INHERITANCE OF RESISTANCE TO GREY LEAF SPOT AND NITROGEN UTILISATION EFFICIENCY IN MAIZE (Zea mays L.)

By

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APPROVAL

The University of Zambia approves this dissertation of Kabamba Mwansa as fulfilling the requirements for the award obamba Mwansa hereby declare that this dissertation represents my own work and that it has not previously been submitted for the degree at this or another University.

Signature

ABSTRACT

Maize is an important staple and cash crop in Zambia. Abiotic and biotic stress conditions, particularly low soil fertility (low nitrogen) and grey leaf spot (Cercospora zeae- maydis), reduce maize yields. Most varieties developed by the Zambian National Programme have neither resistance to GLS nor tolerance to low nitrogen stress. Earlier variety selection was done under optimum conditions and when the disease was absent. In this study 10 inbred lines from the Zambian National Programme were crossed to 12 CIMMYT single cross testers using a North Carolina Design II. The 110 progenies realized were evaluated under fertilizer and no fertilizer (low N) conditions at 6 sites also endemic to grey leaf spot disease in Zambia and Zimbabwe. Objectives were to (i) determine important gene action controlling the traits (ii) estimate GCA and SCA of lines and testers (iii) estimate narrow and broad sense heritability of the two traits, and (iv) identify good hybrids. Results showed that Nlevel, Site(Nlevel) and GCA (lines and testers) were all significant ($p<0.01$) for the variables measured except for SCA (lines x testers). Additive gene action rather than non-additive gene action were involved in controlling the traits. Lines (L12M1(220GY)–150-3-3-1-1and N3-1XN3offtype-4-1-3-3-2-1-1) and testers (CML444/DRB-F2-60-1-1-1-BB and CML444/CML 448) consistently performed well. These parents had high and positive GCA effects for grain yield, plant height, and ears per plant. They were also good combiners for kernel weight, the number of kernels per ear and had reduced leaf senescence and a short anthesis-silking interval (except line: L12M1(220GY)–150-3-3-1-1). Significant and negative GCA for GLS were exhibited by lines (Line 14-1 and 8535-23-1-2-2) and testers (CML 444/ DRB-F2-60-1-1-1-BB and CML 440/ CML 443) while the susceptible parents were lines (L12M1(220GY)–150-3-3-1-1 and N3-1XN3offtype-4-1-3-3-2-1-1) and tester (CML 312/CML 442). High genetic correlations for grain yield at low N, high N and across environments were found

with most secondary traits except for anthesis (lines and testers at low N), SKW (testers under low N), ASI (testers across environments and lines at high N) and leaf senescence (line and testers). High heritability estimates at nitrogen stress were found in GY (h2=0.51), AD (h2=0.51), SD (h2=0.57), PH (h2=0.68), SKW (h2=0.81), and turcicum (h2=0.89). ASI (h2=0.44), leaf senescence (h2=0.29), KNEAR (h2=0.42), and EPP (h2=0.38) had low heritabilities under low N. High heritability was also found for GLS (h2=0.77). Hybrids involving L12M1(220GY)-150-3-3-1-1x CML444/CML448 and Line 14-1 x CML444/CML 448 were among hybrids performing well under low N, high N and across environments.

DEDICATION

To my dearest wife Erica and my lovely daughters Bwalya, Mukuka, Mwaka and Chishala for the support and encouragement.

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A	Shelling %
HCOV	Husk cover
TEXT	Texture (grain)
PN	Plant number
EN	Ear number
EROT	Ear rot

CHAPTER ONE

1.0 INTRODUCTION

Maize (Zea mays L.) is one of the most important food crops worldwide. Among the world's major cereal crops, maize ranks third after wheat (Triticum aestivum L.) and rice (Oryza sativa L.) in global production. In 2000 about 140 million hectares were put to maize globally and of this approximately 96 million hectares were in developing countries (Pingali and Pandey, 2000). Current annual maize

production is estimated at 500 million tones and by 2020 the projected demand for maize in developing countries will surpass the demand for both wheat and rice (Pingali and Pandey, 2000).

In Zambia maize is a staple crop followed by cassava, sorghum, and millet. It accounts for more than 70% of carbohydrates in the diets of many Zambians. Almost 90% of the maize produced is used directly for human consumption, with livestock and industry
(Bear making) taking up the rest (Mungoma and Mwambula, 1996; Ministry of Agriculture Food and Fisheries, 1995). Maize is also an important cash crop grown by the majority of smallholder farmers in the country.

Since maize is a source of human food and income, it therefore means that successful grain production would result in food security in the country. In Zambia cultivation of maize is done throughout the three agro-ecological zones of Zambia namely regions I, II, and III and by all categories of farmers (Bunyolo et al, 1995). The average production stands at 1.5 t/ha and this hardly results in food self-sufficiency in the country (Ministry of Agriculture Food and Fisheries, 2000).

Among the constraints destabilizing maize production and eroding income and food security in Zambia and the southern African region are the drought, low soil fertility, acidic soils (low pH), pest and diseases (Zambezi and Mwambula, 1996; Banziger et al, 2001; Mungoma and Mwambula, 1996; Reddy et al, 1989; Betram et al, 2003).

One of the most serious and recent diseases of maize since 1996 has been grey leaf spot (GLS) caused by Cercospora zeae maydis (Kaula personal communication, 2003; Ngwira and Pixley, 2000; Tembo and Pixley, 1998). On susceptible varieties, disease severity often reaches 60-100% plant coverage

and leaf damage by the time the crop reaches physiological maturity. The severe blighting results in weakened stems, leading to lodging. According to Ngwira and Pixley (2000), the disease can reduce grain yield of maize under heavy infestation by 20-100%.

Since the 1990s Zambia has experienced droughts and the worst one occurred during 1991/92 season that resulted in low production of maize resulting in the importation of the commodity (Mungoma and Mwambula, 1996; Zambezi and Mwambula, 1996). Since then partial droughts have occurred frequently. In addition infertile soils especially low nitrogen has exacerbated the effect of insufficient rainfall. Despite intensifying their cropping, farmers still realize poor yields due to continuous use of non-restorative fallows (Banziger et al, 2001), as well as farm soils that are old and depleted of nutrients. A relatively small number of farmers can afford chemical fertilizers, which is now rarely subsidized and few can obtain credit to purchase inputs. Because rainfall is so unreliable, farmers who do manage to obtain fertilizer cannot be sure when to apply it and when they apply, they usually apply less than the recommended rates. The result of growing maize under low input condition results in wide yield gaps between researchers and smallholder farmers. According to Zambezi and Mwambula (1996) researchers may obtain 10 t/ha compared to smallholder farmers who often reap less than 1 t/ha.

The Zambia National Maize Research Program has since 1983 developed commercial maize varieties currently on the market. Most varieties have been found to display different levels of susceptibility to grey leaf spot and none can be considered to be resistant. Under favorable conditions these varieties will all develop significant levels of the disease. The varieties at the time of development were not selected for resistance to grey leaf spot, as it was not present in Zambia.

In addition the varieties possess little or no tolerance to low nitrogen stress. Earlier selection was only done under optimal fertilizer conditions as opposed to screening the germplasm under stress conditions as well. The program according to Mungoma and Mwambula (1996) relied of the theory that the better performing selections at optimal fertility levels would do better at sub-optimal levels too.

Declining soil fertility, use of marginal areas, high cost of fertilizer, lack of credit facility, and the sub-optimal application of nitrogen fertilizer will continue to affect yields of maize with farmers harvesting less than 1 t/ha.

In mitigating the problems, the Maize Research Program under the Ministry of Agriculture and Co-operatives and the International Maize and Wheat Improvement center (CIMMYT-Zimbabwe) embarked on a programme to develop germplasm with enhanced tolerance to both biotic and abiotic stresses. The improved germplasm would be used as parents for improved maize varieties. It is envisaged that the developed germplasm would tackle the problems of grey leaf spot, drought and low soil fertility leading to more stable yields and incomes, and improvement in the food security of the country and the region as a whole.

The value of developed maize germplasm as parents of commercial hybrid varieties in any breeding programme can be determined primarily by their combining ability. Therefore, the objectives of the study were to:
Determine important gene action for grey leaf spot (GLS) resistance and low nitrogen tolerance, and the interaction between the two traits.
Estimate narrow and broad sense heritabilities of the two traits.
Determine the general combining ability (GCA) and specific combining ability (SCA) of female (tester) and male (line) parents.
4. Identify hybrids suitable for Zambia conditions.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 GREY LEAF SPOT (GLS)

Grey leaf spot of maize, caused by Cercospora zeae-maydis, is considered a disease of major concern in many parts of the world (Ward et al, 1997). The disease was first identified in the United States of America (USA) in 1925. According to Hurrf et al, (1988) GLS developed to epidemic level in the USA in the 1970's. In Southern Africa, the first report of the disease was in South Africa in the 1980's. However, significant epidemics caused by GLS in the country happened during the 1991/92 growing season (Gevers et al, 1994; Ward and Nowell, 1997). Therefore, prior to 1994, GLS was of economic importance in South Africa. Nevertheless, GLS has now become one of the prevalent and severe diseases of maize in Eastern and Southern African regions (Ngwira and Pixley, 2000; Tembo and Pixley, 1998). In 1994, GLS was observed in Uganda and in 1995/96 the disease was seen in Kenya and Zimbabwe (Pixley, 1996).

In Zambia, GLS was observed in 1996 (Kaula personal communication, 2003; Ngwira and Pixley, 2000; Tembo and Pixley, 1998). The disease is wide spread and is now considered as the single most important diseases of maize in the country. Previously, maize streak virus (msv), leaf blight (Exserohilum turcicum),

and common rust (Puccinia sorghi) were the major diseases of maize in Zambia (Rao et al., 1987). As such, research in the maize program is now focusing on selecting germplasm material that has enhanced resistance to grey leaf spot.

2.1.2 DISEASE CONDITIONS

Grey leaf spot is a fungal disease caused by Cercospora zea-maydis on a maize crop. The disease requires a warm or hot and humid rainy weather conditions. Under these conditions, the pathogens or inoculum, would bloom suddenly especially on overcast days (Ngwira and Pixley, 2000), under high relative humidity (Beckman et al, 1983; Donahue et al, 1991) and with the extended leaf wetness (Beckman and Payne 1982; Donahue et al, 1991). Although GLS is highly influenced by the microclimatic conditions, the disease prevalence varies depending on the location and climatic conditions (Donahue et al, 1991). This makes the assessment of the disease for both inheritance studies and resistance breeding very difficult (Saghai maroof et al, 1996). According to Ngwira and Pixley (2000) the disease therefore spreads more rapidly in high rainfall area than in dry areas.

