

**EFFECT OF ENVIRONMENT ON POLLEN – SILK SYNCHRONISATION
IN MAIZE HYBRID SEED PRODUCTION**

By

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University of Zambia in Partial Fulfilment of the Requirement of Masters of
Science in Agronomy (Crop Science)**

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DECLARATION

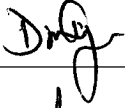
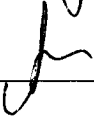
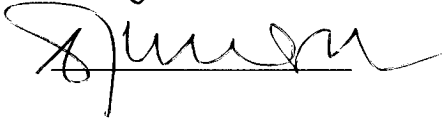
I CHANDA RICHARD do hereby declare that this dissertation represents my own work and that it has not previously been submitted for the degree at this or any other University.

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APPROVAL

The University of Zambia approves this dissertation of Richard Chanda as fulfilling the requirements for the award of the degree of Master of Science in Agronomy

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ABSTRACT

In maize hybrid seed production, the objective is to maximise seed yield of desirable seed grade that is saleable and genetically pure. To achieve this, the timing of pollen shed of the male and silking of the female should be well synchronised. Currently, maize hybrid seed production is based on limited information on the quantity of pollen produced by the male and practical experience synchronising pollen-shed with silking. Therefore, the objective of the research was to look into the aspects of synchronisation as related to hybrid seed maize production, specifically to study the effect of environment on male - female synchrony. Nine inbred lines, used as males and nine single cross hybrids, used as females, producing hybrids of different maturities were used in the study. The parents were grown under optimal, sub-optimal conditions relative to soil nitrogen level and under water stress in the dry season. Irrigation water was withheld for four weeks during flowering. The recommended agronomic practices were used at all the trial sites. During the growing season, the rate of silking and pollen-shedding were collected on each plant daily. In addition, seed yield components and other important agronomic traits were recorded. Significant ($p < 0.05$) genotype x environment interactions were observed on grain yield, 100 seed weight, ear leaf area, plant stand, average tassel length, days to 50% anthesis, anthesis-silking interval and number of tassel branches. The main effects of the environment and hybrids were significant ($p < 0.05$) in most of the traits measured. There was considerable variation in the response of parents to varying environmental conditions. Generally, the onset of flowering was delayed, with water stress having the greatest influence on the onset of silking, tasselling and pollen shedding, compared to optimal conditions. On average, BIPASI and desynchronisation increased under nitrogen stress. Low nitrogen and high plant population with optimal nitrogen increased the duration of pollination and duration of pollen shedding. BIPASI explained only 22% of the observed variation in number of grains per plant. The number of grains per plant were strongly associated to ears per plant ($R^2 = 0.84$), sheddays ($R^2 = 0.75$) and silk spread ($R^2 = 0.75$); moderately associated to duration of anthesis ($R^2 = 0.66$) and to low extent associated to 50% silking ($R^2 = 0.52$). Therefore, it was concluded that seed set depends on the dynamics of silking and pollen shedding. Multiple regression analysis revealed that traits responsible for moderating seed set differed from environment to environment, but averaged across all environments and parents, one hundred seed weight, ears per plant and shelling percentage were the most common traits. Ears per plant had the highest impact, again proving the robustness of this trait in influencing seed yield. Generally, most parents that had BIPASI of ± 5 days, had high seed set, except under low N conditions were N deficiency limited yield. Despite synchronisation being affected by environment, seed production was economically viable for parents planted on the same day when grown in various environments. However, this depended on parental combination. Therefore, in order to maximise seed set, synchronisation studies should be done to simulate actual field production to take care of the differential response of parents to stress conditions.

DEDICATION

To my dearest wife Edina and my lovely children Kunda, Chanda and Emmanuel for their spiritual support, inspiration and love which kept me going.

To mum and dad I would say thanks for giving me a good foundation

God bless you all.

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CHAPTER 1

1.0 INTRODUCTION

Maize (*Zea mays*) is the most important cereal in the Southern African Development Community (SADC) region and the most preferred staple food. About 11 million hectares are grown to maize in the region covering 71 percent of the area planted to cereals (Bänziger et al., 2004). The crop is also a prominent component of the agricultural trade involving various categories of farmers. In Zambia, 90% of maize produced is used directly for human consumption and accounts for more than 70% of the dietary carbohydrates source for most Zambians (Mung'oma and Mwambula, 1996; Ministry of Agriculture Food and Fisheries, 2000).

Maize production in the region is characterised by a big yield gap of between 1.0 t ha⁻¹ to 10 t ha⁻¹ for smallholder farmers and researchers respectively (Waddington and Heisey, 1996). The low yields are mostly attributed to drought, causing yield losses of 10 - 15% on 80% of the area planted annually (Zambezi and Mwambula, 1996) and low soil fertility, nitrogen being the most limiting nutrient followed by phosphorus (Bänziger et al., 2004).

It is for this reason that in 1997 CIMMYT, in collaboration with National Agriculture Research and Extension Systems (NARES), initiated a breeding programme under the Southern Africa Drought and Low Fertility Project (SADLF) (Bänziger et al., 2004 and Pixley et al., 1997). As a result of this project, the development of drought and low nitrogen tolerant varieties has received top priority in most national breeding programmes in the SADC. According to Bänziger et al. (2004), hybrids developed by CIMMYT in this stress breeding programme showed a consistent yield advantage over private company check hybrids at all yield levels ranging from 1.0t/ha to over 10.0 t/ha in the 65 trials done across eastern and southern Africa between 2000 and 2002.

Therefore stress tolerant maize varieties have the potential of contributing to productivity and stability of food supply at both national and small-scale farmer levels. Waddington and Heisey (1996) have estimated that the use of varieties tolerant to low nitrogen would raise the yield by 0.4 t/ha and the use of high yielding varieties (HYV) would raise yield by 0.1 t/ha above the average of 1.1 t/ha in the SADC region. This is in agreement with the findings of Edmeades et al. (1996) who observed that genetic improvement of maize for drought tolerance within species would close the yield gap

between actual and potential water limited yields by 30 – 40%. Despite this, Waddington and Heisey (1996) observed that the yield obtained by using low nitrogen tolerant varieties and high yielding varieties would be far short of the estimated yield of 3.0 t/ha, a yield required to feed the SADC region in the 21st century. Furthermore, Masole and Gumbo (1994) have shown that the use of improved genotypes and technology can increase maize grain yield by about 83% while 11% increment would be due to weather.

The impact of any technology depends on the adoption of that technology by the target group, of which stress tolerant varieties are no exception. Access to the right amount of properly priced seed of improved varieties at the right time ensures food security. This is because; seed is one of the agricultural inputs that sets the upper limit of achievable yield. According to Pixley et al. (1997), the dissemination of improved varieties in the region, is dependent on the state of the seed industry at both the national and regional level. This is in agreement with the findings of Heisey et al. (1997) who observed that in developing countries, the adoption of hybrids depends on the price, market structural conditions and the cost of innovation. In his study, the price of seed was singled out to be the most important factor in the initial adoption and diffusion of hybrid seed, which is of less importance in a country with a mature seed industry. Hence, the timely provision of high quality, affordable seed will lead to faster adoption of these varieties by the smallholder farmers. However, the production of high quality and affordable seed requires the optimization of pollen silk synchronisation. The synchronisation of silking of the ear in the female line and pollen shed of the male line tassel determines seed set and hence yield in a seed crop.

In hybrid seed production, a close synchrony between receptive silks on the female parent and pollen production on the male parent as well as abundant pollen is critical for high seed set (Westgate et al., 2003). However, it has been hypothesized by Vidal – Martinez et al. (2001) that pollen production is a problem in maize hybrid seed production conditions. In addition, Westgate et al. (2003) observed that the management of modern hybrid seed production is not cost effective and not rational. His conclusion was based on the premise that the planting density and male – female ratio is based on practical experience and not on quantitative information on the flowering biology of maize crop.

Research on the role and regulation of pollen – silk synchronisation or anthesis–silking interval has received much attention in the screening of breeding materials for stress conditions as proved from long-term breeding trials done at CIMMYT, Mexico (Edmeades et al., 2000). However, the synchronisation studies have been restricted to self pollination in maize, especially that agronomic studies on maize have demonstrated that there is genetic variability for low nitrogen tolerance or what is known as nitrogen use efficiency (NUE) in maize (Gallais and Hirel, 2004).

There have been no studies reported on the effect of the environment on the pollen – silk synchronisation in hybrid seed production of stress tolerant parental lines. There is also limited knowledge on the correlations of NUE with aspects related to hybrid seed production.

This research study was carried out to determine the effects of environment on the synchronisation of male and female flowering in hybrid seed production of selected three-way cross hybrids. The specific objective of the research was to study the effect of low nitrogen, optimal nitrogen and water stress during flowering on the flowering dynamics of maize inflorescences.

The hypotheses of the study were:

- (a) There is variation in pollen–silk synchronisation between male and female parental lines of maize hybrids
- (b) Optimisation of pollen–silk synchronisation in maize parental lines would improve hybrid seed production in an array of environments.

CHAPTER 2

2.0 LITERATURE REVIEW

2.1 ASPECTS OF MAIZE PRODUCTION IN THE REGION

One of the major challenges facing the Southern African Development Community (SADC) countries is to achieve national food security while reducing environmental degradation and depletion of natural resources. Drought and low soil fertility have been identified as the major abiotic stresses leading to low yields especially among the resource poor farmers (Pixley et al., 1997). These stresses account for the big yield gap between those obtained by small-scale farmers averaging 1.1tons/ha and that obtained at research stations which is over 10tons/ha (Bänziger et al., 2002; Waddington and Heisey, 1996; Zambezi and Mwambula, 1996). In order to reduce the yield gap, a vigorous regional breeding programme was launched by CIMMYT in 1997, called the Southern Africa Drought and Low Nitrogen Project (SADLF). The major objective of the project was to develop, through breeding, maize varieties that are tolerant to drought and low nitrogen (Bänziger et al., 2002; Zambezi and Mwambula, 1996). The varieties developed through SADLF are high yielding and consistent in performance than the existing commercial hybrids (Bänziger et al., 2004).

The other problem that has been identified as a contributor to food insecurity is access to high quality seed by the resource poor farmers. In Sub – Saharan Africa the cost of improved seed is one of the major causes cited for low adoption of improved varieties FAO (1998). Therefore, any technologies that will reduce the cost of seed production, will improve the adoption of improved varieties of maize. Stress tolerance breeding then needs to address the issue of hybrid seed production because even when it is possible to develop stress tolerant hybrids that significantly outperform the current varieties, often it is not possible to produce improved seed at a price that subsistence farmers will be willing and able to pay. Therefore, it is envisaged that the availability of maize varieties tolerant to low nitrogen and drought will be easily adopted due to reduced costs of seed production and at the same time will increase maize yield among resource poor farmers. The fact that smallholder farmers constitute 80% of the crop production in Zambia, underpins the need to address aspects that impede high productivity among smallholder farmers (MACO, 2003).

Adequate pollen production is an essential prerequisite for achieving high yields in commercial maize (*Zea mays* L.) production and for ensuring high levels of genetic purity in the production of hybrid seed (Fonseca et al., 2003). Under field conditions, the quantity of pollen produced would limit seed yield due to the use of male inbreds with small tassels, male sterile blends consisting of 50% male fertile lines and top crosses having 10% male fertile, coupled with environmental effects (Westgate et al., 2003). Similarly, modern maize hybrid seed production is based on practical experience synchronizing pollen shed by male parent with silk emergence by female parent limited information and not on the quantity of pollen shed by the male (Fonseca et al., 2004). This was confirmed by Masole (2006, personal communication) who indicated that 50% silking and 50% anthesis is recorded without recourse to stage of silking, that is, how many silks are exposed per cob and stages of pollen-shed, that is, beginning of pollen shed, maximum pollen shedding or end of pollen shed. Therefore, Vidal – Martinez et al. (2001) hypothesised that pollen production limits kernel set in hybrid seed production. The hypothesis was further supported by simulation studies done by Westgate, Fonseca and Lizaso (2005, personal communications). They found that seed production was limited primarily by pollen availability and flowering dynamics of the inbred pairs. These stages are key in scheduling planting of male and female plants in seed crops to achieve high kernel set. In addition, the maleness or pollination ability of the male is based on experience and not on the quantity of pollen produced. Thus the classification of a male as a good pollinator or poor pollinator is based on this. Seed production, therefore, requires the management of critical processes and operations; good synchronisation of parents with regards to good pollination and adequate fertilisation; to ensure the production of high quality seed maize that is of high genetic and physical purity.

2.2 POLLEN – SILK SYNCHRONISATION IN MAIZE

The time interval between anthesis of the male inflorescence and silking of the female inflorescence is called the Anthesis–Silking Interval (ASI) by many authors or desynchronisation (Struik et al., 1986) or asynchrony (Westgate, 1997 and Herrero, 2003). A short interval or when pollen-shed and silking are well synchronised is necessary to achieve a high kernel set.

Under normal climatic conditions, the tassel sheds pollen before silking. This phenomenon is called protandry. When protandry is large and the duration of pollen

shedding is short, pollen will not be abundant when the silks are present. This will especially affect the florets in the top ear, because these silks emerge later than those of the lower florets (Tollenaar and Daynard, 1987a). However, under stress conditions of low soil nitrogen, drought, pH, plant density, the development of male and female organs are affected differently leading to either protogyny (negative ASI) or protandry (positive ASI) depending on the timing and intensity of stress.

The relationship between ASI and seed yield has been heavily researched in breeding populations. Many of the correlation studies between ASI and yield reported are related to self-pollination, as in breeding materials, than in cross-pollination studies, as is the case in hybrid seed production. Therefore, much review work written here will be on self-pollination.

It was Du-Plessis and Dijkhuis (1967) who first showed that ASI was inversely related to yield in response to water stress in a single cross hybrid, SR 52. The relationship between the number of kernels per plant and ASI, fitted on a logarithmic scale was $Y = 2.714 - 0.0374x$, with a correlation coefficient of $r = -0.969$ while the relationship between yield per plant and ASI, on a logarithmic scale, was $Y = -0.3929 - 0.03928x$ and a correlation coefficient of $r = -0.966$. Maximum seed set is obtained in plants that start silking within 1 – 2 days when 50% of the plants are at anthesis. Westgate, (1997) reported that maximum kernel set was obtained on ears that had their silks exposed within 2 to 3 days of anthesis (ASI = +2 to +3days) and to their surprise, a high kernel set was observed for pioneer 3790 in plants that had silked 6 days before anthesis or in those plants whose silk emergence had lagged behind anthesis for 8 days (Westgate, 1997). However, an ASI of 3 is acceptable, according to Mwambula and Manda (1998), which is in agreement with an ASI of 2 to 3 days, reported by Westgate (1997), for maximum kernel set.

2.2.1 ASI and hybrid seed production in maize

In hybrid seed production, the time lag between the start of silking and start of pollen shedding determines seed-set, seed grade and therefore yield of the seed crop. The time lag also has a bearing on seed quality as it relates to the risk of contamination from foreign sources of pollen or morpho-physiological quality at maturity (Batisela et al., 2002). The interval between 50% plants silking and 50% plants shedding pollen, known

as ASI, is commonly used in identifying parents that 'nick' or for synchronising parents to achieve high kernel set.

The ASI, though is commonly used as an indicator of parents that "nick", is just an interval or time difference and yet kernel set is determined by synchronous silking between ears and within ears, quantity of pollen produced, efficiency of pollination at various pollen densities. ASI in hybrid seed production is useful when quantitative information on pollen shedding and silking dynamics is collected (Lizaso et al., 2003 and Westgate et al., 2003). In cases where the flowering dynamics of the parents are known, Fonseca et al. (2004) had shown that ASI had a greater impact on kernel set amongst all the genetic and management variables used in the test. They further found that a perfect ASI (ASI = 0days) does not result in high seed set, while delaying silking such that ASI is -2.0days relative to an initial ASI of -0.55days resulted in a 35% reduced of kernel set. On the other hand advancing silking prior to 50% pollen shed (increasing ASI to +2.0days) increased kernel set by 38%. High kernel set was obtained when anthesis was delayed by 5 days relative to 50% silking. Westgate, Fonseca and Lizaso (2005, personal communication) found maximum kernel set for inbred pairs at ASI values between +2 to 4 days in a field with initial ASI of 1.2days.

Split planting of the males is commonly done in hybrid maize seed production, to extend pollen availability hence increase kernel set. Maximum kernel set has been reported when the interval between two pollen sources was about 5 to 6 days, for inbred pairs having an ASI of -0.55days relative to the first pollen source (Westgate, Fonseca and Lizaso. 2005, personal communication).

Seed production requires that the genetic purity of the variety be maintained. Therefore, contamination of seed fields should be eliminated or kept within stipulated tolerance levels. In areas where distance isolation cannot be used, time isolation is utilised. The principles behind time isolation is that two seed crops of different varieties of maize grown in close proximity will not be able to contaminate each other since the silk of one field is not receptive to pollen when the contaminant is shedding pollen. Studies done by Havazvidi and Caulfield (1988) on time isolation in Zimbabwe at Rattray Arnold had shown that a time isolation of 21 days is adequate to achieve a very low contamination level.

Even in well synchronised seed production fields, the risk of contamination is not completely eliminated. However, the level of contamination depends on the presence of adventitious pollen relative to local pollen density, genetic factors like pollen-silk compatibility, environmental factors and quantity of receptive silks in the field. Later appearing silks are at a high risk of contamination. Westgate, Fonseca and Lizaso (2005, personal communication) obtained a 1.6% out crossing for late-emerging silks. In the field, adventitious pollen was artificially introduced, with pollen quantity peaking to 7.5 pollen grains cm², when late-emerging silks were receptive to pollen. They further found that the ASI for maximising kernel set and that for minimising contamination were not the same. This suggests that the management of ASI in hybrid seed production would depend on the flowering characteristics of the parents involved and the potential for adventitious pollen entering the field.

Batisela et al. (2002) have shown that the physical, morphological and physiological characteristics of seeds developed at different positions of the ear differ in seed quality attributes. They noted that the physiological qualities of the round proximal and central seeds are equivalent and all are significantly superior to the round distal seeds. They further observed that the seeds located on the proximal sector of the ear was 100% superior in performance; seeds located on the central ear sector had 38% superior seed performance and 62% seeds being of average performance while the seeds located on the distal sector of the ear had 24% of seeds of inferior performance and the remainder had half of average performance and the other half of superior performance.

Flat seeds, produced on the central portion of the ear, are of superior quality (Batisela et al., 2002). Batisela et al. (2002) further report that, the demand for flat seeds is high to the extent that price of round seeds is 60% that of flat seeds. This implies that proper synchronisation is essential for the production of flat seeds as poor synchrony would result in the production of a high percentage of round seeds (Batisela et al., 2002). Under effective pollination, single cross seed parents produce a high proportion of flat than round seeds with a ratio of 60% to 40%, with the small and medium round seeds being less than 10% (Curtis, 1980).

2.2.2 ASI and plant breeding

A survey on the yield increases of modern hybrids has been attributed to many factors, among them being prolific physiology. True prolificacy leads to protogyny whereas

normal maize shows protandry; hence short ASI (Gallais and Hirel, 2004). Duvick (1997) in evaluating maize hybrids from the period 1931 to 1991, showed that increases in grain yield of 53 kg ha⁻¹year⁻¹ have been accompanied by significant decrease in ASI (0.04 days year⁻¹) and an increase in Ears Per Plant (EPP) of 0.02 per year. This was further confirmed by trials done by Sangoi et al (2001) who reported a decrease in ASI of 0.14 days per decade for low N or 0 kg N ha⁻¹ and 0.17 days per decade for optimal N or 200kgN ha⁻¹. On the other hand, selecting for drought tolerance or reduced ASI in tropical maize reduces the number of spikelet on the upper ear by 20%, after more than 8 cycles of recurrent selection (Edmeades et al., 1998).

In plant breeding ASI has been used as an effective secondary trait to select for drought tolerance in maize populations (Bryne et al., 1995), as an indicator of barrenness if EPP is less than 1.0 (Edmeades et al., 1999) or less than 0.9 (CIMMYT, 2005) and an indicator of prolificacy when EPP is greater than 1.0 (Edmeades et al, 1999). It has been shown by many researchers that under moisture stress the genotypic variability for ASI is high and that the heritability does not decline rapidly as grain yield per se. Furthermore, the independence of ASI to maturity differences among varieties makes it a better trait for selection. Edmeades et al (1997b) demonstrated that focusing on EPP and ASI when breeding for water stress tolerance would result in an increase in harvest index and grain yield for all water stress regimes. Westgate (1997) proposed selecting for protogyny or negative ASI and rapid ear growth prior to anthesis for improving drought tolerance in maize. According to Westgate (1997), protogyny and rapid ear growth at anthesis are indicators of increased biomass partitioning to pistillate flowers especially when assimilate supplies become limiting, as under severe drought stress conditions. Biasutti et al (2000) when selecting for adaptation in a broad based population, BC 88, observed a reduction in days to 50% pollen shed and 50% silking of 1.75days and 1.74days per cycle after 4 cycles of selection. This is about 0.01 ASI per cycle. Under drought conditions, direct selection for yield is ineffective but ASI and EPP has been used effectively, especially when the environment allows for genetic variation to be expressed. (Bryne et al., 1995; Diallo et al., 1997 and Edmeades and Bänziger, 1997). This is in agreement with the findings of Bänziger and Lafitte (1997), who showed that using secondary traits plus yield during selection for low soil nitrogen is 20% more efficient than selection for yield alone. In addition, ASI and EPP reflect the ability of a plant to produce a grain-bearing cob under nitrogen stress and hence are important secondary traits when selecting for drought tolerance (San Vicente et al.,

1997; Bolaños et al., 1993 and Edmeades et al., 1995). Bänziger and Lafitte, (1997) were able to confirm that ASI, EPP, leaf chlorophyll concentration and leaf senescence are linked to N stress with EPP and Leaf senescence being the most important. The genetic correlations obtained were -0.47 for ASI, 0.78 for EPP, 0.24 for leaf chlorophyll concentration and 0.42 for leaf senescence. When the site yield is 20% less of the yield potential in unstressed conditions, then the correlation between EPP and ASI on yield, approaches -0.7 and 0.9 respectively (Edmeades et al., 1992). Hence, ASI and EPP are two traits strongly related to yield under stress with EPP being the most affected yield component under stress conditions (Vasal et al., 1997 and Edmeades et al., 1998)

When breeding for stress tolerance, the correlation between environments in relation to the performance of the materials is very important. When evaluating the response of S_4 maize lines, Diallo et al (1997) found a highly significant correlation of yield under high plant density and low nitrogen to yield under natural condition environment. Yield under severe drought stress was correlated to yield under moderate drought only ($r = 0.52$, $p < 0.01$). A positive correlation between yield under low nitrogen and moderate drought stress was also found.

Several reports have shown that yield and ASI are negatively correlated with values ranging from $r = -0.36^{**}$ to $r = -0.73$ (Fischer et al., 1989; Edmeades et al., 1992; San Vasal et al., 1993 and Vicente et al., 1997). Large significant negative genetic correlations were observed mostly under severe stress conditions and weak correlations under well watered conditions (Srinivasan et al., 1997; Betran et al., 2003, Bolaños and Edmeades, 1997). Ears per plant and yield are positively correlated (San Vicente et al., 1997 and Vasal et al., 1997), accounting 25 – 35% of the variation in grain yield (Edmeades et al., 1997).

Bolaños and Edmeades (1997) had described the correlations of ASI, EPP, weight per kernel and kernel number per ear (KNE) to yield. They reported that the genetic correlations between grain yield and ASI or ears per plant were weak under well – watered conditions while under drought, the genetic correlation between yield and ASI was strong and consistent across environments. The genetic variances for grain yield, kernels per ear, kernels per plant and weight per kernel decreased with increasing drought, but those for ASI and ears per plant increased. An exponential relationship between grain yield with ASI and EPP was found with r^2 of 0.70 and 0.94 respectively.

On the other hand, the relationship between grain yield with weight per kernel and kernels per ear was explained by a linear equation with r^2 of 0.74 and 0.89 respectively. The relationship between EPP and ASI was also found to be exponential under well watered and water deficit conditions (Elings et al., 1997). However, this relationship was limited to genotypes with only one ear. In prolific hybrids, the response of EPP was observed to be strongly related to plant growth rate at silking than ASI. The genetic correlation between grain yield and EPP was reported to be a function of ASI and EPP, to the extent that the correlation between grain yield and EPP increased very rapidly to almost 1.0 as mean ASI exceeded 5 days or mean EPP below 0.7 (Bolaños and Edmeades, 1997). In their case, ASI and yield had similar heritabilities. This relationship indicates that grain yield depends on kernels per plant mediated through EPP and less through kernels per ear (Edmeades et al., 1997).

According to Bolaños and Edmeades et al., (1997) grain yield strongly depends on ASI. This is supported by other trial reports where ASI had accounted for 70% of the variation in grain yield. In the variety, Tuxpeño Sequia it was reported that ASI accounted for 76% of the variation in the observed grain yield (Edmeades et al., 1997). There are also instances where ASI has failed to account for more than two thirds of the observed grain yield in a breeding population (Edmeades et al., 2000). Hence, Bolaños and Edmeades (1997) concluded that yield strongly depends on ASI. However, the phenotypic correlation between tassel branch number and yield was zero, which was indicative of the competition that exist between tassel and ear for assimilates. Based on these findings, the two workers proposed a breeding strategy where: (a) direct selection for yield should be done under well watered conditions while under stress conditions ASI should be used as selection tool, (b) drought should be managed so that the mean ASI should exceed 5days and the mean ears per plant to drop below 0.7 at normal plant density, in order to maximise the expected genetic gain. They further concluded that ASI is related to biomass partitioning to the developing ear. Conversely, ASI is a predictor of yield. However, they also observed that the relationship between ASI and yield diminishes as inbreeding of the progenies progresses.

A reduced ASI in populations was observed when selection was done on materials stressed during flowering and grain filling (Bänziger et al., 1999). In four maize populations, namely Tuxpeño Sequia, La Posta Sequia, Pool 26 Sequia and Pool 18 Sequia; Bänziger et al. (2002) observed a reduction in pollen shedding of 2.2, 0.9 and 1.4

days with an increase of 1.4 days in Pool 18 Sequia, after 8 cycles of recurrent selection. However, stability in yield was reduced for populations selected beyond cycle 6 when tested under stress conditions (Bryne et al., 1995). This implies that breeding for specific adaptation is most likely to occur when selections are beyond cycle 6. The heritability of ASI does not decline as rapidly as grain yield *per se* under low nitrogen. In an analysis of 19 progeny trials, the heritability of ASI was 0.52, which was slightly greater than that of grain yield (Edmeades et al., 1993 and Bänziger et al., 1997)

This study led to the proposal of maize ideotype for drought stress. Edmeades et al. (1997) proposed that a drought tolerant maize ideotype should have among other things, rapid ear growth at flowering, short ASI under stress, small tassels and relatively short stature. This ideal maize plant type should also be prolific under well watered conditions, single eared under stress and not barren, have stay green characteristics, high grain yield under well watered conditions and a stable high grain yield under stress.

The value of a trait in breeding depends on its heritability and genetic control. Knowledge of the location of useful genes or Quantitative trait loci (QTL) associated with the trait is useful in improving selection efficiency as well as allowing for marker assisted backcrossing (Kearsey and Pooni, 1998). Six putative QTL for ASI have been identified on chromosomes 1, 2, 5, 6, 8 and 10, under drought conditions. The identified putative QTL accounted for 47% of the phenotypic variance (Edmeades et al., 1998). On the other hand, the QTLs identified by Edmeades et al. (2000) on chromosomes 1, 3 and 6, accounted for 38% of the phenotypic variance. In addition, one position was found to have an allele that was responsible for reducing ASI as well as decreasing grain yield. Based on these findings, Edmeades et al. (2000) proposed using a selection index that combines best QTLs for both traits for Marker Assisted Selection (MAS).

