilized maize plants which could have a higher incidence of GLS. More research on the incidence and severity of GLS through intercropping legumes with maize should be investigated.

It is a common practice to allow maize to dry down after grain-fill before harvesting. This often only takes place just before planting the new crop the following season, during which time dry, GLS infested leaf debris may be disseminated short and long distances to previously non-infected GLS areas.

Nowell (1997) reported that in an observation trial in Greytown, KZN, *Stenocarpella* ear rot increased with increased manure levels. This has implications for small-scale farmers who allow cattle to feed on maize stover. Cattle add manure to the soil which could lead to increased levels of GLS as a result of increased soil nutrients, particularly N, P and K, in the following year's maize crop. Trials with organic products such as cattle manure and chicken litter, with a high N content, should be used to determine their effect on plant growth, *C. zeae-maydis* infection and subsequent disease severity in future research trials. The advantage of allowing cattle to feed on maize stover is that this practice reduces inoculum levels the following season. It is unlikely but nevertheless it has not been substantiated, whether the conidia of *C. zeae-maydis* are viable in cattle manure.

Many small-scale farmers in RSA still grow open-pollinated cultivars which are highly susceptible to GLS (Ward, personal communication)[2]. Some of these farmers have started buying the higher grain-yielding, more stable, hybrid seed. As these farmers plant almost exclusively white-grained hybrids, the level of GLS resistance is usually relatively high (Nowell, 1997). On the other hand, large-scale commercial farmers in RSA have a sophisticated market infrastructure that helps to stabilize income. These farmers are usually able to afford a holistic GLS management programme of resistant hybrids, crop rotation, tillage practices and, if warranted, foliar fungicides (Ward *et al.*, 1999b).

Some agriculturalists contend that small-scale farmers of Africa can be lifted out of poverty without the use of modern agricultural inputs, such as improved seed, fertilizer and agricultural chemicals. Experience has shown that small-scale farmers want access to yield-increasing, drudgery-reducing technology, especially as there is a shortage of labour in rural areas as a result of urban drift (Borlaug, 1997).

The research presented in this thesis shows that if fungicides are not applied to control GLS, as in the case of small-scale farmers, increased applications of N and potassium (K) result in an earlier appearance of the pathogen in the maize crop, and a higher final percentage leaf blighting and standardised area under disease progress curve. Grain yields did not increase with increased applications of K in all three years of the trial. This was probably because grain yield response, which should have occurred at higher K applications, was reduced by increased GLS severity. In contrast, grain yields increased with increasing N applications, but only in the third year of the trial (1997/98).

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Smith (1989) found that P had little or no impact on final percentage leaf blighting. This was confirmed in the GLS : N, P, K trial at Ahrens reported in this thesis. On the other hand, analyses indicated that, despite increased disease levels, increased N and K application, combined with fungicide applications, resulted in increased grain yields, and was significantly higher than in non-fungicide treated maize.

Reducing applications of N fertilizers has been suggested as a disease control measure (Toussoun, 1970) but control at the cost of yield is obviously unacceptable. The final answer probably lies in genetic control, but advances in the commercial production of nitrification inhibitors offer exciting possibilities. Use of these products increases uptake of NH_4-N relative to NO_3-N and the resulting changes in N metabolism of plants have been shown to markedly reduce the incidence of some diseases (Huber and Watson, 1974; Warren *et al.*, 1975). Until such time as the efficacy of N stabilizers has been more thoroughly investigated, the effects of soil nutrition on GLS and other diseases are of rather limited importance to commercial growers.

In future, the effect of soil and plant nutrition on the development of GLS should be investigated under a range of environments in a number of divergent farming practices, including small-scale farming. Soils more severely depleted in N than those used in the research presented in this thesis, should be used to determine the effect of N on GLS.

Results from a wheat trial planted after fungicide treated and non-fungicide treated maize showed that wheat grown on residual fertilizers after GLS blighted maize were higher than wheat grown in soils after fungicide-treated maize. Planting a winter crop to utilize residual fertilizers after a failed maize crop due to intense GLS blighting, could have financial benefits for both commercial and small-scale farmers.

8.7.2 Economic analyses

New problems and concerns in disease management have made the balance between economic inputs and outputs important and perhaps even essential in the development of strategies for plant disease control. With added yield from additional fertilizer and

fungicide applications, agriculturalists should consider the financial implications, especially the added costs of harvesting the higher yield, plus added costs of fertilizers and fungicide treatments.