Apart from warm and humid rainy weather, there are also other factors known to cause the rapid spread of the disease. In Southern Africa for instance presence of inoculum and extensive cultivation of susceptible host plants are some of the factors (Tembo and Pixley, 1998; Ngwira and Pixley, 2000). Other factors are the widespread use of minimum tillage techniques whose practice leave fields covered with infected stover (Thompson et al, 1987). Payne and Waldron, (1983) mentions that the conditions contribute to over wintering of fungus on corn debris thereby serving as a source of disease inoculum. This could lead into early infections to the crop the following season with symptoms appearing about mid season. While increased severity has been associated with no-tillage maize, Perkins et al (1995) however observed the disease under conventional tillage practices.

Minimum tillage is commonly practiced now as a conservation method of farming with the objective of restoring soil fertility. In Zambia, Golden Valley Agricultural Research Trust (GART) and some Non Governmental Organization (NGO) are spearheading and promoting this technology. In areas where this technology is introduced more than 50% of the farmers have already adopted the technique (Moono personal communication, 2004).

In addition, continuous and or extensive cropping of maize is also another contributing factor. In Zambia, like in most growing areas, the practice has been to grow maize traditionally under a system of monoculture and few farmers practice any form of crop rotation.

2.1.3 DISEASE SYMPTOMS

Grey leaf spot is known to affect leaf, sheath, husk and stem tissues of maize plants. Symptoms first appear typically around flowering (Ngwira and Pixley, 2000). However, they may be much earlier if conditions favour disease development (Latterell and Rossi, 1983). Initial symptoms appear as small, rectangular, and elongated tan to brown necrotic spots delimited by the major veins on the maize leaf (Sprague and Dudley, 1988). The lesions on the leaves eventually spread to cover the whole plant (Ngwira and Pixley, 2000).

The lesions then turn grey afterwards when fungus grow on the surface of the dead leaf tissue (Ngwira and Pixley, 2000). When the number and size of lesions increases rapidly, they result in extensive death of leaf tissues. This makes leaves to appear blighted.

In addition GLS may infect maize stalks too. This development weakens the stalk thereby causing lodging (Lipps, 1987). Associated with GLS infections are the

stalk rots as well. Latterell and Rossi (1983) mentions that this arises due to early infection of the fungus on maize plants.

2.1.4 ECONOMIC IMPORTANCE

Under ideal conditions disease severity has been observed to reach 60-100% plant coverage. This causes extensive leaf damage by the time the maize crop reaches crop physiological maturity (Ngwira and Pixley, 1996). As such the quality of silage from maize can be reduced (Ward and Nowell, 1997).

Yield losses due to GLS have been reported. For instance, 20% yield reduction has been mentioned in the USA, in Pennsylvania (Aryers et al, 1984) and in Tennessee (Hilty et al, 1979). Others have mentioned losses of as much as 50% (Strongberg and Donahue, 1986; Strongberg and Flinchum, 1994), whilst losses of between 10-50% have been reported by Gevers and Lake (1994), and Saghai maroof et al (1996). In Africa, yield losses up to 88% have been recorded. This was in Kwa-Zulu Natal in South Africa by Ward et al (1993). In addition 30% losses has been reported to occur in endemic areas (Ward et al (1993). Latterell and Rossi (1983) also mentioned that non-documented losses have undoubtedly been higher when severe disease results in stalk lodging.

Yield losses due to GLS have been attributed to loss of photosynthetic area, increase in lodging, and premature death (Strongberg and Donahue, 1986; Strongberg and Flinchum, 1994). Due to loss of photosynthetic area, carbohydrates are diverted from the stalk and roots to the grain at greater than normal levels. This causes stems to weaken and often lodge, leading to death of the plant and therefore loss in yield.

2.1.5 DISEASE CONTROL.

The disease can partially be controlled through the combined use of crop rotation (Sprague and Dudley, 1988), crop sanitation (Sprague and Dudley, 1988),

fungicides (Ward et al, 1995) and use of genetic resistance (Saghai maroof et al, 1996; Sprague and Dudley, 1988; Stromberg and Donahue, 1986; Ngwira and Pixley, 2000). The use of fungicides increases production costs and it is not usually economically feasible to many farmers. In addition the chemical fungicides are also viewed as environmental hazards with possible adverse effect on the farmer's health (Tembo and Pixley, 1998; Nhlane and Caligari, 1996). Therefore, the main solution lies in the use of genetic resistance (Thompson et al, 1987; Elwinger et al, 1990; Singh, 2003) in maize cultivars which is viewed to be highly effective and cost efficient (Ward et al, 1997) and can be required as a sole solution or as a contribution to a better integrated approach in dealing with the disease problem (Tembo and Pixley (1998).

Development of resistant cultivars however needs the understanding of inheritance of resistance. Most published reports have found additive, with less important, but significant non-additive gene action affecting resistance (Gevers and Lake, 1994; Ulrich et al, 1990). However, dominance (Elwinger et al, 1990), recessive and epistatic (Saghai maroof et al, 1996) gene action have been implicated in GLS resistance in maize as well.

Molecular marker analysis done by Bubeck et al (1993) showed significant association between GLS resistance and chromosome segments whilst Saghai maroof et al (1996) found only four chromosomes to be associated with GLS resistance for one single population from his studies.

2.1.6 DISEASE EVALUATIONS

Evaluations of the disease can be done through artificial inoculation and by natural infections achieved through growing the experiments in hot spot areas that are endemic to GLS. In artificial inoculation as explained by Tembo and Pixley (1998), inoculum is prepared from collected and kept GLS infected leaves kept are under cool conditions. Prior to infestation the leaves are ground and the

pinch of inoculum is placed in whorl of each plant. This is at 6 to 8 leaf stage when plants are growing with young leaves (Ngwira and Pixley, 2000). Natural infestation requires endemic areas where maize is grown year after year using some form of conservation tillage in which there is increased amount of surface debris left.

Since development of GLS disease is highly influenced by microclimatic conditions (Payne and Waldron, 1983), it therefore means that a strong dependency on the environmental effects makes the assessment of the disease, for both inheritance studies and resistance breeding, very difficult. Although the presence of heavy disease pressure is an essential prerequisite to evaluate the level of GLS resistance, it has been observed that such an optimal condition is difficult to achieve through artificial inoculation or supplementary irrigation. Donahue et al (1991) found that the GLS disease prevails in high relative humidity and with extended leaf wetness, which varies among different locations and climatic conditions. The difficulties in disease evaluation have further limited progress in developing GLS-resistance maize hybrids.

Disease assessment is done by visual estimates of percent leaf area affected. In most instances ratings are done on mature plants on a plot basis on a scale of 1 (resistance) to 5 (susceptible) with increment of 0.5 on a scale (Ngwira and Pixley, 2000; Thompson et al, 1987). The term mature plant refers to an approximate stage of development near physiological maturity. Disease symptoms should be scored at least twice. This should be at mid-silk (flowering) and mid to late grain fill (Ngwira and Pixley, 2000).

2.2. NITROGEN AND THE MAIZE PLANT

2.2.1. IMPORTANCE OF NITROGEN

Nitrogen is an essential macronutrient required by the maize plant. It is a component of all enzymes and therefore necessary for plant growth and

development (Banziger et al, 2000). It contributes about one–sixth of the weight of proteins (enzymes) and is a basic element of nuclei acids. Nitrogen is plentiful in leaves, mainly in photosynthetic enzymes, where it may account for up to 4% of dry weight. Because of nitrogen uptake in the maize plant, biomass production and grain yield have shown a strong correlation to each other. Banziger et al, (2000) showed nitrogen requirement of a maize crop as related to grain yields.

2.2.2 LOW NITROGEN (LOW N)

Nitrogen is an important macronutrient that often limits yields in the lowland tropics. Though application of nitrogen fertilizers and amendments can generally correct the situation, these are often not available. Therefore, low nitrogen (Low N) or nitrogen deficiency condition in plants occurs when available nitrogen required for optimal plant growth and development is below optimal-levels required or recommended amounts. The conditions of low N arise due to a number of factors. This includes low inherent nitrogen in soils, mono-cropping, and high cost of inputs especially nitrogenous fertilizers. Others are the use of marginal lands, lack of credit facilities and the reduced or sub-optimal application of nitrogen fertilizers.

Inherent low soil fertility in particular nitrogen is a common feature especially in tropical soils (Betram et al, 2003). The limitation is due to acidic soil (Pandey et al, 1994). Acid soils have poor agricultural quality due mostly to their low pH, low nutrient reserves, low nutrient retention capacity, low organic matter and soils deficient in nutrients (Donahue et al 1983; Tisdale et al, 1985; Narro et al, 1996). In addition production environments for maize are becoming harsher as maize is displaced to more marginal environments by higher value crops (Beck et al., 1997).

Farmers commonly practice mono cropping without crop rotation (Haggblade and Tembo, 2003) and this has led to decline in soil fertility status of soil as organic carbon is depleted (Haggblade and Tembo, 2003, Banziger and Lafitte, 1997).

High cost of inputs is a concern now especially that there are no government subsidies and fertilizers have to be acquired at economic price (Haggblade and Tembo, 2003) and farmers fail to acquire them as it does not justify the producer prices that prevails (Heisey and Mwangi, 1996) or the economic returns (Lafitte and Edmeads, 1994).

Sub-optimal or reduced application of plant nutrients is a common practice among farmers. Banziger et al, 1997 points out that under drought conditions farmers often delay fertilizer application. And when they apply they do so in reduced amounts that contribute little to long-term fertility management. In addition, deficiency may also arise when there are significant risks of drought and frost or of excessive leaching of nitrate (Lafitte and Edmeads (1994).

Studies done show that application of nitrogen can be as much as 36 kg/ha in Brazil (Santos et al, 1996), 14 kg/ha in Malawi (Zambezi and Mwambula, 1996), 10 kg/ha in Africa (Heisey and Mwangi, 1997) and a mere 7 kg/ha in sub-Sahara Africa (Musya and Diallo)

According to Zambezi and Mwambula, (1996), wide yield gaps have been observed between researcher and smallholder farmer yields. Yields of 10 t/ha and less than 1.0 t/ha have been recorded between researcher and smallholder farmer respectively. Other studies have shown yield losses of about 10 - 55% (Logrono and Lothrop, 1996) and 300 to 400kg/ha (Low and Waddington, 1991).