2.2.3 ASI and plant variety evaluation

An evaluation of the performance of maize hybrids released at different decades to nitrogen level in Brazil, revealed that modern hybrids have better synchrony (Sangoi et al., 2001). The linear relationship between decade of introduction and ASI, measured as the difference between days 50% anthesis and 90 silking, was $y = 22.8 - 0.14x$ for zero nitrogen and $y = 22.5 - 0.17x$ for 200kg/ha nitrogen. This close relationship between synchrony and the performance of modern hybrids was also reported by Duvick (1997).

Similarly, Bassetti and Westgate (1994) reports that an ASI of greater than 7 days in hybrids is responsible for poor kernel set due to limited number of pollen grains (< 100 grains $\text{cm}^{-2} \text{d}^{-1}$) per silk.

In a study to evaluate inbred lines, extracted from populations with a background of drought tolerance, grown during the 1991 – 92 drought rain seasons in Zambia, Masole and Gumbo (1994) reported a positive correlation between yield and ASI. They noted that the varieties that yielded highest had the lowest ASI. The best genotype under moisture stress had 2 days of delayed silk emergence (Mwambula and Manda, 1998). Similar results were reported by Diallo et al. (2004) when evaluating hybrids for mid altitude zones of Eastern Africa. Hybrids that had performed well under drought conditions had short ASI and high EPP. Low correlations of -0.5 to -0.6 between ASI and yield were reported for trials where water stress coincided with flowering.

Badu–Aparaku et al (1997) reported that under non-stress conditions, the correlations between grain yield, ASI and EPP were not significant while under drought stress the correlations were significant with grain yield being positively correlated to EPP ($r = 0.67$, $p < 0.01$) and negatively correlated to ASI ($r = -0.28$, $p < 0.05$). In the evaluation of maize hybrids, Setimela (1997) showed that maize hybrids that can do better under poor rainfall distribution can be selected even when the correlation between yield and ASI is weak ($r = -0.149$). This implies ASI can effectively be used to identify adaptable genotypes for variety release.

Genotype by environment interaction for ASI, 50% silking, 50% anthesis and plant height reported by Setimela (1997), implies that varieties are not consistent in the response of ASI to various environments. Similarly, a significant genotype by nitrogen interactions for days to mid silk, ASI, ear height and grain yield has been reported (Sibale and Smith, 1997). In the variety, La Posta Sequia C₄, a negative ASI was observed in well-watered conditions, while an ASI of zero was obtained under drought conditions (Moser, 2004). The interactive effects of N and water levels were significant ($p = 0.05$) for ASI in four varieties.

2.3 FACTORS AFFECTING THE CORRELATION BETWEEN ASI AND KERNEL SET IN CROSS-POLLINATED MAIZE.

Though there are reports that affirm to the fact that ASI is negatively correlated to yield, also positive correlations have been reported. Most of the correlations obtained are based on self-pollination studies on breeding materials. In cross pollinated studies like hybrid seed production, the association between ASI and kernel number can be affected by pollen viability, quantity of pollen produced, pollen transportation in the air, silk receptivity and abortion of kernels under optimal and sub-optimal conditions (Aylor et al., 2005) and period of pollination (Struik and Makonnen, 1992). Low nitrogen influences both the number of florets per ear and the fraction of those that develop into kernels (Edmeades and Lafitte, 1995). The correlation between ASI and yield reported can be weak or strong (Bolaños and Edmeades, 1997). Hall et al. (1982), working on maize using hand pollination, reported that under stress conditions, the time of exposure of silk to pollen and the proportion of pollen shed after 50% and 100% silking affects kernel set. He further confirmed other research findings, that for maximum kernel set, silk needs to be exposed to pollen for 4 days, while Struik and Makonnen, (1992) reported an exposure period of 5 to 6 days. When the amount of pollen is small, at least 10 days of silk exposure is required to achieve maximum grain set (Struik and Makonnen, 1992). This is because pollen production is skewed to early stages of pollen – shedding rather than being evenly distributed. They further observed that the plant to plant variation during pollen-shed can prolong the duration of anthesis.

2.3.1 Quantity of pollen produced

Maize pollen production is generally considered not to be a limiting factor to kernel set in commercial maize production under favourable conditions (Westgate, 1997; Westgate et al., 2003 and UribeArrea et al., 2002). In hybrid seed production, pollen quantity may limit kernel set (Vidal – Martinez et al., 2001) because of reduced tassel size (UribeArrea et al., 2002) or ratio of male to female population in a hectare. A reduced tassel size is one of the results of selection when breeding for drought tolerance (Bolaños and Edmeades, 1997). If the males are inbred lines, then the quantity of pollen produced and the pattern of pollen production can further be reduced by environmental conditions as inbred lines are very sensitive. A reduction in kernel set was observed in a plot where 20% were male fertile or 20% of the population were allowed to shed pollen. However, no significant differences in grain yield were observed between 100% and 20% male fertile plots (Westgate et al., 2003). The amount of pollen developed depends on the

number of staminate flowers per plant and the amount of pollen per anther (Goss, 1968). The number of ears per hectare and exposed silks per ear determines the minimum level of pollen production required to saturate kernel set (Westgate et al., 2003). This implies that, in practice, it is possible to adjust the plant population of the males to match with the number of exposed silks per ear once the quantity of pollen produced per tassel is known.

Several studies have been carried out to establish the threshold amount of pollen, which limits seed set. Varied information has however been generated. According to Sandras et al. (1985a), a density of about 5 pollen grains per silk is necessary to ensure pollination of 90% of the exposed silks, while Waldron, (2005), taking account of the losses due to dispersal, estimated that at least 170 grains per silk should be available. To have a perfect kernel set of 100%, Westgate (1997) estimated a minimum of 100grains $\text{cm}^{-2} \text{d}^{-1}$ or conversely, a perfect kernel set is expected for any silk exposed when the pollen density is at least 100grains $\text{cm}^{-2} \text{d}^{-1}$. According to Westgate et al. (2003), the number of kernels per plant and yield per plant increases as pollen density per silk increases up to a threshold of 3000 pollen grains per silk. At this threshold, a variety having a greater number of florets per ear and more rapid emergence of silks during pollen-shed, will have a greater number of kernels per ear. The threshold beyond which kernel set is affected was finally determined by UribeArrea et al. (2002) as 227 pollen grains at the end of pollen shedding and 2 pollen grains per exposed silk. This confirmed the findings of Waldron, (2005) who reported a fertilisation of 8 – 24% when 1 – 2 pollen grains are applied on an individual hair and a fertilisation level of 25 – 83% when 1, 2 and 3 grains are added to two or more hairs on a single silk. It was Waldron, (2005) who established that a high level of fertilisation could be achieved with low numbers of pollen grains applied to the bases of silks. However, he could not establish the minimum number of grains required on each silk as he did not take care of reduced viability and the number of pollen grains required to stimulate synergistic pollen tube growth.

2.3.2 Pollen dispersal

Maize pollen is released from the anthers in a manner described by Stanely (1974) and Keijzer et al (1996), moderated by the relative humidity around the tassels. Pollen is released when the vapour pressure deficit (VPD) is above 0.2kPa to 0.5kPa (Aylor, 2005). Pollen may be released at once or gradually, the pattern of emission being greatly modified by environmental conditions, while instantaneous wind direction has impact on

the direction of flow of pollen (Ma, et al., 2004). The most favourable condition for pollen release has been determined, being near neutral or very unstable stratification of the atmosphere (Jarosz, 2003).

Once released in the air, pollen is transported within and outside the maize canopy. The dispersal pattern of pollen depends on quantity of pollen available and weather conditions during pollen dehiscence (Goss, 1968). Wind speed and direction, turbulence and settling speed of pollen also affect pollen dispersal (Aylor et al., 2005). The settling speed of pollen depends on pollen size and pollen density. Among all the grasses, maize pollen is the heaviest.

The movement of maize pollen in the maize crop canopy has been well investigated by Aylor (2005). Horizontal deposition of pollen follow a power law over short distances downwind from the source, and the dispersal distance increases with the source canopy height and the roughness length of the downwind canopy (Jarosz et al., 2005).

The movement of pollen at different heights in the canopy has been postulated to be based on the Langragian stochastic (LS) model, called SMOP – 2D (Stochastic Mechanistic Model). This model is used to predict the measured concentrations and fluxes of pollen at different heights in the maize canopy. Studies by Aylor (2005) based on this model showed that only 20% of the pollen released by the tassel at 2.7m height reaches the silks at a height of 1.5m. Using this model, he predicted an increase in quantity of pollen reaching silks of about 3% due to canopy architecture and 5% from rebounds of pollen stuck on leaves. Furthermore, he predicted that 23% of the amount of pollen expected in a solid male – planted field, would be reaching silk for a typical 1:4:1 seed production field.

Freshly released pollen is prone to rebound and re-entrainment from plant surfaces. The critical wind velocities at which re – entrainment occurs is over a range of 0.3 to 0.6m/s (Aylor et al., 2003).

These studies, however were limited to pollen settling down to silks (Aylor, 2006 personal communication), because pollen grains in the air have a tendency to settle down than move upward and then downward (Ma et al., 2004 and Raynor et al., 1972). The tendency of pollen to settle downwards quickly or float has implications on the height

difference between male tassel and female silk. This critical height has not been determined or known (Aylor, 2006 personal communication; Masole, 2006 personal communication), though Masole (2006 personal communication) proposes a height of 50cm to be critical. This is because the wind speed within a canopy is often very low ($\ll 1\text{m/s}$) having a high turbulence intensity ranging between 2 and 5 (Jacobs and Van Boxel, 1991). This suggests that the orientation of rows in the field should be parallel to the prevalent wind direction and the speed of wind may determine the male: female ratio, for success of pollination.

One maize plant is able to pollinate 0.01% of the surrounding plants within a radius of 20m, decreasing to 0.005% at 30m, implying that 50% of the kernels of any individual plant result from pollen of plants within a radius of about 12m (Emberlin, 1999 and Jarosz et al, 2004). This is because most of the pollen is deposited about 30m of the source that is 95% being deposited at 10m from the source and 99% at 30m, under low wind speeds (Jarosz, 2003). The reduction in quantity of pollen from the source is exponential (Ma, et al., 2004). These studies are in agreement with the latest findings on isolation studies related to G.M.O containment (Ma, et al., 2004 and Luna et al., 2001).

The settling velocity (V_s) of maize pollen depends on volume equivalent diameter (D_e), water content, shape and size (Aylor, 2002). The settling speed ranges from 21cm/s for pollen grains with D_e of 76 – 80 μm to 32cm/s for pollen grains with D_e of 103 – 106 μm (Aylor, 2002).

2.3.3 Pollen viability

In hybrid seed production, the viability of pollen relative to the time pollen takes to land on receptive silk is cardinal for maximizing seed set as well as minimizing out crossing. Maize being an allogamic plant, the amount of grain yield is influenced by the viability of pollen (Hidv'egi et al., 2005). The level of nitrogen has an effect on maize pollen viability and longevity (Hidv'egi et al., 2005). Hence, the germination rate, drying rate, water content and the resistance to water loss of maize pollen are important for successful pollination and hence ASI (Aylor et al., 2005). Walter et al. (2004) revealed that spraying glyphosate (1.12 kg a.i ha¹) to glyphosate-resistant maize at V6 growth stage or later stages resulted in the production of deformed pollen with reduced viability. *Pollen is also killed by rain. Pollen soaked by rain forms a paste and is not*

viable (Masole, 2006 personal communication). Similarly, the anthers do not open when there is rain (Masole, 2006 personal communication).

2.3.3.1 Atmospheric conditions and Pollen viability:

Maize pollen is classified into the short-lived pollen group, where loss in viability is inversely related to the duration of exposure to air and the vapour pressure deficit of the air (Hall et al., 1982 and Thomison, 2005). The viability of pollen ranges from 3hrs to 9hrs depending on environmental conditions. Luna et al. (2001); Treu and Emberlin (2000) obtained viabilities of 1 to 2 hrs after pollen was exposed to atmospheric conditions of 28 to 30°C and relative humidity (RH) above 53% in Mexico. Pollen remains viable for 60min at 23 °C and 50% RH (Aylor, 2003).

In favourable atmospheric conditions, pollen is viable for 1 day or for 70 – 80hrs at temperatures of 5 – 10°C with a relative humidity of 50 – 80% (Gross, 1968). Viability periods of 15 – 20 minutes have also been observed (Gross, 1968). Aylor (2004) found that the length of exposure time required for pollen germination to be reduced by 50% ranged from 60 to 240 min, depending on environmental conditions.

At flowering, 60% of pollen fresh weight consists of water; once water content in pollen falls below 40%, then pollen longevity diminishes rapidly (Thomison, 2005), thus confirming the findings of Aylor (2003) that viability increases at higher levels of RH.

2.3.3.2 Pollen viability in storage:

Pollen viability of 200hrs has been recorded when it is stored at -8 to +5°C (Gross, 1968). Studies on pollen viability after storage or through in vitro culture have shown that (a) refrigerated pollen in the tassel had decreased pollination over 9 days, (b) refrigerating isolated pollen in a beaker, showed decreased pollination over 8 days, and (c) Storing maize pollen in plastic bags exposed to sunlight under a maximum temperature of 28°C remained viable for 30hrs.

2.3.4 Pollen desiccation

Pollen in the air is prone to water loss or desiccation. The desiccation is a function of air temperature, relative humidity and time (Fonseca and Westgate, 2005). Pollen desiccation may occur in areas with drought and having temperatures of above 30°C.

Pollen viability is relatively insensitive to solar radiation but is affected most by loss of moisture, which is related to the vapour pressure deficit (Aylor, 2004).

Thus, Fonseca and Westgate (2005) developed a single relationship that described the rate of pollen desiccation for several genotypes. They found that pollen grains are released from anthers at about 55 – 60% moisture content and the rate of pollen desiccation is a function of air temperature, relative humidity and time. Pollen viability decreased linearly ($r^2 = 0.77$ to 0.93) with pollen moisture content (PMC) to zero at $PMC \approx 30\%$.

2.4 FACTORS AFFECTING POLLEN – SILK SYNCHRONISATION

Despite ASI being strongly correlated to grain yield, there are other factors that affect grain yield in maize. Maize grain yield is primarily associated with variations in number of mature kernels per ear, which in turn depends on crop growth rates around silking, a period of approximately 30 days bracketing silking (Sangoi et al., 2001; Echarte and Tollenaar, 2006). The plant growth rate during the critical period of kernel set is a good predictor of the capacity of maize plant to set kernels under a wide range of environmental and management practices (Andrade et al., 2002). However, the observed association between ASI and grain yield is further complicated by the fact that maize is able to compensate for low kernel set by increasing kernel weight hence its shelling capacity (Below et al., 1997).

2.4.1 Drought

Under water stress, the female organ is more sensitive than the male organ on a maize plant. When drought occurs early in maize, the flowering interval is increased and this is associated with reduced turgor and low abscisic acid in reproductive structures. The osmotic adjustment of maize under drought stress is high in the tassel, and this perhaps explains the reason why pollen production continues while silk growth is reduced. (Moreno and Hernandez, 2003). Water deficit during or a few days prior to anthesis delays silk emergence by 1 – 8 days (Ritchie and NeSmith, 1992). Herrero and Johnson (1981) reported that drought increased the interval between initial silking and pollen shed on an average of 3 and 4 days respectively. Moss and Downey (1971), reported ASI values of 3, 13 and 16 for the control, treatment 2 (T2) and treatment 3 (T3) respectively. In their case, maize was exposed to water stress 59 days from sowing for 5 days (T2); water stress applied for 5 days commencing 59 days from sowing, then

watered with 200ml once until day 70 (T_3) and the control with no stress (T_1). Severe early drought led to delayed silking and pollen development. Under severe drought stress, silk would not emerge or silking would occur within the ear leaf sheath (Herrero and Johnson, 1981).

The quantity of pollen is reduced when stress occurs before tasselling, while stress at later stages does not affect pollen numbers (Hall et al., 1982 and Uribebarrea et al., 2002). Hall et al., (1982) reported that water stress before silking increases the duration of pollen shedding per plant apart from increasing the interval of starting of pollen shedding and start of silking on the same plant.

2.4.2 Plant density

When the plant density is high and there is drought, silking is delayed. This has been attributed to reduced assimilates being partitioned to the growing ear around anthesis (Edmeades et al., 1993). Sangoi (2001) reported that increasing maize plant population beyond the optimal, tassel development, ear development and silk extrusion is slow while few spikelet primordia are transformed into functional florets.

In a review of the effects of plant density on maize yields, Dungan et al. (1958) reported an increase in ASI of close to 0.4 days per 1 plant/m increase in planting rate. In seed production where the female is too tall relative to the male, increasing the plant population of the female causes a delay in pollen shedding of the male parent, hence large ASI (Pucavic et al., 1988). However, a high plant population has no significant effect on flowering in three-way cross hybrid seed production (Flores et al., 2004).

Duvick (1997) observed that there is a trend to increase the plant population in seed production to ensure the number of silks pollinated per hectare is at or past the genetic potential for kernel set. However, to achieve a high kernel set, silk exertions should be rapid especially if the female has a greater number of florets per ear (Westgate et al., 2003). Similarly, high plant density causes a large reduction in amount and duration of pollen produced per plant (Uribebarrea et al., 2002). Therefore a balance has to be determined to optimise seed yield.

2.4.3 Fertility level

Nitrogen deficiency results in delayed flowering and slow silk emergence from distal spikelets thereby increasing the interval between tasselling and silking (Edmeades et al., 1993). However foliar fertilization has no effect on flowering (Flores et al., 2004). In lowland tropical maize, ASI was delayed 0.6 days under low N and increased by 1.6 days under optimal N (Edmeades et al., 1993). Oikeh et al (1997) concluded that a better synchronisation of anthesis and silking indicates a better ability to tolerate nitrogen stress. The level of nitrogen also affects pollen viability and preservation of viability (Hidvegi et al., 2005). In an experiment done by Bennett et al. (1989), they observed that N stress delayed tasselling in all three water treatments i.e. optimal irrigation, 10 day wilting period preceding silking and rainfed in maize. Conversely, water stress delayed both tasselling and silking. Manson (1970) studied the effect of N, P and season on the flowering and maturation of SR 52 maize hybrid. He found that the ASI was 9.6 days for treatments without N and P, which reduced to 5.1 days when N and P were applied. The effects of each nutrient were reported as P alone = 0.3 days and N alone = 5.7 days. In prolific and semi-prolific maize, increasing nitrogen reduces the silking interval between the apical and sub-apical ears while the silking period is increased (Kamprath et al., 1984). This tends to result in a high seed set due to synchronous silking between ears.

Nitrogen accumulation is significantly correlated with grain yield at both levels of nitrogen and its uptake at flowering in both low N and high N input conditions. (Below et al., 1997 and Gallais and Hirel, 2003). At low N input levels, N determines kernel number (Gallais and Hirel 2003) and kernel weight, hence shelling percentage (Below et al., 1997). Therefore, the response of maize N availability depends on root uptake, vegetative storage capacity, recycling efficiency from vegetative tissues to developing kernels, which is related to zein accumulation in maize kernels and the dynamics and strength of the kernel sink (Cliquet et al., 1990 and Huber et al., 1994, cited by Edmeades et al., 2000). A poor pollination in maize leads to sink suppression, increasing the source – sink ratio, which in turn reduces the recycling of N from vegetative tissues to developing kernels (Sangoi et al., 2001). Higher N efficient hybrids have been reported to have a better balanced source: sink ratio. Under normal growing conditions, the three blades (upper blades) near the ear are the most important source of N for kernel filling, others being roots and sheath in these hybrids (Cliquet et al., 1990).

However, Seed growth rate is affected by N level only when there is no water stress (Bennett et al., 1989). Both nitrogen level and water management affects N accumulation, the interaction being more evident between 49 and 105 days after emergence. N uptake is reduced when water stress is applied at the vegetative stage only under high N fertilisation (Bennett et al., 1989).

Other mineral nutrients that have been reported to play a significant role in pollen silk synchronisation are Zinc (Zn), Iron (Fe), Magnesium (Mg) and Boron (B). Deficiencies of Zn and Fe delays anthesis and increases ASI in susceptible genotypes (Manson, 1970). Zinc deficiency retards tassel formation, anthers fail to develop, decreases pollen viability and cob dry weight by about 75% (Marschner, 1995 and Sharma et al., 1987). Magnesium deficiency results in the production of few and small pollen grains that are of low germination rates. The plants have poor tasselling and delayed anther development (Marschner, 1995 and Sharma et al., 1991). Though magnesium deficiency does not affect ovule fertility, seed setting and development are adversely affected (Sharma et al., 1991).

Boron deficiency affects silk receptivity to pollen (Vaughan, 1977) and severe boron deficiency delays tasselling and protrusion of anthers (Berzy et al., 1996). Silk receptivity ceases when the content of boron in the silk is less than 3ppm (Vaughan, 1977). The stipulated minimum content of boron in maize seed is 0.08ppm, obtained by foliar spraying of the seed crop with 100 – 150g/ha sodium molybdate or seed dressing of 15g of sodium molybdate per 50kg of seed (Munyaradzi, 2002). This amount is comparable to the minimum boron requirement of 3mg per maize plant for fertilisation and grain set (Vaughan, 1977). Seed produced from boron deficiency plants is of low germination rate and produce a high percentage of abnormal seedlings. According to Vaughan (1977) drought causes boron deficiency through immobilization in leaves apart from making applied boron fertilizer unavailable.

2.4.4 Adaptation and photoperiodic response

The response of maize to various environmental conditions depends on whether maize is photosensitive or not. When cultivars adapted to cool highlands of Mexico were grown in hot lowland tropical environments, ASI increased from 1.9 to 7.3 d and grain yield (GY) fell from 6 to less than 1Mg ha⁻¹. Conversely, when a lowland tropical population

CHAPTER 3

3.0 MATERIALS AND METHODS

Five field experiments were conducted at four locations. Four experiments were conducted under rainfed conditions and one experiment irrigated, in the dry season. Three experiments were conducted under optimal nitrogen conditions and one under sub-optimal nitrogen conditions. The irrigated experiment was conducted under optimal nitrogen conditions in addition to inducing water stress during flowering.

3.1 TRIAL LOCATIONS

The rainfed experiments were conducted at Mount Makulu, 1463 meters above sea level (masl), Magoye at 1022masl and Golden Valley Agricultural Research Trust (GART) at 1189masl in Chisamba during the 2005/2006 rain season in Zambia. The irrigated trial was done at Nanga Irrigation Research Station (NIRS) at 980masl located in Mazabuka district. The locations used represented three zones of the SADC Maize Mega Environments and two agro-ecological zones of Zambia. The general climatic conditions of the locations are presented in Table 1.

Table 1: Description of the SADC Maize Mega-Environments

Zone	Environment	Location	Description of environment		
			Av. max. Temp. °C	Risk of drought	Seasonal rainfall
A	Mid- Altitude Humid Warm	Golden Valley	24 - 27	Low	>700 mm
B	Mid- Altitude Humid Hot	Mount Makulu	27 - 30	Low	>700 mm
E	Low land Tropical Dry	Nanga and Magoye	>30	High	<700 mm

Source: Vivek et al., 2005

3.2 MAIZE GENOTYPES USED IN THE STUDY

Nine female single crosses and nine male inbred lines from CIMMYT – Zimbabwe were used in this study. One hybrid from the Zambia National Research Programme and two hybrids from Zambia Seed Company Limited were also included as checks. The pedigrees and line codes of the materials used in the study are presented in Table 2.

Table 2: Plant population, treatment and inter row spacing used at each site

Location	Acronym	Management	Date planted	Row spacing	Row length (m)	Plant population
Golden Valley - optimal nitrogen	GVOPT	Optimal Nitrogen and low plant population	19 th Dec. 2005	90 cm	5	44, 444
Golden Valley - low nitrogen	GVLN	Low Nitrogen and high plant population	24 th Dec. 2005	75 cm	5	53, 333
Mount Makulu	MAKOPT	Optimal Nitrogen and high plant population	27 th Dec. 2005	75 cm	4	53, 333
Nanga	NANG	Optimal Nitrogen, high population and managed water stress	27 th July 2006	75 cm	4	53, 333

Round up (5L/ha) was applied prior to the day of planting, to control couch grass. The field experiment was further kept weed and pest free by hand weeding and spraying the field with appropriate insecticides.

(b) *Mount Makulu*

Phorate, a systematic insecticide, was applied at a rate of 2kg/ha in the planting hole to control soil pests together with compound D (200kg/ha). Three seeds were sown in a planting hole and later thinned to two plants after emergence. Topdressing was done at 4weeks of age using urea (46%N) at a rate of 200kg/ha.

Weeds were controlled by applying a herbicide, Blazine at a rate of 3L/ha before maize and weeds had germinated. Hand weeding was done to control the weeds that had emerging later. Monocrotophos and Confidor were used to control stalkborer and termites respectively.

(c) *Nanga*

The field used for maize was previously under vegetables during the rain season. The field was kept weed free by hand weeding and stalkborer free by spraying with monocrotophos.

During the growing season, irrigation water was for 3 weeks during the period bracketing flowering.

3.4 DATA COLLECTION

In all the trials, most of the plant characteristics were collected on an average of 5 randomly selected plants per plot, unless stated.

3.3.1 Plant Height (PH):

Plant height was measured as the length of maize from the ground surface up to the flag leaf tip obtained at grain filling.

Table 3: Description of materials used in the trials.

Hybrid name	Maturity	Sex	Stock ID	Pedigree	Origin	Source
	Early	F	A 656-1	CML312/CML442	HA01A-1153-1/2	CIMMYT-Zimbabwe
HY1	Early	M	V 269-78	ZEWAc1F2-277-2-3-B-1-B	MZ03B-2205-97	CIMMYT-Zimbabwe
	Early	F	A 656-1	CML312/CML442	HA01A-1153-1/2	CIMMYT-Zimbabwe
HY2	Early	M	V 269-167	ZM303c1-103-2-B-1-3-B	MZ03B-2205-270	CIMMYT-Zimbabwe
	Early	F	A 656-1	CML312/CML442	HA01A-1153-1/2	CIMMYT-Zimbabwe
HY3	Early	M	V 269-59	ZEWAc1F2-312-7-1-B-1-B	MZ03B-2205-73	CIMMYT-Zimbabwe
	Intermediate	F	J20-7	CML395/CML444	HA01A-1153-3/4	CIMMYT-Zimbabwe
HY4	Intermediate	M	V 237-9	Ent52:92SEW1-2/[DMRESR-W]EarlySel-#L-2-1-B/CML386]-B-22-1-B-4-#-1.B	HA03A-2116-9	CIMMYT-Zimbabwe
	Intermediate	F	A1120-12	CML445/CML395	HA04A-1150-25/26	CIMMYT-Zimbabwe
HY5	Intermediate	M	A281-13	CML440	HA99A-1153-13	CIMMYT-Zimbabwe
	Intermediate	F	J20-7	CML395/CML445	HA01A-1153-3/4	CIMMYT-Zimbabwe
HY6	Intermediate	M	A1154-140	CML443	HA04A-162-65	CIMMYT-Zimbabwe
	Late	F	A1232-18	CML444/CML395	MZ04B-1250-35/36	CIMMYT-Zimbabwe
HY7	Late	M	J26-3143	CML312	HA02A-130-311	CIMMYT-Zimbabwe
	Late	F	J20-7	CML395/CML445	HA01A-1153-3/4	CIMMYT-Zimbabwe
HY8	Late	M	A992-33	ZM621A-10-1-1-1-2-BBBBB (EV7992#[EVPOP43-SRBC3]#b#bst-118//CML444)-B-1-1-3-5-BBBB/CML197	MZ03B-1217-19-B1	CIMMYT-Zimbabwe
	Late	F	A1232-1	CML448	MZ04B-1250-1/2	CIMMYT-Zimbabwe
HY9	Late	M	A557-25	CML448	MZ00B-1219-15-B2	CIMMYT-Zimbabwe
GV 412	Early	F	N/A	COMMERCIAL HYBRID	N/A	ZARI - Zambia
GV 659	Intermediate	F	N/A	COMMERCIAL HYBRID	N/A	ZARI - Zambia
ZMS 737	Late	F	N/A	COMMERCIAL HYBRID	N/A	ZAMSEED - Zambia

3.3.2 Ear Height (EH):

Ear height was measured as height between base of plant to the insertion of the top ear of the same plant.