Economic analyses in this thesis was based on "a worst case scenario" as ZS 206 is highly susceptible to GLS. When GLS became epidemic in KZN in the early 1990s, this hybrid and PAN 6552 accounted for the bulk of the maize plantings in the province. Within three seasons these hybrids had been completely replaced with PAN 6480 (yellow-grained) and PAN 6479 (white-grained). Although resistance is not high enough to eliminate grain yield losses, these hybrids, although infected by *Cercospora zeae-maydis*, still produce higher yields.

New hybrids from Zimbabwe that appear to be relatively resistant to GLS and do not require spraying to achieve relatively high yields, are slowly becoming more popular. However, the yield potential of these hybrids is not as high as the more popular GLS-susceptible hybrids. It appears that in achieving resistance a certain amount of yield potential has been sacrificed (Ward, personal communication). At present farmers still prefer planting the higher yielding susceptible hybrids that require the application of fungicides to achieve their high potential yields. The outstanding efficacy of the current fungicides effectively illiminates the risk of planting high yielding but susceptible hybrids - a strategy which is also economically attractive.

Two scenarios exist. Firstly, genetic load associated with GLS resistance will limit the yield potential of GLS resistant hybrids or, secondly, GLS resistance carries little or no genetic load and therefore does not limit the yield potential of hybrids carrying this resistance.

Economic analyses of the trial reported in this thesis, using ZS 206, showed that in fungicide-treated maize, gross margins increased from R4561 to R4984 with 0-120 kg N ha^{-1}. Similarly, gross margins increased from R3884 to R5096 with 0-150 kg K ha^{-1}. In contrast, in non-fungicide treated maize, gross margins increased from R2878 to R3414 with increasing N applications and from R3386 to R3526 with increasing K

applications. The difference in gross margin between fungicide treated and non-fungicide treated maize ranged from R498 to R1570 with increasing K applications. However, with increasing N applications, there was no increase in gross margin. This could have been due to the high residual levels of N, due to the retention of N on the clay soils and high organic matter at the trial site.

Analyses showed that three fungicide applications resulted in the highest grain yields and gross margins compared to single and double sprays. If fungicides are applied to control GLS, i.e., in commercial maize production, highest grain yields and gross margins were obtained using 120 kg N ha^{-1} and 150 kg K ha^{-1} . In contrast, where fungicides are not used to control GLS, i.e., in small-scale maize production, highest grain yields and gross margins were obtained using 60 kg N ha^{-1} and 50 kg K ha^{-1} because of the higher severity of GLS at the higher N and K application rates.

Analysis of dry matter of pig, chicken, cattle (kraal), horse and sheep manure contains 1-3% N and 0-3 % K (Table 1) (CADI - unpublished data). Therefore, a small-scale farmer would have to transport and apply up to 3 tonnes of manure ha^{-1} if he plans to use manure as a substitute for 60 kg inorganic N and 50 kg inorganic K ha^{-1} . This would be an impractical and uneconomical exercise.

It is difficult to assess with confidence, the economics of a progressive small-scale farmer spraying with a knapsack sprayer. However, by making certain assumptions, it was shown that the cost of three applications of fungicides ha^{-1}, using a knapsack sprayer, is R876 ha^{-1} compared to aerial application of fungicides by commercial farmers which is R624 ha^{-1} i.e. a difference of R252 ha^{-1} . The lower cost for the commercial farmer is mainly because the interest rate on a loan is lower. The commercial farmer is also able to spread costs over a greater area thereby lowering fungicide application rates ha^{-1} and his earning capabilities/opportunity cost value of his time is higher.

However, the commercial farmer stands to lose more in gross margins if timely and efficacious spraying programmes to control GLS in highly fertilized maize lands are not

implemented. However, the optimal treatment chosen will ultimately depend on the individual farmer's risk-aversion preferences and access to capital.