2.2.3. MAIZE UNDER LOW-N STRESS

When maize is grown under low N stress, reproductive development and yield is affected as the result of nitrogen supply (Edmeads et al 2000; Below, 1996). In maize nitrogen is known to influence crop photosynthesis, root growth, and reproductive development and crop development (Banziger et al 2000).

Nitrogen stress reduces crop photosynthesis as it affects leaf area development and leaf photosynthesis rate and it also accelerates leaf senescence. According to Banziger et al (2000) about 50% of all leaf N is directly involved in photosynthesis either as enzymes or chlorophyll. When N becomes scarce plants reallocates N from older tissues such as leaves and stalk to younger tissues which are the leaves and grain leading to early senescence of the older, lower tissues. And with increase in N stress, photosynthesis rate is reduced resulting in little assimilates being manufactured.

Under N stress the absolute amount of root for absorption of water and nutrients are reduced. In addition maize develops shallow roots than they usually do when grown under normal fertilization (Banziger et al, 2000). These conditions predispose the plants to greater risks under drought.

Nitrogen stress has influence on the development of maize reproductive structures as well. Since the initiation and development of reproductive structure occurs in distinct phases, each is affected by N stress. It has been found that the number of potential kernel ovules is established early in plant development. The kernel row number is set by the time most tropical maize plants have 12 – 14 leaves while the number of kernel per row by the time plants have 16 - 18 visible leaves (Banziger et al, 2000; Below, 1996).

The number of ovules that ultimately develop into mature kernels is affected by the extent of kernel abortion two weeks bracketing flowering (Below, 1996). Severe N stress delays both pollen shed or anthesis and silking, but the delay in

silking is relatively more so that the Anthesis – silking interval (ASI) becomes greater under N stress. Silking delay is correlated with kernel and ear abortion (Banziger et al, 2000; Below, 1996).

Nitrogen stress also influences crop development. At the beginning of the season and especially with fertilizer applied, N exceeds crop demand. However, when the season progresses, more N is taken up. Banziger et al 2000 mentioned that Soil N mineralization is usually less than 1 kg N /ha / day, whereas a healthy maize crop can take up and assimilate 4 to 5 kg N / ha / day, leading to N depletion of the soil and N stress in the plant as the season progresses. Plants adjust to some extent to N stress by re-mobilizing N from older tissues, a mechanism that does not affect yields in case of tissues that contributes little to photosynthesis. Depending on the timing of N stress in growing plant parts, different yield determining factors are affected. Nitrogen stress before flowering reduces leaf area development, photosynthesis rate and the number of ear spikelets (potential grains). Nitrogen stress during flowering stage results in kernel and ear abortion, whereas stress during grain filling accelerates leaf senescence and reduces crop photosynthesis and kernel weight (Banziger at al, 2000).

2.2.4. BREEDING APPROACHES UNDER LOW NITROGEN (LOW N).

In developing maize varieties, plant breeders have in the past used optimal conditions during screening phase to select for desirable plant type. When few genotypes remain, they are then evaluated under abiotic stress. At this stage selection intensity is often low and therefore progress in breeding for tolerance to abiotic stress is poor (Banziger et al, 2000). Apprehensions on why breeders have not been making selections under abiotic stresses early in breeding stages have been outlined. Among notable reasons according to Banziger et al (2000), and Lafitte and Edmeads (1994) are that heritabilities and genetic variances decrease under abiotic stress as yield levels fall. In addition the genotype x

environment interactions under stress is high and this make it difficult to identify best genotypes with entries changing ranks and sometimes not being significant from one experiment to another as compared to conditions where yields are high.

Since maize in the tropics is continuously exposed to abiotic stress (N-stress), then there is a need to include extensive screening under stress conditions so that yields under favorable and stress conditions are improved (Banziger et al 2000). Therefore, one approach is to select cultivars that are superior in the utilization of available N. This can either be due to enhanced up take capacity or because of more efficiency use of absorbed N in grain production (Lafitte and Edmeads, 1994).

Cultivars that are less responsive to applied N and sometimes that performs better than do N-responsive hybrids or cultivars have been identified (Pollmer et al, 1979; Thirapon et al, 1987). A suggestion by Blum (1988) was that selection for yield in low target environments (low soil-N status) should be more effective than selection for yield potential alone.

One approach to increasing the efficiency of selection in low N environments relies on the use of secondary traits (Blum, 1988; Banziger et al, 2000)

2.2.5. LOW NITROGEN FIELDS.

These are fields used to screen genotypes at every stage of breeding. They are depleted with available nitrogen. Depletion involves growing non-leguminous crops with high biomass production and then removing it. According to Banziger at al, (2000) the higher the biomass the more nitrogen is removed from the soil. Under these fields, yields of genotypes should be in the range of 25 – 35 % of those obtained under well-fertilized condition and should also represent an uptake of 20% to 25% of N for maize grown under well fertilizer conditions. With this stress, plant traits affecting yields are different from the ones relating to

yields under non- stress conditions and therefore genetic variation for low N tolerance can be observed.

If yields under low N stress are greater that 50% of those obtained under well-fertilized conditions, then they relate more to genotypic yield potential than the mechanism that impact tolerance to Low N stress and N stress tolerance genotypes cannot be easily discriminated (Banziger at al, 2000. When low N fields are developed they have to be used continuously for several seasons. The aim to capitalize on results obtained with Low stress of the past season to manage the N stress of the following seasons (Banziger at al, 2000).

The conditions for operating the Low N fields are that the fields should only have limitations in nitrogen and not other factors (i.e. nutrients, water, soil PH). In these fields no nitrogenous fertilizer either in chemical or organic form should be applied and it is also required that the length of fallow between the previous crop and planting date of maize be reduced. The Stover of the previous crop has to be removed after the harvest so as to avoid nitrogen returning to the soil through organic matter. In the management of the low N site, the fields should not be intercropped or rotated with leguminous crops.

2.2.6. USE OF SECONDARY TRAITS.

In maize breeding programme, secondary traits are used in identifying tolerant genotypes. Under low N these traits improve precision with which Low N tolerant genotypes or nitrogen use efficient genotypes are identified and they also demonstrate the degree to which Low N stressed the crop. Among the suggested traits are the high plant nitrate uptake (Mollaretti et al, 1987), genetic variation for mobilization of N from leaves and stems to grain (Eghball and Maranville, 1991). Others are the large leaf area and high specific N associated with high maize yields under N stress (Muchow and Davis, 1988), leaf chlorophyll concentration (Hardcre et al, 1984), plant height of N stressed plant (Lafitte and Edmeads,

1988), leaf senescence (Wolfe et al, 1988a), and ears per plant as well as anthesis silking interval (Banziger et al, 2000, Edmeades et al, 1993). The use of adaptive value of secondary traits according to Blum (1998) should begin with an assessment of their relationship to productivity in a field environment. Whenever phenotypic correlations are used to determine the underlying associations between characters, care must be exercised to ensure that the associations are not simply a result of environment differences. Falconer (1989) points out that genetic correlations are more useful than phenotypic correlations in determining the relationships between traits.

Therefore the ideal secondary traits should be ones that genetically associate with grain yields, are highly heritable and genetically variable, and should be cheap and fast to measure. At the same time they should also be stable within the measurement period and as a reliable estimator of yields before final harvest (Edmeads et al, 1998; Banziger et al, 2000 and Lafitte and Edmeads, 1994).

Among the secondary traits used for assessing tolerant genotypes in maize in many National Maize Breeding Programmes under Low N are the anthesis to silking interval (ASI), number of ears per plant (EEP), senescence and grain yield (Banziger et al, 2000).

2.2.6.1 ANTHESIS TO SILKING INTERVAL (ASI).

When stress such as drought and low N coincides with flowering, a commonly observed phenomenon in maize is delayed silking resulting in an increase in length of ASI. It has been found that under Low N a shortened ASI contributes significantly to improved grain yield (Banziger and Lafitte, 1997). According to Dow et al, (1984), a shortened ASI in maize is associated with tolerance of stress which occur around flowering. Many researchers have also reported ASI to be a better trait than yield to select for under low nitrogen stress as well as under

drought as its variability increases with increasing (nitrogen) stress (Banziger et al, 1997, Edmeads et al, 1993). In addition its heritability does not decline as rapidly as grain yield per se under low N stress (Banziger et al, 1997, Edmeads et al, 1993). Analysis of 19 progeny trials indicated that the heritability of ASI (0.52) was slightly greater than for GY (0.46) (Banziger et al, 1997).

In maize genetic correlations between GY and ASI stress have been reported. Lafitte and Edmeads (1994a, 1994b), obtained correlation values in the range of –0.30 to –0.55 and these were significant (at $p<0.05$) under low N as opposed to high N conditions. Banziger and Lafitte (1997) managed to obtain values ranging from 0.21 and –0.75 in their progeny trials done under low N.

2.2.6.2. GRAIN YIELD COMPONENTS.

Grain yield components include number of ears per plant (EPP), number of kernels per ear (KNEAR) and the kernel weight (SKW).

The dependence of grain yield under low N on its yield components was well documented by Edmeads et al. (1997a) for several tropical maize populations. Grain yield was linearly related to kernel weight ($r = 0.74$), and kernels per ear ($r = 0.89$), whereas the relationship between grain yield and EPP was curvilinear and highly significant ($r = 0.94$).

High correlations between grain yield and its components are normally found because of lack of independence among them (Blum.1988). EPP is a useful diagnostic tool for low N tolerance because it is easy and fast to measure, and because their relationship with grain yields increases with stress.

Kernel weight is probably important in determining yield only under well fertilized conditions, whereas variability for EPP increases more rapidly with increasing low N stress than the variability for kernels per ear (Bolanos et al, 1993).

2.2.6.3. LEAF SENESCENCE.

Leaf senescence is an orderly, active process in which nutrients in a leaf are reclaimed and mobilized to other parts of the plant. Senescence occurs in response to aging, and under constant environmental conditions, it is relatively constant and predictable. Drought, low N, darkness, detachment and hormone abscissic acid are found to be some of the causes (Banziger et al, 2000, Wilkins, 1984 and Mohr and Schofar, 1994). Under N stress is leaf senescence is accelerated and plants may show differences in the rates. Plants with delayed or reduced leaf senescence stay green and continue to carry out photosynthesis for an extended period than plants than senescence fast. This is important as such plants will continue to reallocate the much needed assimilates to developing grains and may contribute to production of high kernel number and high kernel weight resulting in more ears and yields.

Leaf senescence in addition may determine maturity in maize plants. Early maturing plants tend to senescence their leaves earlier than late maturity plants.