3.3.3 One hundred seed weight (100SWT):

One hundred seed weight was determined as the weight of 100 seeds corrected to moisture content of 12.0%.

3.3.4 Shelling percentage (Shell):

Shelling percentage was calculated based on 10cob samples that were randomly selected, including the second cobs in case of prolific hybrids. A cob having one pip (grain) was considered as a full cob. The shelling percentage was calculated as a ratio of shelled grains to unshelled cobs of the sample.

3.3.5 Yield (yld):

Grain yield (kg/ha) was calculated from plot yield corrected for plant population and moisture content of 12.0%.

3.3.6 Pollen shedding characteristics:

The time to beginning of pollen shedding (beg shed), maximum shedding (max shed) and end of pollenshed (end shed) was observed following the procedures described by Westgate *et al* (2003). On a daily basis, the number of plants at each stage of anthesis were recorded. The data were later used to calculate the proportion of plants at each stage on a daily basis.

3.3.7 Tassel characteristics:

The number of tassel branches (TB) and the average length of all tassel branches (TL) were measured on males only. Both TB and TL were used as proxy to quantify the amount of pollen produced by the males. It was assumed that anthers on the tassel were evenly distributed.

3.3.8 Silking dynamics:

Silking dynamics were determined as the proportion of the number of plants that have silked in a plot to the total number of plants in a day. This involved counting female plants that had silks exposed on a daily basis.

3.3.9 Ears per plant (EPP):

Number of ears per plant at harvest were measured as number of ears with minimum of one fully developed grain divided by number of plants.

3.3.10 Biparental - Anthesis Silking Interval (BIPASI) and Desynchronisation (Des):

BIPASI was determined as the difference in days when 50% of the females have their silks exposed and when 50% of the males are shedding pollen. BIPASI differs from anthesis-silking interval (ASI) in that BIPASI is calculated between two parents, one designed as a male and another as a female, while ASI is on the same plant.

Desynchronisation was determined as the difference in days between 1st date of silking and 1st date of anthesis.

3.3.11 Tasselling and silking interval (TSI):

This was calculated as the interval, in days, between the tasselling of the male plant and the silking of the female plants. 1TSI and 50TSI refers to the interval between the first plants in a plot to flower and when 50% of the plants in a plot have flowered, respectively.

3.3.12 Number of kernels per plant (KPP):

This was calculated by multiplying the number of kernels per ear by EPP. The number of kernels per ear were calculated as:

$$\text{Kernels per ear} = \frac{(100 * \text{FSGW} * \text{NEH})}{\text{FHSW}}$$

Where: FSGW = fresh shelled grain weight (gm)

FHSW = fresh hundred seed weight (gm)

NEH = number of ears harvested

3.3.13 Ear Leaf Area (ELFA):

This was calculated by multiplying the length and width of the leaf located at the node of the apical ear. The area was multiplied by a factor of 0.75 to get the leaf area.

3.4 ESTIMATION OF FLOWERING AND OTHER PARAMETERS

From the data collected, the following parameters were calculated:

3.4.1 Pollenshed period:

(a) **Sheddays:** Is the number of pollen days the average plant in the population sheds pollen. The calculation assumes all plants in the population shed a similar number of pollen grains and that pollen shed per plant were uniform for all sheddays. The formula described by Westgate et al. (2003) was used with slight modifications. The equation is shown below:

$$\text{Sheddays} = 50\% \text{ Endshed} - \frac{(50\% \text{ begshed} + 50\% \text{ maxshed})}{2}$$

Where: 50% endshed = time, in days, when 50% of the plants in a plot are at the end of pollen shedding.

50% maxshed = time, in days, when 50% of the plants in a plot are at maximum pollen shedding.

50% begshed = time, in days, when 50% of the plants in a plot are just beginning shedding pollen.

(b) **Duration of Anthesis (AnthDura):** this is the duration of the period of pollen shedding, determined as the difference between the day when the first plant stops shedding pollen or end shed and when the first plant starts shedding pollen or beg-shed (Struik et al., 1986).

(c) **Anthesis spread (AnthSprd) or anthesis interval (AI):** The difference, in days, between the first male plant starts to shed pollen and the last male plant stops to shed pollen in a plot.

3.4.2 Silking spread:

Silking spread was determined as the differences, in days, between the first female plant to silk and the female last plant to silk the plants in a plot. Silking spread was used as an indicator of interplant variation that may be due to stress or genetic differences.

3.5 STATISTICAL ANALYSIS

3.5.1 Analysis of Variance:

Statistical analysis was carried out according to established procedures (Petersen, 1994). Each trial per environment was analysed as a randomised complete block design. Prior to combining data, error variances were tested for homogeneity, using the ratio of the largest and smallest variance in the set (Petersen, 1994). Response variates with heterogeneous variances were analysed as split – plot design, while those with homogenous variances were analysed following the standard procedure of multi-location trial data analysis. In the split-plot analysis, environments were considered as main-plots and parental combinations (genotypes) as sub plots.

In the analysis of variance, IRRISTAT 4.0 for Windows, a statistical package developed by the Biometrics and Bioinformatics Unit of the International Rice Research Institute (IRRI, 2003) was used. Test of significance for entries and interaction were determined by using appropriate mean squares, following the procedures of Petersen (1994).

3.5.2 Multiple linear regression and correlation analyses:

A simple linear correlation analysis of number of kernels per plant on synchronisation parameters and yield components was calculated for each environment and then across all environments. This was followed by a forward stepwise multiple regression analysis, using IRRISTAT 4.0 for Windows (IRRI, 2003).

3.5.3 Yield stability:

The yielding ability of the seed parents or females across environments was assessed on grain yield only. The stability on number of seeds per cob could not be done because of the non-significant genotype by environment interaction. The Eberhart and Russell (1966) method was used in studying the yield stability of the seed parents.

CHAPTER 4

4.0 RESULTS

4.1 GENERAL

The growing conditions, in terms of weather, under which the trials were done was generally good. The male parent for hybrid 7 had low vigour; resulting in poor field emergence of the variety in all the trials. Therefore, the parents involving the hybrid were discarded in the analysis.

In the drought trial, water stress could not be managed properly due to leakages in the irrigation pipes, which affected certain portions of the trial. Water leakage had occurred in the second week of water stress period.

At Golden Valley under optimal nitrogen, stalk borers and armoured crickets were observed. Crickets mostly attacked anthers and silk, to a less extent, in some plants. Stalkborers were effectively controlled by using insecticides while the control of crickets were not effective.

4.2 SINGLE SITE ANALYSIS:

Appendix 1 shows the significance of each trait at each environment. The homogeneity of variances differed depending on the trait. Variances were homogeneous for most traits (Table 4) and hence were analysed as described above.

4.2.1 FLOWERING PARAMETERS:

Significant differences ($p=0.05$) between parental lines were observed for synchronisation traits, that is 1TSI, Des and BIPASI. The differences in many traits were observed at Mount Makulu followed by Nanga, while at Golden Valley low nitrogen and Golden Valley Optimal nitrogen, there were no differences (Table 4).

Table 4: Main effects of environment on flowering traits and homogeneity of variances

	Trait	ENVIRONMENT				Homogeneity of variances
		MAKOPT	GVLN	GVOPT	NANG	
1	1TSI	NS	*	NS	**	Heterogeneous
2	50TSI	*	*	NS	NS	Heterogeneous
3	Des	**	**	NS	NS	Homogeneous
4	BIPASI	**	NS	NS	*	Homogeneous
5	TL	**	NS	NS	*	Homogeneous
6	TB	**	NS	**	**	Homogeneous
7	AnthSprd	NS	NS	NS	NS	Homogeneous
8	SilkSprd	NS	NS	NS	NS	Homogeneous
9	AnthDura	NS	NS	NS	NS	Heterogeneous
10	Sheddays	NS	NS	NS	NS	Heterogeneous
11	50SILK	*	NS	*	NS	Heterogeneous
12	50ANTH	**	NS	*	*	Homogeneous

1TSI and 50TSI = tasselling silking interval; Des = Desynchronisation; BIPASI = Biparental anthesis silking interval; 50SILK = 50% silking; 50ANTH = 50% anthesis; TL = tassel length; TB = number of tassel branches; AnthSprd = anthesis spread or anthesis interval; SilkSprd = silking spread and AnthDura = duration of anthesis.

* = significant at 1%, ** = significant at 5% and NS = not significant.

4.2.1.1 Anthesis date: The onset of anthesis and silking are shown in Table 5. The time to 50% anthesis was stable across environments. The longest male took 86 days to shed pollen at Nanga followed by 75 days at Mount Makulu, then by 69 days at both Golden Valley Optimal and Golden Valley Low Nitrogen. The differences between the maximum and minimum were 7.3days at Mount Makulu, 9.4 at Golden Valley Optimal, 4.9 days at Golden Valley Low Nitrogen and 10.0 days at Nanga. The variation in time to pollen shed between males was high under water stress and lowest under nitrogen stress. The effect of water stress and low plant population were the same (10 days Vs 9.4 days).

4.2.1.2 Silking date: The time to 50% silking was generally longer at Nanga (85.8days), Golden Valley Low Nitrogen (71.2 days), Mount Makulu (70.0 days) and Golden Valley Optimal (65.0 days) in that order (Table 5). The differences in days

between the early silking and late silking female plants were lowest at Nanga, 3 days and highest at Mount Makulu, 10 days. Golden Valley Low Nitrogen and Golden Valley Optimal had differences of 6 and 5 days respectively. Females for hybrids 1, 2, 3 and 4 varied greatly in time to onset of silking compared to their counterpart males for onset of anthesis. Parents for hybrids 5 to 9, responded similarly resulting in the same range across environments. The differences ranged from 0 to 3 days.

Table 5: Onset of silking and anthesis

(a) 50% Anthesis					(b) 50% silking			
HYB	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	62.0	62.3	65.0	77.0	64.3	66.0	69.7	85.3
2	66.7	61.7	65.7	77.0	70.0	64.3	69.0	86.0
3	63.0	61.7	65.3	76.3	69.0	65.3	69.7	85.0
4	66.0	62.0	64.3	81.3	71.0	65.3	69.7	86.3
5	67.7	59.3	65.3	82.7	67.3	62.3	70.7	84.7
6	74.7	62.0	67.7	86.3	72.7	64.3	71.3	84.7
8	71.3	68.7	69.2	84.7	71.7	65.3	74.0	86.3
9	69.3	62.7	65.3	84.3	74.0	67.0	75.3	87.7
MEAN	67.6	62.5	66.0	81.2	70.0	65.0	71.2	85.8
5%LSD	5.60	4.84	5.16	6.20	3.29	2.40	5.90	2.91

4.2.1.3 Biparental Anthesis-Silking Interval (BIPASI): The biparental anthesis – silking interval though being generally high at Golden Valley Low Nitrogen and Nanga, the range was highest at Nanga (10.7 days) followed by Golden Valley Optimal (7.6 days). Despite Mount Makulu and GOLDEN Valley Low Nitrogen on average having different BIPASI (-2.4 days vs -5.1 days), the range at Golden Valley Low Nitrogen (6.7 days) was bigger than that at Mount Makulu (6.3days). Yet the differences between hybrids were highly significant ($p < 0.01$) at Mount Makulu (Table 11). On average, Mount Makulu and Golden Valley Optimal had the same BIPASI (2.4 vs 2.5) while Nanga and Golden Valley Low Nitrogen had almost the same BIPASI (4.5 vs 5.1) with significant differences between hybrids observed at Nanga. Hybrid 9 had extreme BIPASI of 10 days at Golden Valley Low Nitrogen. All hybrids at Golden Valley Optimal and most hybrids at Mount Makulu had BIPASI within acceptable limits, ± 4 days. In cross pollination studies done by Ma et al. (2004), it was found that, high cross-pollination was possible if pollen shed

started not earlier than five days or later than 3 days relative to silk emergence of the receptor field. This revelation can be used to determine synchronisation for high seed set.

4.2.1.4 Desynchronisation (Des): The interval between the onset of silking and pollen-shed was low for most hybrid-inbred pair (Table 6). At Golden Valley Optimal, most pairs had desynchronisation of 3 days. Most parents had maintained their protandry or protogyny behaviour across all the environments, except for parents for hybrids 5 and 6. On average, desynchronisation higher under stress conditions, with water stress having the highest (Table 6).

Table 6: Synchronisation parameters

(a) BIPASI					(b) Desynchronisation			
HYB	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	-2.3	-3.7	-4.7	-8.3	0.3	2.3	2.7	6.3
2	-3.3	-2.7	-3.3	-9.0	0.7	2.7	0.7	7.0
3	-6.0	-3.7	-4.3	-8.7	5.0	2.0	2.0	7.3
4	-5.0	-3.3	-5.3	-5.0	3.7	2.7	1.7	2.3
5	0.3	-3.0	-5.3	-2.0	-1.7	0.7	2.0	0.7
6	2.0	-2.3	-3.7	1.7	-5.7	0.7	1.0	-3.0
8	-0.3	3.3	-4.5	-1.7	-2.0	-3.0	-2.0	-0.3
9	-4.7	-4.3	-10.0	-3.3	3.7	4.3	7.7	2.7
MEAN	-2.4	-2.5	-5.1	-4.5	0.5	1.5	2.0	2.9
5%LSD	3.80	4.60	4.81	6.64	4.84	4.77	4.10	7.22

4.2.1.5 Tasselling Silking Interval (TSI): The interval between 1st plant and 50% plants tasselling and silking was almost similar for both varieties (Table 7). Generally, the interval was reduced under water stress followed by low N for both 1TSI and 50TSI. The interval between parents for hybrid 8 was low across environments, being between 0 and 3days. Parents for hybrid 1 and 9 had large intervals (Table 7). Most hybrids exhibited stable 1TSI than 50TSI intervals.

Table 7: Tasselling silking interval

(a) 1TSI					(b) 50%TSI			
HYB	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	-6.3	-11.3	-6.7	-2.0	-7.7	-11.7	-8.3	-1.3
2	-6.7	-7.3	-4.7	-2.7	-9.3	-7.7	-7.3	-2.3
3	-7.7	-6.7	-4.7	-2.7	-8.7	-8.3	-6.7	-2.3
4	-5.3	-6.0	-4.0	-1.7	-6.7	-7.0	-7.3	-1.3
5	-3.0	-3.3	-4.0	-2.7	-3.0	-4.0	-6.7	-2.3
6	-3.0	-8.3	-6.7	-2.3	-6.7	-9.3	-9.7	-1.3
8	-1.7	0.3	0.3	-3.0	-3.7	-0.3	-3.4	-3.0
9	-8.0	-8.0	-9.3	-5.3	-8.3	-8.0	-11.7	-4.0
MEAN	-5.2	-6.3	-5.0	-2.8	-6.8	-7.0	-7.6	-2.2
5%LSD	4.74	7.74	4.83	1.65	3.87	7.30	4.15	1.81

4.2.1.6 Anthesis Duration (AnthDur): On average, the lowest duration of pollen shedding was under water stress, with most males shedding pollen for 2 – 3 days. At Golden Valley Optimal, most males had a pollen shedding duration of 3 – 4 days. The performance of the males at Mount Makulu and Golden Valley Low Nitrogen was similar, 5 – 6 days of AnthDur. Therefore, under optimal N conditions, the changes in the period of pollen shedding due to population may reflect the sensitivity of the males. Otherwise, little change would be expected.

4.2.1.7 Sheddays: The pollen sheddays were used as proxy for quantity of pollen available at its maximum. This is because the calculation of this parameter is based on 50% plant population (see Chapter 3, Materials and Methods). At Nanga, most males had pollen sheddays of one day only except for males 1, 5 and 6 which had very brief sheddays (Table 8). The male for hybrid 8 had the longest sheddays of 2, under water stress. At Mount Makulu and Golden Valley Low Nitrogen males behaved similarly, with most males shedding pollen for 4 days. At Golden Valley Optimal, the sheddays were between 2 to 3 days for most males.

Table 8: Pollen shedding

HYB	(a) ANTHESIS DURATION				(b) SHEDDAYS			
	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	8.3	2.7	6.3	3.0	4.5	2.2	4.5	0.3
2	6.0	3.3	6.0	3.0	4.5	2.5	4.5	0.8
3	5.0	2.7	5.7	3.0	4.5	2.0	4.2	0.5
4	4.7	3.0	5.0	2.0	3.3	2.0	3.8	0.7
5	6.3	2.0	5.3	2.0	5.8	2.2	4.0	0.0
6	6.3	4.3	6.6	2.7	4.8	3.7	4.7	0.2
8	6.7	4.3	4.7	3.7	4.5	1.3	3.4	1.5
9	6.0	4.0	5.3	3.0	4.2	1.7	3.8	0.8
MEAN	6.2	3.3	5.6	2.8	4.5	2.2	4.1	0.6
5%LSD	4.78	1.93	2.24	1.64	2.66	2.32	1.72	1.84

4.2.1.8 Tassel Length: The same pattern of tassel length and number of tassel branches were observed at Nanga and Golden Valley Low Nitrogen (Table 9). Tassel length differences were significant at Nanga and Mount Makulu only. At Nanga the longest tassel was 172cm and shortest was 67cm, while at Mount Makulu the longest was 243cm and shortest 115cm. The number of tassel branches ranged from 7 at Golden Valley Low Nitrogen and 11 at Mount Makulu. Most males had 200cm long tassels at Mount Makulu.

4.2.1.9 Number of Tassel Branches (TB): The number of tassel branches at Mount Makulu and Golden Valley Optimal were the same, ranging between 10 and 12 branches (Table 9). Golden Valley Low Nitrogen and Nanga had lower number of tassel branches ranging from 5 to 8 branches except for a few males (Table 9). Males at Mount Makulu and Golden Valley Optimal had the highest number of branches, mostly being greater than 10 branches (Table 9).

4.2.1.10 Anthesis and Silking spread: Table 10 shows interplant variation for anthesis and silking. The interplant variation was high for most males at Mount Makulu. It took more than 10 days between the first plant to start shedding pollen and the last plant to shed pollen. At Golden Valley Optimal, Golden Valley Low Nitrogen and Nanga the period was mostly between 6 to 9 days. At NANGA, it took 6 to 7 days to complete anthesis, which was similar to that experienced at Golden Valley Optimal, 7 to 8 days. Excluding Mount Makulu, most males had consistent

interplant variation in anthesis (Table 10), resulting in a consistent period at all the environments except at Mount Makulu, that had exceptionally long period (Table 10).

While Mount Makulu had the longest interplant variation for anthesis, it was second to Golden Valley Low Nitrogen for inter – plant variation in silking (Table 10). Females mostly took 10 to 11 days to complete silking at Golden Valley Low Nitrogen, 8 to 9 days at Mount Makulu, 6 to 7 days at Nanga and 5 to 6 days at Golden Valley Optimal. The consistency in silking was observed for other environments when Golden Valley Low Nitrogen is excluded.

Table 9: Tassel Index

HYB	(a) Tassel Length in cm (TL)				(b) Tassel branches (TB)			
	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	281.3	143.7	114.7	122.6	14.9	12.0	8.0	6.1
2	207.7	151.0	93.7	138.6	10.6	10.0	6.7	8.6
3	214.1	125.0	104.0	142.1	13.1	10.7	8.0	8.4
4	243.5	142.7	129.3	171.7	11.1	11.7	7.0	8.3
5	212.5	134.7	109.0	127.0	13.5	11.3	8.7	8.2
6	153.5	126.3	123.0	87.2	9.2	10.3	9.7	6.0
8	115.1	95.0	65.7	67.2	5.3	6.0	5.3	3.4
9	182.4	145.7	80.3	84.3	10.5	12.7	6.7	5.0
MEAN	201.3	133.0	102.5	117.6	11.0	10.6	7.5	6.7
5%LSD	50.98	34.45	50.56	55.77	3.12	3.02	3.69	2.46

4.2.2 YIELD AND YIELD COMPONENTS:

Significant differences ($p = 0.05$) between parental lines were observed for some selected yield and yield components (Table 11). Significant differences were observed at Golden Valley Optimal and Nanga in most traits. Variances were heterogeneous for most traits (Table 11) and hence were analysed as a split plot design as described in Chapter 3, Materials and Methods.

Table 10: Pollen shedding and silking dynamics

(a) ANTHSPRD					(b) SILKSPRD			
HYB	MAKOPT	GVOPT	GVLN	NANG	MAKOPT	GVOPT	GVLN	NANG
1	12.3	7.3	10.3	6.7	8.7	5.7	11.0	5.7
2	11.3	7.0	9.3	7.0	8.3	6.0	8.3	5.7
3	10.3	7.0	8.7	6.7	9.0	6.3	9.7	6.0
4	10.7	7.3	7.3	5.7	8.3	5.3	10.0	7.0
5	11.3	6.3	9.0	5.7	8.7	7.7	10.3	7.7
6	8.7	7.7	9.0	6.3	9.0	5.3	10.7	5.7
8	9.7	8.0	7.6	7.3	9.0	5.3	12.3	6.0
9	10.0	8.7	7.7	7.0	7.7	5.0	10.7	5.0
MEAN	10.5	7.4	8.6	6.5	8.6	5.8	10.4	6.1
5%LSD	5.16	2.38	3.07	1.73	2.28	2.08	4.93	2.12

4.2.2.1 Plant stand: On average, plant stand at harvesting was similar for Mount Makulu and Golden Valley Optimal at 38.3; while for Golden Valley Low Nitrogen and Nanga were 32 and 31 respectively (Table 12). The target plant count at harvesting was set at 10% of the maximum plant population. Most environments had more than 50% plant count of the target except for a few environments at Mount Makulu, Golden Valley Low Nitrogen and Nanga. The highest hybrid had a plant stand of 48 at Mount Makulu, 42 at Golden Valley Optimal, 410 at Golden Valley Low Nitrogen and 46 at NANGA. The difference between the highest and lowest were similar at Mount Makulu and Nanga; 25.0 vs 24.7 respectively, Golden Valley Low Nitrogen at 16.7 and the lowest was at Golden Valley Optimal being 10.6.

4.2.2.2 Grain yield (GY): Higher yield of 8.3 tons/ha and 8.4 tons/ha were obtained at Mount Makulu and Golden Valley Optimal on average. Golden Valley Low Nitrogen and Nanga had yields of 5.0tons/ha and 3.1 tons/ha respectively. However, the differences between hybrids at each environment were not significant (Table 11 and 13). The high LSD value observed at Nanga under water stress was expected as the response of the genotypes varied, depending on time to flowering (Table 3). The parents that had flowered later had a high stress intensity during grain filling than those that flowered earlier (Plate 1).

Table 11: Main effects of environments on agronomic traits and homogeneity of variances

Trait	ENVIRONMENT				Homogeneity of variances
	MAKOPT	GVLN	GVOPT	NANG	
1 Plant stand	NS	NS	**	NS	Homogeneous
2 Grain yield	NS	NS	NS	NS	Homogeneous
3 Grains/plant	NS	NS	*	**	Homogeneous
4 Shell	NS	*	**	**	Heterogeneous
5 100SWT	NS	NS	NS	NS	Heterogeneous
6 EPP	NS	NS	NS	NS	Homogeneous
7 PH	*	NS	**	*	Heterogeneous
8 EH	*	NS	**	NS	Heterogeneous
9 ELFA	NS	NS	NS	NS	Heterogeneous

Grns/plt = number of grains per plant; 100SWT = seed weight of one hundred kernels; PH = plant height; EH = ear height; EPP = ears per plant; ELFA = ear leaf area; Shell = shelling percentage; plant stand = number of seed parents at harvesting.

* = significant at 1%, ** = significant at 5% and NS = not significant.

Table 12: Plant stand at harvesting

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	28.3	36.0	29.0	21.3	28.7
2	22.7	33.7	26.7	23.0	26.5
3	33.0	31.7	23.0	21.3	27.3
4	47.7	39.0	30.0	46.0	40.7
5	38.7	40.0	36.7	43.3	39.7
6	45.3	42.3	31.0	35.7	38.6
8	44.3	42.3	38.0	39.0	40.9
9	46.7	41.3	39.7	20.7	37.1
MEAN	38.3	38.3	31.8	31.3	34.9
5%LSD	9.80	13.98	18.85	20.87	8.35

4.2.2.3 Number of grains per plant: Table 14 shows number of grains per plant. Grains per plant were high at Golden Valley Optimal, ranging from 459 to 630; followed by Mount Makulu ranging from 342 to 596. Golden Valley Low Nitrogen and Nanga had lower grain yield per plant, with most seed parents being higher at Nanga. The lowest number was obtained for hybrid 9 at both Golden Valley Low Nitrogen and Nanga, having 19.8 and 98.4 respectively. However, the differences

between hybrids were only significant at Golden Valley Low Nitrogen and Golden Valley Optimal (Table 11).

Table 13: Grain yield (kg/ha) of seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	8544.5	8131.5	5692.8	4405.3	6693.3
2	9537.8	9537.8	3927.2	3150.0	6538.2
3	7647.4	7647.4	5636.6	3989.9	6230.3
4	8700.0	8700.0	5197.3	1608.8	6052.4
5	8816.8	8816.8	4806.0	3155.6	6398.8
6	8555.7	8555.7	5952.2	4014.0	6769.4
8	7773.1	7773.1	5475.3	2768.6	5947.5
9	7231.6	7231.6	3084.0	1693.9	4817.3
MEAN	8350.9	8299.2	4971.4	3098.2	6180.9
5%LSD	1748.04	1730.62	2173.86	3230.00	1083.48

Table 14: Number of grains per plant

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	474.7	167.2	487.2	246.6	343.8
2	596.3	144.1	556.1	178.6	368.8
3	481.7	199.2	508.3	259.2	362.1
4	393.2	72.0	499.4	261.1	306.5
5	443.3	144.3	629.8	288.9	376.6
6	387.6	273.6	485.5	322.0	367.2
8	400.0	142.7	496.5	287.5	331.7
9	342.3	19.8	458.7	98.4	229.8
MEAN	439.9	145.3	515.2	242.8	335.8
5%LSD	124.84	238.20	248.78	101.37	87.46

4.2.2.4 Shelling percent: Table 15 shows the shelling percentage at each environment. At Mount Makulu, the highest shelling % was obtained in female 5, 83% and lowest in female 9, 76%. At Golden Valley Optimal the highest were females 2, 3 and 5 with 84% and the lowest being female 9 with 81%. Golden Valley Low Nitrogen and Nanga had the highest variation with Nanga having a range of 84% for female 1 and 59% for female 9 while Golden Valley Low Nitrogen had a shelling percentage of 83% for female 5 and 73% for female 9. On average, most females had shelling percentages greater than 75%.