Table 1. Analysis of dry matter of pig, chicken, cattle, horse and sheep manure levels. (CADI - unpublished results)

Sample identification	N(*)	Protein	Ca	Mg	K	Na	P	Zn	Cu	Mn
	(%)	(%)	(%)					(ppm)		
Pig manure	1.77	11.04	3.91	0.88	0.14	0.04	3.02	1487	672	652
Chicken litter	1.02	6.37	5.66	0.72	1.19	0.20	1.41	446	91	1217
Cattle (kraal) manure	1.57	9.83	1.75	0.92	2.65	0.49	1.18	178	41	770
Horse manure	1.19	7.47	0.80	0.28	0.70	0.18	0.34	106	37	2062
Sheep manure	2.60	16.27	3.06	1.05	2.58	Na	0.78	109	Na	Na

(*) Kheldahl test Na = not analysed

8.8 Hybrid resistance and conidial germination

Although hybrids with greaer levels of resistance to GLS have been identified in RSA, commercial farmers still prefer to use the higher yielding, less resistant hybrids protected by fungicides. However, the small-scale farmer could benefit from the introduction of commercially available GLS resistant hybrids if he does not have access to fungicides, but can afford the hybrid seed.

The most sustainable and long term GLS management strategy will be the development of high yielding, locally adapted, GLS-resistant hybrids. This may be more easily attainable in Africa where a wider range of germplasm possessing acceptable levels of quantitative resistance to GLS is recognized and readily available to the maize seed

industry. However, until such time, the use of susceptible hybrids and fungicide applications in an integrated GLS management strategy programme will continue. Unfortunately many of these strategies are not available to many small-scale farmers in many parts of the world (Ward, *et al.*, 1999b).

Ward *et al.* (1999a) showed that hybrids in the RSA can be grouped into highly resistant/tolerant, intermediate and susceptible to GLS. Resistant hybrids, e.g., SC 625 showed no yield response to 1, 2 and 3 fungicide applications. In contrast, susceptible hybrids, e.g., ZS 206, only achieved maximum grain yields following three fungicide applications.

Conidial germination trials of *C. zeae-maydis* on the susceptible maize hybrid ZS 206 and the resistant hybrid SC 625 reported in this thesis, showed that there were two different responses to germination of these two hybrids. These results reflect the findings by Ward *et al.* (1999a) that there are distinct groups of maize hybrids based on their resistance or susceptibility to GLS. Conidial germination on the maize hybrid ZS 206 was shown to have a wider range of temperature conditions favourable for germination, i.e., making it more susceptible to GLS than SC 625. In addition, conidial germination on ZS 206 was far less affected by desiccation and interrupted dew periods than SC 625.

8.9 Disease forecasting

In order to sustain a profitable maize industry, growers must find ways to reduce the cost of production and yet maintain high yield and quality. These needs are expected to increase the demand for technology that can minimize input costs while effectively managing risk for losses of yield and quality. At present an integrated approach using resistant hybrids and foliar sprays of fungicides are amongst the most effective methods of GLS control. However, the extensive use of fungicides could also result in resistance build-up in future years.

As GLS is a highly weather-dependent disease, monitoring of environmental conditions is the cornerstone of determining the incidence and severity of GLS. Therefore up-to-date sources of accurate weather data can be important decision-making aids for maize producers. As *C. zeae-maydis* significantly reduces the yield of infected plants and develops rapidly under certain environmental conditions, the correct timing of fungicide applications is critical for disease control.

Observations over the past few years have indicated the need for a more realistic and less arbitrary basis for scheduling fungicide applications rather than relying on individual GLS assessments or calendar-based operations. Detailed studies by Beckman and Payne (1982) and Caldwell (Chapters 5 and 6) have provided data of the effects of weather conditions on spore production, germination, infection, growth and latent periods. These data are being used to create a model to identify periods of infection and disease development and the most economic use of fungicide applications for the control of GLS (Ward, personal communication).

Modelling, using mathematical language, describes a set of ideas and methods that are particularly useful for investigating and describing large, complex systems, e.g., pathosystems. In all aspects of epidemiology, models complement common-sense, simple, logical observations and experiments to reduce crop losses caused by pathogens. Disease forecasting ensures the judicious use and timing of fungicide applications. Often this results in a reduction in the use of fungicides and delays disease onset. This may extend the "life-span" of registered fungicides, e.g. prevent development of resistance to fungicides.

Simulation and modelling will be used much more extensively by researchers in the new millennium. The models developed may be too complex for use directly in the field, but could form the basis for simplified field decisions. These models will also help to define data gaps, test theories, and undertake simulations that are too expensive or too complex to do in the field.

