

GENETICS OF MATURITY AND PHOTOPERIOD  
SENSITIVITY IN MAIZE

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**ABSTRACT**

Ninety tropical-adapted maize inbreds were evaluated for maturity and photoperiod sensitivity under short daylength (SD) environment in Hawaii, and under long daylength (LD) environments in Iowa, and Korea. Extensive genotypic variations were observed for the two traits among these inbreds. There was no single inbred classified as strictly day-neutral. Inbreds that exhibited early maturity and low photoperiod sensitivity were mostly temperate-derived, while those that exhibited late maturity and high photoperiod sensitivity were exclusively tropical-derived.

Diallel analysis (Analysis III of Gardner and Eberhart, 1966) revealed that variations among general combining ability (GCA) estimates were much larger than variations among specific combining ability (SCA) estimates for days to anthesis, silking, blacklayer formation, and their respective delays. GCA and SCA variations contributed more or less equally to the expression of anthesis to silking interval, and grain filling period.

High GCA/SCA ratios indicated large additive genetic variation for maturity and photoperiod sensitivity traits. Estimates of heterosis included in the model, however, were high in most cases which suggested that non-additive genetic variation was also important in the inheritance of these traits.

Generation mean analyses showed that additive and dominance gene effects were highly significant in a majority of the crosses. Magnitude of estimates varied with types of crosses, but in general, dominance gene effects had greater magnitude than additive gene effects for maturity and photoperiod sensitivity. Significant amounts of epistatic gene effects were detected, but they seemed to cancel each other, thus leaving dominance gene effects as the main contributors to the inheritance of the two traits. Maturity appeared to be controlled by few genes (between two and four).

Three cycles of divergent mass selection for silking dates of two tropical maize composites were evaluated under SD environments in Waimanalo and Kauai and under extended daylength in Waimanalo. Selection was effective in diverging silking dates in both populations. Selection for early and late silking resulted in decreased and increased photoperiod sensitivity, respectively. The strong correlated effects of selection on photoperiod sensitivity suggested that short-day maturity and photoperiod sensitivity were under common genetic control. Pleiotropic effects of genes were most likely behind this relationship.

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## 1. INTRODUCTION

Effective selection for acceptable maturity is one of the problems encountered in breeding exotic germplasm for local adaptation. Confounding maturity is the effect of photoperiod as genetic materials moved from low to high latitudes and vice versa. Thus, problems in practical breeding due to photoperiod sensitivity become evident in two different situations: a) when integrating tropical germplasm in temperate breeding programs; and b) when temperate cultivars are to be used in the tropics (Salamini, 1985).

Maize is basically a quantitative short-day plant. In essence, the photoperiodic response of maize refers to an increase of the length of the growth cycle in response to longer days. Consequently, most maize cultivars from the tropics and subtropics develop excessive vegetative growth and exhibit delayed floral initiation when brought into the long day environment of the temperate zones (Troyer and Brown, 1972). On the other hand, temperate cultivars also express photoperiod sensitivity in the tropics, where they grow very short with fewer leaves and extreme earliness (Brewbaker, 1981). Photoperiod effects on maturity and morphology, therefore, limit the rapid exchange of germplasm across latitudes. This constraint is felt more in the U.S. Corn Belt where there is a need to widen genetic diversity. Wellhausen (1965) and Geadelmann (1984) emphasized the

tremendous potential for the improvement of maize in the Corn Belt with the use of exotic germplasm.

Substantial variation has been established among cultivars for maturity per se (Brewbaker et al., 1989; Hallauer and Russell, 1962; Giesbrecht, 1960a, 1960b; Jones, 1955) and photoperiod sensitivity (Aitkin, 1977; Francis et al., 1969, and 1970; Spencer, 1974; Stevenson and Goodman, 1972; Lee, 1978; Russell and Stuber, 1985). However, the genetics of these variations are not well understood, and the use of different measurements has contributed more to the confusion. The key question, largely unanswered, is whether the genetic control of photoperiod sensitivity is distinct from the maturity expressed under short days (Russell and Stuber, 1983). Genetic information about maturity, photoperiod sensitivity and the interaction between them is important in the formation of breeding pools that are insensitive to changes in daylengths.

General objectives of the study were as follows:

- 1) to evaluate a worldwide collection of tropical-adapted inbreds for maturity and photoperiod sensitivity;
- 2) to determine combining abilities as well as the type and magnitude of gene action for maturity per se and photoperiod sensitivity; and
- 3) To determine the genetic relationship between maturity and photoperiod sensitivity.

## 2. LITERATURE REVIEW

### 2.1 Floral Development in Corn

Corn plant development has been described by a number of workers (Bonnett, 1940; Kiesselbach, 1949; Leng, 1951; Weatherwax, 1955). Tassel initiation marks the beginning of the reproductive stage, considered to be the stage at which the growing points have elongated and lateral projections or branch initials had arisen acropetally from the growing point of the central axis (Bonnett, 1940, 1953, 1954, 1956). Siemer, Leng and Bonnett (1969) later defined tassel initiation as the lengthening of the shoot apical meristem prior to the appearance of tassel branch or spikelet primordia, when the growing meristem reached 0.4 mm in length. They further defined ear initiation as the lengthening of the axillary meristem prior to the appearance of the spikelet-forming branch primordia, usually to a length of 0.5 mm. Ear differentiation initially appears very similar to tassel differentiation. One difference between the two is that the ear has prominent subtending ridges (Hanway, 1985). Ear differentiation occurs when spikelet-forming branch primordia develop from the apex just above the subtending ridges (Bonnett, O. T., 1953, 1966). Genetic differences in days to tassel and ear initiation in corn were reported by Martin and Hershey, 1934; Kiesselbach, 1949; Leng, 1951, and Siemer et al. 1969. Methods and models for estimating tassel initiation in corn

have been provided by Aitkin (1971, 1974, 1976) and Colligado and Brown (1957b).

Time relationships of the series of developmental events leading to the emergence of the tassel and the ear shoot, and subsequently anthesis and silking were discussed by Leng (1951) and Siemer et al. (1969). Timing of anthesis and silking has been primarily used to determine the relative maturities of corn cultivars.

### **2.1.1 Factors Affecting Flowering in Corn**

Environment plays a major role in the development of corn inflorescence from the time of flower initiation to actual flowering. Major (1980) described the general response of maize to environmental factors that influence flowering. Among the most important are daylength, temperature, moisture, and soil fertility. Probably the most important and most studied in corn are the effects of temperature and photoperiod and their interaction. The general response to temperature in corn is positive (Aitkin, 1974) as in other temperate cereals but with a higher threshold (above 15 C). Flowering or maturity can be accurately predicted by using growing degree units (Nanda et al., 1984; Cross and Zuber, 1972; Russelle et al., 1984). Photoperiod sensitivity has generated much interest since it is one of the most important factors affecting flowering, hence adaptation of corn. Studies have devoted to the photoperiodic response in corn are reviewed in the

next sections. Much information has been gathered on the effects of these environmental factors on the flowering of cereal crops (Friend, 1965; Friend et al., 1963; Bonaparte, 1975; Puckridge, 1968. Warrington, 1977; Aitkin, 1966; Williams and Williams, 1968).

### **2.1.2 Timing of Flowering as Measure of Corn Maturity**

Maturity is an important objective in corn breeding, thus a reliable measurement is necessary. Determination of the relative maturity of a cultivar is a problem particularly acute for commercial corn breeder working in the Northern Corn Belt, where frost is a continual threat to the crop (Gunn and Christensen, 1964). Jugenheimer (1976) reviewed the measures of maturity that were utilized by different workers. They included days or heat units from planting or emergence to midsilking or midtasseling; days or heat units from planting or emergence to physiological maturity (blacklayer formation) or maximum dry matter accumulation; percentage of dry matter or moisture in the grain at harvest; and leaf number.

Choice of maturity parameters is dictated more by practical considerations. For example, to a plant breeder, flowering time (anthesis and silking) is usually the most important, while for the farmers grain moisture at harvest is probably the most critical (Gunn and Christensen, 1964). Timing of flowering has been a popular and convenient way of measuring maturity because it is relatively less tedious

compared to other methods. Studies by Shaw and Tom (1951) and Hallauer and Russell (1962) indicated that maturity could be predicted at silking time since the interval from silking to maturity is constant. Some workers, however, found variation among inbreds for this interval (Carter and Poneleit, 1973; Daynard and Kannenberg, 1976). Earlier studies noted a very high correlation between silking and maturity parameters. Jugenheimer (1958) obtained a 0.93 correlation between silking and physiological maturity. Similar results were reported by Snelling and Hoener (1940) and Aldrich (1942). Allen et al. (1973) reported high and positive correlations between leaf number and silking date and moisture at harvest. Other workers reported high associations among maturity parameters (Chase and Nanda, 1966 and 1967; Gunn and Christensen, 1964; Shaw and Tom, 1951). Most studies on the inheritance of maturity have used the date of silking or pollen shedding as their basis of maturity (Hallauer and Russell, 1962; Lee, 1978).

## **2.2 Photoperiodism in Plants**

Photoperiodism has been defined as a response of plant to daylength which enable it to adapt to seasonal changes in the environment (Thomas and Vince-Prue, 1984). Hillman (1969) defined it as a control of some aspect of the plant life cycle by the timing of the light and darkness. Photoperiodism regulates the seasonality of many biological processes, because daylength changes in the regular annual

pattern almost everywhere in the world. Biological effects of daylength on the regulation of the flowering time in plants was first noticed by Julian Tuornois (Vince-Prue, 1975). Garner and Allard (1920, 1923), however, determined that differences in daylength cause different flowering responses in plants. They were the first to report that for some maize cultivars, flowering is delayed under long days relative to short day photoperiod.

It has been a common impression that most corn lines, notably the temperate, ones are day neutral and show no response to long days. This has been refuted, however, by the findings of several researchers (Russell and Stuber, 1983). In Waimanalo, Hawaii, at 20° N latitude and considered as a day-neutral environment (Brewbaker, 1985), all corn inbreds showed some delay in flowering under 16-hour day using artificial lights.

### **2.2.1 Photoperiodic Response Categories**

Response to photoperiod can be classified into three main groups: 1) Short-day plants (SDP) which only flower, or flower most rapidly, under daylength shorter than a particular period of light in each 24-hour cycle; this certain number of light hours is called the "critical daylength"; 2) Long-day plants (LDP) which only flower, or flower most rapidly with daylength longer than the critical; and 3) Day-neutral plants (DNP) which flower at the same time regardless of daylength. These groups are further

subdivided into two types of response: qualitative or absolute photoperiodic response, and the quantitative photoperiodic response. The former refers to a response in which particular daylength is essential to flowering, while the latter is when a particular daylength promotes but is not essential to flowering. Vince-Prue (1975) listed plants according to their different photoperiodic classifications.

The difference between LDP and SDP does not lie in the absolute value of the critical daylength itself, but rather in whether the process in question, e.g., flowering, takes place at daylengths longer or shorter than the critical value. Thus, a plant categorized as SDP may have a longer critical value than a plant categorized as LDP. As an example, Hyoscyamus niger (LDP) has a critical daylength of only 11 hours, while Xanthium strumarium has a critical daylength of 15.5 hours (Thomas and Vince-Prue, 1984).