Table 15: Shelling percentage

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	81.3	83.4	81.0	83.7	82.3
2	82.2	83.6	78.0	71.8	78.9
3	81.3	83.6	78.9	80.9	81.2
4	78.9	82.9	78.7	79.2	79.9
5	82.7	83.7	82.8	80.7	82.5
6	78.8	82.5	81.8	81.4	81.1
8	79.4	81.6	79.7	75.8	79.1
9	75.9	81.4	72.9	59.2	72.4
MEAN	80.1	82.8	79.2	76.6	79.7
5%LSD	2.50	2.12	5.42	11.90	5.10

4.2.2.5 One hundred seed weight (100SWT): Generally, grains at Golden Valley Optimal were heavier ranging from 43.9 to 32.4 grammes for 100seeds. The weight for seeds at Golden Valley Low Nitrogen and Nanga was the same being 31.8 and 31.7 respectively (Table 16). Despite the weight of grains between Golden Valley Low Nitrogen and Nanga being the same, the difference between the heaviest and lightest seed parents at each environment was higher at Golden Valley Low Nitrogen. Grain weight differences of 8.6 and 7.5 were obtained at Nanga and Mount Makulu respectively. At each environment the differences between hybrids were not significant (Table 11).

Table 16: 100 seed weight (g) for seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	28.9	35.0	46.3	35.2	36.3
2	29.3	43.0	32.1	31.9	34.1
3	26.8	32.4	30.9	33.2	30.8
4	31.4	36.5	34.7	30.6	33.3
5	34.3	34.5	29.1	27.2	31.3
6	29.5	43.9	27.5	29.5	32.6
8	29.6	39.1	28.0	30.3	31.8
9	30.2	39.3	26.9	35.8	33.0
MEAN	30.0	38.0	31.9	31.7	32.9
5%LSD	4.38	12.41	23.71	8.69	6.46

4.2.2.6 Ears per plant (EPP): Prolificacy was high at Mount Makulu and Golden Valley Optimal (Table 17). Under low N conditions at Golden Valley Low Nitrogen most seed parents were barren, having $EPP < 0.80$ except for seed parents for hybrid 6.

Table 17: EPP for seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	0.97	0.97	0.72	0.81	0.87
2	1.08	1.10	0.73	0.73	0.91
3	1.08	0.95	0.75	0.81	0.90
4	1.02	0.93	0.84	0.82	0.90
5	0.99	1.06	0.68	0.88	0.90
6	0.94	1.09	0.96	0.86	0.96
8	0.99	1.06	0.75	0.86	0.91
9	1.02	1.05	0.58	0.63	0.82
MEAN	1.01	1.03	0.75	0.80	0.90
5%LSD	0.20	0.23	0.35	0.22	0.12

4.2.2.7 Plant Height (PH): Plants were taller at Golden Valley Optimal and Mount Makulu, being in the range of 255 to 176cm; giving an average of 200cm. At Golden Valley Low Nitrogen and Nanga plants were generally shorter, ranging from 135 to 178cm. Table 19 shows plant height at different environments. The differences between hybrids were significant at all the environments except at Golden Valley Low Nitrogen (Table 11).

Table 18: Plant height (cm) of seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	191.5	196.3	150.7	150.9	172.4
2	190.1	216.0	137.0	135.6	169.7
3	193.5	175.7	135.3	142.5	161.8
4	226.3	226.3	155.0	169.3	194.2
5	204.9	205.7	135.3	143.9	172.4
6	233.9	255.3	145.7	178.0	203.2
8	229.3	253.0	149.7	169.4	200.4
9	219.2	205.3	145.7	144.5	178.7
MEAN	211.1	216.7	144.3	154.3	181.6
5%LSD	10.98	46.58	26.57	26.31	28.36

4.2.2.8 Ear Height (EH): Ear height ranged from 158cm for female 6 at Golden Valley Optimal to 25cm at Nanga for female 5. Ear placement was higher at Golden Valley Optimal averaging 125cm and then followed by Mount Makulu averaging 119cm (Table 19). At Nanga, ear placement was below half a meter while at Golden Valley Low Nitrogen, were below one meter but above 50cm for all the seed parents (Table 19).

Table 19: Ear placement (cm) of seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	91.1	101.3	79.3	28.1	75.0
2	91.4	130.0	62.0	27.3	77.7
3	102.0	90.7	63.0	26.5	70.6
4	137.6	134.0	79.3	27.3	94.6
5	106.3	102.0	70.7	25.1	76.0
6	139.5	158.3	77.3	28.5	100.9
8	139.3	154.3	81.0	26.6	100.3
9	141.7	125.7	82.0	27.0	94.1
MEAN	118.6	124.5	74.3	27.1	86.1
5%LSD	12.56	45.33	20.95	2.48	20.57

4.2.2.9 Ear Leaf Area (ELFA): Table 20 shows the area of the leaf covering the primary ear. Seed parents at Mount Makulu had the largest leaf area followed by Golden Valley Optimal, Nanga and Golden Valley Low Nitrogen in that order. However, the range between the highest and lowest were narrow at Mount Makulu (800 – 900cm²) being similar to that at Golden Valley Low Nitrogen (300 – 400cm²). The differences in leaf area between the highest and lowest at Golden Valley Optimal and Nanga were the same being 200cm² (Table 20). Across all the environments, the lowest ear leaf area was obtained at Golden Valley Low Nitrogen; 244cm² for female 3 and the highest, 912cm² for female 6. However, differences between hybrids were not significant at all the test environments (Table 11).

Table 20: Ear leaf area (cm²) for seed parents

HYB	Environment				Across environments
	MAKOPT	GVOPT	GVLN	NANG	
1	802.6	526.1	385.1	770.0	621.0
2	791.1	564.0	392.6	627.7	593.9
3	832.3	526.1	244.0	619.2	555.4
4	894.8	637.0	394.0	746.0	667.9
5	845.3	556.6	261.4	706.7	592.5
6	911.5	739.8	406.2	850.2	726.9
8	865.1	741.8	332.3	743.0	670.6
9	905.7	590.5	433.7	605.6	633.9
MEAN	856.0	610.2	356.2	708.6	632.7
5%LSD	91.18	293.14	252.17	270.51	86.02

4.3 COMBINED ANALYSIS OF VARIANCE:

4.3.1 FLOWERING DYNAMICS:

The combined analyses of variance for flowering traits are shown in Table 21. The interaction between genotypes and environments were significant ($p=0.05$) for BIPASI and highly significant ($p=0.01$) for TB and TL. Environmental effects were highly significant ($p=0.01$) for most traits except for 1TSI. Non-significant ($p<0.05$) environmental effects for desynchronisation were also observed. The main effects of genotypes were also highly significant ($p=0.01$) for most traits except for BIPASI that was significant at 5%. In addition, non-significant differences between genotypes were observed for sheddays, silk spread and anthesis spread.

4.3.1.1 Silking date: Though the genotype x environment interaction was not significant for days to 50% silking, both genotypic and environmental effects were highly significant ($p<0.01$). Averaged across all environments, the earliest female to silk took 71 days and the late one took 76 days.

4.3.1.2 Anthesis date: Both the main effects of the environment and genotype were highly significant ($p<0.01$). The earliest male to start shedding pollen was male 5 at Golden Valley Optimal taking 59 days and the latest was male 6 taking 86 days. Males took shorter time to start shedding pollen at Golden Valley Optimal (63 days) and took 81 days at Nanga (Table 6).

4.3.1.3 Biparental Anthesis-Silking Interval (BIPASI): The interaction between genotype and environment was highly significant ($p=0.01$). Averaged across all environments, BIPASI ranged from -1days to -6days. Most of the hybrids were within acceptable intervals of ± 5 days for high kernel set.

The response of BIPASI for each parental pair varied from hybrid to hybrid, both linear and non-linear responses were obtained (Figure 2).

Table 21(a): ANOVA across environment for homogeneous variances of flowering parameters

SOURCE OF VARIATION	DF	MEAN SQUARES							
		50%ANTH	DES	BIPASI	TB	TL	SILKSPRD	ANTHSPRD	
ENVIRO	3	1611.23**	23.29ns	47.62**	111.74**	45640.70**	112.26**	71.93**	
REP*ENVIRO	8	3.06	12.99	6.68	1.94	297.271	2.16	3.65	
HYB	7	82.70**	74.38**	51.25**	36.11**	9117.06**	3.02ns	2.44ns	
HYB*ENVIRO	21	15.37ns	14.20ns	16.44*	6.62**	1642.77**	1.97ns	2.43ns	
RESIDUAL	55	9.77	9.37	8.37	3.14	770.50	3.12	3.64	

** , significant at 1%, * , significant at 5%, ns = not significant

Table 21 (b): ANOVA across environment for heterogeneous variances of flowering parameters

SOURCE OF VARIATION	DF	MEAN SQUARES							
		50%SILK	ANTDUR	SHEDDAYS	1TSSI	50%TSSI			
REP	2	4.67	0.83	0.06	46.01	38.49			
HYB	7	19.76**	3.69 ^{ns}	1.43 ^{ns}	69.78**	54.19*			
Error A	14	8.24	1.42	3.53	26.78	23.65			
ENVIRO	3	2299.71**	39.23**	50.64**	67.12**	151.93**			
HYB*ENVIRO	21	3.60 ^{ns}	1.06 ^{ns}	0.80 ^{ns}	10.53 ^{ns}	12.36 ^{ns}			
RESIDUAL	48	3.57	1.04	0.77	6.65	6.95			

** , significant at 1%, * , significant at 5%, ns = not significant

4.3.1.4 Desynchronisation: despite having highly significant ($p=0.01$) genotypic effects, environmental effects and their interaction were non-significant (Table 21). Across environments, most pairs had intervals of 2 to 3 days between the onset of silking and anthesis, except in hybrid 5. In this hybrid, the interval was zero.

4.3.1.5 Tasselling Silking Interval (TSI): Both the effects of 1TSI and 50TSI were similarly, though TSI was more affected. There were significant differences observed between hybrids and the response of the genotypes to environment ($p<0.05$). However, the interaction was non significant for both 1TSI and 50TSI. Comparing the information generated, TSI would be an alternative synchronisation parameter in the absence of BIPASI and Des. The difference between the highest and lowest environments for 1TSI was 3 days while for 50TSI was 6 days.

4.3.1.6 Pollen shedding: Both the period of pollen shedding (AntDur) and pollen sheddays (Sheddays) were highly significantly ($P<0.01$) affected by environment. Differences between males were non significant for these two traits. Therefore, pollen shedding was the same for males at each environment. Table 9 shows that, pollen sheddays were long; Mount Makulu (5 days) and reducing, almost to zero, at Nanga. Similarly, the duration of anthesis was longest at Mount Makulu (6 days) and shortest at Nanga and Golden Valley Optimal (3 days).

4.3.1.7 Pollen yield parameters (TB and TL): For both TB and TL, the effects of genotype, environment and their interaction were highly significant ($p=0.01$). The differences between males in the number of tassel branches were significant ($p<0.05$) at all the environments except under low N conditions. Tassel length differences were significant under water stress conditions and optimal N with high plant population only. At Nanga the longest tassel was 172cm and shortest was 67cm, while at Mount Makulu the longest was 243cm and shortest 115cm. number of tassel branches ranged from 7 at Golden Valley Low Nitrogen and 11 at Mount Makulu.

4.3.1.8 Duration of silking or silking spread: The differences between genotypes and the interaction were not significant ($p>0.05$). However, the effects of the environment were strong being significant at 1%. The period between the first plant

to silk and the last plant to silk in a population was shortest at Golden Valley Optimal and Nanga, 6 days and longest at Golden Valley Low Nitrogen, 10 days.

4.3.2 YIELD AND YIELD COMPONENTS:

The combined analyses of variance for yield and yield components are shown in Table 23. The interaction between genotypes and environments were significant ($p=0.05$) for shelling percentage and ear height only. Environmental effects were highly significant ($p=0.01$) for all the yield and yield components. Significant ($p<0.05$) differences between hybrids were observed for all the traits except for EPP.

4.3.2.1 Grain yield

Across all the environments, the lowest yield were obtained under low nitrogen conditions (site average of 3.2 tons/ha) compared to optimal conditions (site average of 8.2 tons/ha). The yields at the two optimal sites, Golden Valley Optimal and Mount Makulu, were not significantly different from each other. The significant G x E interaction obtained on grain yield, implies that it is possible to find hybrids with specific and general adaptation. This can be seen from the changes in grain yield components, namely 100SWT, number of grains per cob, and EPP across environments (Mwansa, 2005). For example, despite the observed significant effects of environment on 100SWT and EPP (Table 22), non-significant differences between hybrids were observed at all the environments (Table 11). All these components were responsible for the grain yield stability and the observed significant G x E interaction.

4.3.2.2 Number of grains per plant

Though the interaction was non significant, the main effects, environment and genotypes, were highly significant ($p=0.01$) and significant ($p=0.05$) respectively (Table 22). Hybrid 5 had the highest number of grains per plant of 377 and entry 9 the lowest, having 230 grains.

4.3.2.3 Shelling percentage

Highly Significant ($p<0.01$) differences between varieties, environment and their interaction were obtained (Table 22). The hybrid that had the highest number of grains per plant had the highest shelling percentage of 83 and the one with the lowest number of grains per plant had the lowest shelling percentage of 72.

Table 22(a): ANOVA across environment for homogeneous variances of yield and yield components

SOURCE OF VARIATION	DF	MEAN SQUARES				
		PLTSTND	GRNYLD	GRNS/PLT	EPP	
ENVIRO	03	369.86**	1.61E+08**	703251**	0.482818**	
ENVIRO*REP	08	26.28	1.01E+06	11733	2.37E-02	
HYB	07	477.33**	4.66E+06*	28446*	1.94E-02 ^{ns}	
ENVIRO*HYB	21	96.718 ^{ns}	1.63E+06 ^{ns}	10614 ^{ns}	1.93E-02 ^{ns}	
RESIDUAL	56	88.23	1.56E+06	10960	2.13E-02	

** , significant at 1%, * , significant at 5%, ns = not significant

Table 22 (b): ANOVA across environment for heterogeneous variances of yield and yield components

SOURCE OF VARIATION	DF	MEAN SQUARES					
		SHELL%	100SWT	PH	EH	ELFA	
REP	02	14.22	224.51	448.49	564.28	32734.80	
HYB	07	115.50**	52.89**	2901.73**	1877.25**	35633.30**	
Error a	14	19.90	34.00	259.80	233.68	9736.32	
ENVIRO	03	157.77**	322.55**	33938.90**	49271.40**	1.06E+06**	
HYB*ENVIRO	21	36.85**	49.02 ^{ns}	417.56 ^{ns}	586.86*	10266.90 ^{ns}	
* RESIDUAL	46	13.76	67.32	380.72	308.39	22791.30	

** , significant at 1%, * , significant at 5%, ns = not significant

4.3.2.4 Ears per plant (EPP)

The effect of environment on prolificacy was highly significant ($p=0.01$) while the interaction and genotypic effects were non significant. Most females had an EPP = 0.90.

4.3.2.5 Plant height and ear height

Genotypic and environmental effects were significant ($P<0.01$) for PH and EH. Ear height depended on genotype as well as environment, the interaction being significant ($p<0.05$). Across all environments, the tallest plant had the highest cob placement, being similar with the shortest plant (Tables 18 and 19).

4.3.2.6 Ear Leaf Area (ELFA)

Averaged across environments, ELFA ranged between 550 – 730 cm² (Table 20). There were highly significant ($P=0.01$) differences between genotypes and environments (Table 22). Ear leaf area was low under nitrogen stress, ranging between 200 to 400cm² and the highest being obtained at MOUNT Mount Makulu, ranging from 700 to 900cm². Hybrid 1 had consistently higher ear leaf area while hybrid 3 had consistently lower leaf area.

4.4 CORRELATION ANALYSIS

To determine the traits that were closely associated with number of grains per plant at each environment and across environments, simple linear correlations were calculated. The results are shown in Table 23.

4.4.1 Correlations at Nanga

High positive significant ($p<0.05$) correlations were observed for 1TSI, 50% silking, Shelling percentage, EPP and ELFA. Significant negative correlations were also observed for 100SWT. Strong positive correlations, though not significant, were obtained for PH, plant stand, 50TSI and Silk spread (Table 23).

4.4.2 Correlations at Golden Valley Optimal

High positive significant ($p=0.05$) correlations were observed for silk spread only. Anthesis spread and 50% silking were negatively correlated to grains per plant, the correlations being highly significant ($p=0.01$). Other traits that were strongly

correlated to grains per plant were duration of anthesis and shelling percentage though non significant (Table 23)

Table 23: Simple linear correlations of 19 traits with number of grains per plant at each environment and across all environments.

TRAIT	Environment [‡]				
	NANG	GVOPT	GVLN	MAKOPT	COMBINED*
BIPASI	0.39	0.02	0.67	-0.16	0.44*
Desynchronisation (Des)	-0.46	-0.19	-0.41	0.08	-0.25
1TSI	0.75*	0.45	-0.01	-0.26	-0.22
50TSI	0.66	0.44	0.03	-0.38	-0.13
Duration of anthesis (AntDur)	-0.22	-0.55	0.71*	0.10	-0.08
Sheddays	-0.30	0.06	0.66	0.19	0.06
Anthesis spread	-0.42	-0.78**	0.63	0.57	0.19
Silk spread	0.55	0.88**	0.03	0.17	-0.38*
50% Anthesis	0.18	-0.45	0.37	-0.50	-0.41*
50% Silking	-0.78**	-0.90**	-0.35	-0.52	-0.57**
Tassel Branches	0.04	-0.08	0.70*	0.33	0.63**
Tassel length	0.04	0.05	0.39	0.36	0.51**
100 Seed Weight (100SWT)	-0.71*	-0.15	0.05	-0.26	0.23
Shelling percentage	0.88**	0.56	0.64	0.80**	0.56**
Ears per plant (EPP)	0.98**	0.32	0.72*	0.59	0.91**
Plant stand	0.62	-0.12	-0.46	-0.94**	0.29
Plant Height (PH)	0.60	-0.10	-0.21	-0.81**	0.77**
Ear Height (EH)	-0.005	-0.25	-0.24	-0.87**	0.60**
Ear Leaf Area (ELFA)	0.75*	-0.23	-0.19	-0.90**	0.50**

BIPASI = Biparental Anthesis – silking interval; 1TSI = tasselling silking interval when the first plant in a plot silks or sheds pollen; 50TSI = tasselling silking interval when 50% of the plants in a lot are tasselling or silking.

*,** = significant at 5% and 1% respectively.

‡ = based on n=8

* = based on n = 32

4.4.3 Correlations under low nitrogen: GVLN

High positive significant ($p=0.05$) correlations were observed for duration of anthesis, number of tassel branches and EPP. Non significant ($p>0.05$) high correlations for BIPASI, Anthesis spread and shelling percentage were also obtained (Table 23).

4.4.4 Correlations at Mount Makulu

High positive significant ($p=0.01$) correlations were shelling percentage only. Highly significant ($p=0.01$) negative correlations were also observed for plant stand, PH, EH and ELFA. EPP, 50% silking, 50% anthesis and anthesis spread were also strongly correlated to number of grains per plant (Table 23).

4.4.5 Correlations across all environments: Combined

The number of grains per plant were significantly ($p\leq 0.05$), negatively and strongly correlated to silk spread, 50% anthesis and 50% silking. Significant ($p\leq 0.05$) and positive correlations with BIPASI, Tassel branches, Tassel length, shelling percentage, EPP, PH, EH and ELFA were also observed.

4.5 MULTIPLE REGRESSION ANALYSIS

The ability of a maize plant to compensate for seed yield and ear number by adjusting kernel weight and shelling percentage can complicate the association between ASI and yield. Therefore, the traits that were responsible in determining seed set at each environment and across all the test environments were determined by multiple regressions and results are presented in Appendix 2. A total of 19 traits viz Plant stand, 100SWT, Des, 50%Anth, 50%Silk, AnthDur, PH, EH, ELFA, Shell, 1TSI, 50TSI, EPP, BIPASI, TB, TL, sheddays, AnthSprd and SilkSprd; were used in the analysis.

4.5.1 Mount Makulu: optimal nitrogen and high plant population

The traits that were responsible for determining grain number per plant are shown in Table 24. The traits explained 92% of the variation observed on the number of grains per plant. The coefficients were significant ($p<0.05$) for all the traits. Three of the traits in the equation are related to flowering and these are pollen sheddays, days to 50% silking and anthesis spread. The effect of sheddays were almost equal in strength to that of 50% silking (12 vs 13), though sheddays had a negative effect.

4.5.2 Golden Valley Optimal Nitrogen: optimal nitrogen and low plant population

Four traits namely, 100seed weight, shelling percentage, EPP and anthesis spread, were responsible for determining the number of grains per plant (Table 25). The traits explained 85% of the variation observed on seed set. The coefficients were



significant ($p < 0.05$) for all the traits except for anthesis spread. Majority of the traits that were responsible for moderating kernel set were yield components, viz shelling %, EPP and 100SWT (Table 25).

Table 24: Traits influencing kernel set at Mount Makulu

TERM	Coefficient	Std. Error	Probability
100SWT	-4.83	1.86	0.020
SHELL%	29.04	4.19	0.000
PLTSTND	-3.45	1.19	0.011
EPP	200.05	87.69	0.036
50%SILK	13.28	4.32	0.008
SHEDDAYS	-12.17	5.35	0.036
ANTHSPRD	7.86	3.74	0.051
Y - intercept	-2771.79	635.37	0.001
R²	= 94.4%		
Adjusted R²	= 91.7%		

4.5.3 Golden Valley Low Nitrogen: low nitrogen and high plant population

Five traits namely, plant stand, shelling percentage, EPP, 50% silking and sheddays were responsible for determining the number of grains per plant at Golden Valley Low Nitrogen (Table 26). The traits explained 83% of the variation observed on seed set. The coefficients were significant ($p < 0.05$) for all the traits except for days to 50% silking. Pollen sheddays were second after EPP in influencing kernel set, having a coefficient that is 3 times bigger than 50% silking (Table 26).

Table 25: Traits influencing kernel set at Golden Valley Optimal Nitrogen.

TERM	Coefficient	Std. Error	Probability
100SWT	-11.02	1.52	0.000
SHELL%	24.90	7.28	0.003
EPP	717.16	88.43	0.000
ANTHSPRD	-14.76	8.18	0.085
Y - intercept	-1750.70	621.23	0.011
R²	= 87.5%		
Adjusted R²	= 84.7%		

Table 26: Traits influencing kernel set at Golden Valley Low Nitrogen.

TERM	Coefficient	Std. Error	Probability
Shell%	19.15	5.27	0.005
PltStnd	-4.15	1.86	0.051
EPP	256.13	95.91	0.025
50%Silk	13.49	7.35	0.097
Sheddays	46.90	19.41	0.038
Y - intercept	-2564.90	815.95	0.012
R²	= 89.2%		
Adjusted R²	= 83.2%		

4.5.3 Nanga: optimal nitrogen, high plant population and water stress

The traits that were responsible for determining the number of grains per plant at Golden Valley Low Nitrogen were all yield components (Table 27). The traits explained 89% of the variation observed on seed set and their coefficients were significant ($p < 0.05$) for all the traits except for 100SWT. The largest contributor to kernel set was EPP.

Table 27: Traits influencing kernel set at Nanga.

TERM	Coefficient	Std. Error	Probability
100SWT	-2.02	1.18	0.099
SHELL%	3.98	0.70	0.000
EPP	358.63	54.38	0.000
ELFA	0.11	0.04	0.020
Y - intercept	-358.16	70.64	0.000
R²	= 90.7%		
Adjusted R²	= 88.7%		

4.5.5 Across all environments

Across all the test environments, the traits explained more than 77% of the variation in grains per plant. Time to silking and the heterogeneity in the silking of the females having similar influence ($b = -10$). However, the effect of time to silking was highly significant ($p < 0.01$) compared to silk spread (Table 28).

Table 28: Traits influencing kernel set across all environments.

TERM	Coefficient	Std. Error	Probability
100SWT	-3.91	1.18	0.002
SHELL%	3.62	1.95	0.065
EPP	443.00	71.46	0.000
PH	2.00	0.60	0.001
EH	-1.89	0.63	0.004
50%SILK	-10.07	2.30	0.000
SILKSPRD	-9.51	4.81	0.049
Y - intercept	400.20	299.65	0.182
R²	= 79.2%		
Adjusted R²	= 77.3%		

4.6 SEED YIELD POTENTIAL OF SEED PARENTS

The response of seed parents to environmental conditions for number of grains per plant was well described by linear equations, explaining more than 92% of the variation of the number of grains per plant (Figure 1).

Most of the seed parents were stable with their slopes equal to the mean response ($b = 1.00$). Females 2 and 5, had slopes greater than 1.00. These females are among the low yielding seed parents (Figure 1) in low yielding environments, but were top most in high yielding environments. Therefore, they are sensitive to environmental improvement.

Female 6 having a slope less than unity non responsive to environmental improvement. Under low yielding environments, the variety is the highest in yield, while as the environmental conditions improve; the variety yield drops drastically (second from the least). Hybrid 9 had a consistently low average yield followed by hybrid 4, as shown in Figure 1.

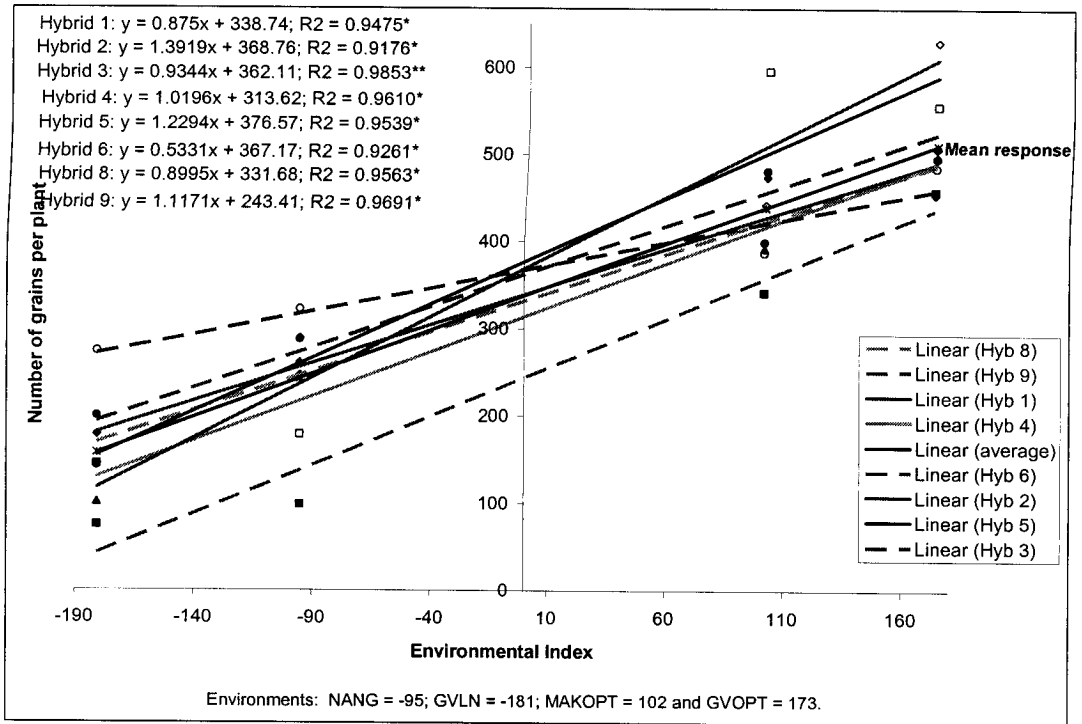


Figure 1: Response of seed parents to environment: genotypes with above average performance.

CHAPTER 5

5.0 DISCUSSION

To understand the effects of environment on phenological development of maize, the growing conditions at Mount Makulu were used as control. The agronomic practices used at Mount Makulu were similar to those used in hybrid seed production (Ristanovic, 2006 personal communication).

5.1 FLOWERING TRAITS

5.1.1 Floral development

The effect of environment on floral development of the parents is shown in Table 30. As expected, stress had an effect on floral development, the impact being great under water stress conditions at Nanga. The effects of low plant population at high N (Golden Valley Optimal) and low N (Golden Valley Low Nitrogen) for desynchronisation, 1TSI and 50TSI were not significantly different from the control (Mount Makulu). Under water stress (Nanga), females had their silks exerted 3 days after the males had commenced pollen shed.