8.9.1 Automatic weather monitoring networks

At present the CADI in KZN currently maintains five automatic, battery-powered weather stations (Adcon Telemetry, Worcester, South Africa) at permanent sites in commercial fields that represent the macroclimate of the area as much as possible. These are based at CADI (29°32'S, 30°17'E), Karkloof (29°30' S, 30° 15'E), Greytown (29°04' S, 30° 35'E; and Paulpietersberg (27°25'S, 30°50'E) and are used to identify the correct timing for effective fungicide application. Each station is equipped with sensors and data loggers to provide accurate recordings of maximum and minimum temperature, maximum and minimum relative humidity and leaf wetness at 15 minute intervals. A computer at CADI retrieves data from each field station and down loads the processed data with telecommunication and radio links with computer modems. These data are used to explore fungicide application programmes for disease forecasting. Good husbandry of the crop is essential as low populations and weed infestations can greatly influence environmental readings.

These automatic weather stations have helped improve the accuracy of previous models, but problems still occur when the sensors are dirty or when the canopy has not formed. This can lead to underestimation of GLS if readings are too low or overestimation if readings are too high.

8.9.2 Prediction model

The advantage of avoiding unnecessary application, or in providing additional protection, based upon predicted meteorological considerations is obvious. To assist growers in making profitable decisions regarding the application of foliar fungicides, CADI is creating computer-based prediction models for *C. zeae-maydis,* using the weather data from the automatic weather stations. These are in the process of being tested in KZN (Ward, personal communication). Weather variables resulting in spore production and release, spore germination, infection and latent periods are used in the prediction model.

The models provide information for timing fungicide applications so a producer can tailor applications to specific localities rather than rely on a fixed, calendar-based spraying schedule, regardless of climatic factors and epidemiological criteria. A prototype model has been running since 1995/96 and is able to closely predict the onset of GLS in a number of areas.

However, predictions are not equally accurate for all regions. A limiting factor is that the exact temperature requirements of the pathogen under local conditions have not been established, particularly the effect of temperature lower than 20 °C. This system could be used to warn farmers when to start monitoring crops closely. For maximum benefit when planning a fungicide programme, each farm would have to have their own weather monitoring system. Residual debris and hybrid resistance will have to be built into the model. Considerable work is still needed before this model can be used for anything more than an early warning system for the start of a GLS epidemic or warning of favourable conditions for infection. It is anticipated that the model will provide information when subsequent sprays should be applied, based on prevailing weather conditions and effective periods of control by fungicides.

When the advisories are introduced in 2001, maize growers in KZN will be among the first in the RSA to adopt weather-based advisories for making disease management decisions.

8.9.3 Economic benefits of the model

Economic benefits gained from the model are too early to predict. However, the more favourable the weather conditions for the development of GLS, the more important timely fungicide applications become. It takes only a modest return in yield to offset the costs of fungicide and application (Ward, *et al.,* 1997a). When use of the model extends the length of the spray interval and results in one less fungicide application, savings are enormous. For example, on 60, 000 hectares under maize, a farmer can save over R9 million based on the cost of three aerial fungicide applications of R405 ha^{-1} (Ward, personal communication).

The expense of the automatic weather station at present defines the limits of the model and thus affects disease control and economic benefits. However, chemical companies and more progressive farmers could together buy stations and charge a fee to neighbouring farmers for advice of GLS.

8.9.4 Implementation of the model

The fungicide programme based on the GLS model should be integrated with other *control options, e.g., rotations, conservation tillage practices and resistant cultivars.* Reliable environmental data based on the geographical area covered by the weather stations are needed as data collected from distant sites are inadequate when disease is sporadic or when disease pressure is low but cumulative.

Implementation and validation of the model will commence in the 2000-2001 maize growing season through farmer's days, articles in farming magazines, radio interviews as well as cooperation of industry, producers and university personnel. This will enable modifications to be made as the model develops.

Early in the season, the advisory will alert farmers to the need to inspect fields to make decisions on their initial fungicide application. The necessity for subsequent sprays will be based on prevailing weather conditions, the last spray date and genetic resistance of the host. Daily advisories will be available for each area surrounding the weather stations. Growers will use the advisory from the weather station nearest their fields.