### 2.2.2 Timing of Photoperiod.

Timing rather than the total energy received is crucial in photoperiodism. This was shown by the experiment whereby some species with a critical daylength for SD response of 14 hours had a long day response to 18 hours of white fluorescent light of about 20,000 lux. Reducing the incident light to 5,000 lux did not have a short-day effect, but reducing the total light period to less than the critical produced a short day effect. Reducing the quantity



of light is different from reducing its duration in the normal 24-hour cycle of the same factor.

Two generalizations have been advanced to account for the scheduling of light and darkness. Either different basic mechanisms may be involved, depending on the species, or differences in mechanisms which were unrelated to major phylogenetic groups (Head, 1979).

For the type of mechanism involved in photoperiodic timing, two different hypotheses were postulated: 1) Hourglass timing hypothesis which states that the timing is a result of a series of unidirectional biochemical reactions beginning at the start of the dark period, and when not interrupted by light, proceeds to completion and induction. An analogy is made with an hourglass which does not cycle on its own like a clock, but must be turned over to continue timing; 2) The second hypothesis states that photoperiodism involves the biological rhythms or circadian clock. Most of the accumulated evidence support this hypothesis. Control of flowering by photoperiod may be related to the rhythmic changes in response to light.

### **2.2.3 Photoreception and Induction**

The site of daylength perception occurs in the leaf, although response is expressed in the plant apex. Photoperiodism is independent of photosynthesis which might have some value for their evolution and survival.

Studies have shown that flowering can be induced by exposing a single leaf to favorable light/dark cycles. Grafting experiment (Zeevart, 1976) confirmed the role of leaves in photoreception. These experiments suggested that photoreception is separate from evocation which is the transition of flowering to the apex, and that the transmission of a floral stimulus is required. Induction, an important aspect of photoperiodism, is the degree to which the response persists after the treatment that starts them. This phenomenon means that the effect of a relatively brief exposure to a particular light schedule is subsequently expressed no matter what light schedule is imposed later on. Some plants showed weak while others showed strong induction.

The molecular basis of photoperiodism was first elucidated by Borthwick et al. (1948) and S. B. Hendricks (1960). They were able to identify the substance that absorbed the photoperiodically effective light. In their experiments with soybean and cocklebur, which are SDP's, they found out that the most effective wavelength for inhibiting flowering was in the red spectrum (660 nm). Effect of the red light break, either to inhibit flowering in SDP, or to promote it in LDP, could be prevented by a light break with a wavelength of 730 nm (far red). This was called the "reversal effect" of far red light. Outcomes of successive light breaks in inhibiting flowering depends on

the wavelength given last, i.e., effective if red and ineffective if far-red. This led to the identification of phytochromes: the Pr (red-absorbing) and Pfr (far-red absorbing). Pfr may be the physiologically active material.

#### **2.2.4 Hormonal Control of Photoperiodism**

Chailakhian, a Russian botanist, first postulated the existence of a hormone that control flowering. He termed this hormone "florigen" (flower-maker), which moves from induced leaves to the meristem where it promotes flowering. Later, many studies indicated that this substance is produced by both the photoperiodic and day-neutral plants. A major objection to the florigen hypothesis was that its only effective transfer is by grafting. Extraction of the substance also failed to confirmed the hypothesis. This was explained however by the substance being unstable or difficult to extract. The concept of florigen so far remain obscure. Some investigators explain the hormonal mechanism in terms of flower inhibiting substances, rather than the flower-promoting one (Thomas and Vince-Prue, 1984).

#### **2.2.5 Interaction of Photoperiod with other Factors**

Effects of temperature, age, and other physiological states cause changes in photoperiodic responsiveness. For example, vernalization, the promotion of flowering by cold treatment, can alter plant responses. Varieties of wheat and rye (winter annuals) would not flower as quantitative

long-day plants unless seedlings were exposed to several weeks of low temperature (0-15° C) (Head, 1979). In corn, sensitivity to photoperiod was altered by temperature. Warrington and Kanemasu (1983) noted a more linear increase in leaf initiation and appearance rate under 18° C than under 28° C. Temperature similarly affects flowering response in corn (Russell and Stuber, 1983). Breuer et al. (1976) and Stevenson and Goodman (1972) found that photoperiod sensitivity was more or less the same at lower temperature. Other researchers reported that sensitivity were expressed more at lower temperatures (Colligado and Brown, 1975a; Francis, 1972a; Hesketh et al., 1969). Hunter et al. (1974) observed, however, that temperature and photoperiod were independent of each other. There is no general rule for the effects of age on photoperiodic response. In some species, however, small seedlings can achieve flowering with the same photoperiodic conditions as mature plants. In corn plant studies, flowering response to daylength was found to interact with temperature, light intensity, and nutritive status of the plant.

### **2.3 Responses of Maize to Photoperiod**

Sensitivity of corn to photoperiod is very apparent when tropical cultivars are brought into temperate areas and vice versa (Garner and Allard, 1923; Kiesselbach, 1949; and Francis, 1972c). This sensitivity is primarily manifested in change of maturity. Tropical maize varieties when grown

in higher latitudes, where growing daylengths are longer, extend their period of vegetative growth and anthesis is seldom early enough to set seed in the field before frost. It is accompanied by increased number of leaves, greater plant and ear heights and heavy braceroots (Francis, 1972c; Spencer, 1974; and Chaudry, 1968). In contrast, corn belt (temperate) cultivars grown near the equator, where days are relatively shorter, mature more rapidly and under many conditions do not attained characteristic plant height and node number (Francis et al., 1969).

The effect of photoperiod on plant development is manifested in the period which ends with tassel differentiation; hence, the number of days from emergence to tassel initiation (TI) has been a reliable guide in determining sensitivity. Daylength in excess of 14 hours was shown to delay tassel initiation resulting in an average delay in anthesis of 14.8 days and the addition of 5.03 leaves (Brewbaker, 1981). Warrington and Kanemasu (1983) reported lengthening of time between both sowing and TI and TI and anthesis. Temperature did not alter the response of corn to photoperiod. Time from TI to anthesis is much less affected by temperature than the time from sowing to TI.

Stevenson and Goodman (1972) observed that the race "Tehua" produced at least 28 more leaves under long days than under short days. Moreover, some of the lines showed increased rates of leaf initiation and leaf appearance with

increased rates of leaf initiation and leaf appearance with an increase with daylength (Warrington and Kanemasu, 1983).

Dry matter yield is directly affected, with the sensitive plants producing higher yield than the insensitive lines, primarily due to the increased plant height and number of leaves per plant. Reduction in grain yield, however, was reported under extended daylength using artificial lights (Faungfupong, 1976). Grain-stover ratios was also decreased when sensitive cultivars were grown in extended daylength, but no effects were observed in insensitive cultivars.

Other reported effects of extended daylength included slow ear development, increased spikelet number and kernel initials per row (Ragland et al. 1966). There was no direct evidence that the extended maturity due to photoperiod sensitivity resulted in an increase in carbon assimilation rate. Increased dry matter yield resulted from longer time for photosynthesis during the growing period.

Studies on the interaction between photoperiod and temperature gave significant interaction for TI and number of leaves; however the relative importance of interaction effects compared to the main photoperiod effect was minor. Roberts and Struckmeyer (1938) observed that at 21° C night temperature there was no photoperiod sensitivity between 9 and 16-hours daylength. At 13° C night temperature, differences in flowering response were observed. Francis

(1972c) corroborated the findings that sensitivity increased with decreasing temperature. Duncan and Hesketh (1968), and Bonaparte (1975) reported that leaf number increased with increasing temperature. Grain filling was also affected by temperature. Under low temperature and long photoperiod, corn required more days from silking to physiological maturity (Hunter et al. 1977)

#### **2.4 Inheritance Studies of Flowering and Photoperiod Sensitivity**

Flowering has been used as a criterion in measuring photoperiod responses in corn. Most inheritance studies on maturity used number of days to tasseling or anthesis and number of days to silking as their basis of maturity. Giesbrecht (1960a, 1960b) reported that four to five gene pairs controlled flowering time. He further suggested the presence of partial phenotypic dominance for earliness and of interallelic interaction of maturity factors. Mohamed (1959) reported that flowering was controlled by two or three major genes. Hallauer (1965) reported that a maximum of three effective factors governed days to silking in a cross between Oh43 (Early) and B14 (Late) and that additive genetic variation was of major importance. Selection studies for early flowering using recurrent selection schemes were effective in decreasing maturity, indicating large amount of additive genetic variation (Troyer and Larkins, 1985; Troyer and Brown, 1972, 1976).

Many corn cultivars and inbred lines were reported to be day-neutral and exhibited no delay in flowering (Sprague, 1934 and Mes, 1953). Inbred lines tested in Hawaii showed wide range of maturity when comparing 12-hour and 16-hour daylength using artificial lights. The presence of genetic variability is the first requirement for breeding for insensitive lines.

Any successful breeding programs involving tropical x temperate crosses is dependent on the knowledge of the inheritance of sensitivity or insensitivity to photoperiod and of the nature of the gene action operating in the population.

Several studies established that major or few gene pairs are controlling photoperiod sensitivity. Francis (1972a, 1972c) indicated that the trait was qualitative and seemed controlled by few genes. Spencer (1974) further suggested that the photoperiod response was due to discrete number of genes showing no or little dominance. Most of the studies used number of days to flowering (anthesis or silking) as the main criterion. Studies by Giesbrecht (1960a, 1960b) and Mohamed (1959) indicated that flowering was governed by not more than five gene pairs. Hallauer (1965) suggested that a maximum of three gene pairs controlled days to silking and that additive genetic variation was of major importance. Lee (1978), using days to tassel, tassel initiation, silking, and anthesis as



parameters, concluded that both additive and non-additive genes contributed to the genetic variation of photoperiod sensitivity. Heritability of the trait ranged from 73.9-94.7%. Lee further stated that sensitivity expressed as increasing leaf number was controlled by a minimum of two genes showing some degree of dominance. The preponderance of additive gene action was also shown by Russell and Stuber (1985) using generation mean analysis.

Many aspects of the genetics of photoperiodism are still not yet thoroughly understood. In particular, many questions remain concerning the nature and importance of photoperiod x temperature interactions. Low sensitivity to long days, however, can be easily transferred genetically. In genetic studies of photoperiod sensitivity in maize, a key question is whether or not photoperiod sensitivity is distinct from the maturity expressed under short days (Russell and Stuber, 1983). Studies by Russell and Stuber, 1983 indicated a significant positive correlation between photoperiod sensitivity and short-day maturity among 70 inbred lines. Among inbreds expressing moderate and or late short day maturity, however, a wide range of responses occurred. This suggested that genes for maturity under short days and photoperiod sensitivity might be under the control of different loci.