2.2.6.4. PLANT HEIGHT

Genotypes that allocate assimilates more to vegetative plant parts like leaves as well as plant height tend not give higher yields. It is important that an ideal plant height that is not detrimental (i.e. lodging) to economical productivity is selected and attained in genotypes. Stresses like drought and nitrogen have been found to reduce plant height. Under nitrogen stress plant height is reduced.

2.3. NORTH CAROLINA DESIGN ll (DESIGN II).

Mating designs are used to develop progenies for the purpose of obtaining genetic information from the experimental populations. North Carolina Design II is one type and was developed Comstock and Robinson in 1948. In developing experimental progenies, different sets of parents are used as males and females.

Each male parent is mated to each female, but male parents are not crossed to each other and female parents are not crossed to each other. Design II is a cross-classification design in terms of analysis and in this design the expectations of males and females are equivalent to general combining ability (GCA), whilst the male x female source is equivalent to specific combining ability (SCA). Since two sets of parents are used in this design, two independent estimates of GCA are obtained. Appropriate F-test are made for the differences among males and among females and for the interactions of males x females.

Though design II has not been used as extensively in maize as the diallel, Hallauer and Miranda (1988) mentions that it has advantages over the diallel designs if one is interested in estimating components of variance of a reference population. The merits include: (1) more parents can be included for a given level of resources, (2) two independent estimates of (A2 are available, (3) an estimate of (D2 is determined directly from the mean the mean squares, and (4) a greater number of parents can be included by subdividing parents into sets.

2.4. ESTIMATES OF GENETIC VARIANCE AND COMBINING ABILITY.

Development of maize varieties with enhanced resistance and tolerance to biotic and Abiotic stresses require the knowledge of inheritance of the traits and effective screening techniques. Inheritance studies so far have indicated presence of genetic variability in genotypes regarding presence of genes for the resistance of GLS (Thompson et al, 1987; Elwinger et al, 1990) as well as tolerance to low N (nitrogen use efficiency) in maize (Pollmer et al, 1979; Thirapon et al., 1987). Regarding Nitrogen use efficiency, different traits are known to determine tolerant types of genotypes and these only occur or show under stress conditions (Blum, 1988; Banziger et al, 2000). Heritabilities, for such tend to be high compared to grain yield that is known to decrease with stress. Effective selection in the early generation of the segregating materials can be

achieved only when additive genetic effects are substantial and heritability is high.

Estimation of genetic parameters of the population is useful in plant breeding process in deciding appropriate breeding strategy that will utilise the genetic presence (Duddly and Moll, 1969; Hallauer and Miranda, 1988). The estimation of genetic variance component is useful in determining whether there is sufficient variation in a population to follow further improvement to take place, as well as to identify the most promising genetic populations. In addition, estimation of genetic variances is useful in the selection of the most rapid and efficient breeding procedure in improving important characters. In estimating the genetic variation among genotypes knowledge of the heritabilities is important as it indicates the probability and extent to which improvement is possible through selection. Heritability can therefore be estimated either by the analysis of variance or through the regression of offspring on parents.

In determining mode of inheritance of GLS and NUE, it is important to estimate the general combining ability (GCA), and specific combining ability (SCA) effects. The concept of combining ability is used in connection with testing procedures to study and compare genotypes as well as predict the potential of lines in hybrid combination for many traits especially where the objective is to develop superior hybrids.

The general and specific combining abilities represent the major divisions of types of gene action for quantitative traits (Cukadar-Olmendo et al, 1997; Hallauer and Miranda, 1988). General combining ability of a line refers to the average value of a line estimated on the basis of its performance of that genotype in hybrid combination with other lines and is largely due to additive genetic effects and higher order additive interactions. The importance of the significance GCA is in the selection from the cross, parents that have the highest

GCA that may produce the best performing progeny (Cukadar-Olmendo et al, 1997, Hallauer and Miranda, 1988 and Fehr, 1987). Significant GCA effects indicated the greater role of additive gene effects controlling a particular trait.

However the performance of a particular cross may deviate from the average general combining ability of the two parental lines. This deviation is the specific combining ability (SCA) of the cross (Griffing, 1956, Hallauer and Miranda, 1988). SCA is largely a function of non-additive dominance and other types of epitasis (Cukadar-Olmendo et al, 1997). It is not possible to predict the potential of lines in hybrid combination for many traits; therefore, combining ability should be examined when objective is to develop superior hybrids for quantitative traits (Cukadar-Olmendo et al, 1997). Ratios of mean square components associated with variance of GCA and SCA effects are computed to estimate the relative importance of GCA in explaining progeny performance. The closer the ratio is to unity, the greater the predictability of progeny performance based on GCA effects alone and therefore suggests that additive gene effects were relatively more important than non additive gene effects among hybrid combinations. However, significant SCA effects imply the contribution of the non-additive gene effects to variations expressed among hybrids (Cukadar-Olmendo et al, 1997; Hallauer and Miranda, 1988)

CHAPTER THREE

3.0 MATERIALS AND METHODS

The study was conducted in two stages; the first involving the development of the experimental materials while the second involved the genetic evaluation of the experimental materials.

3.1 STAGE 1. GENETIC MATERIALS.

Ten inbred lines in advanced generations of inbreeding and twelve Testers (single crosses) from Zambia National Research Program and CIMMYT – Zimbabwe respectively, were used in this study. The pedigree and line codes for inbreds as well as testers used in the study are presented in Table1. Inbred lines

have been selected for tolerance to low N and resistance to grey leaf spot. These lines have also exhibited various levels of resistance to other prevailing major diseases like maize streak virus, turcicum and rust, and they are also tolerant drought. The testers were elite materials selected for combining ability and agronomic performance across stress and non-stress environments.

Each inbred line was crossed to twelve single cross testers representing each of the major heterotic pattern or group from CIMMYT-Zimbabwe. Crossing was done by hand pollination at Muzarabani-Zimbabwe (429 masl, 16.37o S, 31.02o E) during the 2003 winter nursery (dry season). Pollen from the male plants (lines) ware collected using tassel bags and bulked prior to pollination on the female plants (testers). One hundred and ten line x tester combinations (testcrosses) were generated from the crosses while ten line x tester combinations escaped pollina_____

3.2. STAGE 2. EVALUATION

3.2.1 LOCATION AND CULTURAL PRACTICES

A total of six trials were planted in six locations in Zambia and Zimbabwe respectively (Table 2). Three trials were planted under optimal fertilized (high N) conditions and the remaining with no fertilizer (low N). The locations for low N are sites, which have been developed after depleting the soil of nitrogen for some years (Banziger et al., 2000). These are managed continuously by not applying N fertilizer (either in chemical or organic form), and by cutting and removing the plant biomass after each crop season. The optimum or well-fertilized sites used were sites, which are also hot spots for screening, grey leaf spot disease in Zambia and Zimbabwe.

Fertilizer was applied at the rate of 180-80-40 kg per hectare in terms nitrogen, phosphorous and potassium. 40 kg N per hectare was incorporated as compound D prior to sowing, and 140 kg N per hectare as urea was side dressed about 4-6 weeks after sowing. No chemical N fertilizer was applied to low N experiments.

All trials received standard cultural practices to control soil eating insects and weeds. Furadan was used prior to planting and both herbicides and hand weeding were used to control weeds. Spraying the bases of plants with Antkil as well as Dursban controlled termites, especially at low N at Golden Valley.

Sampling of soils at all trial sites was taken at two soil depths: 0 – 20cm and 20 – 60cm. This was prior to planting and results for the analyses are shown in Table 2 and Appendix A.

Table2: Description of Sites where 110 line x tester cross combinations were evaluated

Experiment	Country	Site	Altitude	Latitude	Longitude	Fertilizer level	Soil type
1	Zambia	Golden Valley	1170masl	14.17oS	28.37oE	High N	Clay loam
2	Zambia	Golden Valley	1170masl	14.17oS	28.37oE	Low N	Clay loam
3	Zambia	Kabwe	1207masl	14.27oS	28.28oE	Low N	Sand loam
4	Zambia	Mount Makulu	1281masl	15.53oS	28.25oE	High N	Sand clay loam
5	Zimbabwe	Cimmyt-Harare	1489masl	17.80o S	31.02o E	Low N	Medium Grained Sand clay
6	Zimbabwe	ART-Farm	1489masl	17.80o S	31.02o E	High N	-

3.2.2 EXPERIMENTAL DESIGN

The 110 testcrosses were evaluated with four check entries in an alpha (0,1) lattice design with two replicates (Patterson and Williams, 1976) with incomplete block sizes of six plots for testcrosses. The experimental unit consisted of one 5m long row in Zambia and one 4m long row in Zimbabwe. In all experiments, the rows were spaced at 0.75m except for high N trial at Golden Valley that was row spaced at 0.90m. Planting between hills was done with a spacing of 0.50m. Each hill was over planted and later thinned to 2 plants per hill when seedlings reached 4-leaf stage. Two borders rows surrounding the experiments were also planted.

3.3. DATA COLLECTION

3.3.1 Field weight: The weight of ears harvested from each plot was measured in the field using hanging scales (CARDINAL, Model No HSDC 20 Kg in Zimbabwe and SALTER ENGLAND, Model 23563 25kg x 100g in Zambia).

3.3.2 Grain yield: Harvested ears were shelled to obtain grain weight per plot in kilogram. Grain weights were then adjusted to 12.5% grain moisture and converted to tones per hectare using the formular:

$$GY\ (t/ha) = \frac{\text{grain weight (per plot)} \times (100 - \text{moisture}) \times 10,000}{87.5 \times \text{plot size} \times 1000}$$

3.3.3 Moisture content (MOI): The moisture content of a sample of kernels for each sample plot was measured with a hand-held moisture meter (Dickey-John Mult-Grain, Model. 46233-12223A)

3.3.4 Ears per plant (EPP): Number of ears per plant at harvest, measured as number of ears with a minimum of one fully developed grain divided by the number of plants.

3.3.5. Anthesis date (AD): Measured as number of days after planting when 50% of the plants shed pollen.

3.3.6 Silking date (SD): Measured as number of days after planting when 50% of the plants produced silk.

3.3.7 Anthesis Silking Interval (ASI): Determined by the difference in days between Silking date and Anthesis date

3.3.8 Plant height (PH): Measured as average height in centimeters between the base of a plant to the insertion of the first tassel branch of the same plant on 10 randomly selected plants.

3.3.9 Ear height (EH): Measured as average height in centimeters between the base of a plant to the insertion of the uppermost ear of the same plant on 10 randomly selected plants.