Water stress and low nitrogen generally, increased the time lag between silking and pollen shedding. BIPASI and desynchronisation were increased by 2.1 and 1.9 days respectively. Similar results were reported by Herrero and Johnson (1981), who reported an increase of 1day in ASI or desynchronisation due to drought. However, higher increments of 3 days and 4 days due to drought have been observed (Herrero et al.,1981). In their case they were looking at ASI between reproductive organs on the same plant. In this study, ASI was between organs from two plants, hence called biparental anthesis – silking interval (BIPASI). Plant population had a non - significant effect on BIPASI, which is contrary to other reports (Pucavic et al., 1988). Plant population caused an increment of 0.1 days at Golden Valley Optimal.

Table 29: Main effects of environments on kernel set, floral development and other traits.

Parameter	Environments			
	MAKOPT (control)	GVOPT	GVLN	NANG
Synchronisation parameters				
- BIPASI	-2.4	-2.5	-5.2*	-4.5*
- Desynchronisation	0.5	1.5	2.0	2.9*
- 1TSI	-5.2	-6.3	-5.0	-2.8*
- 50TSI	-6.8	-7.0	-7.7	-2.3*
Pollen shed and silking intervals				
- Anthesis spread	10.5	7.4**	8.7*	6.5**
- Silking spread	8.6	5.8*	10.4	6.1*
Duration of Pollen shed				
-Anthesis Duration	6.2	3.3**	5.6	2.8**
-Sheddays	4.5	2.2**	4.1	0.6**
Onset of flowering				
-50% anthesis	67.6	62.5*	66.0	81.2**
-50% silking	70.0	65.0**	71.2	85.8**
Pollen yield components				
-tassel branches (number)	11.0	10.6	7.5**	6.7**
-tassel length (cm)	201.3	133.0**	102.5**	117.6**
Yield and yield components				
Grains per plant (number)	440	511*	157**	243**
Shelling percentage (%)	80.0	83.0*	79.3	75.5*
Grain yield (Kg/ha)	8265	8240	3155**	4845**
100 seed weight (g)	30.0	38.4**	32.2	31.7
EPP	1.01	1.02	0.75**	0.80**
PH (cm)	213	221	140**	152**
EH (cm)	120	128	73**	27**
ELFA (cm ²)	843	620**	353**	675**

BIPASI = biparental anthesis - silking interval, EPP = ears per plant; PH = plant height; EH = ear height; ELFA = ear leaf area, 50% tasselling silking interval and 1st plant tasselling silking interval.

** , * significantly different from Mount Makulu at 5% and 1% respectively.

The significant ($p = 0.01$) interaction between genotypes and environments for BIPASI entails that you can find environments where parents synchronise and where they don't synchronise. Therefore, it is possible to find areas of suitability of parents for seed production. Both linear and non linear responses (Figure 2) were obtained with coefficient of determination ranging from 74% to 100%. This indicates the complexity of this trait if it has to be used to identify parents that synchronise.

BIPASI for hybrids 1, 2 and 3 was low under low nitrogen, increased under water stress and thereafter reduced. Similarly, for hybrids 4, 5, 6 and 8, BIPASI was fluctuating within limits of ± 5 days (Bassetti and Westgate, 1994), with hybrid 4 and 8 having well described linear responses ($R^2 = 0.74$ and $R^2 = 0.97$ respectively). However, the response of hybrid 3 was exceptional (Figure 2).

The yield response of hybrids 1, 2 and 3 (Figure 1) and the response of BIPASI for these hybrids (Figure 2) are consistent with the suggestions of Westgate (1997) and those reported by Moser (2004). Westgate (1997) suggested selecting for protogyny, adding that a large negative ASI under drought would result in stable yields due to parents being synchronised. Moser (2004) on the other hand had reported high kernel set under drought conditions for the population, La Posta Sequia C₄, which had an ASI of -2.5 days under well watered conditions. Figure 3 gives an in-depth preview of the response of genotypes to environment as it relates to yield and BIPASI.

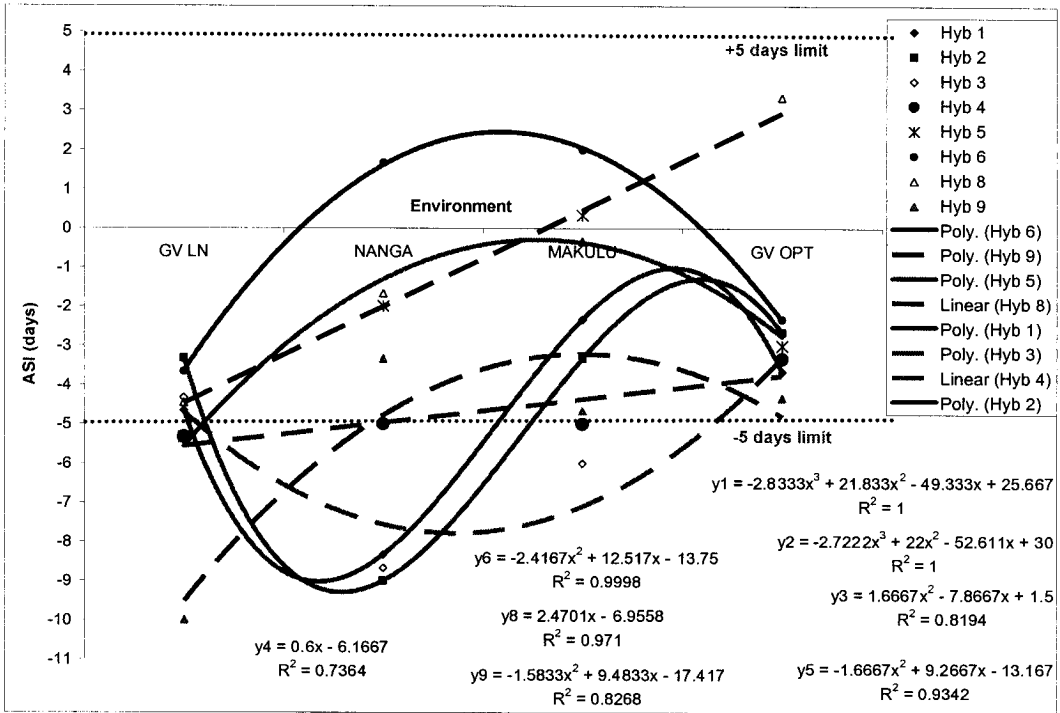


Figure 2: Response of BIPASI to environmental conditions for each hybrid

The graphs in Figure 3 indicate that each genotype has maximum kernel set at different BIPASI, depending on the interaction of anthesis and silking. For example, hybrid 6 had optimal GPP when BIPASI was -1day ($R^2 = 0.72$); hybrid 8 at +3days ($R^2 = 0.95$) and hybrid 9 at -7days ($R^2 = 0.85$). The only hybrid that had a linear response was 8 (Figure 3). Westgate (1997) had obtained similar results with Pioneer hybrid 3790. He noted that there were no yield reductions for ASI^s between -6days and +8days. It is also important to note that hybrid 9 had a narrow range of response ($R^2 = 0.85$).

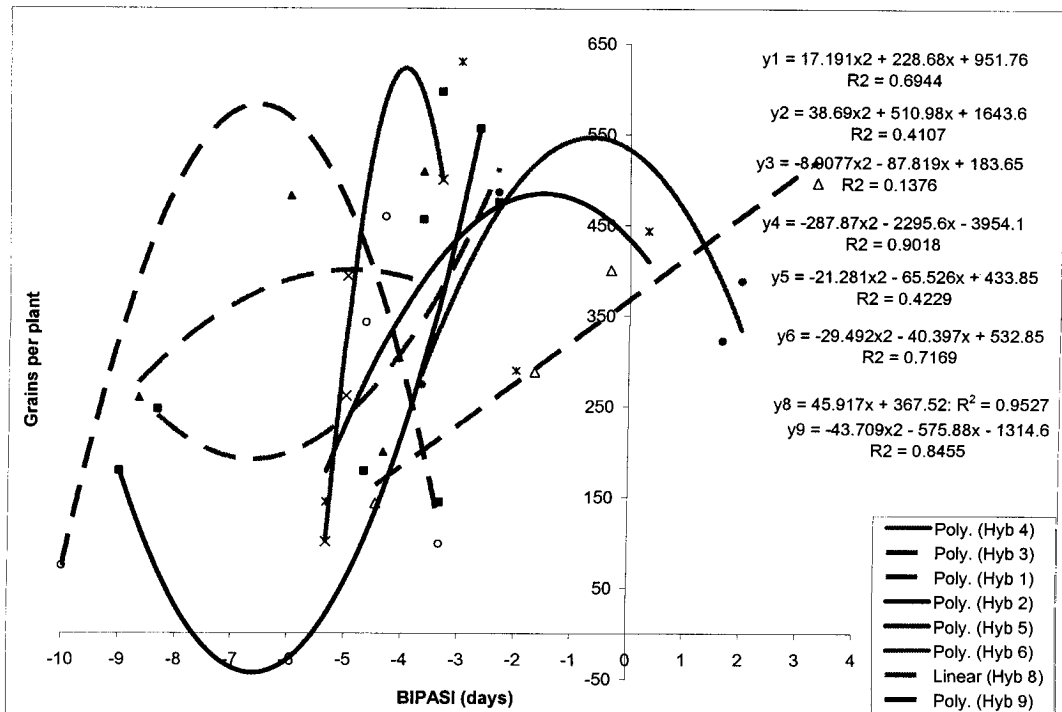


Figure 3: Response of GPP on BIPASI for each hybrid across all the environments.

The observed increment in time lag between anthesis and silking, homogeneity in silking and pollen shed due to stress were translated into differences in number of kernels per plant (Table 29). Low N and water stress reduced the number of kernels per plant significantly compared to the control. The high kernel set observed at low plant population, at Golden Valley optimal, than at high plant population, at Mount Makulu, could be attributed to better moisture supply as a result of lower plant population since EPP was on average similar and non-signifocant (Table 11 and

Table 17). Kernels from sub-apical ear and increased kernel number on the apical ear could have also contributed to the differences observed (Svečnjak et al., 2006). In addition, high plant population has been reported to affect both the apical and sub-apical ears, but not the number of grain rows per ear (Svečnjak et al., 2006). This is confirmed by the mostly lower EPP under high plant population than low plant population (Table 17).

Low nitrogen delayed the onset of 50% pollen shedding by 0.7 days and 50% silking by 3.7 days. The effects of water stress were the same on the male and female plant organs, delaying both 50% pollen shed and silking by 15 days. This suggests that the onset of 50% pollen-shed is stable under low and optimal nitrogen conditions. These findings confirm the simulation studies done on maize by Gungula et al (2003). They reported a linear relationship between nitrogen rates and days to silking of R^2 values greater than 0.70. Therefore, it can be concluded that low N had greater effects on silking than pollen-shed phenology. This conclusion is further supported by the observed considerable increase of BIPASI between optimal and low N conditions (Table 29).

Although the sensitivity of ear development to water stress has been reported (Struik et al., 1986), in this study, sensitivity of the tassel was observed. This response can be attributed to the sensitivity of maize inbred lines to stress as well as the competition from the hybrids. Water leakage that had occurred in some portions of the trial field at the time of water stress could have contributed greatly to the disparity observed.

Previous research results have shown that 80% of the variation in pollen production could be accounted for by number of tassel branches (Fonseca et al., 2003) and tassel length. In this study, the number of tassel branches and average tassel length were used as a proxy for estimating the quantity of pollen produced per male parent. It was further assumed that flowers were evenly distributed along the tassel length. The number of tassel branches affects the onset of different stages of anthesis, hence duration of pollen-shed. The length of the tassel affects the quantity of pollen produced and duration of pollen-shed. Males had a tendency of maintaining the number of tassel branches between Mount Makulu and Golden Valley Optimal, as well as between Golden Valley Low Nitrogen and Nanga. However, tassel length

varied greatly (Table 29). Hence, the quantity of pollen produced was highest at Mount Makulu followed by Golden Valley Optimal, Nanga and Golden Valley Low Nitrogen in that order. The interaction between TB and TL as it varies with environment could better be understood using an index. Figure 4 shows the response of pollen yield components, using the tassel index developed by Vidal Martinez et al. (2001). In the equation, all parameters were assumed to be unit, except for TB and TL. The male for hybrid 8 had consistently lower tassel index while male 9 was very sensitive to environment (Figure 4).

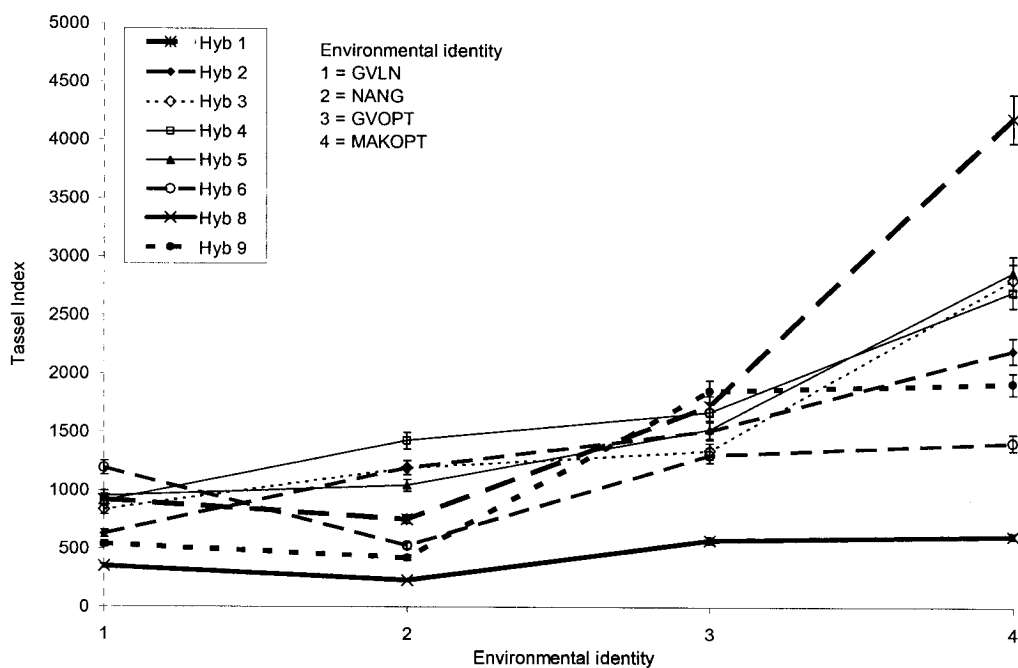


Figure 4: Response of Tassel Index of each male to environment.

Vidal – Martinez et al. (2001) had hypothesized that the variation in pollen production could either be due to genotypic or environmental effects. Yet in their study of inbred lines, they reported strong genotypic effects for the expression of pollen yield components. In this study, however, the phenotypic expression for pollen yield components was influenced by genotype, environment and the interaction between genotype and environment, the interaction being significant ($p < 0.05$). The environmental variance for TB and TL were 36.5% and 48.8% of the

total variance respectively, while that due to hybrids were 27.5% and 22.7% of the total variance for TB and TL respectively (Table 21).

The effect of environment on the silking duration of the female is shown in Appendix 3. According to Fonseca et al. (2005) females taking 8 days to 95% plants silking are more uniform for silking than those taking 20 days. In this study, plants took 14 days to reach 95% silking at Mount Makulu and Golden Valley Low Nitrogen. At Nanga and Golden Valley Optimal, the females took 8 days. This implies that silking uniformity could not have affected seed set. However, their interaction with pollen shed dynamics could have affected seed set as demonstrated by photos in Plate 2.

5.1.2 Pollen shedding and silking dynamics

Appendix 4 shows the interaction of silking dynamics, anthesis spread and pollen sheddays. Struik and Makonnen (1992) explained the different causes of desynchronisation, hence seed set. Based on their proposal, the following can be mentioned about the observed variation in grain number at each environment.

At Golden Valley Optimal, anthesis spread was shorter than silking spread. Therefore, when pollen was shed, a high proportion of females had their silks exposed and pollen shed lagged behind silking by 2 days. This had resulted in high kernel set interpreted as number of grains per plant. At Mount Makulu, with the same BIPASI of -2 days, a lower grain number could have resulted due to the fact that at peak pollen-shed, few silks were exposed. Pollen production has been shown to be skewed towards the early stages of pollen-shedding (Struik et al., 1982; Struik et al., 1986 and Westgate, 2003), with a peak period being within 2 days after on set of anthesis (Westgate, 2003). Therefore, at Mount Makulu, the amount of pollen was not adequate to pollinate the late emerging silks. The low plant population of inbred lines (1 row male compared to 3 rows females), interprets to low pollen load per exposed silk if pollen shed is over stretched. At Golden Valley Low Nitrogen, the high BIPASI (- 5.2 days) against a background of a short anthesis spread with a long silk spread, would have resulted in high grain number. However, low nitrogen had limited the potential number of kernels through limited assimilate supply (Lemcoff and Loomis, 1994); quantity of pollen produced and pollen viability (Hidv'egi, 2005) and rate of silk exertion coupled with number of silks exposed (Fonseca et al., 2004).

The almost equal anthesis and silking intervals (6.5 vs 6.1 days) at Nanga, is a good recipe for low kernel set. However, since pollen commenced 5.2 days after silking, then more females had their silks exerted at peak pollen shed to the extent that more pollen was being made available even after no plant was silking. In this case, even silk that had exerted latter were pollinated. However, the detrimental effects of water stress on silk receptivity and kernel support limited kernel number (Plate 4).

Though the rate of silk exertion per ear was not assessed in this study, Fonseca et al. (2004) had demonstrated that a plant taking 9 days to expose 95% of silks on the ear and that taking 4 days would have different kernel sets. The results confirm the above observations, as shown in figure 5, the number of grains per plant being strongly associated to silking spread ($R^2 = 0.69$). However, anthesis spread had a low association with seed yield ($R^2 = 0.33$). In line with the findings of Fonseca et al. (2004) a linear relationship between silking uniformity and number of grains per plant was obtained in this study. These results seem to indicate that the duration of silking can have a far reaching consequence on the success of hybrid seed production among the resource poor farmers.

All in all, it can be said that the rate of silk extrusion, timing of pollen-shed and quantity of pollen produced could have played a major role in establishing seed set (Plate 1).

5.1.3 Relationship between number of grains per plant with synchronisation and pollen shedding traits

Figure 6 shows that at Golden Valley Optimal, parents that had BIPASI within limits had the number of grains per plant above the average (>336). Similarly, most genotypes at Golden Valley Low Nitrogen were within limits, but had low number of grains per plant (<336). The response of genotypes at Nanga and Mount Makulu Optimal was however not well defined. The association between number of grains per plant and BIPASI was weak, explaining only 22% (Figure 7) while Desynchronisation (Des) explained only 12%. The figure, 22%, is close to the figures, 25 – 35% reported by Edmeades et al. (1997) as the variation in grain yield explained by ASI. However, Desynchronisation shows that high kernel set cannot be achieved

with perfect synchronisation, which is in agreement with those reported by Westgate (1997); Edmeades et al. (2000) and Moser (2004).

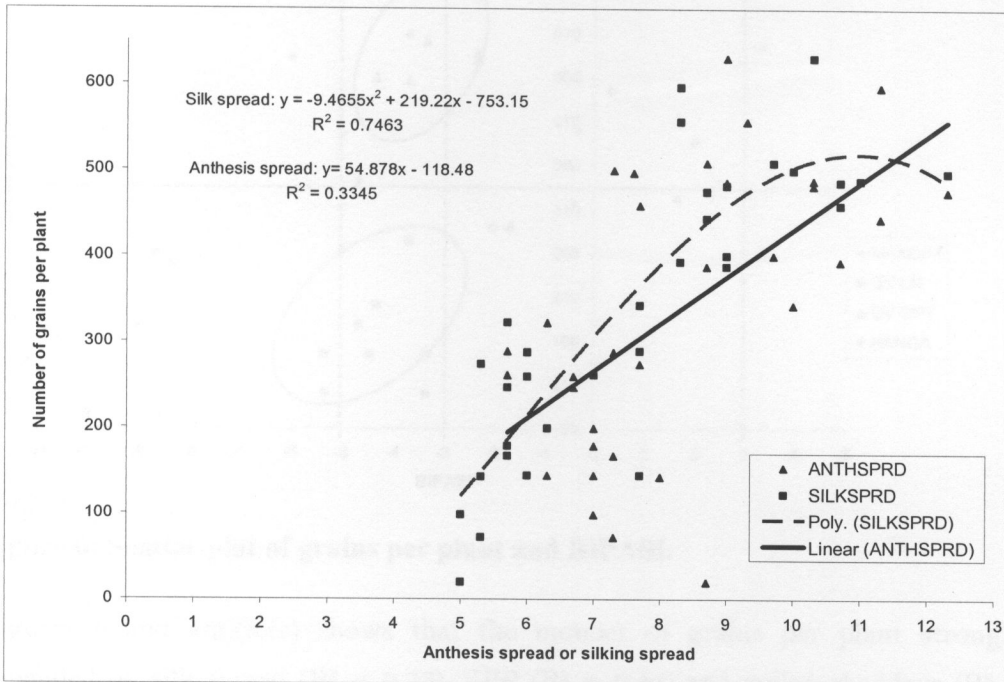


Figure 5: Relationship for number of grains per plant with the duration of silking and anthesis for 8 genotypes tested across 4 environments.

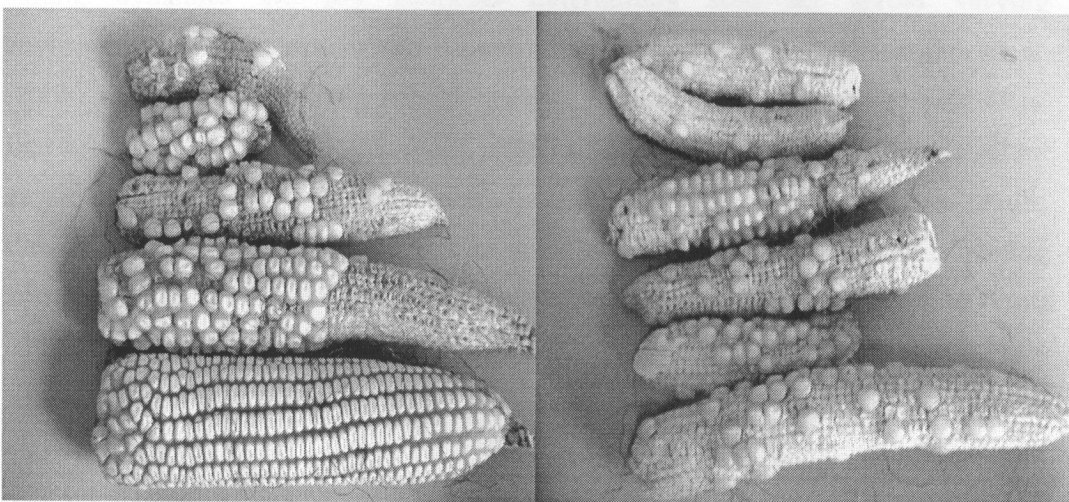


Plate 1: Effect of silking uniformity between plants and silking rate of silks on the cob on seed set under water stress for synchronised (left) and unsynchronised (right) parents.

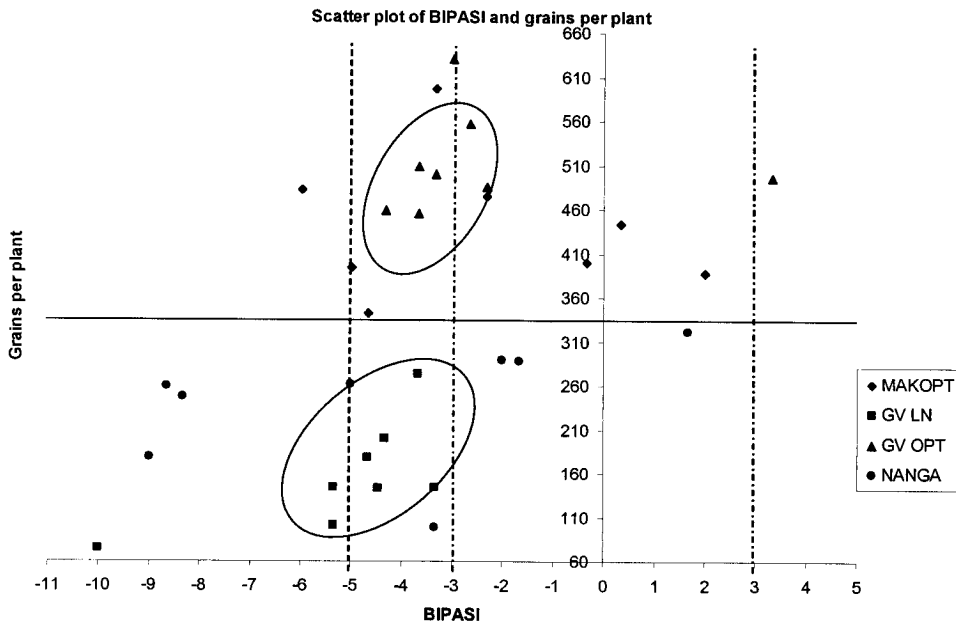


Figure 6: Scatter plot of grains per plant and BIPASI.

Figures 5 and 8(a)(b)(c) shows that the number of grains per plant strongly depended on silk spread ($R^2 = 0.75$), EPP ($R^2 = 0.84$) and pollen sheddays ($R^2 = 0.75$); moderately to duration of anthesis ($R^2 = 0.66$) and to a low extent on 50% silking duration of anthesis ($R^2 = 0.52$). This confirms that pollen shedding and silking dynamics are key elements determining seed set across varying environments. These results are consistent of those reported by Westgate et al. (2003). In respect of selecting suitable parents for seed production, the graphs reveal that using males with pollen average pollen sheddays of 4 – 5 days with interplant variation of around 6 days would result in high kernel set. In case of female plants, the interplant variation should not be more than 10 days. Hence parents having anthesis duration of 6.5 to 7.5 days and silking spread of 9.5 to 11 days would result in high kernel set. In this respect, females that were achieving a 50% silking early were most favoured ($R^2 = 0.52$).

The inter-relationships between some of these traits were strong [Figure 8(d)(e)], indicates that they can be used in place of another.

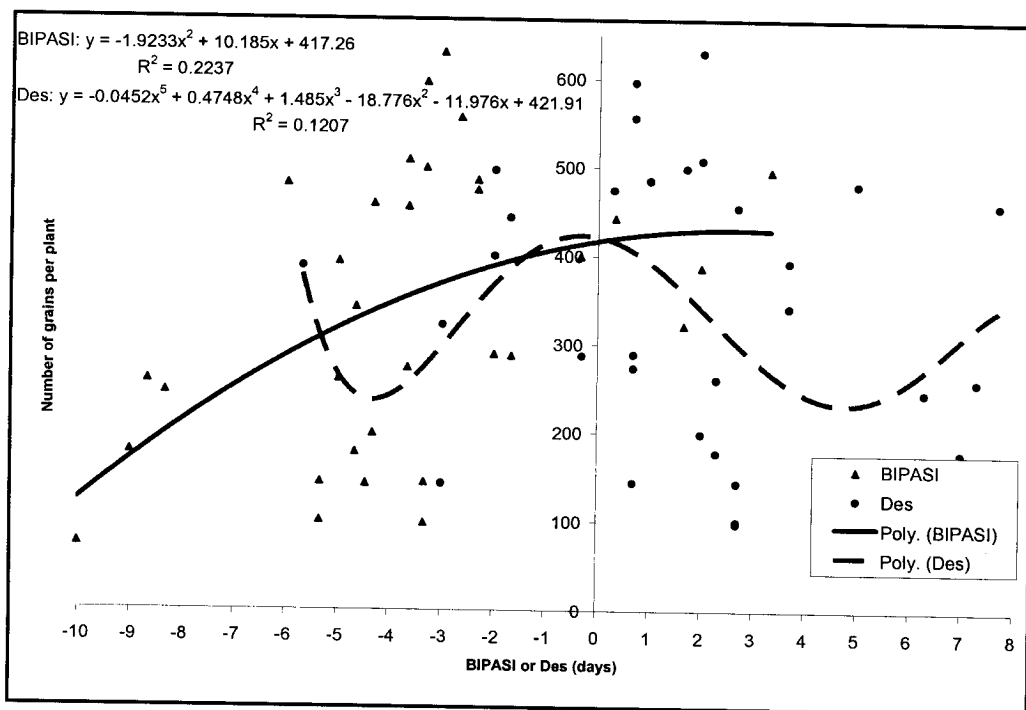


Figure 7: Relationship for number of grains per plant with BIPASI and Des for 8 genotypes tested across four environments.