## 2.5 Breeding Methods in Screening Lines Insensitive to Photoperiod

Screening Techniques. Efficient identification of photoperiod insensitive lines is dependent on the effectiveness of the screening technique. Early corn breeders basically relied on seasonal variations from location to location to test plant response. The use of phytotrons or growth chambers facilitated the rapid evaluation of different breeding lines with excellent reliability. Limitation in space, however, has put a constraint on the continued use of growth chambers. Breeders have hundreds of lines to test, hence more space is needed. This led to the placement of artificial lights over corn plants in actual field conditions. Francis et al. (1970) used 300 W incandescent bulbs to light a field 40 x 50 meters which allowed him to rapidly test photoperiod sensitivity in a large number of genotypes. Lee (1978) installed 150 W bulbs in his genetic studies with good results. A key question is what is the minimum light intensity and for how long should the plants be exposed to elicit the true response to daylength. Warrington and Kanemasu (1983) suggested that the use of higher light intensity elicited a greater response in terms of increased leaf number than using low light intensity. Brewbaker (1981) indicated that under Hawaiian condition an excess of 14 hours of daylength and an exposure of up to 6 weeks are necessary to create a significant response in all tested

lines. Francis (1970) found that an intensity of at least 7 foot-candles (75 lux) and a 15-hour daylength were enough to accurately identify insensitive individuals in a heterogeneous or segregating population in the field. He further constructed a photoperiod response curve that included all the months of the year and all latitudes from 70 degrees N to 60 degrees S. This should be an aid to determine the appropriate date of planting in a given location. One limitation of the artificial light technique in the field is its vulnerability to changing cloud cover that can affect the effective photoperiod. Several traits have been used to evaluate photoperiod responses in maize. Among the most common are: days to tassel initiation (Hunter et al, 1974; Francis et al, 1969, 1970; Breuer et al, 1976; Lee, 1978), total leaf number (Hanway, 1963; Russell and Stuber, 1984; Chase and Nanda, 1967; Hunter et al, 1977; Tollenaar and Hunter, 1983; Moss and Harrison, 1968), and number of days to anthesis and to silking (Brewbaker, 1981; Lee, 1978). Determining tassel initiation and counting the total number of leaves is tedious; whereas recording the days to pollen shed or silking does not require much time and labor. In fact the latter traits were considered adequate and precise when used as indices for photoperiod sensitivity. Days to flower were found to be correlated to maturity (Troyer and Brown, 1972, 1976).

Breeding Methods. There are very few maize breeders currently active in breeding photoperiod insensitive corn. This is probably due to experimental costs. Most of the studies conducted so far dealt in identification and quantitative genetic analysis. Francis (1970) suggested that a continued backcrossing program is a rapid way of incorporating the desirable genes. However, this breeding method is effective only if the inheritance is controlled by a major gene. Population improvement methods such as selfed progeny selection, half and full sibbing are effective in accumulating desirable alleles in a heterogeneous population. The ultimate objective is to incorporate the gene(s) into a usable line with a wide range of adaptability. Salamini (1985) discussed breeding schemes and the cooperative program for the development of a broad based photoperiod insensitive populations.

## **2.6 Methods in Estimating Genetic Variance or Effects**

The choice of mating designs depends on several interdependent factors. Some of these were given by Cockerham (1963) as follows: 1) the natural mode of reproduction and mating flexibilities of the species; 2) the objectives in estimating genetic variances such as general interest in knowledge of gene actions for quantitative characters, choice of alternative selection and breeding procedures, and the prediction of response to selection; 3) the joint purposes such as estimating genetic variances and

simultaneously selecting among progenies or evaluating of hybrid combinations; and 4) the reliability of the estimates. The choice is generally dictated by the simplicity and the cost of the design which will give the desired information. Hallauer and Miranda (1981) summarized the basic steps in the estimation of genetic parameters: 1) development of progenies from mating designs and their evaluation over environments in an appropriate experimental design; 2) appropriate components of variance are expressed in the expected mean squares (EMS) in the analysis of variance (ANOVA); 3) translations are made to the appropriate relationships of relatives based on the mating design used; and 4) translations are made from the relationships of relatives to the theoretically determined functions of components of genetic variance for the covariance of relatives. These variances and covariances among relatives were shown in terms of additive and non-additive genetic variances (Falconer, 1989 and Kempthorne, 1957). Mating designs have been classified into one-, two-, three-, or four-factor designs depending on the number of ancestors per progeny over which control is exercised.

One-factor Mating Design. A set of half sib families or polycross progenies would constitute a one-factor design, wherein only one component of variance for progenies or covariance of relatives can be estimated.

Two-factor Mating Design. Examples are designs I, II, and III of Comstock and Robinson (1948, 1952), and the diallel cross which was first analyzed through statistical genetic techniques by Sprague and Tatum (1942).

Design I or the nested mating design involves mating randomly chosen pollen parents (males) with randomly chosen seed parents (female) to produce half-sib and full-sib families. Assuming no epistasis, variance among males and among females/male is equal to  $1/4 V_A$  and  $1/4 V_A + 1/4 V_D$ , respectively. Design II or the factorial mating design involves a set of randomly chosen parents divided into two groups. One group of parents used maternally are mated to each of another group of parents used paternally. Variance among males or females is equivalent to  $1/4 V_A$  while variance among male x females is equivalent to  $1/4 V_D$ . This design is excellent for multi-flowered plants or inbred lines. Design III involves mating randomly chosen F2 or more advanced generation plants back to both of the parent inbred lines producing pairs of backcross progenies. Variance among males and male x parent is equivalent to  $1/4 V_A$  and  $V_D$ , respectively. Design III is very useful in estimating the degree of dominance.

To derive the mean square expectations and the genetic interpretations for the above mating designs, it is assumed that the individuals used as parents are randomly selected; that genotypes are randomly distributed relative to

variations in environments; absence of non-genetic maternal effects; regular diploid behavior of meiosis; no multiple allelism; linkage equilibrium; and no epistasis. Diallel crosses are perhaps the most commonly used among the two-factor mating designs. Hayman (1954b) defined the diallel cross as the set of all possible matings among several genotypes. The genotypes may be individuals, clones, homozygous lines, and others and if there are  $n$  of them, there will be  $n^2$  mating combinations including reciprocals. Diallel analyses differ in three main ways: 1) in the materials ultimately under investigations; 2) in the postulated underlying genetic mechanisms; and 3) in the methods of estimation.

Statistical analysis of diallel cross in evaluating general combining ability (GCA) and specific combining ability (SCA) was first made by Sprague and Tatum (1942). The GCA estimate obtained provided for an indication of additive gene effects while SCA estimate gave information on dominance and epistatic gene effects. Since then diallel crosses have been used extensively in elucidating genetic properties not only in crosses among inbred diploids, but also in many crops which included heterozygous polyploids (Dunn and Wright, 1970; Levings and Dudley, 1963, Wynne et al., 1970; Miller, 1977; Goose et al, 1988).

There are several approaches to diallel analysis with Hayman's and Griffing's approaches being the earliest

developed. Hayman's approach is similar to the one advanced by Jinks (1954). The line approach introduced by Kempthorne (1956) could also be a distinct one. The main difference in Hayman's (1954a, 1957, 1958) approach from that of Kempthorne's lies on whether the parents should be considered as the population on which inferences are to be made (model I or fixed model), or as a random sample from some larger population of parents (model II or random model). Hayman and Jinks used model I while Kempthorne used model II. The analyses developed by Griffing (1956) were based on both models and were probably the most popular ones. He gave four methods of diallel analysis depending on the number of entries used. They are: Method I - parents, F1's, and reciprocals; Method II - parents and F1's only; Method III - F1's and reciprocals; and Method IV - F1's only.

Hayman (1960) discussed statistical and genetic differences among the different approaches mentioned. He established parameters related to those of Kempthorne's (1956), and Griffing's (1956). Baker (1978) elaborated critical issues in using a diallel analysis. He pointed out that from the statistical point of view the critical issue concerns the the choice of a model with fixed and random genotypic effects, but from the genetic point of view, the assumption of the independent distribution of genes in the parents and the assumption of no epistasis are the most



critical. The latter assumption is generally regarded as unjustifiable in the genetic interpretation of diallel statistics. Workers then developed general theoretical expectations that included higher order epistasis such as interactions among average effects of two or more non-allelic genes ( $V_{AA}$ ,  $V_{AAA}$ , and etc.); interactions of two or more non-allelic dominance effects ( $V_{DD}$ ,  $V_{DDD}$ , etc.); and interactions between dominant and additive effects of two or more non-allelic genes ( $V_{DA}$ ,  $V_{DDA}$ , etc.) (Cockerham, 1954; Li, 1954; Kempthorne, 1955; Henderson, 1954; Horner et al., 1957). Sprague and Eberhart (1977) described different approaches for estimating epistatic variance. These included use of the genetic variances and covariances from design I and II analyses, evaluation of F1 crosses in Design II experiments and derived S1 progenies from each F1, and the use of selected parents (fixed models). Models of Gamble (1962a, 1962b), Hayman (1958), and Anderson and Kempthorne (1954) were based on generation mean analyses that allowed for the estimation of digenic epistatic effects.

A model was presented by Gardner and Eberhart (1966) and Eberhart and Garner (1966) which is appropriate not only for inbred lines and pure line varieties but also for random mating varieties in Hardy-Weinberg equilibrium. It allows the estimation of heterosis effects in addition to the main genetic effects from fixed lines or varieties; hence a fixed

model. The model is actually similar to Hayman's (1954b, 1957) if only the diallel cross is considered. However, Hayman did not discuss the problem of a fixed set of parents. The model was further extended to permit the inclusion of multiple alleles and additive x additive effects assuming that higher order epistasis are negligible. Deviation from the model would provide a test for epistasis and linkage. Gardner and Eberhart presented three types of analysis based on the diallel cross: Analysis I, when five groups of populations are present; Analysis II, when heterosis was estimated including its partitioning; and Analysis III, when crosses are subdivided into GCA and SCA components. Baker (1978) later showed the relationships of the different parameters of the diallel analysis of various authors. The model was later expanded by Hammond and Gardner (1974) and Smith (1979) to evaluate progress from recurrent selections.

Other Designs. Cockerham (1963) discussed other complex designs such as three-factor and four-factor mating designs as shown by the triallel and quadrallel analysis, respectively. He noted co-designs such as covariance analysis of parent and offspring or of grandparent and grandoffspring.

### 3. MATERIALS AND METHODS

#### 3.1 Maturity and Photoperiod Sensitivity of Tropical-Adapted Maize Inbreds

The Hawaii Foundation Seed Facility of the University of Hawaii maintains a worldwide collection of about 300 open-pedigree maize inbreds of tropical background. These inbreds represented some of the best combining lines developed by public research institutions. About half of the inbreds were bred in the tropics (between 23° N and 23° S latitude). The origin and derivation of these lines were reported by Brewbaker et al., 1989; many of them were bred in Nigeria (IITA), Thailand, India, Columbia, and Hawaii. Most of them were subjected to pest and disease screening trials conducted in several countries.

##### 3.1.1 Field Experiments

Ninety maize inbreds were evaluated in three trials in Waimanalo, Hawaii (20° N) and one trial each in Ames Iowa, (42° N) and Suwon, South Korea (37° N). Trials were set up in a randomized complete block design with two replications in Hawaii trials, four in Iowa, and three in Korea. Plot size was 0.75 x 0.25 m giving an effective population of 53,333 plants per ha. Two seeds per hill were planted at a distance of 0.25 m between hills, and carefully thinned to one plant about 10 days after emergence. Fertilizers were applied at the rate of 160 kg of N and 80 kg of P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O per ha.

The primary trait considered in this study was the number of days from planting to silking which was the basis for relative maturity. Silking date was recorded when silk emerged from at least half of the plants in a plot. Accumulated thermal units expressed as Growing Degree Days (GDD) were calculated using the following formula:

$$\text{GDD} = [(T_{\text{max}} + T_{\text{min}})/2] - 10^{\circ} \text{ C}$$

Maximum temperature above  $30^{\circ} \text{ C}$  were entered as 30 and minimums below  $10^{\circ} \text{ C}$  were entered as 10. Means from Hawaii were considered as estimates for maturity under a short daylength (SD) environments, while the means from Iowa and Korea were estimates for maturity under a long daylength environments (LD).