3.3.10 Ear position (EPO): Calculated in percentage as a ratio of ear height to plant height.

3.3.11 Stem lodging (SLODGE): measured as percentage of plants that showed stem lodging, i.e. those stems that were broken below the main previous to harvest time.

3.3.12 Root lodging (RLODGE): measured as percentage of plants that showed root lodging, i.e. those stems that were inclined by more than 45° at harvest time.

3.3.13 Grey leaf spot (GLS): Score for the severity of grey leaf sport (Cercospora zeae-maydis) symptoms rated on a scale from 1 (= clean, no infection) to 5 (= severely diseased).

3.3.14 Northern leaf blight (NLB): Score for the severity of northern leaf blight (Exserohilum turcicum) symptoms rated on a scale from 1 (= clean, no infection) to 5 (= severely diseased).

3.3.15 Maize streak virus (MSV): Score for the severity of maize streak virus symptoms rated on a scale from 1 (= clean, no infection) to 5 (= severely diseased).

3.3.16 Common rust (rust): Score for the severity of common rust (Puccinia sorghi) symptoms rated on a scale from 1 (= clean, no infection) to 5 (= severely diseased).

3.3.17 Ear rot (EROT): percentage of ears that were rotten.

3.3.18 Leaf senescence: Leaf senescence was visually estimated under low N stress on plot basis as the proportion of live green vs. senesced dried at leaves. This measure was taken in all trials on 3 occasions 4-5 weeks after flowering (or grain filling) using a scale of 1-10 described by Banziger et al (2000), where:

1 = 10% dead leaf area

2. = 20% dead leaf area

3 = 30% dead leaf area

4 = 40% dead leaf area

5 = 50% dead leaf area

6 = 60% dead leaf area

7 = 70% dead leaf area

8 = 80% dead leaf area

9 = 90% dead leaf area

10 = 100% dead leaf area

3.3.19 100 Kernel weight (gm): 100 kernels for each entry were counted at random and weighed using SARTORIUS AG GOTTINGEN Type BL 6000 Serial 91105058. The weights were adjusted to 12.5% moisture.

3.3.20 Single Kernel eight (gm)

FHSW = fresh hundred seed weight (gm)

NEW = Number of ears harvested

3.4. ANALYSIS.

Analyses of variance were computed for each location (referred to as site hereafter) separately using spatial analysis software ASREML OR REMLTOOL (Burgueno et al, 2000). This was to generate means and mean square (standard)

errors. In the analysis, genotypes (testcrosses) were considered as fixed objects while incomplete blocks were taken as random objects. Significance of entries were tested using mean square errors

Combined analysis of variance was computed using PROC GLM in SAS (SAS, 1997). In the combined analysis sites or environmental effects were treated as random effects and crosses as fixed effects.

General combining ability (GCA) and Specific combining ability (SCA) effects were calculated according to the line x tester model using adjusted means and pooled mean square errors. Check entries were not included in the analysis and each site was considered as a separate environment. In addition parents where pollination was not completed due to lack of synchronization were also dropped from the analysis. The combining ability analysis was carried out using an array totals over replications following the procedure of Kempthorne (1957) related to methods of Comstock and Robinson (1952). The mean squares due to lines and testers were tested against the mean squares due to lines x testers. The mean squares due to lines x testers and other interactions were tested against the pooled error mean squares. In addition mean squares due Nlevel was tested against mean squares due to site(Nlevel) while that of Site(Nlevel) was done by mean squares due to site x line x tester(Nlevel).

The simple linear (genetic) correlation of GY for lines and testers with secondary traits was performed by regressing GY on the secondary traits using the formular described by Steel and Torrie (1980) and Gomez and Gomez (1984). The formular used is:

r = (replication; n = number of parents

The components of genetic variance are calculated using the following formular explained by Hallauer and Miranda (1988):

(f2 = 1/8Dr

(m2 = 1/8Dr

(fm2 = 1/16Hr + Eb

(w2 = 1/4Dr +3/16Hr + Eb

Where Dr = additive genetic variance; Hr = dominance; Eb = non-heritable error

Heritability estimates are also obtained through the formular described by Hallauer and Miranda (1988):

peratures recorded for the sites were 23.6, 23.7 and 21.1 o C. The rainfall amounts received at Golden Valley and Kabwe sites were less than the amounts normally received in the normal year. On two occasions hailstorm was experienced at Mount Makulu and this caused lodging and leaf damage to plants. Only the experiment at ART farms received irrigation each time there was moisture stress. Appendix A shows 2003/04 season meteorological data for the sites.

4.2. Analyses of Variance

Combined analyses of variance across environments for all measured variables are presented in Tables 3, 5 and 6. Appendix C shows summary results for the same variables in terms of significance differences (probability levels) for the 9 x 9 as well as 10 x 7 line and tester analysis. This was after dropping parents (lines and testers together or testers only) where crossing of parents was not complete due lack of synchronization. Since maximum information regarding line and tester performance could be sought from a 9 x 9 line and tester analysis, discussion in this report, therefore, is based on this analysis.

4.3. Grain Yield (GY)

Differences in grain yield (GY) were observed across Nlevel and Site(Nlevel) and (Table3 and Appendix C). Yield averaged 1.56, 8.01, and 4.79 t/ha under low N, high N and for across environments (table 4). Nitrogen stress reduced grain yield by 80% relative to the high N environments.

Differences were also observed among lines and testers as well as Nlevel x tester and Site x tester(Nlevel) (Table 3). Average GY of crosses across environments ranged from 4.5 to 5.05 t/ha for testers while for lines the range was from 4.35 to 5.56 t/ha respectively (Table 4). Most testers gave higher grain yield in crosses than the mean yield of the trial both across environment and well-fertilized conditions with the exception of T1, T3 and T5. Under no fertilizer T1, T6, T7 and T9 had higher yields in crosses.

Among lines, L1, L2 and L11 gave higher GY for across environments. Under nitrogen stress higher GY in crosses was produced by L1, L7, L8 and L11. At optimal conditions all with the exception of L2, L6 and L7 gave higher yields. L11 and L1 generally did exceptionally well under all conditions (Table 4).

No differences ($P>0.05$) were observed for GY for Line x Tester as well as for other interactions (Table3)

4.4. ANTHESIS DATE (AD)

Analysis of variance for 50% days to anthesis show significant differences for Site(Nlevel), line, tester and for Nlevel x tester (Table3 and Appendix C). No differences ($p>0.05$) were observed for line x tester including other sources of variations.

Mean anthesis days are summarized in Table 4. It took 73.6 days, 71.4 days and 72.4 days for genotypes to shade pollen under no fertilizer, with fertilizer and across environments. Anthesis was earlier in T5 and was later in T12 for across environments. The earliest line to shade pollen was L2 (70.54 days) while the later ones were L7, L8, L10 and L11.

Shading pollen under low N and high N was early in T1 and T5 while T8, T9 and T12 were late under both conditions. In lines, male flowering was slightly earlier as can be seen in Table 4 at optimal fertility. However, L2 was the earliest at reduced fertility.

Although application of fertilizer resulted in plants flowering early, the differences in days in terms of male flowering under low N and high N was only slightly (< 2days on average).

4.5. SILKING DATE (SD)

Table 3 shows analysis of variance for silking while mean silking days are noted in Table 4. Silking days were different ($p<0.001$) across Site(Nlevel) and also differed among lines and testers as well as Nlevel x line ($P<0.01$). No differences ($p>0.05$) were observed for other sources of variation.

The average days to silking were 78.3 and 72.7 days at nitrogen stress and optimal fertility levels. Silking was delayed by about 6 days on the average relative to high fertility in both line and testers. For across environments, low N and high N, the earliest and late testers to produce silk were T5 and T12 while in lines it was L2 and L11 respectively.

4.6. ANTHESIS SILKING INTERVAL (ASI).

There were significant differences in the anthesis-silking interval between Site(Nlevel), among lines as well as Nlevel x line. No differences were noted for other sources of variations (Table3)

Environmental means for ASI was 4.7 days, 1.27 days and 3.0 days for low N, high N and for across environments (Table 4). L2, L9, L10 and T1, T5, T7 and T9 had ASI below the mean of the trial. Under no fertilizer L8 (4.14 days), L9 (4.15 days) and T9 (3.65 days) gave lowest ASI. Nitrogen stress in general increased ASI in both lines and testers.

Table 3. Mean squares for grain yield, anthesis, silking, anthesis-silking interval, ears per plant and plant height
Across all 9 x 9 lines and testers grouped in 3 low N and 3 high N sites in Zambia and Zimbabwe

SOURCE	DF	GY	AD	SD	ASI	EPP	PH
NLEVEL	1	50.60**	616.53ns	3811.53ns	1390.91ns	10.55***	639310.98ns
SITE(NLEVEL)	4	155.53***	1409.77***	1229.05***	275.62***	0.12***	152167.05***

LINE (GCA)	8	2.05*	51.22***	65.37***	8.02***	0.04***	2533.12***		
TESTER (GCA)	8	6.34***	47.58***	58.36***	2.83	0.031**	3476.63***		
NLEVEL X LINE	8	1.76ns	3.79ns	10.37**	6.98***	0.015ns	409.11***		
NLEVEL X TESTER	8	1.98*	4.96*	5.92ns	0.45ns	0.015ns	166.01ns		
LINE X TESTER (SCA)	64	0.89ns	2.91ns	4.21ns	2.13ns	0.0093ns	126.78ns		

NLEVEL X LINE X TESTER	64	0.87ns	1.72ns	2.35ns	1.81ns	0.012ns	98.59ns
SITE X LINE(NLEVEL)	32	1.02ns	3.71ns	7.14ns	2.81ns	0.017ns	128.83ns
SITE X TESTER(NLEVEL)	32	1.91**	3.00ns	4.47ns	1.21ns	0.0099ns	126.20ns
SITE X LINE X TESTER(NLEVEL)	256	0.76ns	2.28ns	4.11ns	2.08ns	0.011ns	107.71ns
POOLED ERROR	526	1.16	3.31	6.79	3.07	0.021	262.16

LSD					
0.865	1.457	2.086	1.404	0.116	12.956
MEAN					
4.79	72.5	75.5	3.0	0.88	186.2
CV					
22.56	2.51	3.45	58.47	16.51	8.70
# LOW N SITES					
3	3	3	3	3	3
# HIGH N SITES					
3	3	3	3	3	3

DF=degree of freedom; GY=grain yield; AD=anthesis date; SD=silking date; ASI=anthesis silking interval; EPP=ears per plant; PH=plant height

*, **, *** Significant at 5%, 1% and 0.1%; ns = non significant at 5%

Table 4. Data of Grain yield and Secondary traits, units, lattice-adjusted means across (AC),
Low N (level 0) and high N (level 1) environments for lines and testers.