By 2001 the central computer at CADI will print an advisory for each location at 1600 hrs every day. Once the advisories have been verified, a recorded message will be prepared for producers in the maize growing areas. A toll-free telephone hot line will be installed at CADI and will probably be the most popular and up-to-date advisory for farmers and chemical companies. This hot line will deliver regional advisories based on weather data collected by the five regional weather stations. This method of delivery will ensure timeous updates and make them accessible 24 hrs a day including public holidays and week-ends.

Farmers participating in the programme will be used in a survey to be run in 2002, to ascertain number of fungicide applications for GLS control in the 2000-2001 maize-growing season. This will determine if, and how many, fungicide applications were saved and the average savings in production by using the CADI advisory system.

8.9.5 Educating the public

Traditional methods of information dissemination will be used to inform farmers of the advisory, e.g., farmers' days, radio interviews, popular articles in farming magazines, newsletters, extension officers, short courses, crop production guides and other extension publications which are updated regularly. While these are useful tools for informing farmers of new developments, the publications can lack recent changes in fungicide registrations and methods of use. The information may also lack relevance to prevailing crop conditions and not make the best use of cost-saving, site specific integrated management strategies.

It is hoped that the advisory will become part of the daily regional weather reports. The best approach would be to use electronic systems such as the Internet, but many rural producers are limited to only long-distance telephone access. Telephonic communication using dedicated telephone lines may be an interim solution until electronic communication becomes widespread.

8.9.6 Future considerations

The choice of fungicides is another variable that can affect the performance of a disease management programme. Various degrees of GLS and length of control have been reported with different fungicides sprayed according to various spray programmes (Ward *et al.,* 1997a). This may require adjustment depending on hybrid choice, rate of plant growth, environmental factors and fungicide chemistry. To accommodate these options, the dimensions of the advisory programme should be expanded to form part of resistance-management strategies in the years ahead.

Modifications to the model after field tests, together with further epidemiological studies in following years will, no doubt, improve reliable forecasting of GLS. The model has opened up exciting new possibilities for GLS control for the maize industry, increasing growers' awareness of environmental conditions that favour disease and enabling intelligent decisions for correct timing of fungicide sprays. Despite some limitations and modifications still required, this model signals a logical departure from fungicide applications based on calendar dates and longevity of fungicides and results in more judicious application of fungicides for improved GLS control and reduced production costs.

Reducing the need for fungicide applications for the control of GLS, continues to be challenging and difficult. The present GLS forecasting system offers some of the most advanced technology in electronic weather monitoring. Part of the mission of the CADI is to create knowledge, to validate and fine-tune the advisory and to transmit relevant information to clientele. An ongoing challenge to all involved in the GLS prediction model is to continually update the model. This will result in the release of improved GLS advisories with greater efficiency and a wider margin of dependability in future years.

8.10 Conidiogenesis of *Cercospora zeae-maydis*

In general, the process of conidiogenesis in *C. zeae-maydis* is similar to that observed in *C. beticola* by Pons *et al.* (1985). Sympodial proliferation of conidiogenous cells in *C. zeae-maydis* is characteristic of other species in the genus *Cercospora* (Pons *et al.*, 1985). In addition, conidial measurements and observations are also similar to other taxonomic descriptions of this pathogen (Tehon and Daniels, 1925; Chupp, 1953; Kingsland, 1963; Beckman and Payne, 1982; Latterell and Rossi, 1983; Wang *et al.*, 1998).

The granular wall material laid down on both the half of the septum remaining on the conidiogenous cell and the half constituting the base of the conidium, compliments observations on *C. beticola* by Pons *et al.* (1985). This further confirms the

differentiation of genera of *Cercospora* and *Cladosporium* from *Alternaria, Dendryphiella* and *Drechslera*, which have a ring of electron opaque material on the geniscars in the secondary layer of the conidiogenous cell wall.

In this study, diurnal conidial release has been shown to correspond to increasing vapour pressure deficits and temperature and decreasing leaf wetness. This was confirmed with multiple regression analyses of conidial release related to environmental variables. This hygroscopic process that appears to be involved in the release of conidia in *C. zeae-maydis* has also been found in *C. beticola* (Meredith, 1967; Pons *et al.*,1985) and *C. asparagi* (Cooperman, 1986).