### **3.1.2 Maturity and Photoperiod Sensitivity Classification**

Inbreds were classified for maturity per se based on silking date under SD environment in Waimanalo only since maturity data in Iowa and Korea were confounded by photoperiod. Photoperiod sensitivity was expressed as a delay in silking and was computed by subtracting mean SD from LD silking dates (both days and GDD). Classification of inbreds according to maturity and photoperiod sensitivity are given in Table 3.1.

Table 3.1. Maturity and photoperiod sensitivity classification.

Maturity	Days to Silk	Photoperiod Sensitivity	Silking Delay
Early	<60	low	<15
Medium Early	60-64	moderately low	15-21
Medium Late	64-68	moderately high	22-28
Late	>68	high	>28

### 3.2 Diallel Analysis

#### 3.2.1 Test Materials

The nine selected inbred lines were Ant C-S5, B73 (Hi), Hi 29, Hi32, Hi34, Narino 330-S6, Oh43 (Hi), Tx601 (Hi), and Tzi4. These parents were chosen for their relative maturities and photoperiod sensitivities so that each category was represented. Crosses in all possible combinations (diallel), excluding reciprocals, were accomplished by a paired-row system at Waimanalo. At least 20 ears were harvested and bulked for each cross. Parental inbreds were seed increased at the same time by sibbing.

#### 3.2.2 Field Experiments

Short Daylength Trials. Evaluations under SD environments were made in Waimanalo and Kauai. A total of 45 entries (9 parents and 36 crosses) were planted in a modified randomized complete block design hybrids. This modification involved segregation of the inbred parents and hybrids in the same block. Randomization was then made within groups. This set up minimized competition effects

among inbreds and hybrids. Plot size was 7.5 m<sup>2</sup> with plant spacing of 0.25 m. Cultural practices were the same as described in Section 3.1.

Long Daylength Trials. The same entries were evaluated under LD environments in Iowa and Waimanalo. The experimental procedures were the same as SD trials, except in Waimanalo where daylength was extended to 16 hours by supplemental artificial lighting at night. Figure 3.1 shows the lighting set up as seen during the day and at night. This set up was similar to the one described by Lee (1978), except that two additional electric poles were added (one on each side of the field) to accommodate 10 more 150-W incandescent bulbs (Philips) strung along the. There were five electric lines, 51 meters long and spaced at 4.6 m between lines. Bulbs (10 on each line) on adjacent lines were staggered to provide more uniform light distribution. This lighting system covered about 930 m<sup>2</sup> of land area and provided an average light intensity of three mmol/sec/m<sup>2</sup> recorded by LI-1776 solar monitor at ground level. Lights were turned on and off automatically by clock timer hooked up to a 3-pole magnetic contactor at predetermined times at night. Average daylength at time of planting was about 13.0 hrs, so that the added three hours of lighting approximated the 16-hour daylength required for the experiment.

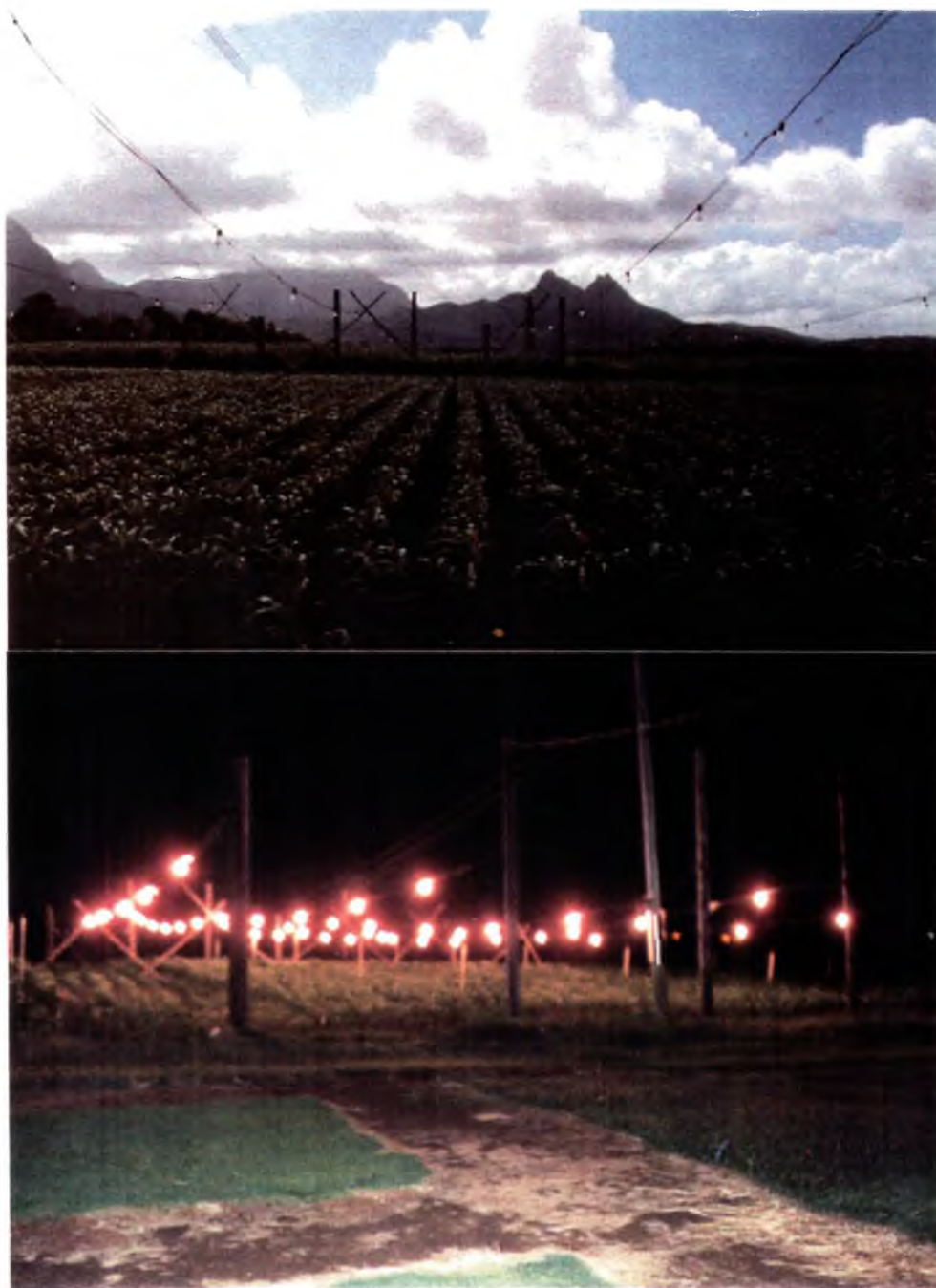


Figure 3.1. Light set-up at the University of Hawaii Research Station, Waimanalo, Hawaii.

### 3.2.3 Traits Measured

The following traits were recorded from each plot:

- 1) Days to anthesis - number of days from planting to time when 50% of the plants had shed pollen.
- 2) Days to silking - number of days from planting to time when 50% of the plants had emerged silks.
- 3) Anthesis to silking interval (ASI) - days to silking minus days to anthesis.
- 4) Days to blacklayer formation (BLF) - number of days from planting to time when half of the plants exhibited the blacklayer at the base of the kernels (Waimanalo only). This is a measure of physiological maturity.
- 5) Grain Filling Period (GFP) - time between silking and blacklayer formation.
- 6) Leaf number - total number of leaves per plant averaged over five plants. Leaf number six was marked to keep track of the younger leaves that fall off early.
- 7) Plant height (cm) - average height of five plants measured from the ground up to the tip of the tassel.
- 8) Total dry matter yield (kg/ha) - total above-ground yield (dried to constant weight).
- 9) Grain yield and components - grain yield was computed in kg/ha at 15% moisture content. Yield components included number of ears/plant, ear length 1 (base to tip, in cm), ear length 2 (filled ear length), ear diameter, kernel row number, and number of kernels/row.



### 3.2.4 The Genetic Model

Analysis III as described by Gardner and Eberhart (1966) was used to estimate general combining ability (GCA) and specific combining ability (SCA) effects. The model also included parental effects and heterosis effects. The model for the parents is as follows:

$$Y_j = M_p + p_j$$

where

$Y_j$  = mean of the  $j$ th parent

$M_p$  = mean of all the parents involved in the diallel

$p_j$  = effect of the  $j$ th parent.

The model for the crosses is:

$$Y_{jj'} = M_c + g_j + g_{j'} + s_{jj'}$$

where

$Y_{jj'}$  = mean of a cross

$M_c$  = mean of all the crosses

$g_j$  = general combining ability (GCA) effect of  $j$ th parent

$g_{j'}$  = general combining ability effect of the  $j'$ th parent

$s_{jj'}$  = specific combining ability effect of hybrid.

The difference between  $M_c$  and  $M_p$  provided for an estimate of heterosis (H).

The restrictions are that sum of GCA's = 0 and sum of SCA's = 0. The combined analysis of variance of nine parents and their 36 hybrids evaluated in four environments is given in Table 3.2. The entries and entries x

environments were further partitioned into different components as shown in Table 3.3. The ratio between GCA and SCA gave an indication of the relative magnitude of gene action. GCA and SCA estimates were derived by least square methods of estimation.

Table 3.2. Combined analysis of variance of nine parents and 36 hybrids.

Source	df
Environments (E)	3
Reps/E	8
Entries	44
Entries x E	132
Pooled Error	352

Table 3.3. Components of entries and entries x environments.

Source	df
Entries	44
Parents	8
Parents vs crosses	1
Crosses	35
GCA	8
SCA	27
Entries x E	132
Parents x E	24
Parents vs crosses x E	3
Crosses x E	105
GCA x E	24
SCA x E	81
Pooled Error	352

### 3.3 Generation Mean Analysis

#### 3.3.1 Generation of Populations

Five groups of populations were generated in this study: parents,  $F_1$ ,  $F_2$ ,  $BP_1$ , and  $BP_2$ . The four inbred

parents used in this study are Ant C-S5, Hi34, Oh43 (Hi), and Tx601 (Hi). One of the assumptions of GMA is that the two parents must possess two opposing traits under consideration. Strictly speaking, only the cross Oh43 (Hi) x Hi34 and Oh43 (Hi) x Tx601 (Hi) would pass the test for maturity, and the crosses involving Oh43 (Hi) and the other three parents for photoperiod sensitivity. All possible combination crosses were nevertheless derived to detect any canceling of genetic effects (Hallauer and Miranda, 1981).  $F_2$  populations were generated by selfing the  $F_1$ 's, while  $BP_1$  and  $BF_2$  were derived by backcrossing the  $F_1$  to parent 1 and parent 2, respectively. At least 50 plants were used to derive each population.

### 3.3.2 Field Experiments

Trials were conducted under SD environments at Waimanalo and on Kauai and under extended daylength at Waimanalo as described in Section 2.2. A total of 28 entries were arranged in a randomized complete block design, replicated three times. The plot size was 7.5 m<sup>2</sup> for parents and  $F_1$ 's, 15.0 m<sup>2</sup> for the backcrosses, and 22.5 m<sup>2</sup> for the  $F_2$ 's. At the plant spacing of 0.75 x 0.25 m, those plot sizes gave populations of 40, 80, and 120 plants, respectively. Silking date was the primary data collected. Sample plants were tagged and data were recorded from individual plants. Sample size per plot was 20 for parents and  $F_1$ 's, 35 for backcrosses, and 60 for  $F_2$ 's, or a total of

60, 105, and 180 plants, respectively for one trial.