Table 4. Cont/. Data of Grain yield and Secondary traits, units, lattice-adjusted means across (AC),

Low N (level 0) and high N (level 1) environments for lines and testers

Table4. cont/. Data of Grain yield and Secondary traits, units, lattice-adjusted means across (AC),

Low N (level 0) and high N (level 1) environments for lines and testers

4.7. EARS PER PLANT (EPP).

Table 3 and Appendix C show differences in the number of ears per plant across Nlevel, Site(Nlevel), and for lines and testers respectively.

The average ears per plant produced under reduced fertility and at high N were 0.74 and 1.03 ears respectively. Low N reduced ear number per plant as much as 28% compared to optimal conditions (Table 4).

T12 (0.69) had the least number of ears at low N condition while highest EPP for lines were in L1, L2, L11 and L9 under nitrogen stress. However, all testers and lines showed same numbers of EPP under high N (Table 4).
Differences were not observed for other variations (Table 3)

4.6. PLANT HEIGHT (PH)

Highly significant differences ($p<0.001$) were observed across Site(Nlevel) as well as for lines, testers and the Nlevel x testers (Table3 and Appendix C)

Table 4 shows mean heights for lines and testers in crosses. The average plant height under low N was 149.91cm while under high N it was 222.45cm. Plant height was reduced by 33% under N stress compared to well - fertilized conditions.

Plant height for across analysis ranged from 171.47cm to 197.06cm for testers. Under reduced fertility the lowest and highest average heights were in T5 and T8 respectively.
At high fertility levels T7, T8, T9 and T12 had higher average heights compared to mean of the trial.

Most lines attained lower heights than the average of the trial both at low and high N conditions. Only lines L1 and L11 gave higher average heights at both environmental conditions.

4.9. SINGLE KERNEL WEIGHT (SKW)

Differences for single kernel weight were observed for N(level), Site(Nlevel). Kernel weight differences were also noted in lines, testers as well as N(level) x tester (Table 5 and Appendix B).

Average single kernel weights were 224.75mg under low N and 330.2 mg under high N respectively (Table 4). Increased nitrogen increased single kernel weight compared to zero nitrogen.

Kernel weight for testers ranged from 207.12 for T5 to 259.25 mg for T12 with no fertilizer. Testers T6 and T12 had higher SKW both at low N and high N while T8 was higher at low N only. In addition T1 and T3 gave higher SKW but at high fertility conditions.

Among lines, higher SKW in crosses under low N included L1, L7 and L11. Under high N high SKW were from L2 and L8 apart from L1 and L11.

4.10. NUMBER OF KERNELS PER EAR (KNEAR)

Across analysis for numbers of kernels per ear shown on table 5 and appendix B indicates differences in number of kernels per ear observed across Nlevel and site(Nlevel). In addition, numbers of kernels differed among lines and testers and Nlevel x tester but not for other interactions.

Table 4 shows average kernel weights for lines and testers. Mean number of kernels per ear under reduced fertility was a 227.71 while at high fertility it was 523.5. Nitrogen stress reduced number of Kernels each parent produced. Most testers had higher kernel numbers at low N except T3, T8 and T12. For lines, L4, L8 and L11 produced more kernels per ear in crosses under all environments whilst L7 and L10 gave higher kernels at high N only.

4.5. LEAF SENESCENCE (SENESC)

Highly significant differences for Site(Nlevel) and among lines and testers as well as for Nlevel x lines and Nlevel x testers were observed for leaf senescence (Table 5 and Appendix B).

Senescence was recorded both under low N and high N. It was earlier observed around flowering and during grain filling stage in trials subjected to nitrogen stress (low N). Under well-fertilized condition, leaf senescence occurred late and after physiological maturity.

Table 4 gives mean values for senescence scores. Under low N senescence scores ranged between 47.97 to 51.72% for lines while for testers leaf senescence scores ranged from 47.83 to 52.65%. The least leaf senescence in testers was observed in T4, T5 and T7 while the rest of the testers had leaf senescence scores above the mean of the trial. Among lines, the least scores were in L 1, L4, L7 and L10 with the least score of 47.83% exhibited by L10.

Generally senescence was accelerated under lowN than at high N.

TABLE 5. MEAN SQUARES FOR SINGLE KERNEL WEIGT, NUMBER OF KERNELS PER EAR AND SENESCENCE
ACROSS ALL 9 LINES AND 9 TESTERS GROUPED IN 3LOW N AND 3 HIGH N IN ZAMBIA AND ZIMBABWE

SOURCE	DF	SKW	KNEAR	DF	SENESCENCE
NLEVEL	1	1330230.5**	10556115**	1	12230.43ns
SITE(NLEVEL)	4	42348.12***	580778.85***	3	10032.99***

LINE (GCA)	8	9113.71***	12150.22**	8	216.57***
TESTER (GCA)	8	8920.31***	8410.89**	8	288.51***
NLEVEL X LINE	8	1106.01ns	11264.86ns	8	326.66***
NLEVEL X TESTER	8	2227.10**	3447.22ns	8	312.39***
LINE X TESTER (SCA)	64	702.18ns	6334.44ns	64	52.77ns
NLEVEL X LINEXTESTER	64	710.74ns	4665.55ns	64	58.97ns
SITE X LINE(NLEVEL)	32	781.23ns	3828.06ns	24	42.11ns

SITE X TESTER(NLEVEL)	32	942.25ns	4962.11ns	24	86.14ns
SITE X LINE X TESTER(NLEVEL)	254	609.91ns	4642ns	192	46.29ns
POOLED ERROR	338	922.49	6692.05ns	495	167.11

LSD
26.623 71.705
11.331
MEAN
252.0 375.6
45.6
CV
10.95 21.78
28.35
#LOW N SITES
3 3
3
#HIGH N SITES

2 2

2

*,**,*** significant at 5%, 1% and 0.1%

4.8. DISEASES.

Grey leaf spot (GLS), Exserohilum turcicum (Et) and rust were observed in the trials. GLS was recorded in two trials grown under high N at Golden Valley and at Mount Makulu in Zambia. Turcicum affected all trials planted in Zambia while rust was only recorded at ART Farms in Zimbabwe.

Analyses of variance for the diseases are shown in Table 6 and Appendix C. Highly significant differences for GLS were observed across Site(Nlevel) and among lines and testers. Disease establishment occurred late and after the grain filling stage. The average disease score for GLS was 1.92. Across environment score for testers ranged from 1.52 to 2.47 while for lines the range was 1.40 to 2.47 (Table 4). T1, T4 and T6 had higher disease ratings while T5 had the least (Table 4). Higher disease ratings for lines were recorded in L1, L7, L8 and L11 with L10 having the lowest score of 1.40.

Differences were also observed for Exserohilum turcicum (Table 6) under low N and high N conditions. Mean disease scores are shown on Table 4. General observation was that disease score was higher under low N than high N. Mean score for the trials was 1.9 for across environment while the average scores under low N and high N were 1.70 and 2.14 respectively. Most testers and lines with the exceptions of T3, T6 and T8 as well as L7, L8 and L11 showed lower disease score across environment compared to mean of the trial (Table 4). At low fertility the lowest score was in T9 (score 1.76). Table 4 also shows that disease incidence for turcicum in terms of scores were higher on low N compared to high N environments.

Table 6 and Appendix C show analysed data for rust. Rust disease differences were noted among entry as well as for lines and testers. Average disease score was 2.0 (Table 6). The least disease pressure was in T3, T4, and T6 and in L4, L10 and L11 respectively.

TABLE 6. MEAN SQUARES FOR GREY LEAF SPOT, TURCICUM, RUST ACROSS ALL 9 LINES AND 9 TESTERS GROUPED IN 3 LOW N AND 3 HIGH N SITES IN ZAMBIA AND ZIMBABWE

SOURCE	DF	GLS	DF	Et	DF	RUST		
NLEVEL	0	50.08ns	1	18.59ns	-	-		
SITE(NLEVEL)	1	50.07***	3	18.94***	-	-		

LINE (GCA)	8	1.48***	8	1.431***	8	3.22***
TESTER (GCA)	8	1.82***	8	0.79***	8	0.73**
NLEVEL X LINE	-	-	8	0.16ns	-	-
NLEVEL X TESTER	-	-	8	0.21ns	-	-
LINE X TESTER (SCA)	64	0.15ns	64	0.10ns	64	0.21ns
NLEVEL X LINEXTESTER	-	-	64	0.083ns	-	-

SITE X LINE(NLEVEL)	8	0.25ns	24	0.26ns	-	-
SITE X TESTER(NLEVEL)	8	0.31ns	24	0.21ns	-	-
SITE X LINE X TESTER(NLEVEL)	64	0.16ns	192	0.10ns	33	-
POOLED ERROR	212	0.29	495	0.21	6	0.24

LSD

0.647

0.457

0.977

MEAN

1.9

1.9

2.0

CV

28.78

23.37

24.93

#LOW N SITES

-

2

-

#HIGH N SITES

2

2

1

*, **, *** Significant at 5%, 1% and 0.01%; ns = non significant differences

4.11. COMBINING ABILITY

Mean squares due to general combining ability (GCA lines and GCA testers) were significant for all variables measured (tables 3, 5 and 6). However, the mean squares due to specific combining ability (SCA line x tester) were not significant the same traits.

4.11.1. GCA FOR LINES

Estimates of GCA effects for lines for various traits are presented in tables 7.

Positive and significant GCA effects for GY were exhibited in L1 (except under high N) and L11 while L2 was negative and significant in all environments. Negative and significant GCA effects were also found in L9 (low N) and in L6 (high N and across environment).

Most lines showed significant GCA effects for AD and SD with three lines (L1, L2 and L9) being negative and one line (L11) being positive in all testing environments. At low nitrogen condition L6 was not significant while L1 and L10 were not significant for the two traits at high fertility.

Positive and significant GCA effects for plant height were observed in L1 and L11 while the rest of the lines were negative and significant with the exception of L6 (high N and across environment) and L2 and L4 (low N).

GCA effects for nitrogen use efficient traits are shown in table 7. Superior GCA for EPP and SKW were obtained from L1 and L11 while L6 and L7 were poor combiners for the two traits in all environments. The GCA effects for KNEAR were positive and high for L8, L10 and L11 in all environments whereas the rest of the lines had either there GCA values negative in all environments or a combination of positive and negative depending on N level. Low and negative significant GCA values for leaf senescence were showed by L7 and L10 while L2 was a poor combiner for leaf senescence. The rest of the lines were had moderate leaf senescence.