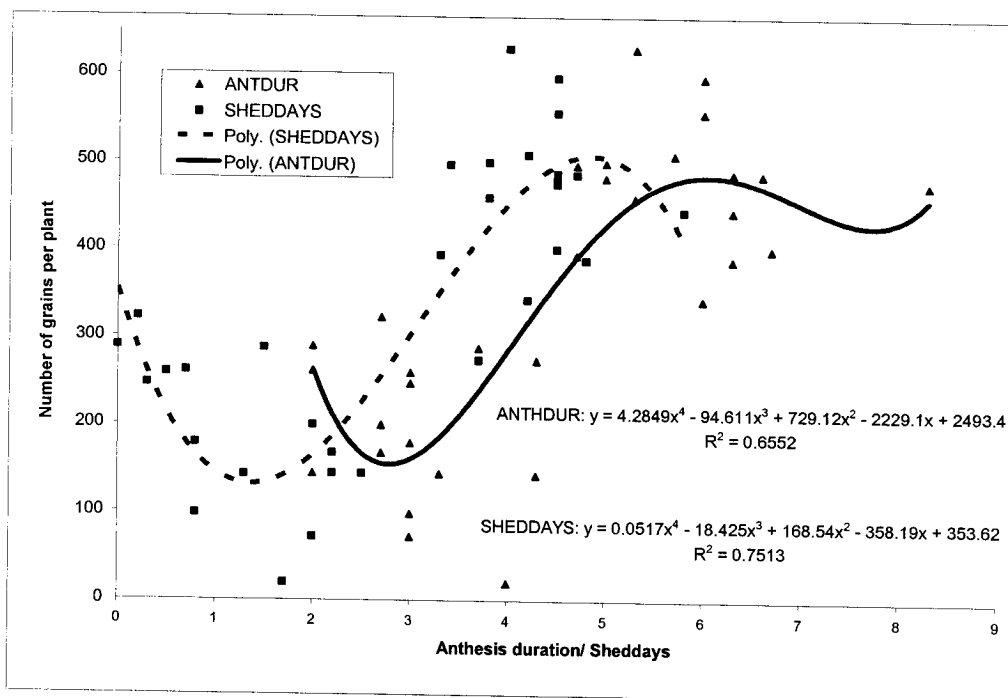


Figure 8(a): Relationship for number of grains per plant with pollen shedding traits for 8 genotypes averaged across four environments.

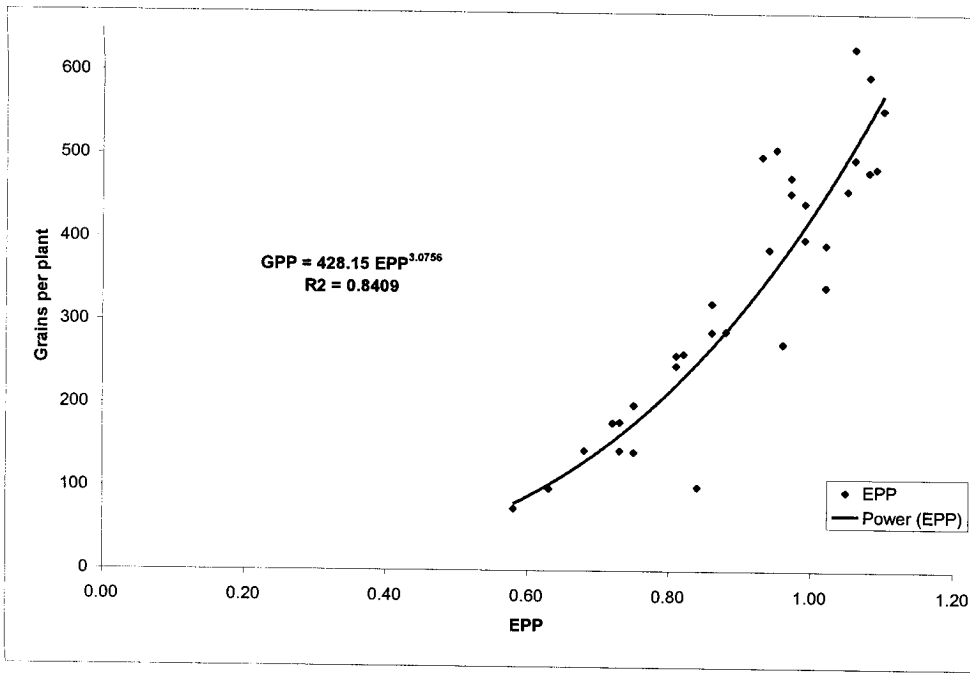


Figure 8(b): Relationship between numbers of grains per plant with ears per plant for 8 genotypes averaged across four environments.

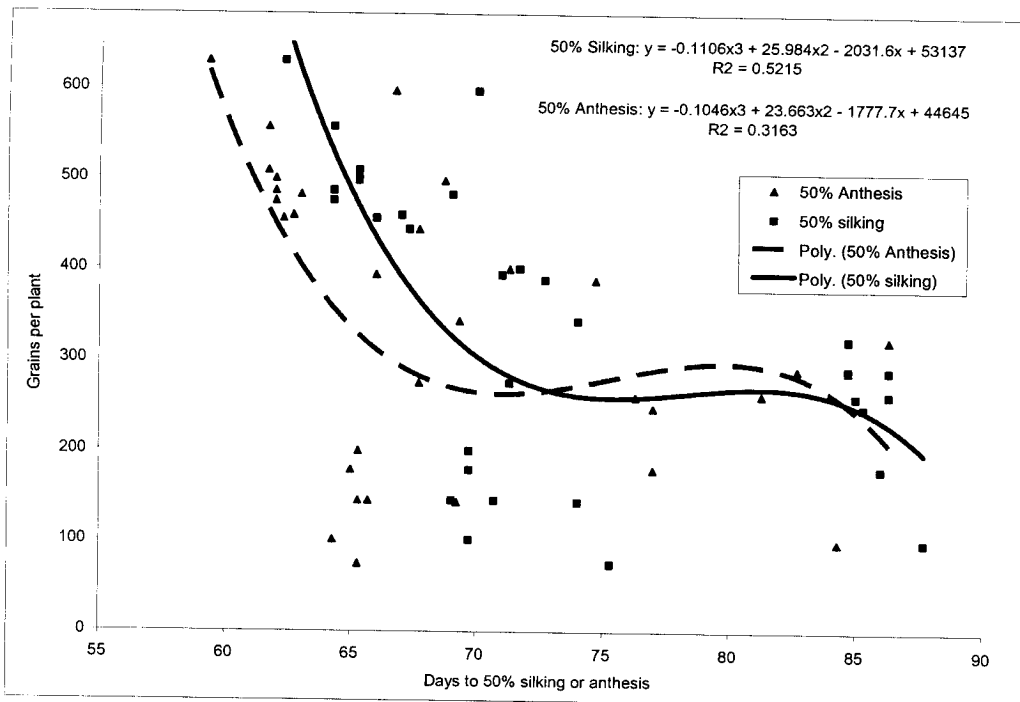


Figure 8(c): Relationship between number of grains per plant and days to 50% silking for 8 genotypes averaged across four environments.

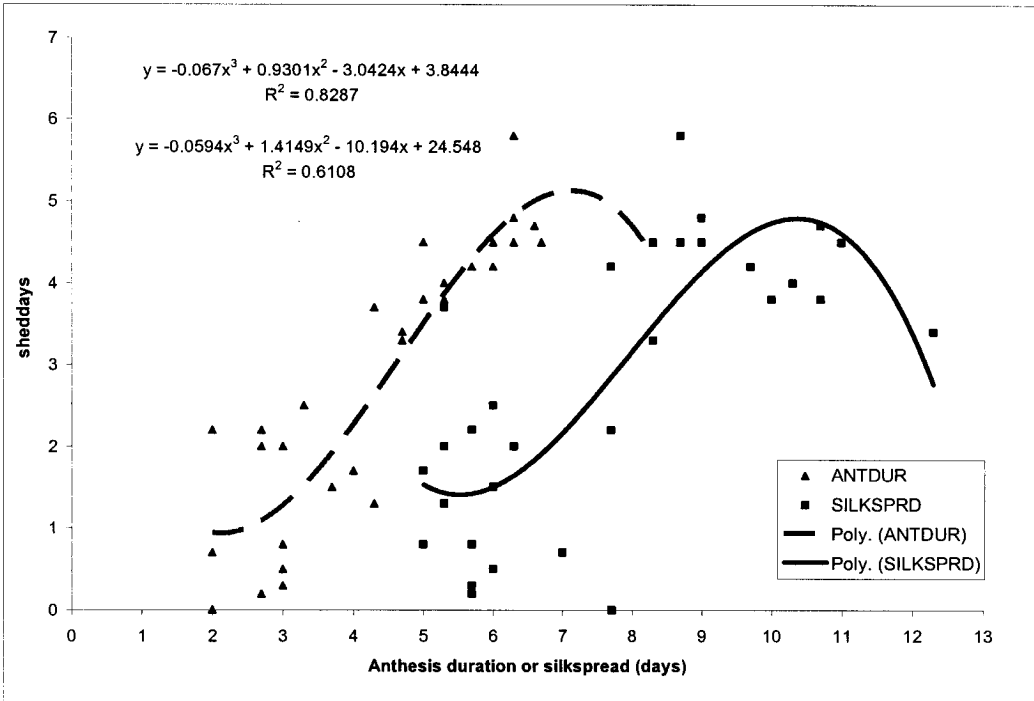


Figure 8(d): Inter-relationships among sheddays, silk spread and anthesis duration for 8 genotypes averaged across four environments.

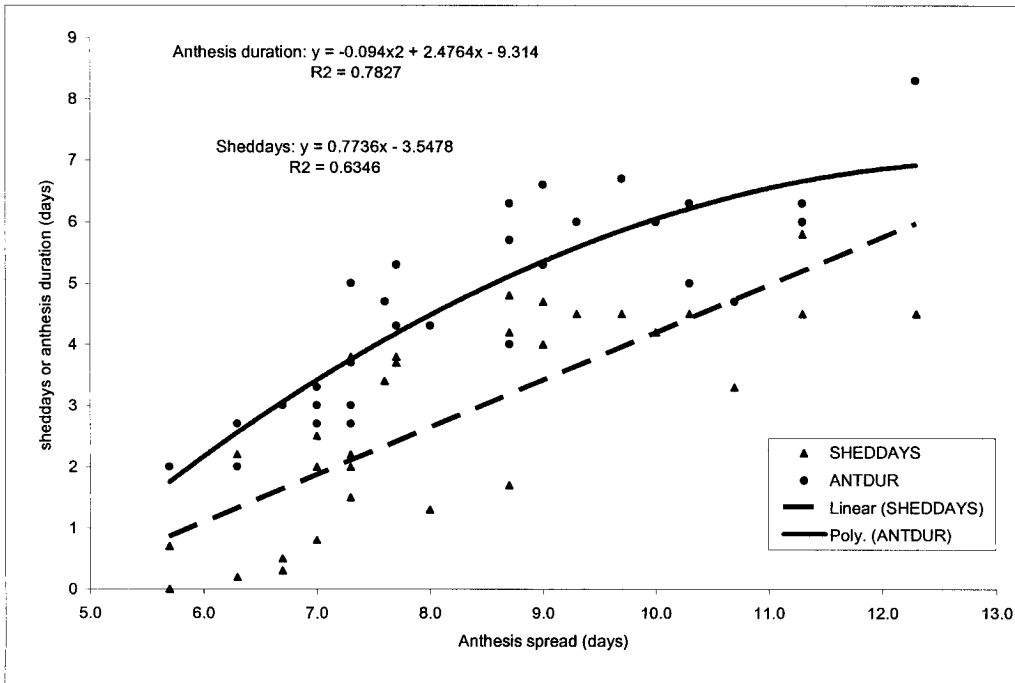


Figure 8(e): Inter-relationships among sheddays, anthesis duration and anthesis spread for 8 genotypes averaged across four environments.

Low nitrogen prolonged the silking pattern (Appendix 3) and to fertilise the late exposed silks, a prolonged duration of pollen shed is required, the pollen quantity of pollen increasing with the number of branches. Low nitrogen prolongs silking and the rate of silk extrusion (Lemcoff and Loomis, 1994; Dase et al., 1997 and Sangoi et al., 2001). Therefore, the period of pollen shed should not only be long, but the quantity of pollen released to fertilise the exposed silk should be more than the threshold of 100grains $\text{cm}^{-2} \text{d}^{-1}$ (Westgate, 1997). Hence determining the quantity of pollen produced per male is important to assess whether the pollen parent is a good or poor pollinator. The period of pollination can be increased by split planting of the males and or decreasing the male to female ratio, as determined by the number of tassel branches.

The above observation is supported by regression results shown in Table 26; with shelling percentage and time to 50% silking having similar effects ($b=16$). Plant stand had a significant negative effect ($b=-3.96$) implying that reducing the plant population to maximise the limiting resource, nitrogen, would result in efficient seed production.

5.2 YIELD AND YIELD COMPONENTS

On average, all the plants were barren except for hybrid 6 having EPP of 0.96. (CIMMYT, 2005). Hybrids 9, 11 and 12 were greatly affected by low N resulting in EPP values of 0.52 to 0.58. Hybrid 6 despite being prolific and having a high number of grains per cob was not the highest yielding. This shows that yield cannot be compensated by grain set and kernel weight under low N conditions. This observation is in agreement with the research findings of Sangoi et al. (2001), Otegui (1997), Lemcoff and Loomis (1994); and Otegui and Melon (1997). Studies done by Lemcoff and Loomis (1994), had shown that nitrogen fertilisation had less influence on kernel mass with a high influence ($p<0.05$) on total number of kernels of the first ear.

The plant heights of more than 200cm obtained under optimal nitrogen conditions had made detasselling difficult. This could have resulted in low yields due to removal of the first top leaves. Tall plants have also been known to delay pollen shedding (Pucavic et al., 1988) due to shading of the males.

The tendency of the female parents to have pseudo or tiller cobs at the apical cob node (plate 2) has implications on the source: sink ratio. These structures apart from competing for assimilates, they could be principle sources of the remobilised assimilates during terminal drought. Therefore, the role of 'pseudo cobs' in sustaining yield need to be investigated.

The low number of grains/plant and low EPP observed under low N conditions is due to the limited number of spikelets that differentiated on the ear as a result of N stress (Lemcoff and Loomis, 1986; and Lemcoff and Loomis, 1994). Nitrogen stress also reduced the number of cobs with synchronous silking in all the female hybrids. In prolific hybrids, stress reduces prolificacy and the synchrony between the two ears (Anderson et al., 1984). Nitrogen supply before anthesis affects yield through grain number (Pearson and Jacobs, 1987; Lemcoff and Loomis, 1987), and has been reported to account for 64% of the variation in yield (Otegui, 1997).

On the other hand, the low kernel number observed under water stress could have been mainly due to kernel abortion (Plate 3). Drought during flowering has the primary effect on the number of aborting kernels (Kiniry and Ritchie, 1985; Schussler and Westgate, 1991). Under these conditions, it was expected that the good pre-anthesis environment had resulted in high dry matter accumulation, which when remobilised would have resulted in high grain set (Otegui, 1997).

In view of the above, the variation in number of kernels per cob between varieties under water stress, therefore, is directly related to BIPASI, as ovaries that expose their silks late during pollen shedding are deleteriously affected by drought (Otegui et al., 1995). In addition, a poor BIPASI leads to sink suppression, increasing the source: sink ratio, thereby affecting the pattern of assimilate remobilisation and partitioning (Sangoi et al., 2001).

5.3 CORRELATION COEFFICIENT

Correlation coefficients are useful in identifying relationships that change from one environment to another (Lafitte and Edmeades 1994). In this study, the number of grains per plant were used as an indirect measure of pollen availability, each pip or grain representing a fertilised ovule. In addition, grain yield in maize depends on

kernels per plant mediated through EPP and less through kernels per ear (Edmeades et al., 1997).



Plate 2: Number of pseudo or tiller cobs at the apical ear node, under optimal growing conditions

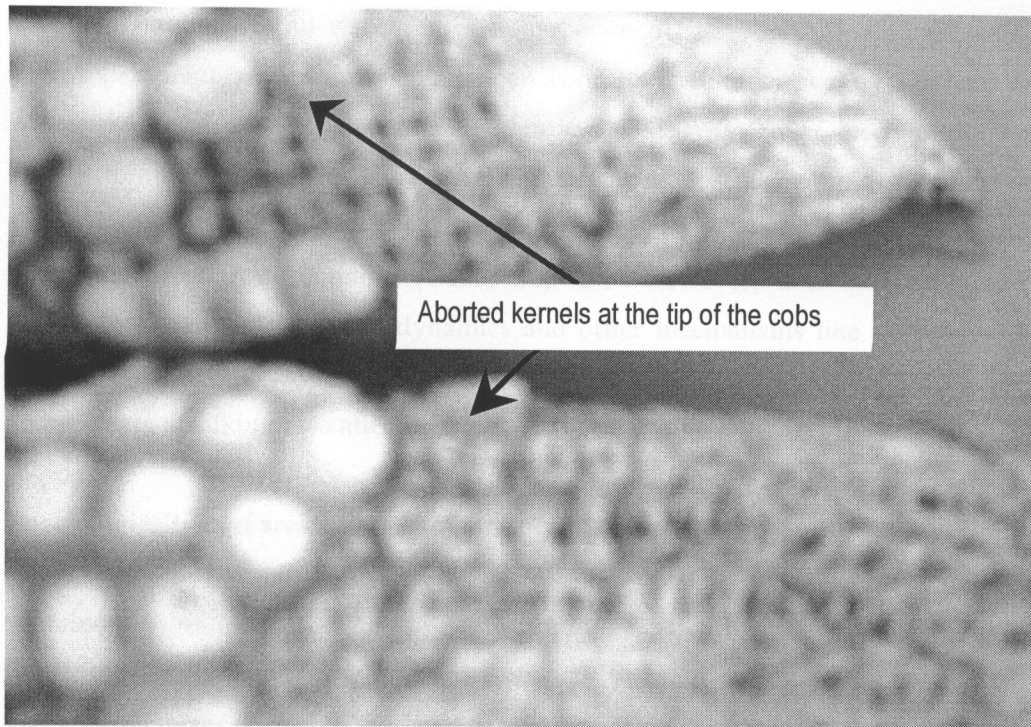


Plate 3: Kernel abortion in late exposed silks under water stress conditions at Nanga

In this study, EPP was strongly associated with number of grains per plant under water stress ($r=0.98^{**}$, $n=8$) and low N ($r=0.72^*$, $n=8$), conditions. BIPASI was only strongly associated to grain number under low N conditions ($r=0.67$, $n=8$). Strong associations of ASI and EPP with yield under low N and drought conditions has been reported before by Bolaños et al. (1993) and Edmeades et al. (1997, 1998). However, across all the test environments, BIPASI and EPP were positively and significantly ($r=0.44^*$, $n=32$ and $r=0.91^{**}$, $n=32$ respectively), associated to grain number (Table 24). The positive correlation between ASI and grains per plant observed in this study is contrary to those reported by other researchers (Fischer et al., 1989; Edmeades et al., 1992; Vasal et al., 1993 and San Vicente et al., 1997). Such contrasting results would be expected because the ASI in breeding populations is calculated from the same plant and therefore is an indicator of competition between the tassel and ear, while the ASI, herein referred to as BIPASI, as in hybrid seed production, is between two different genotypes. Therefore, BIPASI has no bearing on the competition between tassel and ear of the same plant but rather is an indicator of the interaction between two different genotypes.

The non-significant and weak correlations between EPP, BIPASI with number of grains per plant, under optimal nitrogen conditions (Golden Valley Optimal and Mount Makulu), suggest that other pollen and silking dynamics mechanisms were responsible for moderating kernel set in maize. Under stress conditions, yield and yield components viz 100SWT, shelling percentage, PH, EH and EPP were strongly associated with grain number (Table 24). This however, does not exclude the interaction between flowering dynamics and other mechanisms like hormones that control seed set (Carcova et al., 2000). Plant population and individual plant components of silking also affect kernel yield (Fonseca et al., 2004).

Physiologically, leaf area and the amount of radiation intercepted during grain filling affect seed set in maize (Struik et al., 1986). In this study, ear leaf area was highly correlated to number of grains per plant under water stress ($r=0.98^{**}$) and low N ($r=0.72^*$). Under low N conditions, carbon flow to grain sink is highly correlated to leaf area per plant (Lemcoff and Loomis, 1986).

The positive correlations of grains per plant with EPP under water stress and with BIPASI under low N implies that high number of kernels per hectare in hybrid seed production can be achieved by growing females that are prolific under water stress and increasing ASI under low N. Alternatively, a high seed set can be achieved with short BIPASI as long as there is synchronous pollination of silks on the ear. This implies that females that exhibit synchronous silk exertion should be grown when BIPASI is short. This is in agreement with the findings of Carcivoca et al. (2000) and Käser-Schneider (2002). They observed that delaying pollination until 5 days after silking of the apical ear increased kernel set of the apical and sub-apical ear, under optimal conditions. The increased kernel set was also related to synchronous silking between apical and sub apical ears. The premise that delaying pollination improves kernel set is based on the fact that:

- (i) Silk remains receptive to pollen for more than 6 days
- (ii) Pollination of the apical ear prevents seed set of the sub-apical ear (Carcova et al., 2000). In addition, the occurrence of sub-apical ear is triggered by the apical ear when it achieves maximum potential kernel set (Svečnjak et al., 2006) and
- (iii) Through dominance and hormonal effects (Carcova et al., 2000).

The negative association of grains per plant with duration of anthesis under water stress (Nanga) could be due to abortion of apical fertilised ovules seen in the field (Plate 4) and the high rate of silking between female plants recorded (Appendix 3). Conversely, the high rate of silking combined with a long duration of anthesis ensures the pollination of late exposed silks, in cases where the parents are synchronised. However, under water stress, this has a negative effect on number of grains per cob because late pollinated silks are aborted due to either water stress or early fertilised ovule preventing the development of late fertilised ovule or both (Westgate and Boyer, 1986; Schussler and Westgate, 1991a and Schussler and Westgate, 1991b). Abortion occurs when low silk water potential is imposed for less than 4 days after silking while silk receptivity is lost when low silk water potential is imposed for more than 5 days (Bassetti and Westgate, 1993). In this study, loss in silk receptivity could not have been the major cause of low kernel set. This was because the leakage in the irrigation pipes could have moderated the severity of water stress.

The results observed, support the selection strategy suggested by Westgate (1997) when breeding for drought tolerance. He suggested using selection strategies that improves ear/silk growth and /or modify the pattern of pollen shed. Therefore, seed parents should be assessed for these attributes for a successful seed production. This underpins the need for synchronisation research studies that simulates actual hybrid seed production.

Table 30 shows the multiple regression results in a matrix form. Amongst all the traits, EPP had the largest influence on grain set. Other traits of importance were 100SWT and shelling percentage. These results confirm the reports of Kiniry et al. (2002) that seed number in maize responds to ear growth rate and intercepted IPAR. At what level does the quantity of pollen limits kernel number in maize is a matter under debate and therefore needs further investigation.

Assimilates from leaves immediately below the primary ear and those above, preferentially supply the ear with assimilates (Fairey and Daynard, 1978). ELFA and plant height at anthesis are closely correlated to the amount of nitrogen in a plant (Lafitte and Edmeades, 1994a) hence, an indirect measure of the potential amount of assimilates that can be remobilised to the ear. This implies that prolific seed parents

with large ear leaf area should be grown in areas where mid season drought is expected or experienced. In terms of breeding, selection for prolificacy under mid drought stress would result in such hybrids. Conversely, a hybrid that had high kernel set under water stress could be considered to be efficient in nitrogen utilisation (Krone and Lambert, 1995).

Table 30: Multiple regression table matrix showing partial regression coefficients

Term	MAKOPT	GVOPT	GVLN	NANG	Combined
100SWT	-4.83	-11.02	-	-2.02	-3.91
SHELL%	29.04	24.90	19.15	3.98	3.62
PLTSTND	-3.45	-	-4.15	-	443.00
EPP	200.05	717.16	256.13	358.63	-
50%SILK	13.28	-	13.49	-	-10.07
SHEDDAYS	-12.17	-	46.90	-	-
ANTHSPRD	7.86	-14.76	-	-	-
ELFA	-	-	-	0.11	-
PH	-	-	-	-	2.00
EH	-	-	-	-	-1.89
SILKSPRD	-	-	-	-	-9.51
Y - intercept	-2771.79	-1750.70	-2564.90	-358.16	400.20
R²	94.4%	87.5%	89.2%	90.7%	79.2%
Adjusted R²	91.7%	84.7%	83.2%	88.7%	77.3%

Under adequate pollen, low nitrogen determines kernel number, kernel weight and hence shelling percentage (Gallais and Hirel, 2003). This is confirmed by the results in Table 61, where shelling percentage; plant stand and EPP influenced seed set. The role low nitrogen played in affecting crop development and pollen production was translated into days to 50% plants silking and pollen sheddays were second to EPP in level of influence.

Plant population has been shown to affect the number of kernels per cob (Otegui, 1997), the effect of plant population was observed under low N and high population (Table 30). This indicates that under optimal nitrogen conditions, female parents are sensitive to plant population and other environmental factors. This further demonstrates the need to test seed parents for their environmental suitability. High 100SWT under low N conditions (Table 29) could be attributed to poor kernel set.

Therefore, high kernel mass is negatively related to the number of grains per plant, being strong at low plant population.

Across all environments, the role of PH and EH in regulating seed set was surprising. Apart from being involved in determining yield, as sources of assimilates, they influence pollination. The negative association between grain set and ear height cannot be well understood. It can only be hypothesized that when the ear height of the female is very high relative to the tassel of the male, pollen may not rich the exposed silk. This is because maize pollen is heavy and has been shown to have a tendency of falling downwards (Ma et al., 2004 and Raynor et al., 1972). Hence to fertilise a high placed cob entails high wind speeds are required to blow pollen upwards and as it settles down it pollinates the exposed silks (Aylor, 2006 personal communication). Similarly, the quantity of pollen produced could be limited due to reduced number of tassel branches and tassel length. This limits the quantity of pollen produced hence reaching the ear and at this stage ear height may become critical.

The above hypothesis is supported by the practical experience by Pannar Seed Company, where seed set was limited by a very short male. The farmer had to use a blower to improve pollination (Mwansa, 2006 personal communication). Masole (2006 personal communication) proposed a height of 50cm to be critical. This critical height yet remains to be determined and if it exists may play a role in the suitability of parents for seed production.

In breeding studies, EPP is a good indicator of stress tolerance (Duque-Vargas et al., 1994). This study further confirms and demonstrates the robustness and universality of EPP. The relationship between GPP and EPP shown in figure 5 is similar to the one reported by Edmeades et al (2000) on breeding populations. In the matrix, 100SWT and shelling percentage were moderated by the efficiency of pollination, hence synchronous emergence of the silks per ear is a key factor in achieving synchronous pollination of the silks (Cárcova and Otegui, 2001 and Cárcova et al., 2002).