### 3.3.3 The Genetic Model

Scaling tests as outlined by Singh and Chaudhary (1976) were conducted to determine whether a three-parameter (Jinks and Jones, 1958; Mather and Jinks, 1971) or a six-parameter model (Hayman, 1958, 1960) was appropriate. Adequacy of scale must satisfy two conditions: a) additivity of gene effects and b) independence of heritable components from non-heritable ones. The first condition provides information regarding absence or presence of epistasis or gene interactions. The following were the four tests for scale effects:

$$A = 2B_1 - P_1 - F_1$$

$$B = 2B_2 - P_2 - F_1$$

$$C = 4F_2 - 2F_1 - P_1 - P_2$$

$$D = 2F_2 - B_1 - B_2$$

where  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BP_1$ , and  $BP_2$ , were means of parent 1, parent 2, cross between  $P_1$  and  $P_2$ ,  $F_1$  selfed, backcross to  $P_1$ , and backcross to  $P_2$ , respectively. When the scale was adequate, the values of A, B, C, and D should be zero within the limits of their respective standard errors. The significance of any one of these scales was taken to indicate the presence of non-allelic interaction.

Following Gamble's (1962a) notation, the following genetic effects were estimated:

**m** = mean

**a** = additive genetic effect

**d** = dominance effect

**aa** = additive x additive effect

**ad** = additive x dominance effect

**dd** = dominance x dominance effect

The three-parameter model included only the **m**, **a**, and **d**, whereas the six-parameter model included all the genetic effects described above. These genetic effects were estimated following the procedures outlined by Singh and Chaudhary (1976). Estimates of additive, dominance, and environmental variances were calculated based on the assumption that there was no epistasis and linkage (Mather, 1949). The following formulae were used to derive these variances:

$$\text{Additive variance } (V_A) = 2VF_2 - (VBP_1 + VBP_2)$$

$$\text{Dominance variance } (V_D) = VF_2 - (V_A + V_E)$$

$$\text{Epistatic variance } (V_E) = (VP_1 + VP_2 + VF_1)/3$$

where  $VP_1$ ,  $VP_2$ ,  $VF_1$ ,  $VF_2$ ,  $VBP_1$ , and  $VBP_2$  were phenotypic variances for  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BP_1$ , and  $BP_2$ , respectively. Heritabilities were computed by using these variances:

$$\text{Narrow sense } (nh) = V_A / (V_A + V_D + V_E)$$

$$\text{Broad sense } (bh) = (V_A + V_D) / (V_A + V_D + V_E)$$

The minimum number of genes were estimated by:

- 1) Castle-Wright formula (Mock and Schuetz, 1974) which was given by:

$$n = (P_1 - P_2)^2 / 8(VF_2 - VF_1)$$

2) A formula attributed to Sewall Wright:

$$n = [0.25(0.75 - h + h^2)D^2 / (VF_2 - VF_1)]$$

where

$$D = P_2 - P_1 \text{ and } h = (F_1 - P_1) / D.$$

### 3.4 Divergent Mass Selection for Silking Date

#### 3.4.1 Selection Materials and Procedures

Two open-pollinated composites were used as base populations for divergent mass selection. One was MIRSYN 1, a synthetic developed for Northern Corn Leaf blight (E. turcicum) resistance, and the other was HIC 4g, a composite derived from temperate by tropical crosses. Divergent mass selection was initiated by selecting the earliest and latest individuals for each population. Selection intensity was 10% for a population size of 3000 plants. The selection area was stratified (Gardner, 1961) into blocks of 500 plants to minimize soil fertility gradients. The earliest and latest 50 plants to silk in each block were spray-painted. At harvesting, two kernel rows were sampled from each selected ear and then bulked for the next cycle. Two separate populations (early and late) were then planted in isolation, either by time or space, and where another 10% of the plants were selected. This procedure was repeated for three cycles of selection.

### 3.4.2 Field Experiments

The selected generations were evaluated in three trials, one each in Waimanalo and Kauai, and one under lights in Waimanalo. Table 3.4 shows the entries entered in the three-replication (RCB design) evaluation trials.

Table 3.4. Entries included in the evaluation trials.

Populations	No. of entries
MIRSYN 1 C0 (base population)	1
MIRSYN 1 C1 Early and Late	2
MIRSYN 1 C2 Early and Late	2
MIRSYN 1 C3 Early and Late	2
HIC 4g C0 (base population)	1
HIC 4g C1 Early and Late	2
HIC 4g C2 Early and Late	2
HIC 4g C3 Early and Late	2

Plot size was 15 m<sup>2</sup> (4 rows, 5 meters long) with the plants in the 2 middle rows used for data sampling. Silking was recorded from individual plants (40 plants per replication), and other morphological data measurements such as leaf number and plant height were taken from 10-plant averages. Grain yield was taken from all ears harvested from the middle rows. The silking date difference between LD and SD in Waimanalo provided estimates of photoperiod sensitivity.

### 3.4.3 Statistical and Genetic Analysis

The form of the combined analysis of variance is shown in Table 3.5. Comparisons were made among means of selection cycles for each population using the Duncan's multiple range test. Genetic advance ( $G$ ) due to selection was computed for each population by taking the difference between the mean of the original population and the mean of the selected population divided by three cycles of selection

Table 3.5. Combined analysis of variance.

Source	df
Environments (E)	2
Reps/E	6
Entries	13
Populations	1
Cycles	6
Populations x cycles	6
Entries x E	26
Error	78

The formula for  $G$  as given by Falconer (1989) is:

$$G = H^2 \times S$$

where

$H^2$  = heritability (narrow sense)

$S$  = selection differential = mean of the original population - mean of selected individuals of that population.

The formula for  $G$  can also be simplified into

$$G = \frac{k \frac{1}{2} V_A^2}{V_P}$$



where

$k$  = selection intensity in standardized units; at 10%  
selection intensity,  $k = 1.76$  (Becker, 1984)

$V_A^2$  = additive genetic variance

$V_p$  = phenotypic standard deviation of the  
population.

Heritability can therefore be derived:

$$H = G/S \text{ or}$$

$$H = 2G/kV_p$$

#### 4. MATURITY AND PHOTOPERIOD SENSITIVITY OF TROPICAL-ADAPTED MAIZE INBREDS

Ninety inbreds were evaluated for maturity (days to silking) in five environments: three in Waimanalo, Hawaii, and one each in Ames, Iowa, and in Suwon, South Korea. The time of the evaluation, latitude, actual daylength (measured as the average time between sunrise and sunset), and average temperature from planting to flowering for each of the locations are presented in Table 4.1. Waimanalo had short daylengths ranging from 11:54 hrs to 13:22 hrs, while South Korea (14.16 hrs) and Iowa (15:30 hrs) were considered long daylengths. Waimanalo has been described as a neutral environment (Brewbaker, 1974) where changes in daylength among seasons do not elicit photoperiodic response from tropical lines.

Table 4.1 Evaluation trials for days to silking.

Environments	Date planted	Latitude	Daylength (hr:min)	Average Temp.
Waimanalo, Hi	02/21/85	20	12:30	22.6
Waimanalo, Hi	05/22/86	20	13:22	25.2
Waimanalo, Hi	01/29/87	20	11:54	22.1
Ames, Iowa	04/24/87	42	15:34	21.6
Suwon, S. Korea	05/30/88	37	14:16	24.2

Although photoperiod sensitivity increases with daylength, studies in the field and controlled environment have shown that significant delays in flowering occur at 14-hr daylength (Lee, 1978; Francis, 1970). Daylengths never exceed 14 hours between latitude 25° N and 25° S. Waimanalo

therefore is designated short daylength (SD), while Korea and Iowa are long daylength (LD) environments.

#### **4.1 Silking Date Variations Among Inbreds**

Days to silking for 90 inbreds in the five environments are summarized in Table 4.2. Silking dates in Waimanalo ranged from 58-74 days (1985), 47-61.5 days (1986), and 64-80.5 (1987), with means of 66.3, 55.1, and 72.1, respectively. Averages over the three Waimanalo trials gave an estimate of the number of days to silking under short daylength. Frequency distribution of these data (Figure 4.1) showed that about 50 percent of all inbreds silked between 64-67 days. Under the maturity classification scheme, 6% of all inbreds were early, 40% medium early, 46% medium late, and 9% late (Figure 4.2).

Variations in the number of days to silking among the three trials in Waimanalo could not be attributed to the differences in daylength, since the trial in 1987 had the lowest daylength yet it gave the highest mean. Likewise, the trial in 1986 had the highest daylength, but gave the lowest mean. The variation could best be attributed to the differences in temperature. Accumulated heat unit data summarized in Table 4.3 showed comparable values for inbreds in three Waimanalo trials. Means of all inbreds obtained in 1985 and 1986 were basically identical. The most notable discrepancies occurred when comparing averages of the 1985 and 1986 data with the 1987 data. Correlations between days

Table 4.2. Number of days to silking of tropical-adapted maize inbreds evaluated in five environments.

Inbreds	Short Daylength				Long Daylength		
	Hi_85	Hi_86	Hi_87	Mean	Iowa	Korea	Mean
A619 (Hi)	58.5	47.5	66.5	57.5	78.0	69.7	73.8
A632 (Hi)	60.0	48.0	64.0	57.3	80.3	66.3	73.3
ANT CS-S5	61.0	51.0	66.5	59.5	101.3	80.7	91.0
B73 (Hi)	61.0	49.5	67.5	59.3	80.0	65.0	72.5
B77 (Hi)	63.5	52.0	71.0	62.2	84.3	70.7	77.5
CI64 (Hi)	64.5	55.0	67.0	62.2	88.5	71.7	80.1
CI66 (Hi)	60.5	55.5	67.5	61.2	84.8	69.7	77.2
CIM.A-21 (Hi)	68.0	58.0	73.5	66.5	112.5	79.0	95.8
CIM.A-6 (Hi)	72.5	56.5	76.5	68.5	142.8	81.7	112.2
CIM.T11-ES	74.0	61.5	80.5	72.0	134.0	89.7	111.8
CM116	66.0	55.0	71.0	64.0	104.0	81.0	92.5
CM117	65.5	55.0	68.5	63.0	94.8	74.3	84.5
CM118	66.0	55.5	68.0	63.2	111.8	80.7	96.2
CM201 (Hi)	62.5	54.0	70.5	62.3	84.5	68.0	76.3
CM207	64.5	55.5	71.5	63.8	95.3	72.0	83.6
Fla2AT113	64.5	56.5	74.5	65.2	99.8	78.0	88.9
Fla2AT114	67.0	56.0	69.5	64.2	99.3	75.0	87.1
Fla2AT115	68.0	55.5	77.5	67.0	110.0	80.7	95.3
Fla2AT116	68.0	56.5	72.5	65.7	113.0	79.3	96.2
Fla2BT106	67.0	54.5	73.0	64.8	104.0	78.0	91.0
Fla2BT54	67.5	55.0	75.5	66.0	103.5	80.0	91.8
Fla2BT73	69.5	55.0	75.0	66.5	103.3	77.7	90.5
Ga209 (Hi)	65.0	54.0	73.5	64.2	93.3	70.7	82.0
GT112Rf	75.0	59.0	73.0	69.0	107.5	80.3	93.9
H55 (Hi)	64.5	56.0	77.0	65.8	91.0	82.7	86.8
H632F	68.5	59.0	73.0	66.8	95.5	74.0	84.8
H95 (Hi)	62.0	54.5	66.5	61.0	82.3	67.3	74.8
H98 (Hi)	64.0	56.0	67.0	62.3	81.8	72.3	77.0
Hi25	61.0	54.0	72.0	62.3	81.8	70.7	76.2
Hi26	61.5	55.0	73.5	63.3	85.3	73.0	79.1
Hi27	68.0	57.5	75.5	67.0	108.3	79.7	94.0
Hi28	60.5	54.0	68.0	60.8	96.5	75.0	85.8
Hi29	63.5	55.0	69.5	62.7	90.8	70.0	80.4
Hi30	65.0	55.0	72.0	64.0	85.8	72.0	78.9
Hi31	60.5	55.0	76.0	63.8	86.0	70.7	78.3
Hi32	59.0	50.5	66.5	58.7	79.0	69.3	74.2
Hi33	61.0	53.0	67.5	60.5	81.0	66.7	73.8
Hi34	68.5	58.5	77.0	68.0	107.5	80.7	94.1
Hi35	65.0	56.0	72.5	64.5	99.0	79.7	89.3
Hi39	68.5	55.5	74.5	66.2	94.8	73.0	83.9
Hi40	62.5	55.5	74.5	64.2	91.8	72.7	82.2
Hi41	72.5	55.5	75.0	67.7	98.3	79.7	89.0
HIX4231	67.0	54.0	74.5	65.2	87.3	72.3	79.8
HIX4263	63.5	52.0	70.0	61.8	86.3	71.7	79.0
HIX4267	67.5	57.0	74.5	66.3	87.0	73.0	80.0
HIX4269	64.5	56.5	73.0	64.7	89.0	72.0	80.5