Good combiners for GLS were L2, L6, and L10 while the poor combiners were L1 and L11. The remaining lines showed moderate GCA effects for GLS. For turcicum L11 (low N and across environment) and L8 (low N) showed positive

and significant GCA effects. At high N all lines showed moderate GCA effects to turcicum.

Figure 1 show general picture of GCA effects of the traits for lines across environments. Lines L1 and L11 consistently performed well due to their high GCA effects in most of the traits.

4.11.2. GCA TESTERS

Table 8 shows GCA effects for traits for testers. Four testers showed positive GCA effects for GY under low N with T1 and T9 being significant. At high fertility T4, T9 and T12 had superior GCA values while poor combiners were T1 and T5 for GY.

Significant and negative GCA effects for male and female flowering were observed in T1 and T5 while the converse was true for T8 and T12 at both reduced and increased fertility. Other lines had the sign (negative and positive) of the GCA effects opposite to each other at both levels of N for the AD (T4) and SD (T9).

Under low N positive and significant GCA effects for plant height were seen in T3, T6 and T8 while positive GCA were recorded in T4, T7 and T12. However, T1 and T5 had their GCA values negative at both N levels while T3 was positive and significant.

For nitrogen use efficient traits, T1, T5, T7 and T9 possessed negative and significant GCA effects for anthesis-silking interval under N stress. Good combiners at high N were T9, T12 and T4. Good combiners for leaf senescence were T4, T 5 and T7 while poor combiners for the same were trait were T3, T6, T9 and T12.

Positive and significant GCA effects for grain yield components were exhibited by T5, T7 and T9 in all environments for ears per plant. Under N stress neutral GCA effect was depicted by T6 while T1 was positive. High and positive effects for single kernel weight were recorded in T6, T8 (except high N) and T12. T4 and T9 showed positive and significant GCA effects for number of kernels per ear. Under low N, T3, T8 and T12 were negative with significant GCA effect for KNEAR.

Most testers showed that they were good combiners for GLS and turcicum. The best combiners for GLS were T3, T5, T7 and T8 while testers with moderate GCA effects were T9 and T12. The remaining lines (T1, T4 and T6) were poor combiners for GLS. For turcicum positive and significant effects were exhibited by T3 and T8 in all environments. Good combiners were T9 and T12. At low N

other lines with superior GCA effects were T4 and T5 while T1 and T6 were neutral. At high N most showed moderate effects to turcicum.

Figure 2 illustrates GCA effects for traits for each tester across environments. T8, T9, and T12 showed high GCA values for more traits. Testers T6 had mostly low and positive effects while T4 and T7 had both low negative and positive GCA effects. T1, T3 and T5 exhibited high and negative GCA for most measured traits.

4.11.3. Specific combining ability (SCA)

Mean squares due to specific combining ability (SCA) were not significant ($p>0.05$) for all traits measured (Table 3, 5 and 6).

The estimates of SCA effects for three-way cross hybrids for grain yield and secondary traits are presented on Table 9 and appendix D, E and F for both nitrogen levels and across environment. 20 hybrids (across environment), 24 hybrids (low N) and 17 hybrids (high N) had significant and positive GCA effects for GY. However, crosses L11 X T3, L4 X T4, L10 X T1, L7 X T7, L11 X T9 and including L8 X T4, L9 X T1 and L1 X T8 possessed significant SCA effects at both N levels and across environments for GY. In addition some crosses as well possessed good GCA effects for ASI, EPP, leaf senescence, GLS, and number of kernels per ear (Table 9).
Generally good combinations for SCA involved at least one high or intermediate general combiner as a parent. Very few low x low or low x intermediate general combiners had good SCA effects (Table 9 and Appendix D, E and F).

Combinations included parents with high x high GCA effects such as L11 x T9 and L1 x T9 (grain yield) as well L2 x T7 (grey leaf spot). In addition good SCA effects also included, high x intermediate SCA effects such as L7 X T7 (grain yield) and L10 x T9 and L9 x T8 (for grey leaf spot).

4.12. CORRELATION

Linear genetic correlations (rg) of grain yield (GY) and secondary traits for lines and testers are shown on Table 10.
Significant genetic correlations were observed between GY and many of the secondary traits measured in both lines and testers (except for leaf senescence).

Anthesis-silking interval, silking, plant height, ears per plant, and kernel weight all measured under low N were either negative or positive, and significantly associated with grain yield except for kernel weight (r= -0.06ns) regarding testers, which was non significant. There was no association between leaf senescence and anthesis with GY under low N for both lines and testers.

Grey leaf spot, turcicum and rust all correlated with grain yield except turcicum (r= -0.26ns) and rust (r= 0.23ns) with testers at optimal conditions.

There were significant correlation involving ears per plant (r= 0.32*) and number of kernels per ear (r= 0.42**) for lines under low N.

Correlation values for ASI was high in lines and testers under low N while plant height (r= 0.73**) and kernel weight (r= 0.85**) values were high in lines only. On the other hand, significant correlation values for ears per plant and number of kernels were observed in testers.

4.13. Heritability

Table 11 shows broad and narrow sense heritability estimates for measured traits. For all traits broad sense heritability estimates was higher than the narrow sense. However, both heritability estimates were generally high for grain yield, anthesis, silking, plant height, and single kernel weight under N stress and optimal conditions. In addition heritabilities for grey leaf spot, turcicum and rust were also high.

Low heritabilities were realized for anthesis silking interval, leaf senescence and number of kernels per ear and ears per plant under nitrogen deficiency.

Values of heritabilities for grain yield, anthesis silking interval, plant height, single kernel weight as well as number of kernels per ear tended to smaller across environments than in either N environments except for anthesis, silking and the three diseases.

Table 11. Broad and Narrow Sense Heritability estimates for Grain Yield and Secondary traits for Across, Low N and
High N Environments.
TRAIT ACROSS Lcrosses across locations, low N and high N are presented in Appendix G, H and I.

The highest grain yield across location was 6.04 t/ha while the lowest was 3.56 t/ha. Under low N testcross L1 x T1 (2.27 t/ha) was the highest yielder while at high N, the highest yield was obtained from cross L9 x T12 (10.2 t/ha).

The number of ears per plant ranged from 0.53 to 0.91 ears under low N and 0.91 to 1.2 ears under high N. Under high N the number of ears per plant was greater or equal to one while under low N it was less than one. Plant height

ranged from 127.5 cm (L6 x T8) to 176.9cm (L9 x T1) under low N while high N the tallest was 2.67 cm for L9 X T12 while the lowest was 187.61 cm for L3 x T3.

Silking days at high N ranged from 67.5 to 75.7days. At reduced fertility the days ranged from 74.5 to 84.0 days. Anthesis days under low N ranged from 70.1 to 78 days while under high N days ranged from 66.2 to 74.0 days. Under low N the lowest ASI was in cross L8 x T9 (2.4 days) while cross L11 x T4 averaged 7.5 days and was the highest.

Grey leaf spot scores ranked as low as 1.02 (L6 x T3) to as high as 3.27 (L4 x T12). Leaf senescence score ranged from 41.5 % to 57.6 % with the least score attained in cross
L11 x T1.

CHAPTER FIVE
5.0. DISCUSSION

Performance of lines and testers differed significantly. Differences could have been caused by variations in nitrogen levels and differences in testing sites (locations). However, it is possible that differences observed could represent real genetic differences among genotypes. The results imply that the genotypes tended to produce dissimilar response when grown in different environments. Therefore, rankings were not the same for lines and testers when grown under low N and high N environments. This would be expected given the differences in the degree of selection and improvements done to the genotypes.

Selection of suitable lines and testers in this case becomes critical without the consideration of associated traits that impact greater performance of maize under

stress. This is important since the final product has to be grown in low N soils, important in limiting yields, which are frequently found in farmer's fields where fertilization is not commonly used and organic matter is rapidly mineralized (Banziger and Lafitte, 1997). Hence development of maize germplasm with high nitrogen use efficient and resistance to disease is crucial if productivity of maize-based farming system is to be sustained or increased.

In this study addition of fertilizer in particular nitrogen enhanced growth and development in the genotypes. Similar reports have been made by Kumwenda and Benson, 1998 and Ikerra et al 1998 in their study involving maize response to increased nitrogen fertilizer levels. However, the converse was true under nitrogen stress (low N). Grain yield was reduced by as much 80% relative to high fertility levels. In addition anthesis date on average was delayed by 6 days and nitrogen stress also retarded plant height on the whole in both lines and testers. In general nitrogen deficiency had a negative impact on the kernel weight, number of kernels per ear, ears per plant, and leaf senescence.

Many researchers have made similar observations of yield reduction in maize grown under nitrogen stress. Yield reductions of 37-78 % (Banziger and Edmeads, 1998), 51- 65% (Betran et al, 2003), and 68% (Lafitte and Edmeads, 1995) for maize grown under low N have been reported. Such level of intensity of stress observed for low soil nitrogen fall within the range of stress levels applied during selection of populations and inbreds for tolerance to low N (Bolanos and Edmeads, 1993a; Lafitte and Edmeads, 1994). Therefore, different lines and testers differed in there per se performance in crosses when grown under low N and when under high fertility. For example L1, L7, L8 and L11 did well in crosses under low N while for testers it was T1, T6, T7 and T9. At high fertility lines L1, L4, L11, and most testers (except T1, T3 and T5) performed better in crosses. However, only L1, L11 and T6, T7 and T9 had better performance at both N levels.

Differences in performance of genotypes under stress relative to non-stress environments simply indicate that other traits were responsible for good performance. These traits known as adaptive secondary traits are responsible for the differential expression between (only expressed under stress) stress and non-stress environments and are genetically variable and they correlate with grain yield (Bolanos et al., 1993; Bolanos and Edmeades, 1996; Banziger and Lafitte, 1997, Betram et al, 2003). Some adaptive traits include anthesis-silking interval, ears per plant, and leaf senescence.

Anthesis as well as silking (days) in both parents was influenced by N deficiency. However, it was silking that was mostly delayed compared to anthesis. Girardin et al (1987) and Banziger et al (2000) have reported similar results when flowering in maize coincides with nitrogen deficiency. In this study silking was extended by 6 days on the average while there was little effect on anthesis.