The variation in the traits determining the number of grains per plant, suggests the development of holistic models for prediction of the performance and

synchronisation of maize hybrid seed production under diverse environments. This would facilitate the production of maize hybrid seed in diverse environments. This is important especially in the wake of climate change and the unpredictability of weather, if smallholder participation in maize hybrid seed production is envisaged.

5.4 YIELDING ABILITY OF SEED PARENTS

The ability of a seed parent (female) to maintain seed yield and quality in variable environments is very important for successful seed production of new hybrids. Generally, when single crosses are used as parents, 60% of the seed produced are flat types, 40% being round seeds and less than 10% are small and medium sized round seeds (Curtis, 1980). Therefore, seed size distribution may not be an issue for seed parents used in this study, as long as pollen quantity is not limiting. In this respect, optimisation of seed yield by using adapted genotypes is critical. Based on average yield and sensitivity (b-value) of seed parent recommendations were made as shown in Table 31, depending on the location of the seed parent in the quadrant.

Table 31: Yield ability of seed parents for number of grains per plant

Hybrid	Slope	Average	Quadrant	Recommendation
Hyb 1	0.87	339	II	Smallholder sector
Hyb 2	1.39	369	I	All sectors
Hyb 3	0.93	362	II	Smallholder sector
Hyb 4	1.02	314	IV	Commercial sector
Hyb 5	1.23	377	I	All sectors
Hyb 6	0.53	367	II	Smallholder sector
Hyb 8	0.90	332	III	Discard
Hyb 9	1.12	243	IV	Commercial sector
Mean	1.00	338		

LSD_{0.05} (grains per plant) = 87.46

The economic feasibility of hybrid seed production depends on the amount of seed used per hectare of commercial production and the amount of hybrid seed produced per hectare. The economic feasibility for commercial use of hybrid seed is greatest when the ratio is largest (Curtis, 1980). Hence, for these hybrids under these

conditions, seed production would be economically feasible for parents having a ratio of 1:100. For most hybrids, seed production under low nitrogen conditions would not be economically feasible (Appendix 5) when 60% of the seed yield are flat seeds except for hybrid 6. In this respect, seed production for hybrid 6 can be done across all the environments under test. Under stress conditions, seed production of parents whose yield comprises of 40% flat seeds would not be viable. The result in Appendix 3 shows that increasing the plant population for hybrid 9 would result in high seed price if the farmer has to recoup his costs.

CHAPTER 6

6.0 CONCLUSION AND RECOMMENDATION

6.1 CONCLUSION

Synchronisation studies involving male inbred lines and female single cross hybrids were grown under four different environments to establish the response of BIPASI and kernel set. Based on the results obtained the following conclusions may be drawn:-

1. Though the interval between silking of the females and pollen shedding of the males or BIPASI is used to identify parents that “nick” or are synchronised for hybrid seed production, the trait could only account for 22% of the observed variation in number of grains per plant across varying environments. In addition, BIPASI was not strongly associated to traits that explained the largest portion of the variation in KPP observed. Therefore, it is concluded that BIPASI is used as an indicator of parents that “nick” than a predictive tool of high seed set.
2. The number of grains per plant in hybrid seed production, strongly depends on pollen sheddays, EPP and silking spread, moderately depends on duration of anthesis and to a low extent on time to 50% silking. The interrelationships between these traits were strong, implying that one trait can be used for another without loss of information.
3. Field testing of the parents to determine their suitability and adaptability for hybrid seed production, especially among the smallholder farmers, should form an integral part of maize breeding.

This is also supported by the fact that each parent had a BIPASI where optimal seed set was achieved, and this BIPASI was different from the other parents. In addition, linear and non-linear response of BIPASI across different environmental conditions was observed.

4. Most of the seed parents used in the trial had acceptable number of grains per plant and were stable in performance. Seed production under these conditions was also assessed to be viable for most parents. Therefore, suitable areas of seed production for a specific hybrid could be identified.

6.2 RECOMMENDATIONS

Despite the above conclusions made, it is recommended that similar studies be done to further verify the factors that are responsible for determining seed set in maize hybrid seed production fields. This will not only provide guidance to efficient seed production technologies but also allow hybrid seed production at smallholder farmer level a reality. As a result, seed production will be optimised.

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Appendix 1: Single Site Probabilities

1.0 YIELD AND YIELD COMPONENTS

(a) NANGA

ANALYSIS OF VARIANCE SUMMARY TABLE FILE YLD2NANG 22/ 2/ 7 11:25 :PAGE 13

F-PROBABILITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 36)	STANDARD TOTAL SS	DEVIATION		C OF V SD/MEAN %	REP	HYB
			BASED ON RESID SS	BASED ON SS			
PLTSTND	36 32.333	13.877	10.473	32.4	0.9910		0.0053
SHELL%	36 75.522	11.888	10.185	13.5	0.7496		0.0480
GRNYLD	36 4844.7	1565.7	1536.7	31.7	0.7940		0.3087
100SWT	36 31.457	4.5222	4.3828	13.9	0.1470		0.4700
GRNS/COB	36 288.90	88.311	73.067	25.3	0.3053		0.0374
EPP	36 0.81525	0.18866	0.20964	25.7	0.3303		0.9566
PH	36 151.84	18.156	15.244	10.0	0.6391		0.0368
EH	36 26.889	1.5758	1.3259	4.9	0.8760		0.0342
LFA	36 675.14	143.55	134.20	19.9	0.4182		0.2103
LEAFROLL	36 4.4444	1.2058	1.1237	25.3	0.2653		0.2373
LEAFSENE	36 4.0556	1.6724	0.96792	23.9	0.6893		0.0000

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 36)	STANDARD TOTAL SS	DEVIATION		C OF V		HYB
			BASED ON RESID SS	BASED ON RESID SS	SD/MEAN %	REP	
PLTSTND	36 34.556	10.154	9.4883	27.5	0.5990	0.1843	
SHELL%	34 79.280	3.3555	3.1119	3.9	0.4607	0.0990	
GRNYLD	31 3155.3	1454.7	1589.2	50.4	0.5215	0.4874	
100SWT	32 30.249	10.171	10.568	34.9	0.3899	0.5948	
GRNS/COB	29 217.14	111.00	132.55	61.0	0.4244	0.8469	
Epp	36 0.70714	0.21737	0.21600	30.5	0.2784	0.4951	
PH	36 139.69	19.783	18.624	13.3	0.7557	0.1875	
EH	36 72.556	13.563	11.800	16.3	0.8019	0.0594	
LFA	36 353.36	128.88	124.90	35.3	0.0695	0.6027	

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 36) OBS.	STANDARD TOTAL SS	DEVIATION BASED ON RESID SS	C OF V		HYB
				SD/MEAN %	REP	
PLTSTND	36 40.278	8.8563	5.0913	12.6	0.9550	0.0000
SHELL%	36 80.015	2.5399	2.1188	2.6	0.2923	0.0435
GRNYLD	35 8265.3	1033.7	964.77	11.7	0.6249	0.1774
100SWT	36 30.817	5.8054	5.4770	17.8	0.0125	0.8115
GRNS/COB	36 413.17	98.458	74.279	18.0	0.0042	0.0468
EPP	36 1.0303	0.12306	0.11533	11.2	0.2638	0.2558
PH	36 212.59	17.259	6.8072	3.2	0.2063	0.0000
EH	36 119.52	21.352	7.6749	6.4	0.4741	0.0000
LFA	36 842.85	75.785	59.108	7.0	0.6469	0.0107

(d) GOLDEN VALLEY - OPTIMAL NITROGEN

ANALYSIS OF VARIANCE SUMMARY TABLE FILE YLD2GVOP 20/ 2/ 7 17:25 :PAGE 11

F-PROBABILITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 36) NO. OBS.	STANDARD DEVIATION		C OF V SD/MEAN %	REP	HYB
		BASED ON TOTAL SS	BASED ON RESID SS			
PLTSTND	36	7.4948	7.3916	19.1	0.7927	0.3263
SHELL%	36	1.3287	1.1611	1.4	0.0915	0.1431
GRNYLD	36	8239.5	973.64	11.8	0.7735	0.1948
100SWT	35	38.357	6.4146	16.4	0.8092	0.2926
GRNS/COB	35	495.18	86.984	17.3	0.9624	0.2800
EPP	36	0.99435	0.21582	23.9	0.2801	0.9491
PH	36	220.64	32.907	10.8	0.0167	0.0112
EH	36	127.72	32.164	17.9	0.0050	0.0131
LFA	36	619.73	162.36	25.9	0.2356	0.4945

2.0 FLOWERING PARAMETERS

(a) NANGA

ANALYSIS OF VARIANCE SUMMARY TABLE FILE NANGAFLO 11/12/ 6 21:55

: PAGE 27

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 24) OBS.	STANDARD TOTAL SS	DEVIATION BASED ON RESID SS	C OF V SD/MEAN %	REP	HYB
1TASEL	24 80.333	1.3726	1.5256	1.9	0.9831	0.7067
1SILK	24 83.125	2.3648	1.9211	2.3	0.0193	0.2551
1BEG	24 80.250	4.7112	3.6702	4.6	0.8410	0.0256
1MAX	24 84.708	4.8497	3.8730	4.6	0.7410	0.0355
1END	24 83.042	4.9911	4.1854	5.0	0.8906	0.0579
50TASEL	24 83.500	1.6681	1.7576	2.1	0.3637	0.7122
50ANTH	24 81.208	4.7087	3.5423	4.4	0.7829	0.0174
50SILK	24 85.750	1.9836	1.6637	1.9	0.0193	0.3828
50BEG	24 81.208	4.7087	3.5423	4.4	0.7829	0.0174
50MAX	24 85.667	4.6966	3.5624	4.2	0.6776	0.0200
50END	24 84.042	4.9386	4.0444	4.8	0.9908	0.0429
ANTDUR	24 2.7917	0.93153	0.93541	33.5	0.5369	0.4244
DES	24 2.8750	5.0846	4.1209	143.3	0.2047	0.0688
SHEDDAYS	24 0.60417	1.0319	1.0522	174.2	0.1768	0.7468
HYPODURA	24 -.83333E-01	5.2163	4.4071	*****	0.2171	0.1098
ASI50	24 -4.5417	4.9342	3.7914	83.5	0.2803	0.0317
ITSI	24 -2.7917	1.7932	0.94176	33.7	0.0001	0.0111
50%TSI	24 -2.2500	2.0483	1.0351	46.0	0.0000	0.0712
SI2575	24 2.7500	1.0734	1.1339	41.2	1.0000	0.5050
TBRCHS	24 6.7458	2.1859	1.4065	20.8	0.3732	0.0031
TL	24 117.58	41.999	31.844	27.1	0.8328	0.0187
TML	24 31.083	3.5656	2.6601	8.6	0.5940	0.0171
TUBL	23 23.687	3.0943	2.5676	10.8	0.4975	0.0617
SILKSPRD	24 6.0833	1.2482	1.2125	19.9	0.9727	0.2536
TSPREAD	23 3.8261	1.0292	0.90734	23.7	0.7494	0.1107

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 24) OBS.	STANDARD		DEVIATION RESID SS	C OF V SD/MEAN %	REP	HYB
		TOTAL SS	BASED ON				
1TASEL	24	62.292	3.7472	3.0851	5.0	0.4534	0.0602
1SILK	24	67.250	3.3395	3.2468	4.8	0.9203	0.2609
1BEG	24	65.292	3.5075	3.1670	4.9	0.3103	0.1968
1MAX	23	67.826	3.3798	2.8992	4.3	0.1331	0.1831
1END	23	70.739	3.1220	2.6623	3.8	0.1493	0.1610
50%TASEL	22	62.773	2.6714	2.8633	4.6	0.8171	0.2425
50%ANTH	23	65.826	2.6569	2.9269	4.4	0.8438	0.5200
50%SILK	24	71.167	3.5098	3.3692	4.7	0.5793	0.2792
50%BEG	23	65.826	2.6569	2.9269	4.4	0.8438	0.5200
50%MAX	22	68.273	2.1198	2.3288	3.4	0.5021	0.5701
50%END	22	71.091	2.2659	2.4603	3.5	0.4797	0.5599
DURATION	23	5.5652	1.1610	1.2706	22.8	0.7581	0.5852
DES	24	1.9583	3.2900	2.3389	119.4	0.2259	0.0129
SHEDDAYS	22	4.1136	0.85818	0.96701	23.5	0.7371	0.7040
HYPODURA	23	3.5652	3.5525	2.8881	81.0	0.3439	0.0665
ASI50	23	-5.1739	2.9795	2.7294	52.8	0.6139	0.1809
1TSI	24	-4.9583	3.4826	2.7570	55.6	0.6223	0.0341
50%TSI	22	-8.0455	2.6811	2.3300	29.0	0.4805	0.0367
SI2575	24	3.0833	0.77553	0.76765	24.9	0.4241	0.4194
TB	24	7.5000	2.1264	2.1058	28.1	0.7037	0.3428
TL	24	102.46	30.553	28.873	28.2	0.9875	0.1943
SILKSPRD	24	10.375	2.5335	2.8126	27.1	0.5749	0.8210
TSPRD	23	3.7391	1.4212	1.13465	36.0	0.4403	0.2046

(c) MOUNT MAKULU - OPTIMAL NITROGEN

ANALYSIS OF VARIANCE SUMMARY TABLE FILE MAKUFLO 11/12/ 6 22:24 : PAGE 27

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	GRAND MEAN (N= 24)	STANDARD BASED ON TOTAL SS	DEVIATION BASED ON RESID SS	C OF V		HYB
				SD/MEAN %	REP	
1TASEL	24 60.917	4.3928	3.0237	5.0	0.7546	0.0060
1SILK	24 66.125	3.2878	2.1283	3.2	0.5776	0.0030
1BEG	24 65.625	5.0201	3.4122	5.2	0.9582	0.0049
1MAX	24 68.042	5.2542	3.4165	5.0	0.8957	0.0029
1END	24 71.792	5.0042	2.9930	4.2	0.7031	0.0011
50% T	24 63.250	4.2758	2.9307	4.6	0.5840	0.0061
50%ANTH	24 67.583	4.7358	3.1988	4.7	0.8227	0.0047
50%SILK	24 70.000	3.3622	1.8788	2.7	0.3011	0.0005
50%BEG	24 67.583	4.7358	3.1988	4.7	0.8227	0.0047
50%MAX	24 69.708	5.0775	3.2842	4.7	0.8978	0.0027
50%END	24 73.167	5.2143	3.7281	5.1	0.9374	0.0088
ANTHDURA	24 6.1667	2.4613	2.7288	44.3	0.5616	0.8210
DES	24 0.50000	4.0860	2.7613	55.2	0.5034	0.0052
SHEDDAYS	24 4.5208	1.4102	1.5182	33.6	0.5001	0.7293
HYPODURA	24 5.6667	4.7701	3.2395	57.2	0.9497	0.0048
ASI50	24 -2.4167	3.2157	2.1671	89.7	0.8472	0.0045
1TSI	24 -5.2083	3.1894	2.7091	52.0	0.4483	0.0864
50%TSI	24 -6.7500	2.8014	2.2106	32.8	0.9754	0.0283
SI2575	24 3.7083	1.1971	1.0607	28.6	0.2374	0.1808
TB	24 11.033	3.1742	1.7838	16.2	0.9253	0.0005
TL	24 201.26	54.730	29.109	14.5	0.5064	0.0003
TMBRCH	24 41.650	5.5222	3.6459	8.8	0.3724	0.0043
TUB	24 26.742	3.7274	2.3583	8.8	0.5534	0.0023
SILKSPRD	24 8.5833	1.1389	1.3025	15.2	0.6411	0.8996
TSPRD	24 6.3333	2.4077	2.2214	35.1	0.5850	0.1885

(d) GOLDEN VALLEY - OPTIMAL NITROGEN

ANALYSIS OF VARIANCE SUMMARY TABLE FILE GVOPTFLO 11/12/ 6 22:54 :PAGE 25

F-PROBABLIITY VALUES FOR EACH EFFECT IN THE MODEL. SECTION - 1

VARIATE	NO. OBS.	GRAND MEAN (N= 24)	STANDARD		DEVIATION BASED ON RESID SS	C OF V		REP	HYB
			TOTAL SS	RESID SS		SD	MEAN %		
1TASEL	24	56.083	5.0812	4.7491	8.5	0.4769	0.2335	0.2335	
1SILK	24	62.417	2.1247	1.8708	3.0	0.9536	0.0960	0.0960	
1BEG	24	60.875	3.3010	3.0394	5.0	0.5416	0.1906	0.1906	
1MAX	24	62.458	3.7530	3.2977	5.3	0.5660	0.1146	0.1146	
1END	24	64.167	4.0931	3.7639	5.9	0.7529	0.1647	0.1647	
50%TASEL	24	57.958	4.7041	4.2454	7.3	0.4548	0.1664	0.1664	
50%ANTH	24	62.542	3.4133	2.7635	4.4	0.5051	0.0477	0.0477	
50%STLK	24	65.000	1.7195	1.3693	2.1	0.6411	0.0362	0.0362	
50%BEG	24	62.542	3.4133	2.7635	4.4	0.5051	0.0477	0.0477	
50%MAX	24	63.750	3.4421	3.0667	4.8	0.7000	0.1222	0.1222	
50%END	24	65.333	3.7144	3.7009	5.7	0.8194	0.3401	0.3401	
DURATION	24	3.2917	1.1971	1.1019	33.5	0.8729	0.1570	0.1570	
DES	24	1.5417	3.0925	2.7212	176.5	0.3604	0.1397	0.1397	
SHEDDAYS	24	2.1875	1.2407	1.3234	60.5	0.7980	0.5862	0.5862	
HYPDURA	24	1.7500	3.6025	3.2660	186.6	0.5867	0.1573	0.1573	
ASI50	24	-2.4583	3.1205	2.6266	106.8	0.7516	0.0642	0.0642	
1TSI	24	-6.3333	4.9840	4.4192	69.8	0.3989	0.1455	0.1455	
50%TSI	24	-7.0417	4.8137	4.1683	59.2	0.3626	0.1167	0.1167	
SI2575	24	2.4167	1.0180	1.0494	43.4	0.3390	0.6320	0.6320	
TB	24	10.583	2.4480	1.7269	16.3	0.3113	0.0105	0.0105	
TL	24	133.00	23.692	19.672	14.8	0.4048	0.0694	0.0694	
SILKSPRD	24	5.8333	1.3406	1.1852	20.3	0.1402	0.2264	0.2264	
TSPRD	24	5.4167	1.4116	1.5099	27.9	0.4332	0.7353	0.7353	

Appendix 2: Multiple regression analysis results

(a) MAKOPT

FORWARD STEPWISE REGRESSION: TEST LEVEL = 0.20, MAX STEPS = 46,

STEP	VARIATE	RESIDUAL MS.	DF	CHANGE IN RSS	F-VALUE	PRBF
1 ADD	SHELL% (9)	5196.56	21	155619.	29.95	0.00
2 ADD	100SWT (8)	3546.40	20	38199.7	10.77	0.00
3 ADD	EPP (11)	1797.26	19	36780.0	20.46	0.00
4 ADD	PLTSTND (10)	1625.80	18	4883.67	3.00	0.10
5 ADD	50%SILK (16)	1397.32	17	5509.84	3.94	0.06
6 ADD	SHEDDAYS (19)	1206.91	16	4444.01	3.68	0.07
7 ADD	ANTHSPRD (26)	994.641	15	4390.87	4.41	0.05

TERM	NO	COEFFICIENT	STD. ERROR	F-VALUE	PRBF	TOLERANCE
CONSTANT	28	-2771.790	635.374	19.031	0.001	0.1071E-03
100SWT	8	-4.830203	1.86451	6.711	0.020	0.5117
SHELL%	9	29.04328	4.19410	47.953	0.000	0.4021
PLTSTND	10	-3.445888	1.18627	8.438	0.011	0.3194
EPP	11	200.0459	87.6925	5.204	0.036	0.5312
PH	12	ZERO		0.445	0.521	0.2551
EH	13	ZERO		0.118	0.735	0.1249
LFA	14	ZERO		0.001	0.969	0.6271
50%ANTH	15	ZERO		0.534	0.482	0.2280
50%SILK	16	13.28220	4.31846	9.460	0.008	0.2553
ANTHDURA	17	ZERO		0.108	0.745	0.1843
DES	18	ZERO		1.192	0.293	0.5603
SHEDDAYS	19	-12.16551	5.34558	5.179	0.036	0.7650
ASI50	21	ZERO		0.534	0.482	0.5335
TB	23	ZERO		0.385	0.551	0.5435
TL	24	ZERO		0.006	0.939	0.3786
STILKSPRD	25	ZERO		0.047	0.826	0.8004
ANTHSPRD	26	7.856409	3.73923	4.415	0.051	0.4413

SOURCE	SS	DF	MS	F	PRBF
REGRESSION	249827.6	7	35689.66	35.882	0.0000
RESIDUAL	14919.61	15	994.6409		
TOTAL	264747.2	22			

R-SQUARED = 94.4%, (ADJUSTED FOR D.F. = 91.7%)

(b) GVOPT

FORWARD STEPWISE REGRESSION, TEST LEVEL = 0.20, MAX STEPS = 46,

STEP	VARIATE	RESIDUAL MS.	DF	CHANGE IN RSS	F-VALUE	PRBF
1 ADD	EPP (11)	10247.3	21	104046.	10.15	0.00
2 ADD	100SWT (8)	4042.29	20	134347.	33.24	0.00
3 ADD	SHELL% (9)	2486.94	19	33593.9	13.51	0.00
4 ADD	ANTHSPRD (26)	2222.93	18	7239.14	3.26	0.08

TERM	NO	COEFFICIENT	STD. ERROR	F-VALUE	PRBF	TOLERANCE
CONSTANT	28	-1750.703	621.225	7.942	0.011	0.2504E-03
100SWT	8	-11.01963	1.52336	52.327	0.000	0.9557
SHELL%	9	24.89893	7.27738	11.706	0.003	0.9517
PLTSTND	10	ZERO		1.544	0.228	0.7263
EPP	11	717.1589	88.4319	65.768	0.000	0.8646
PH	12	ZERO		0.153	0.701	0.6693
EH	13	ZERO		0.031	0.856	0.6267
LFA	14	ZERO		0.732	0.408	0.5284
50%ANTH	15	ZERO		0.255	0.625	0.5682
50%SILK	16	ZERO		0.039	0.840	0.7192
ANTHDURA	17	ZERO		0.087	0.769	0.2590
DES	18	ZERO		0.042	0.833	0.9059
SHEDDAYS	19	ZERO		0.014	0.901	0.8221
ASI50	21	ZERO		0.132	0.720	0.7999
TB	23	ZERO		0.001	0.969	0.9010
TL	24	ZERO		0.760	0.399	0.9408
SILKSPRD	25	ZERO		0.288	0.604	0.6742
ANTHSPRD	26	-14.75544	8.17658	3.257	0.085	0.8067

SOURCE	SS	DF	MS	F	PRBF
REGRESSION	279226.9	4	69806.72	31.403	0.0000
RESIDUAL	40012.72	18	2222.929		
TOTAL	319239.6	22			

R-SQUARED - 87.5%, (ADJUSTED FOR D.F. - 84.7%)

(C) GVLN

FORWARD STEPWISE REGRESSION, TEST LEVEL = 0.20, MAX STEPS = 46,

STEP	VARIATE	RESIDUAL MS.	DF	CHANGE IN RSS	F-VALUE	PRBF
1 ADD	PLTSTND (10)	6817.91	13	122471.	17.96	0.00
2 ADD	SHELL% (9)	4762.89	12	31478.2	6.61	0.02
3 ADD	SHEDDAYS (19)	3952.59	11	13676.2	3.46	0.09
4 ADD	EPP (11)	3123.64	10	12242.1	3.92	0.07
5 ADD	50%SILK (16)	2525.98	9	8502.56	3.37	0.10

TERM	NO	COEFFICIENT	STD. ERROR	F-VALUE	PRBF	TOLERANCE
CONSTANT	29	-2564.895	815.949	9.881	0.012	0.2529E-03
100SWT	8	ZERO		0.085	0.773	0.6161
SHELL%	9	19.14658	5.26816	13.209	0.005	0.6597
PLTSTND	10	-4.150379	1.86075	4.975	0.051	0.4176
EPP	11	256.1325	95.9092	7.132	0.025	0.5949
PH	12	ZERO		1.262	0.291	0.9667
EH	13	ZERO		0.879	0.376	0.5676
LFA	14	ZERO		0.035	0.849	0.3156
50%ANTH	15	ZERO		0.005	0.945	0.6671
50%SILK	16	13.49296	7.35440	3.366	0.097	0.4035
ANTHDURA	17	ZERO		1.820	0.209	0.2230
DES	18	ZERO		0.440	0.529	0.6857
SHEDDAYS	19	46.90339	19.4051	5.842	0.038	0.6892
ASI50	21	ZERO		0.005	0.945	0.4457
TB	23	ZERO		0.213	0.658	0.3713
TL	24	ZERO		0.237	0.642	0.5381
SILKSPRD	25	ZERO		0.141	0.715	0.3343
ANTHSPRD	26	ZERO		0.072	0.789	0.3829

SOURCE	SS	DF	MS	F	PRBF
REGRESSION	188370.5	5	37674.10	14.915	0.0005
RESIDUAL	22733.83	9	2525.981		
TOTAL	211104.3	14			

R-SQUARED - 89.2%, (ADJUSTED FOR D.F. - 83.2%)

(d) NANG

FORWARD STEPWISE REGRESSION, TEST LEVEL = 0.20, MAX STEPS = 46,

STEP	VARIATE	RESIDUAL MS.	DF	CHANGE IN RSS	F-VALUE	PRBF
1 ADD	EPP (11)	2384.47	22	107913.	45.26	0.00
2 ADD	SHELL% (9)	1058.42	21	30231.6	28.56	0.00
3 ADD	LFA (14)	865.858	20	4909.66	5.67	0.03
4 ADD	100SWT (8)	789.168	19	2322.98	2.94	0.10

TERM	NO	COEFFICIENT	STD. ERROR	F-VALUE	PRBF	TOLERANCE
CONSTANT	28	-358.1591	70.6394	25.707	0.000	0.6590E-02
100SWT	8	-2.022683	1.17894	2.944	0.099	0.9052
SHELL%	9	3.975614	0.699276	32.323	0.000	0.7833
PLTSTND	10	ZERO	0.692	0.421	0.421	0.7321
EPP	11	358.6335	54.3805	43.493	0.000	0.7269
PH	12	ZERO	0.156	0.699	0.6867	0.9014
EH	13	ZERO	0.025	0.870	0.9062	0.9062
LFA	14	0.1052861	0.416255E-01	6.398	0.020	0.9062
50%ANTH	15	ZERO	0.625	0.444	0.8204	0.8204
50%SILK	16	ZERO	0.867	0.366	0.5299	0.5299
ANTHDURA	17	ZERO	0.616	0.448	0.8542	0.8542
DES	18	ZERO	0.210	0.656	0.8546	0.8546
SHEDDAYS	19	ZERO	0.013	0.908	0.8022	0.8022
ASI50	21	ZERO	0.196	0.666	0.8602	0.8602
TB	23	ZERO	1.587	0.221	0.7264	0.7264
TL	24	ZERO	1.303	0.267	0.8461	0.8461
SILKSPRD	25	ZERO	0.059	0.805	0.8010	0.8010
ANTHSPRD	26	ZERO	0.270	0.615	0.6768	0.6768

SOURCE	SS	DF	MS	F	PRBF
REGRESSION	145377.0	4	36344.24	46.054	0.0000
RESIDUAL	14994.18	19	789.1676		
TOTAL	160371.2	23			

R-SQUARED - 90.7%, (ADJUSTED FOR D.F.- 88.7%)