Table 4.2 cont.

Inbreds	Short Daylength				Long Daylength		
	Hi_85	Hi_86	Hi_87	Mean	Iowa	Korea	Mean
HIX4283	68.0	56.5	76.0	66.8	93.8	77.3	85.5
ICA L210	67.0	56.0	73.0	65.3	106.8	79.7	93.2
ICA L219	71.5	57.5	72.0	67.0	113.5	87.3	100.4
ICA L221	69.0	58.5	78.0	68.5	105.8	82.0	93.9
ICA L224	68.0	58.0	76.5	67.5	114.0	80.3	97.2
ICA L27	69.5	59.0	76.0	68.2	105.0	79.7	92.3
ICA L29	69.0	56.0	77.5	67.5	109.0	81.3	95.2
ICA L36	71.0	59.0	75.5	68.5	104.0	78.7	91.3
INV 138	65.0	52.5	68.5	62.0	95.8	74.0	84.9
INV 302	65.0	53.5	72.0	63.5	97.0	76.7	86.8
INV 534	62.0	54.5	68.5	61.7	106.5	81.3	93.9
INV 575	61.0	54.5	66.5	60.7	84.3	70.0	77.1
KU1409	67.0	54.0	70.5	63.8	135.0	83.7	109.3
KU1414	70.0	55.5	74.0	66.5	132.5	82.7	107.6
KU1418	71.0	56.0	74.5	67.2	142.5	83.7	113.1
Ky226 (Hi)	66.5	54.0	74.5	65.0	89.0	75.3	82.2
MIT 11-S3	66.0	54.0	67.0	62.3	111.5	82.3	96.9
Mo20W	67.0	51.5	70.5	63.0	84.8	66.7	75.7
Mo5 (Hi)	65.5	52.0	67.0	61.5	86.3	67.0	76.6
Mp496	72.5	57.5	72.5	67.5	107.5	77.7	92.6
Mp68:616 (Hi)	63.0	55.0	66.0	61.3	92.8	73.7	83.2
N139	67.5	55.0	74.0	65.5	87.3	73.3	80.3
N28 (Hi)	68.0	55.0	70.5	64.5	83.8	69.7	76.7
Narino 330-S6	71.5	59.0	76.0	68.8	109.0	80.3	94.7
NC246	69.0	52.5	74.0	65.2	96.8	76.0	86.4
NC248	69.5	53.5	71.5	64.8	95.0	73.0	84.0
Oh43 (Hi)	58.0	50.5	66.0	58.2	79.8	70.0	74.9
PAC90038	61.0	54.0	67.5	60.8	81.3	66.3	73.8
Phil DMR-S6	65.5	57.5	69.0	64.0	111.8	85.7	98.7
SC213	65.0	58.5	75.5	66.3	103.0	77.0	90.0
SC301D (Hi)	69.0	54.5	74.0	65.8	94.5	72.3	83.4
SC43	66.5	54.0	71.5	64.0	94.3	73.7	84.0
T232	67.5	55.0	73.5	65.3	94.3	75.7	85.0
T256	68.5	56.5	75.0	66.7	98.3	77.0	87.6
T258	68.5	54.5	74.5	65.8	93.0	71.7	82.3
Tuxpeno-S5	73.0	56.5	74.5	68.0	111.3	79.3	95.3
Tx29A (Hi)	68.5	53.0	76.0	65.8	94.3	74.7	84.5
Tx5855	67.0	53.5	74.5	65.0	89.3	74.7	82.0
Tx601 (Hi)	73.5	58.5	74.0	68.7	103.0	80.0	91.5
Tzi17	69.5	55.0	76.0	66.8	97.3	75.7	86.5
Tzi3	70.0	57.0	74.0	67.0	140.5	81.7	111.1
Tzi4	74.5	58.0	78.0	70.2	127.5	74.3	100.9
Va35 (Hi)	61.5	51.0	66.5	59.7	76.3	65.7	71.0
W64A (Hi)	62.5	52.5	66.5	60.5	82.3	66.3	74.3
Mean	66.3	55.1	72.1	64.5	98.4	75.5	86.9
LSD (0.05)	1.71	1.58	2.98	2.09	3.33	3.49	3.41

Percentage of inbreds

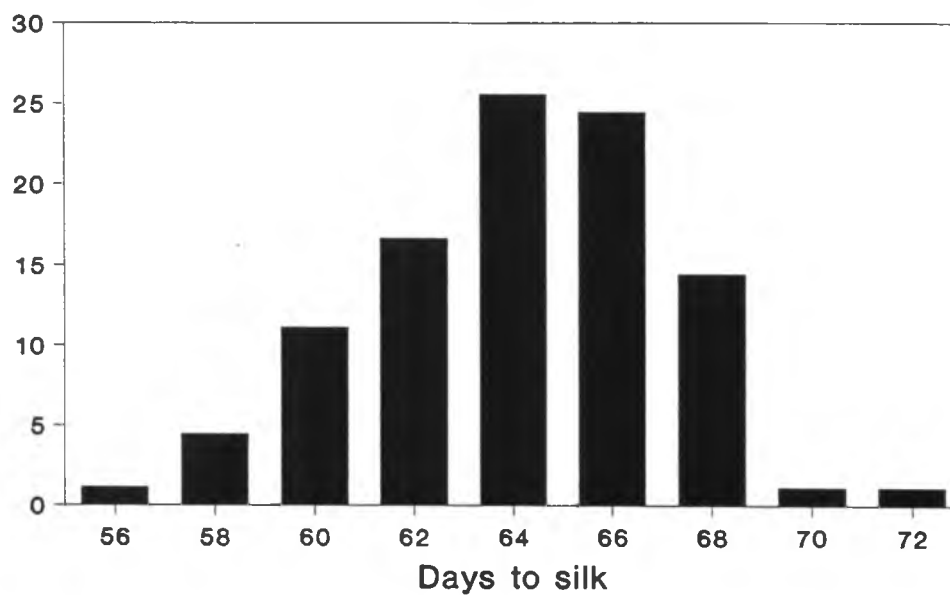


Figure 4.1. Frequency distribution among tropical-adapted maize inbreds for days to silking under short daylength.

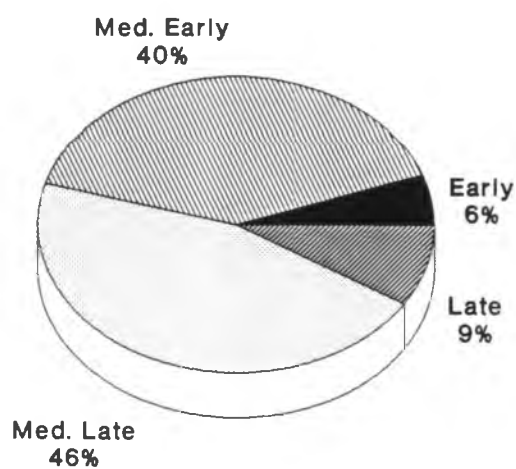


Figure 4.2. Percentage of inbreds under each maturity group.

Table 4.3. Growing degree days (GDD) to silking of tropical-adapted maize inbreds evaluated in five environments.

Inbreds	Short Daylength				Long Daylength		
	Hi_85	Hi_86	Hi_87	Mean	Iowa	Korea	Mean
A619 (Hi)	723	716	794	744	866	970	918
A632 (Hi)	744	724	757	742	896	907	902
ANT CS-S5	758	771	794	774	1219	1166	1192
B73 (Hi)	758	748	810	772	889	885	887
B77 (Hi)	794	786	864	815	939	988	964
CI64 (Hi)	808	834	802	814	1005	1007	1006
CI66 (Hi)	751	843	810	801	945	970	957
CIM.A-21 (Hi)	857	883	900	880	1370	1137	1254
CIM.A-6 (Hi)	919	859	948	909	1647	1182	1414
CIM.T11-ES	941	938	996	958	1572	1289	1430
CM116	829	834	863	842	1261	1163	1212
CM117	822	834	825	827	1107	1056	1081
CM118	829	843	817	830	1361	1166	1264
CM201 (Hi)	779	818	856	817	941	940	941
CM207	808	843	871	840	1116	1013	1064
Fla2AT113	808	859	915	860	1196	1122	1159
Fla2AT114	843	851	841	845	1188	1068	1128
Fla2AT115	857	843	954	884	1338	1166	1252
Fla2AT116	857	859	886	867	1373	1145	1259
Fla2BT106	843	826	893	854	1260	1122	1191
Fla2BT54	850	834	927	871	1256	1155	1205
Fla2BT73	877	834	921	878	1252	1116	1184
Ga209 (Hi)	815	818	900	844	1072	988	1030
GT112Rf	955	898	893	915	1297	1161	1229
H55 (Hi)	808	851	948	869	1046	1193	1119
H632F	864	898	907	890	1120	1050	1085
H95 (Hi)	772	826	794	797	914	926	920
H98 (Hi)	801	851	802	818	911	1020	965
Hi25	758	818	879	818	910	988	949
Hi26	765	834	900	833	952	1031	992
Hi27	857	875	928	887	1314	1150	1232
Hi28	751	818	817	795	1139	1067	1103
Hi29	794	834	840	823	1041	976	1008
Hi30	814	834	879	842	961	1014	988
Hi31	751	834	935	840	964	988	976
Hi32	730	763	794	762	879	964	921
Hi33	758	802	810	790	902	914	908
Hi34	864	890	947	901	1304	1166	1235
Hi35	815	851	886	851	1184	1149	1167
Hi39	864	843	915	874	1107	1031	1069
Hi40	779	843	915	845	1058	1025	1042
Hi41	919	843	922	894	1170	1150	1160
HIX4231	843	818	915	859	985	1019	1002
HIX4263	794	786	848	809	968	1007	987
HIX4267	850	867	915	877	979	1031	1005
HIX4269	808	859	893	853	1012	1013	1012

Table 4.3 cont.