The delay in silking thus increased the anthesis-silking interval. ASI averaged 4.7 days under stress. On average most lines showed slightly lower ASI days than testers relative to the mean. Extended ASI resulted in late and fewer extrusion of silk produced. In some crosses plants failed to produce silk especially at Kabwe site were N stress was high. This resulted in barrenness, reduced ears per plant and as well as number of kernels per ear. All this happened due to reduced (or no) pollination or lack of synchronization between male and female flowers, which was impaired due to increased ASI. This could have contributed to T12 and L4 produce fewer ears per plant. In addition, the fewer grains per ear in T8 , T12 , L9 , and in L10 could have resulted from increased ASI. Reduced ears per plant and number of kernels per ear all affect grain yield in maize, as they are the most important yielding components.

Nitrogen is an important macronutrient and plays a major role in photosynthesis. N stress accelerated leaf senescence and variations in the genotypes were observed. Lower leaf senescence scores were attained in testers T4 and T5 while for lines it was in L4, L7 and L10. Others had either moderate or high leaf senescence. High senescence caused reduction in photosynthesis area diminishing assimilates allocated to new developing parts like kernels. Diminishing assimilates contributed to reduction in number of kernels per ear and eventually the number of ears per plant such as the ones noted in T12 and L6. In addition lower kernel weight may have been caused by reduced period of grain filling, as may have been the case in most lines and testers with the exception of L1, L7, L11, T8 and T12. Reduction in ears per plant, fewer number of kernels per plant and lowering of kernel weight was mainly due to kernel abortions at developmental stage when assimilate to developing grains reduced substantially (Bolanos et al, 1993b; Banziger et al, 2000). Therefore, parents with delayed leaf senescence managed to continue photosynthesis contributing to longer duration of grain filling and high grain yield under low N status.

Nitrogen also had an effect on plant height one of the important agronomical traits. Plant height may indicate plants having adequate number and well developed leaves all-important for photosynthesis. Generally most lines showed lower heights except for L1 and L11. Lower heights are expected from inbred lines that have been selfed for many generations. In this study increased height resulted in increased yield as was the case in L1 and L11. This concurs with findings of Beck et al, 1989 and Lafitte and Edmeads, 1988 that height reductions were accompanied by yield reductions.

The diseases observed in the trials included GLS, turcicum and rust. GLS and rust occurred at optimal condition while turcicum infections happened both at high N and N stress. The diseases occurred in different sites. The occurrence of the diseases especially GLS was necessary to determine the potential of

genotypes to resist the onset and progress of GLS, to determine the magnitude of genetic factors that contribute to resistance. Since sites used in this study may have all the elements favored for pathogen such as continuous production of maize, the disease occurrence and the replicated evaluation of experiments made it possible to assess performance of the genotypes to the disease. The disease scores observed might have not been higher since the establishment of GLS was late. However, disease infection and development varied between genotypes. T5 and L10 showed lower disease scores compared to L1, L7, L8 L11, and T1, T4 and T6. In the former, parents were to resistance to GLS while the later parents were moderately resistant. Late establishment of GLS in maize has been mentioned by many researchers and in many instances leads to minimal yield losses as disease infection does not end in high leaf damage to affect photosynthesis. In addition parents that showed high disease score to GLS such as L1 and L11 also showed similar trends to Exserohilum turcicum. The converse was true for those that did not. In case of leaf rust, the observations were that susceptible parents in this case to GLS and Exserohilum turcicum were the ones that exhibited resistance to the disease. The pattern of disease occurrence may indicate that GLS and rust were highly influenced by high fertility levels and lush growth of plants where as for Exserohilum turcicum both high fertility and N stress were important for the disease to develop. However, N stress on the whole had higher influence on turcicum disease infection, as the disease pressure on stressed plants happened to be higher.

Significant genetic correlations (rg) were observed between grain yield and many secondary traits for lines and testers measured under high N and low N except for anthesis and leaf senescence under nitrogen stress. However, correlations were lower for ears per plant and number of kernels per ear. This indicates that higher grain yields was associated with traits that had higher correlations whilst traits such as ears per plant and number of kernels per ear had minimal contribution to yield due to their low correlations. Though there was no

correlation between grain yield and leaf senescence studies by Banziger and Lafitte, 1997; Lafitte and Edmeads, 1994a and 1994b) and Edmeads et al, 1997a have indicated high relationship of leaf senescence to yield.

Realized broad sense (0.57) and narrow sense heritabilities (0.51) for grain yield were generally larger for grain yield under low N and high N but was low for across environments. While it has been observed that heritabilities of grain yield often declines under stress (Blum, 1988; Banziger and Lafitte, 1997), the result in this study only agrees with that of Lafitte and Edmeads, 1994 who obtained higher heritability (0.58) for grain yield under nitrogen stress. The observed low heritabilities for ears per plant, number of kernels per ear, anthesis silking interval and leaf senescence indicate that these traits were not highly heritable in the progenies. This is in disagreement with other studies where these traits have been found to have high heritability than grain yield (Banziger and Lafitte, 1997; Banziger et al, 1997 and Edmeads et al. (1997a)

Combining ability mean squares for GCA for lines and testers were highly significant for all traits measured except for SCA for line x tester which was not for the same variables. In addition mean squares for GCA for lines and testers were much higher than that of SCA (line x tester). This indicated the preponderance of additive gene action rather than non-additive genes for influencing the traits in the germplasm studied. Several studies involving inheritances have revealed dosage effect or predominance of additive gene actions (Stangland et al., 1983; Zambezi et al., 1986, and Nigussie and Zelleke, 2001). In studies involving inheritance of GLS, Gevers and Lake, 1994 and Ulrich et al, 1990 found mainly additive gene actions being involved. On the contrary studies by Elwinger et al, (1990) and Saghai maroof et al, (1996) indicated that inheritance was non-additive and that dominance as well as epistasis was important in their testing materials. Therefore, the result has breeding implications in that the parents with good general combining ability (GCA) and

per se performance can be crossed to develop high yielding hybrids that can be recommended and be used directly by farmers.

Table 7 and 8 GCA effects for lines and testers for measured traits. Positive and significant effects for GY observed in L1, L11, and T9 at both N levels and across environments significantly increased grain yield while L2 significantly reduced yield. L9 and T3 significantly reduced yield under low N while L6, T1 and T5 did so under high N. In additional EPP and SKW were significantly increased by L1 and L11 as opposed to L6 L7 and T3. Parents L4, T4and T9, increased number of kernels per ear. Under low N L7 L10, T4, T5, and T7 significantly contributed to duration of photosynthesis, as they remained green longer compared to L12, T3 and T12. In terms of diseases L2, L6, L10 and testers TT3, T5, T7 and T8 significantly reduced GLS as opposed to L1, L11, T1, T4 and T8. For turcicum L8 (low N and across environment), L11 (low N) as well as T3 and T8 increased turcicum disease. Since GLS and turcicum are under additive gene action, it important that lines that consistently performed but lacked superior GCA effects were improved further for GLS and turcicum resistance by backcrossing to resistant genotypes.

Negative GCA for male and female flowering shown by L1, L2, L9 and T1, T5, T6 and T7 may indicate early maturity in the parents. T1, T5, L2 and L9 with reduced plant height also had grain yields for the reason that earliness has inverse relation with grain yield (Bolanos and Edmeads, 1993b). In general, L11 and T12 contributed to lateness in tasselling and silking, and to increased height and grain yield. It is common for maturity and plant height to be associated with higher grain yield (Hallauer and Miranda, 1988). However, L1, T6 and T7 may have reduced days to flowering but this did not affect grain yield.

Despite SCA not being significant, crosses with desirable SCA effects generally involved parent combinations with at least one high or intermediate general

combiner as a parent. Very few low x low or low x intermediate general combiners had good SCA effects (Table 9 and Appendix D, E and F). This reveals that the productive lines under low N, high N and across environment involved lines and testers with high x high and high x low general combining ability (GCA) status respectively for important agronomic and physiological traits related to nitrogen use efficiency as well as productivity traits and resistance to GLS. The least productive lines and testers all had low and negative GCA status cross combinations with respect to nitrogen tolerance, resistance to diseases and productivity traits.

The highest yielding hybrids across locations were L 9 x T12 (6.04 t/ha), followed by L10 X T12 (6.00 t/ha). Under low N the highest yielder was L1 x T1 (2.27 t/ha) while at high N, L9 x T 12 (10.2 t/ha) was the highest. However, some hybrids (L11 x T9 and L10 x T9) performed well in terms of low disease pressure (>2.0), low leaf senescence and ASI, more EPP as well as more grain yield across all environments indicating that it is possible to combine stress tolerance and plant performance in terms of yield potential in maize hybrids. Similar results have been reported with temperate maize hybrids where improvements for tolerance to abiotic and biotic stresses have been associated with the ability to maximize yield under non-stress growing conditions (Duvick, 1997). High performance of some crosses was the result of reduction in barrenness and increases in grain number and kernel weight, and were accompanied by a reduction in the anthesis-silking interval (ASI) and a delay in leaf senescence (Bolanos and Edmeads, 1993b, Edmeads et al, 1999). In addition these hybrids showed highly and moderate resistant GLS, turcicum and rust.

CHAPTER SIX

6.0. CONCLUSION

The results of the study have demonstrated the importance of North Carolina mating design II analysis in identifying lines and testers with good combining abilities that help develop hybrids suitable for desirable traits. Additive gene action rather non-additive gene action predominated all characters studied.

Lines (L12M1(220GY)–150-3-3-1-1and N3-1XN3offtype-4-1-3-3-2-1-1) and testers (CML444/DRB-F2-60-1-1-1-BB and CML444/CML 448) consistently performed well. These parents had high and positive GCA effects for grain yield, plant height, and ears per plant. They were also good combiners for kernel weight, the number of kernels per ear and had reduced leaf senescence and a short or negative anthesis-silking interval (except line: L12M1(220GY)–150-3-3-1-1).

High and negative GCA for GLS were exhibited by lines (Line 14-1 and 8535-23-1-2-2) and testers (CML 444/ DRB-F2-60-1-1-1-BB and CML 440/ CML 443) while the highly susceptible parents were lines (L12M1(220GY)–150-3-3-1-1 and N3-1XN3offtype-4-1-3-3-2-1-1) and tester (CML 312/CML 442).

Hybrids involving lines L12M1(220GY)-150-3-3-1-1x CML444/CML448 and Line 14-1 x CML444/CML 448 were among the top performing hybrids across low N and high N conditions.

6.1. RECOMENDATIONS

Lines (L12M1(220GY)–150-3-3-1-1and N3-1XN3offtype-4-1-3-3-2-1-1) which were superior in their combining ability but lacked tolerance to grey leaf spot should improved further through backcrossing them to genotypes with high resistance to GLS.

All the best three way hybrids in this study should be evaluated further and released with their special attributes of tolerance to low N and resistance to GLS.

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