(e) COMBINED

FORWARD STEPWISE REGRESSION, TEST LEVEL = 0.20, MAX STEPS = 46,

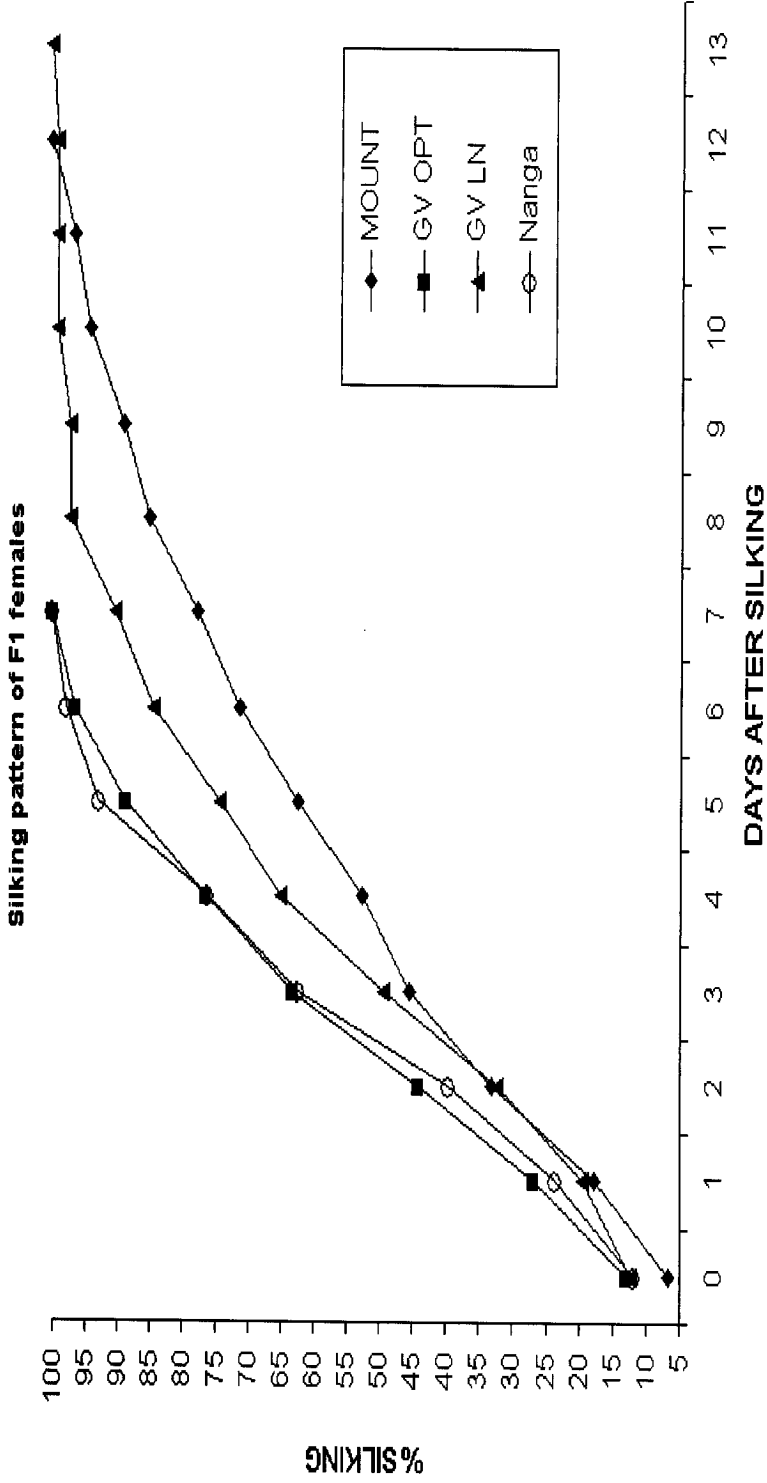
STEP	VARIATE	RESIDUAL MS.	DF	CHANGE IN RSS	F-VALUE	PRBF
1 ADD	EPP (11)	11155.5	83	0.166788E+07	149.51	0.00
2 ADD	SHELL% (9)	9628.94	82	136333.	14.16	0.00
3 ADD	TB (23)	8999.99	81	60574.6	6.73	0.01
4 ADD	PH (12)	8650.10	80	36990.8	4.28	0.04
5 ADD	100SWT (8)	8275.04	79	38279.5	4.63	0.03
6 ADD	SILKSPRD (25)	7968.70	78	32170.0	4.04	0.05
7 ADD	50%SILK (16)	7625.71	77	34379.2	4.51	0.03
8 ADD	EH (13)	6958.94	76	58300.3	8.38	0.00
9 DROP	TB (23)	6996.53	77	-9853.80	1.41	0.24

TERM	NO	COEFFICIENT	STD. ERROR	F-VALUE	PRBF	TOLERANCE
CONSTANT	30	400.2020	299.652	1.784	0.182	0.9167E-03
100SWT	8	-3.908730	1.18075	10.959	0.002	0.8646
SHELL%	9	3.618503	1.95472	3.427	0.065	0.6417
PLTSTND	10	ZERO		0.102	0.749	0.6150
EPP	11	442.9952	71.4644	38.425	0.000	0.5073
PH	12	2.001157	0.596874	11.241	0.001	0.1426
EH	13	-1.885995	0.628431	9.007	0.004	0.9363E-01
LFA	14	ZERO		0.034	0.848	0.3745
50%ANTH	15	ZERO		0.677	0.418	0.1628
50%SILK	16	-10.07480	2.30211	19.152	0.000	0.2171
ANTHPURA	17	ZERO		0.346	0.565	0.7524
DES	18	ZERO		1.610	0.206	0.8246
SHEDDAYS	19	ZERO		1.646	0.200	0.5176
ASI50	21	ZERO		0.677	0.418	0.7854
TB	23	ZERO		1.408	0.237	0.5881
TL	24	ZERO		0.362	0.556	0.7880
SILKSPRD	25	-9.508578	4.81019	3.908	0.049	0.6955
ANTHSPRD	26	ZERO		0.589	0.451	0.7778

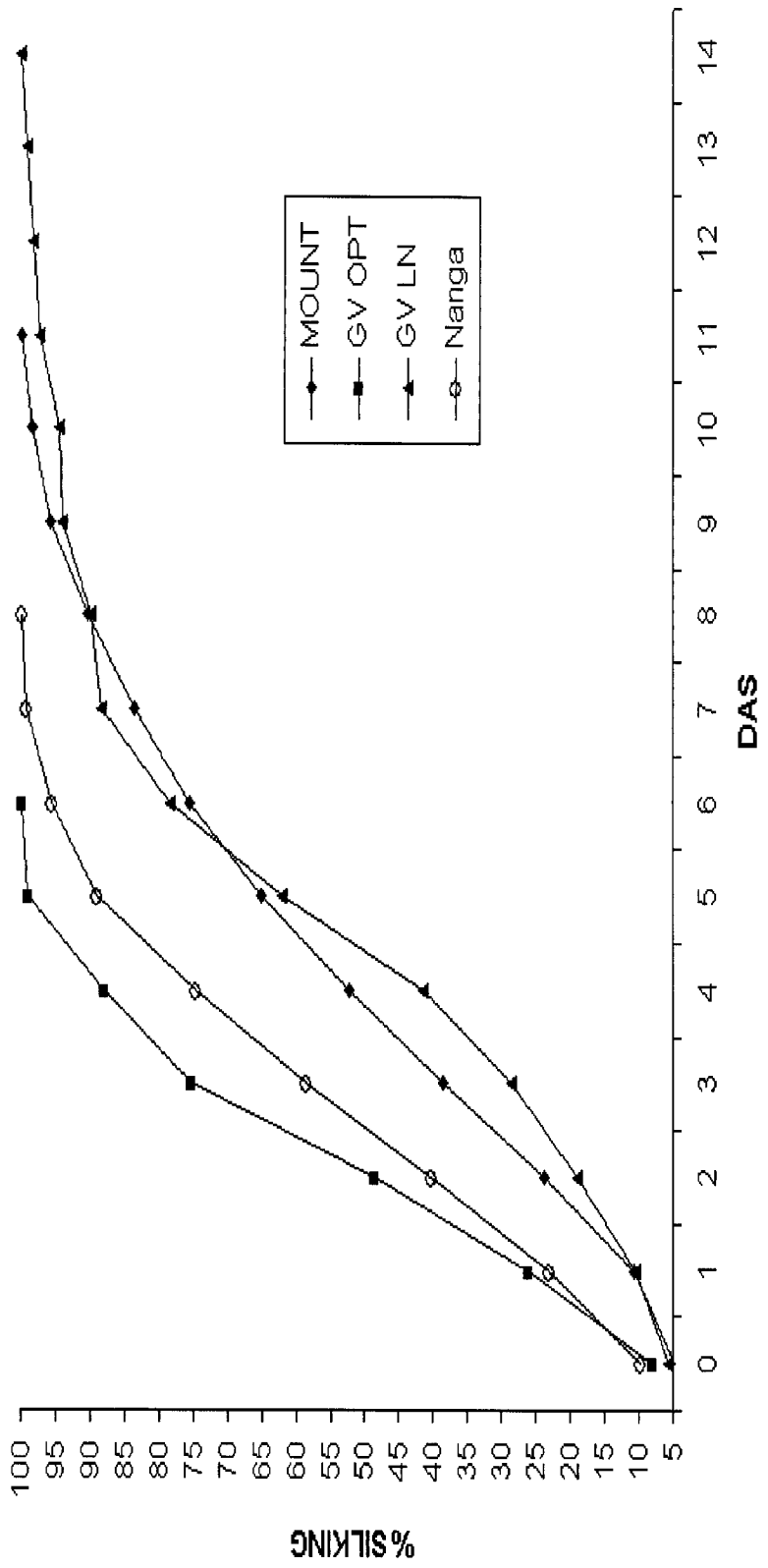
SOURCE	SS	DF	MS	F	PRBF
REGRESSION	2055057.	7	293579.6	41.961	0.0000
RESIDUAL	538732.9	77	6996.531		
TOTAL	2593790.	84			

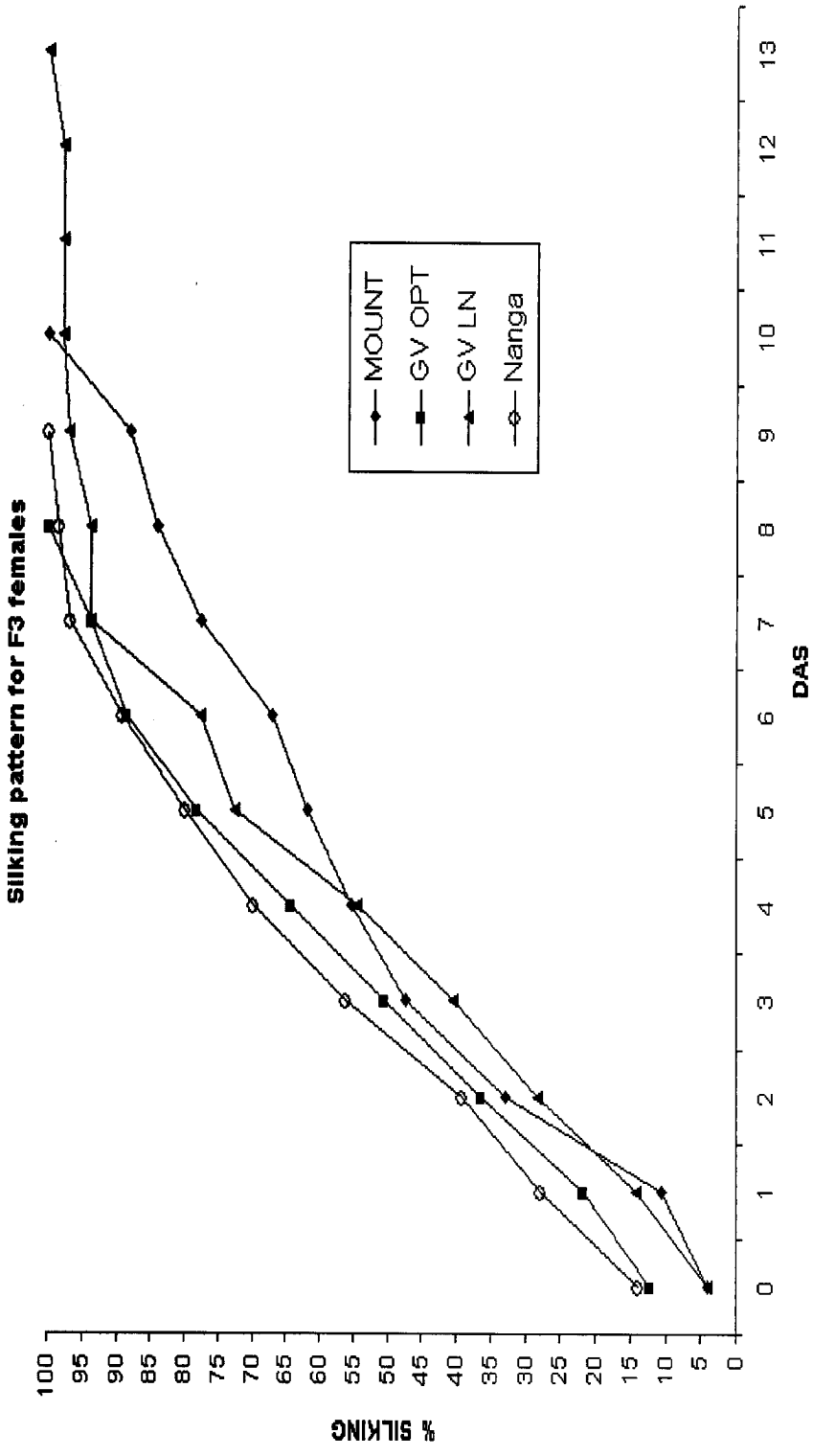
R-SQUARED = 79.2%, (ADJUSTED FOR D.F. = 77.3%)

Appendix 3: Silking dynamics of the grouped females (females 1 – 3) under low N, Water stress, Optimal N and Optimal N with high plant population.

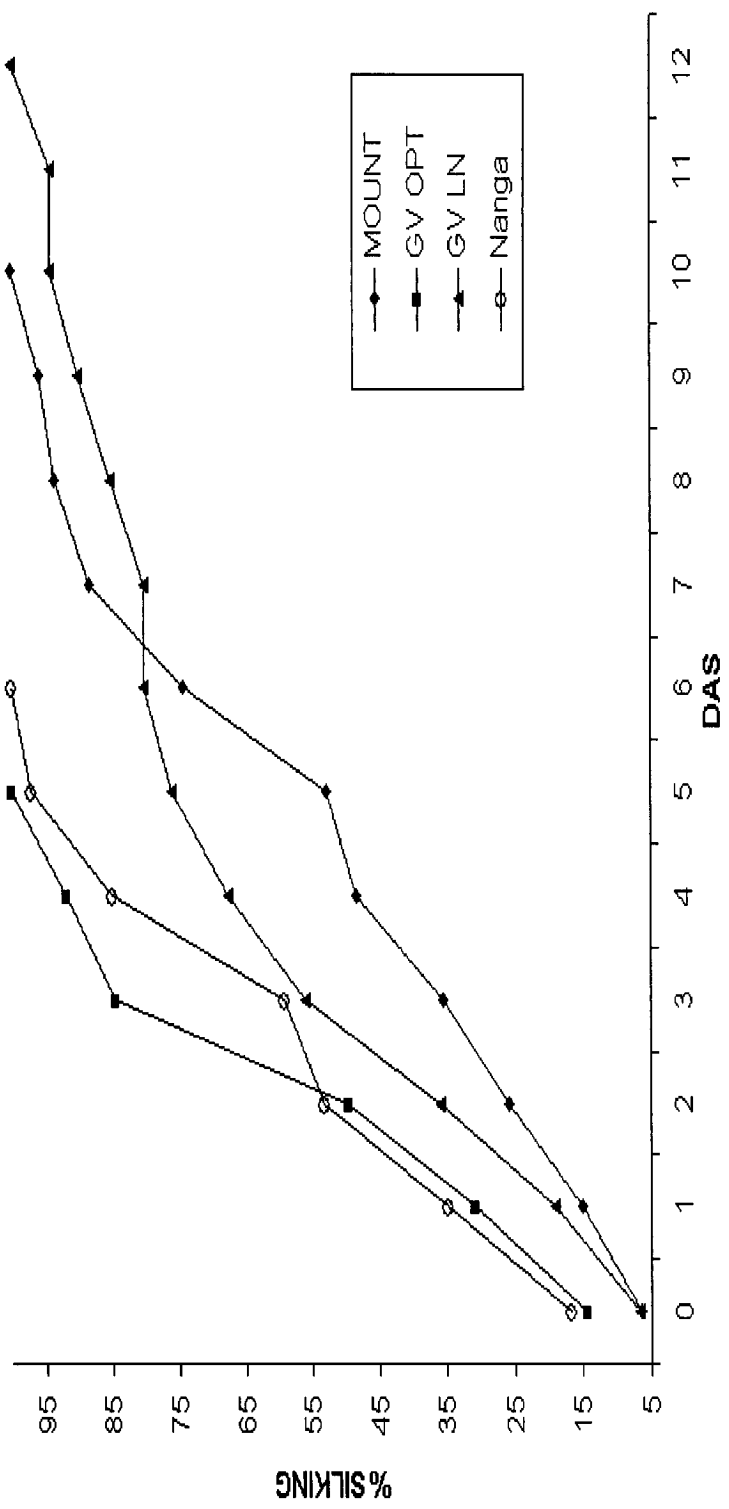


Silking pattern for F2 females



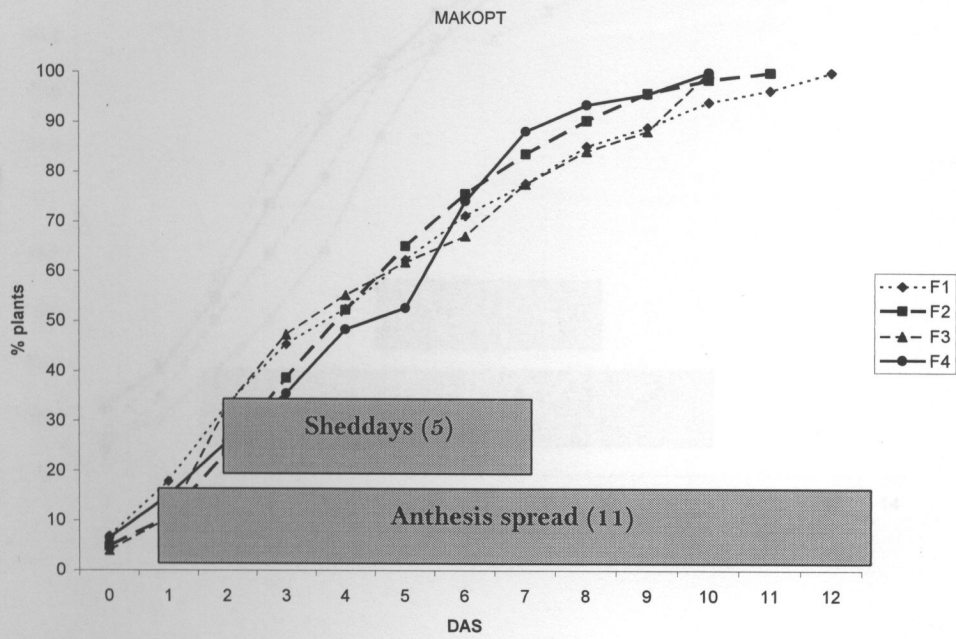


Silking pattern for F4 females

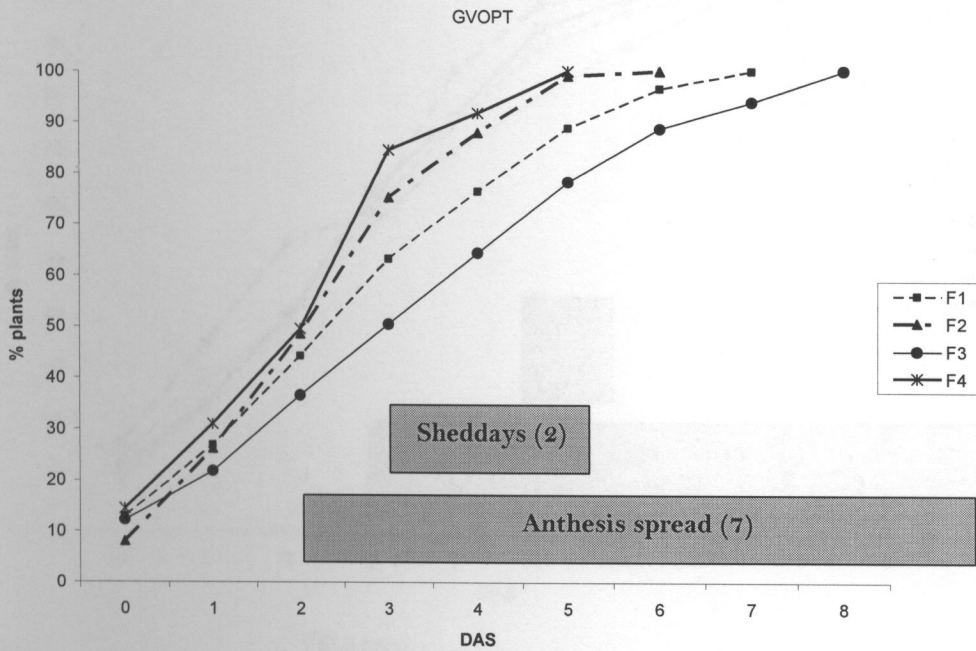


Appendix 4: Dynamics of pollen shedding and silking for different females at each environment

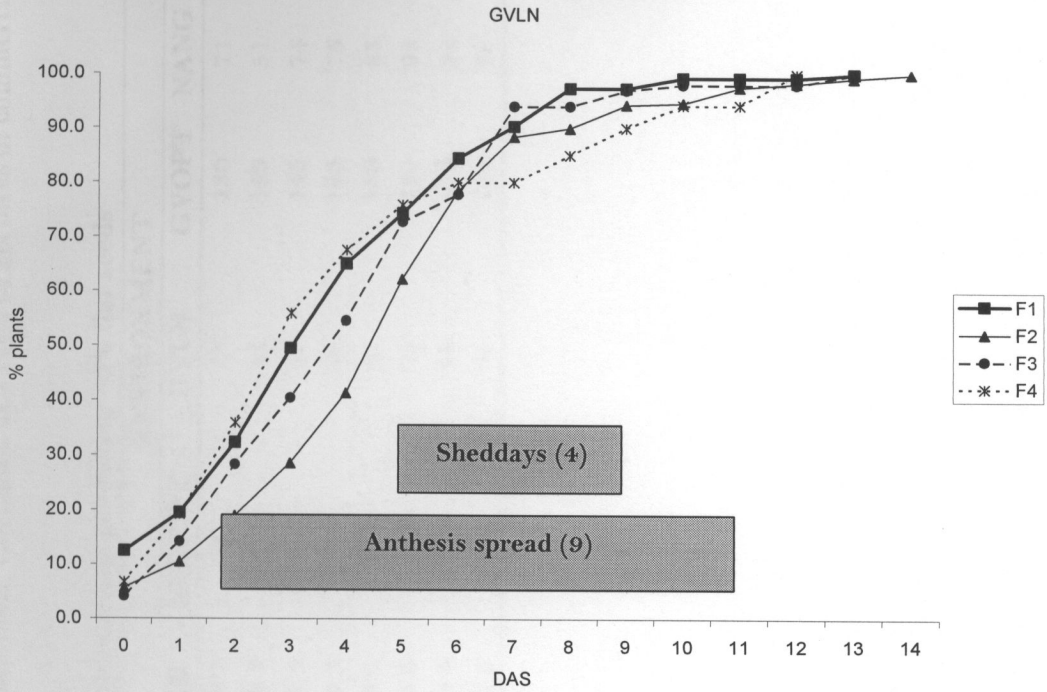
(a) MOUNT MAKULU OPTIMAL



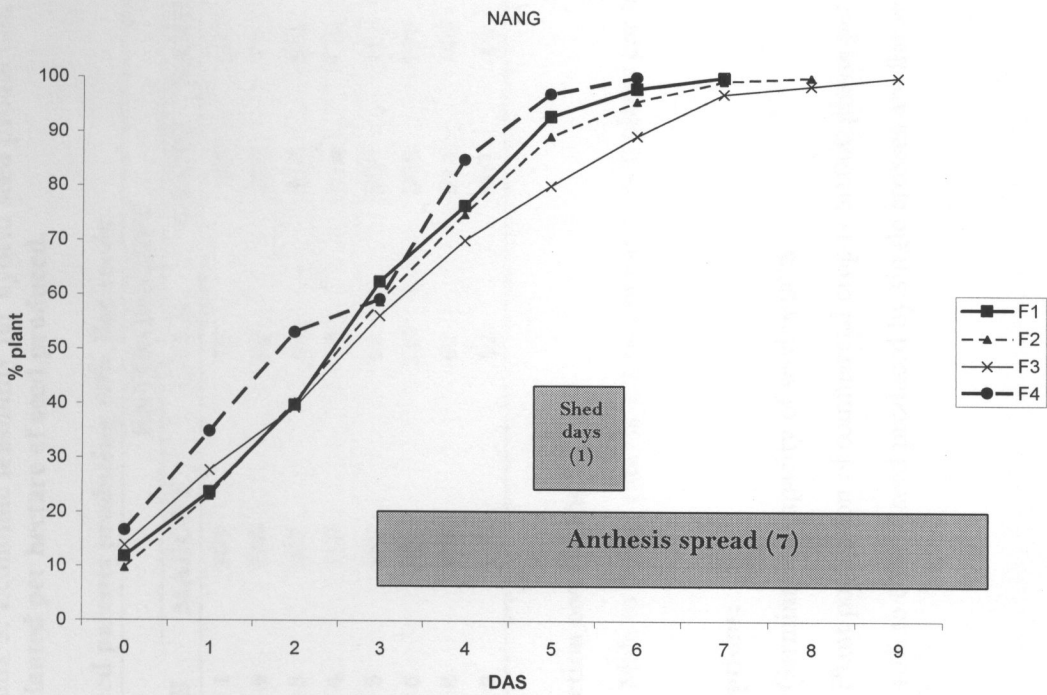
(b) GVOPT



(c) GVLN



(d) NANG



Appendix 5: Economic feasibility for hybrid seed production under various conditions, calculated as a ratio of hectares of commercial crop planted per hectare of seed produced.

(a) Seed parents producing 60% flat seeds

HYB	MAKOPT	ENVIRONMENT		
		GVLN	GVOPT	NANG
Hyb 1	204	76	196	106
Hyb 2	256	62	239	77
Hyb 3	207	86	218	111
Hyb 4	169	43	214	112
Hyb 5	190	62	270	124
Hyb 6	166	117	208	138
Hyb 8	172	61	213	123
Hyb 9	147	32	197	42

(b) Seed parents producing 40% flat seeds

HYB	MAKOPT	ENVIRONMENT		
		GVLN	GVOPT	NANG
Hyb 1	136	51	130	71
Hyb 2	171	41	159	51
Hyb 3	138	57	145	74
Hyb 4	113	29	143	75
Hyb 5	127	41	180	83
Hyb 6	111	78	139	92
Hyb 8	114	41	142	82
Hyb 9	98	21	131	28

Production conditions:

- Male to female ratio is 1:3, planted at 53,000 plants per hectare.

Assumptions:

- Germination capacity of seed is 90%
- Plant population of commercial crop is 50,000 plants per hectare
- 40% to 60% of seed produced by single crosses are flat seeds (Curtis, 1980)