Inbreds	Short Daylength				Long Daylength		
	Hi_85	Hi_86	Hi_87	Mean	Iowa	Korea	Mean
HIX4283	857	859	934	883	1090	1110	1100
ICA L210	843	851	893	862	1294	1149	1222
ICA L219	905	875	877	886	1382	1261	1321
ICA L221	871	890	967	909	1282	1187	1235
ICA L224	857	883	941	894	1390	1161	1276
ICA L27	877	898	935	903	1271	1150	1211
ICA L29	871	851	955	892	1322	1177	1249
ICA L36	898	898	928	908	1263	1134	1198
INV 138	815	794	825	811	1125	1049	1087
INV 302	814	810	878	834	1147	1099	1123
INV 534	772	826	825	808	1285	1177	1231
INV 575	758	826	794	793	938	976	957
KUL409	843	818	856	839	1581	1210	1396
KUL414	884	843	908	878	1556	1196	1376
KUL418	898	851	915	888	1644	1210	1427
Ky226 (Hi)	836	818	915	856	1013	1074	1043
MIT2-S6	814	810	810	811	1355	1191	1273
Mo20W	843	778	855	826	945	915	930
Mo5 (Hi)	822	786	802	803	968	920	944
Mp496	919	875	886	893	1297	1116	1207
Mp68:616 (Hi)	786	834	786	802	1073	1044	1058
N139	850	834	906	863	984	1037	1011
N28 (Hi)	857	834	856	849	931	970	950
Narino 330-S6	905	898	935	912	1322	1161	1242
NC246	871	794	908	857	1143	1085	1114
NC248	877	810	870	852	1112	1032	1072
Oh43 (Hi)	716	763	786	755	892	977	934
PAC90038	758	818	810	795	906	907	907
Phil DMR-S6	822	875	833	843	1359	1238	1298
SC213	898	890	928	905	1250	1105	1177
SC301D (Hi)	871	826	908	868	1103	1020	1061
SC43	836	818	871	841	1098	1044	1071
T232	850	834	900	862	1098	1081	1090
T256	891	859	921	890	1170	1111	1140
T258	864	826	914	868	1077	1007	1042
Tuxpeno-S5	926	859	914	900	1354	1143	1249
Tx29A (Hi)	857	802	935	865	1099	1062	1080
Tx5855	843	810	914	856	1017	1062	1039
Tx601 (Hi)	933	890	908	910	1250	1156	1203
Tzil7	877	834	935	882	1152	1080	1116
Tzi3	884	867	908	886	1629	1182	1405
Tzi4	948	883	960	930	1518	1056	1287
Va35 (Hi)	765	771	794	777	843	896	869
W64A (Hi)	779	794	794	789	916	909	912
Mean	834	835	879	849	1151	1073	1112
LSD (0.05)	23	25	44	31	41	60	51



and heat unit values were all 0.99 suggesting that the relative order of inbreds in each environment did not change.

The long daylength led to often drastic delays in silking. Silking in Iowa was delayed for all inbreds, ranging from 76 to 142 days with a mean of 98.4 days (Table 4.2). The overall mean in Korea, 75.5 days, was also higher than the combined mean (64.5 days) at Waimanalo, but considerably less than the Iowa mean. Heat unit values did not change the relative order and magnitude between short and long daylength environments indicating the strong effect of daylength.

Growing degree days (GDD) values in Iowa and Korea were relatively similar (Table 4.3). Many inbreds such as A632 (Hi), CI64 (Hi), and Hi33, silked later in Iowa than in Korea, but basically had the same GDD. Large differences between Iowa and Korea were detected both for calendar days and GDD among several lines such as CIM. A-6 (Hi), CIM.T-11ES (Hi), Hi34, KU inbreds and Tzi3 and Tzi4. The frequency distribution for combined data from Iowa and Korea, representing maturity under long daylength is presented in Figure 4.3.

Analyses of variance revealed highly significant differences among inbreds in all environments using both calendar days and GDD (Table 4.4). Combined analysis of variance (Table 4.5) detected the presence of interaction

Table 4.4.1. Analyses of variance for the number of days and GDD's to silking in three environments in Waimanalo.

Source	df	Hi_85		Hi_86		Hi_87	
		Days	GDD	Days	GDD	Days	GDD
Reps	1	0.14 ns	3 ns	4.05 *	1017 *	4.7 ns	996 ns
Inbreds	89	30.46 **	6128 **	12.31 **	3142 **	27.0 **	5902 **
Error	89	0.73	139	0.63	161	2.2	487
CV (%)		1.29	1.41	1.45	1.52	2.08	2.51
R-SQUARE		0.98	0.98	0.95	0.95	0.92	0.92

Table 4.4.2. Analyses of variance for the number of days and GDD's to silking in Iowa and Korea.

Source	df	Iowa		Korea		
		Days	GDD	Days	GDD	
Reps	3	34.0 *	4923 **	2	17.4 *	6855 *
Inbreds	89	902.9 **	160909 **	89	88.6 **	26888 **
Error	247	5.8	874	178	4.8	1416
CV (%)		2.44	2.57		2.89	0.04
R-SQUARE		0.98	0.98		0.90	0.91

Table 4.5. Combined analysis of variance for days and GDD's to silking.

Source	df	Mean Squares	
		Days	GDD
environments	4	69147 **	5534140 **
reps/enviroment	8	6.0 ns	2090 **
inbreds	89	585.1 **	121578 **
inbreds x environments	356	119.1 **	20348 **
Pooled error	712	3.9	800

\* Significant at 0.01 level of probability.

\*\* Significant at 0.05 level of probability.

between inbreds and environments, but it only accounted for a small proportion of the total variation among means.

#### 4.2 Photoperiod Sensitivity of Inbreds

Photoperiod sensitivities of inbreds were expressed as silking delay, the difference between days to silk under long and short daylength (Table 4.6). All inbreds exhibited varying amounts of silking delay ranging from 11.3 days (93 GDD's) for Va35 (Hi) to 45.5 (540 GDD's) for KU1418. Overall average silking delay was 22.4 days (262 GDD's). The correlation coefficients for days to silk and GDD was 0.99. Frequency distribution (Figure 4.4) was highly skewed with no inbreds found as day-neutral. About one-third of all inbreds had a silking delay between 15-19 days. Inbreds with low sensitivity to photoperiod (14 days or less silking delay) accounted for 12% of the total number (Figure 4.5), 41% for moderately low, 28% for moderately high, and 19% for high sensitivity.

Most of the lines that exhibited low photoperiod sensitivity were derived from temperate germplasm such as the Minnesota lines (A619 and A632), Iowa lines (B73 and B77), Indiana lines (H95 and H98), Missouri lines (Mo20W and Mo5) and lines from North Carolina, and Ohio. Conversely, lines that showed high sensitivity were of tropical origin. Means of all tropical and temperate derived lines when grown under short and long daylength are presented in Figure 4.6. Tropical and temperate lines did not differ much under short

Percentage of inbreds

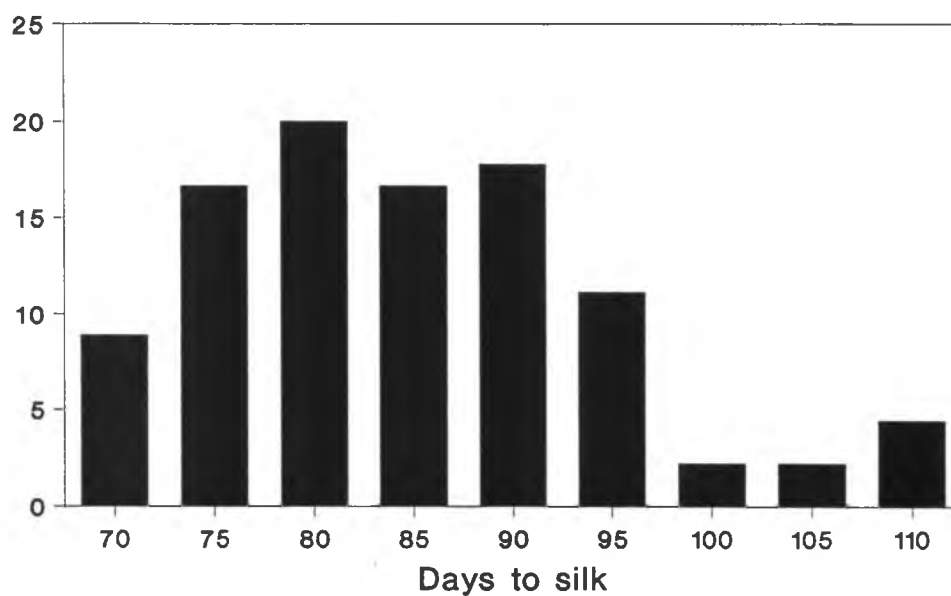


Figure 4.3. Frequency distribution among tropical-adapted maize inbreds for days to silking under long daylength.

Percentage of inbreds

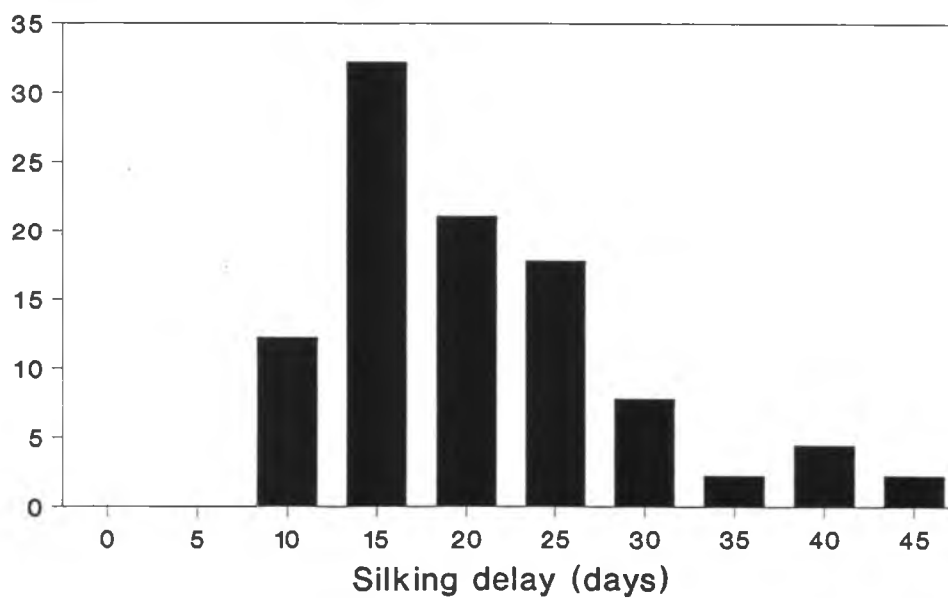


Figure 4.4. Frequency distribution among tropical-adapted maize inbreds for silking delay.

Table 4.6. Photoperiod sensitivity expressed as silking delay of tropical-adapted maize inbreds.