8.11 Future research needs

The maize hybrid (ZS 206) used in this thesis is very susceptible to GLS. This was important to ensure that fertilizers had an effect when the severity of GLS is very high. Consequently, the outcome of the research reported represents the worst case scenario. To give a more complete overview of the effect of soil applied nutrients on the progress and severity of GLS, the research needs to be repeated using different fungicides, foliar application of nutrients, and different hybrids with different levels of susceptibility to GLS in different geographic areas. At the same time, these effects on other diseases of maize could also be investigated. As this research has implications for the small-scale farmer, different cultural practices and cultivars used by small-scale farmers should be investigated. Maize grown on poorly fertilized soil has been shown to have a lower protein content than maize grown on well-fertilized soils (CADI - unpublished data). Analyses of the nutritional status of maize grown under different practices, particularly different fertility levels, would be a further advantage to the small-scale farmer. A study is also needed to determine whether maize is its only host, if *C. sorghi* can infect maize and if the pathogen is seed-borne.

The studies reported in this thesis have made a contribution to the biology of *C. zeae-maydis*. However, there is still much to be learnt about the biology, host resistance and cultural practices to reduce the impact of this pathogen on maize production world-wide.

8.12 The challenges ahead

Although there will be considerable variation in the incidence and severity of GLS between seasons and geographical locations, GLS will continue to increase in importance throughout the world, particularly in the sub-tropical and tropical maize production regions of the world. If environmental losses are appropriate, it will create significant yield losses in the short term (Ward *et al.*, 1999b).

In areas where GLS is not epidemic, reducing initial inoculum levels through tillage, crop rotations and residue management, would be the most suitable management strategy for control of GLS. However, once GLS is endemic within an area of maize production, management strategies must focus on protecting the maize crop by reducing the development of the pathogen. The increased use and advantages of reduced tillage practices means that GLS is here to stay.

The short term GLS management strategy is to use less susceptible hybrids and fungicide sprays, together with crop rotation and residue management to reduce initial inoculum. The long term strategy is to develop high-yielding, locally adapted, GLS resistant hybrids.

The concern in the last three decades about environmental quality has forced attention on policies and programmes to balance the need for an adequate food supply at reasonable prices with the need to reduce the use of pesticides, especially those with more lasting environmental effects. Regulation of the registration of new agro-chemicals has made it increasingly expensive and time-consuming for new compounds to reach the market. In addition, the general trend towards no-till operations greatly

favours the build up of inoculum levels. These factors will serve to focus even more attention on the use of host resistance and cultural practices to control diseases in the future. The emphasis will and must be to tie together science and practice, and take full advantage of the results of the former to perfect the latter. Increased costs of labour and energy, with resultant mechanization, will bring about changes in cultural practices beyond those that would normally occur in agriculture in RSA.

One of the goals of sustainable agriculture is to reduce agrochemical inputs, such as pesticides, without decreasing quality, yield or gross margins of crops. The long-term promise of increased economic gains through improved disease management practices offered by manipulation of nutrient amendments provides incentives to agriculturalists to begin the transition away from costly fungicide control programmes. Manipulation of host nutrition, in conjunction with other cultural practices such as the use of less susceptible hybrids, crop rotations, and weed and pest control provide an effective tool for controlling GLS without the use of costly fungicide control programmes.

Recognition of the role of nutrients in plant health, and in particular, resistance of plants to disease provides opportunities to understand and control plant diseases. The direct correlation of disease response to N and K uptake by maize may provide the needed insight to understand and manipulate fertilizer practices leading to GLS resistance.

As growers attempt to manipulate more of the interrelated factors in plant production, disease management is becoming increasingly complex. Individual methods of disease control will be blended with each other in integrated pest management (IPM) strategies. To devise a successful IPM programme requires an understanding of plant ecosystems, the epidemiology of major pathogens, biological control, imagination, lateral thinking, combining different agronomic disciplines, and much testing in field trials. This type of investigation may well become a dominant type of research in the future, as control focuses on altering cultural practices rather than intensified agrochemical applications. Computer technology should help put these disease

management strategies in concert with the entire production system. The sophisticated knowledge from the knowledge explosion of the past three decades must be applied to result in increased food production "to feed more people and feed people more" (Borlaug, 1997).

8.13 Literature cited

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