Inbreds	Days	GDD	Inbreds	Days	GDD
A619 (Hi)	16.3	174	HIX4283	18.7	217
A632 (Hi)	16.0	160	ICA L210	27.9	359
ANT CS-S5	31.5	418	ICA L219	33.4	436
B73 (Hi)	13.2	115	ICA L221	25.4	325
B77 (Hi)	15.3	149	ICA L224	29.7	382
CI64 (Hi)	17.9	192	ICA L27	24.2	308
CI66 (Hi)	16.0	156	ICA L29	27.7	357
CIM.A-21 (Hi)	29.3	374	ICA L36	22.8	290
CIM.A-6 (Hi)	43.7	505	INV 138	22.9	276
CIM.T11-ES	39.8	472	INV 302	23.3	289
CM116	28.5	370	INV 534	32.3	423
CM117	21.5	255	INV 575	16.5	164
CM118	33.0	434	KU1409	45.5	557
CM201 (Hi)	13.9	123	KU1414	41.1	498
CM207	19.8	224	KU1418	45.9	540
Fla2AT113	23.7	298	Ky226 (Hi)	17.2	187
Fla2AT114	23.0	283	MIT 11-S3	34.6	462
Fla2AT115	28.3	368	Mo20W	12.7	104
Fla2AT116	30.5	392	Mo5 (Hi)	15.1	141
Fla2BT106	26.2	337	Mp496	25.1	314
Fla2BT54	25.8	335	Mp68:616 (Hi)	21.9	256
Fla2BT73	24.0	306	N139	14.8	147
Ga209 (Hi)	17.8	186	N28 (Hi)	12.2	101
GT112Rf	24.9	314	Narino 330-S6	25.8	329
H55 (Hi)	21.0	250	NC246	21.2	257
H632F	17.9	195	NC248	19.2	219
H95 (Hi)	13.8	123	Oh43 (Hi)	16.7	179
H98 (Hi)	14.7	148	PAC90038	13.0	111
Hi25	13.9	131	Phil DMR-S6	34.7	455
Hi26	15.8	159	SC213	23.7	272
Hi27	27.0	345	SC301D (Hi)	17.6	193
Hi28	24.9	307	SC43	20.0	230
Hi29	17.7	186	T232	19.6	228
Hi30	14.9	145	T256	21.0	250
Hi31	14.5	136	T258	16.5	174
Hi32	15.5	159	Tuxpeno-S5	27.3	349
Hi33	13.3	118	Tx29A (Hi)	18.6	216
Hi34	26.1	335	Tx5855	17.0	184
Hi35	24.8	316	Tx601 (Hi)	22.8	293
Hi39	17.7	195	Tzi17	19.6	234
Hi40	18.0	196	Tzi3	44.1	519
Hi41	21.3	266	Tzi4	30.8	357
HIX4231	14.6	144	Va35 (Hi)	11.3	93
HIX4263	17.1	178	W64A (Hi)	13.8	123
HIX4267	13.7	128			
HIX4269	15.8	159	Mean	22.4	262.9

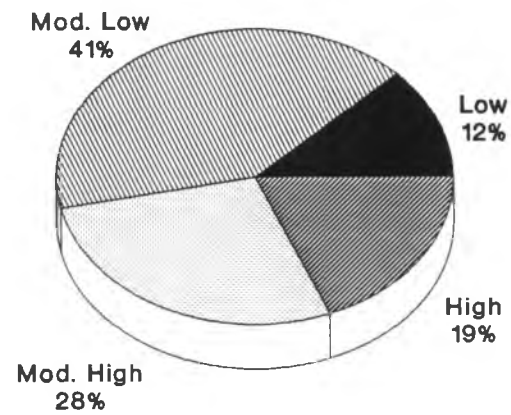


Figure 4.5. Percentage of inbreds under each photoperiod sensitivity group.

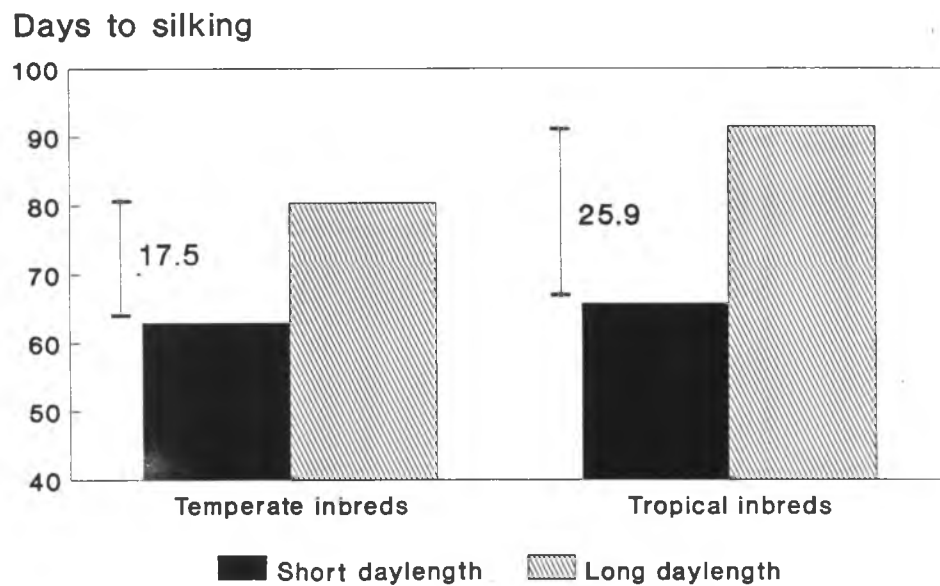


Figure 4.6. Mean number of days to silking for inbreds with tropical and temperate genetic background.

daylength, but showed wide divergence under long daylength. Silking delay was 17.5 and 25.9 days for the temperate and tropical derived lines, respectively.

#### **4.3 Relationship Between Maturity Under Short Daylength and Photoperiod Sensitivity**

Days to silking for the four maturity groups under short and long daylengths are illustrated in Figure 4.7. Silking delay appeared to increase generally with increasing maturity. A closer look at the data in Tables 4.2 and 4.6, however, revealed the presence of wide genotypic variation within each maturity group. For example, Ant C-S5 was classified as early maturing under short daylength, but extremely late under long daylength due to its high sensitivity to photoperiod. Lines such as HIX4267 and N28 were classified as medium late but showed low photoperiod sensitivity. No line, however, showed both late maturity and low sensitivity. Regression analysis showed a very weak relationship with  $r^2=0.21$  (Figure 4.8). It is clear that photoperiod sensitivity of tropical-adapted maize inbreds can not be predicted by their silking date under short or long daylength conditions.

#### **4.4 Discussion**

Inbreds evaluated for maturity and photoperiod sensitivity represented a worldwide collection from the major corn growing zones. Many of them are well-known inbreds such as B73 and Mo17 (Hi33), A619, and W64A, and are

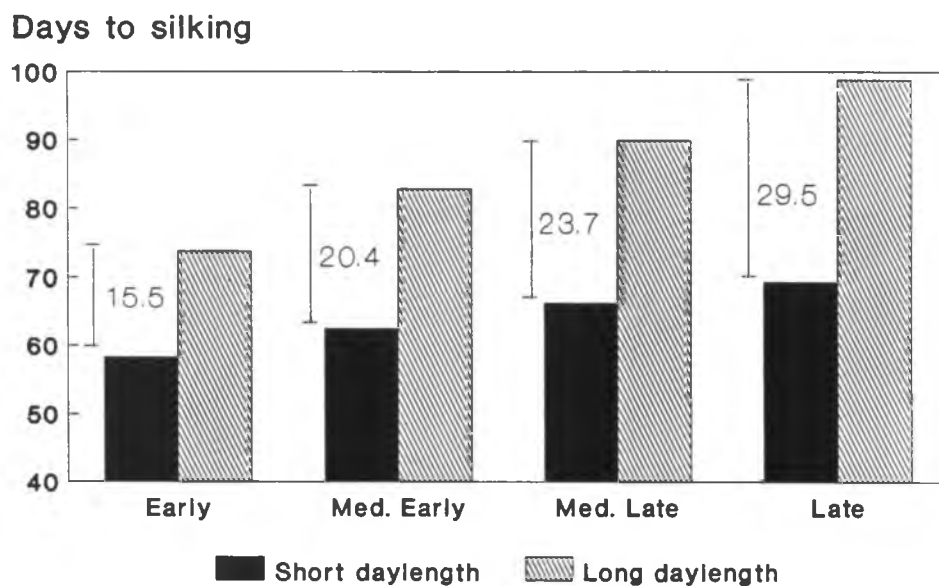


Figure 4.7. Mean number of days to silking for each maturity group under short and long daylength.

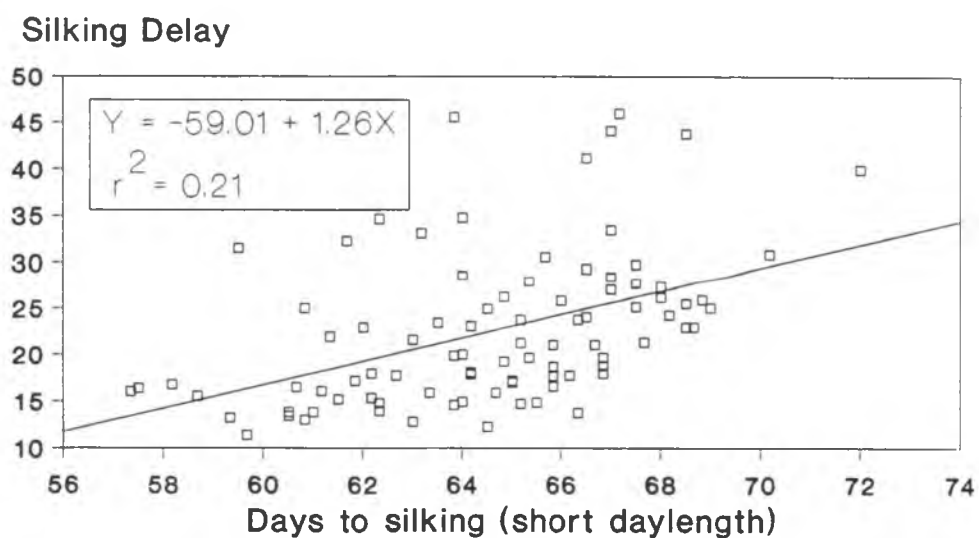


Figure 4.8. Relationship between days to silking under short daylength and photoperiod sensitivity (silking delay).



of 1950 and 1960 vintage. Temperate inbreds that carried the Hi suffix were converted by Brewbaker for resistance to Maize Mosaic Virus (MMV) and adaptation in Hawaii, hence they are sort of "tropicalized" (Brewbaker, 1974). Tropical lines from India, Colombia, Thailand and Nigeria had been derived at least 50% from tropical background and selected for high resistance to pests and diseases as well as for combining abilities. All the inbreds used in this study were part of the Maize Inbred Resistance (MIR) trials conducted in about 15 countries. So far, 46 trials have been conducted for important pests and diseases both in the tropics and temperate areas (Brewbaker et al., 1989). These inbreds are elite lines that could be tapped by breeding programs anywhere in the world. It is imperative, therefore, to accurately measure their maturity and photoperiod sensitivity for their systematic and rapid deployment across latitudes.

Various measures of maturity utilized by different workers included days from planting or emergence to silking or tasseling; days from planting or emergence to physiological maturity (blacklayer formation); percentage of dry matter or moisture in the grain at harvest; leaf number; and growing degree days or heat units for the different phenological stages (Jugenheimer, 1976). Days to silking or tasseling are popular way of measuring maturity because they are less laborious to quantify compared to other methods.

Shaw and Thom (1951) and Hallauer and Russell (1962) showed that maturity could be predicted at silking time since interval from silking to maturity is quite constant, although some workers found variation for this interval among inbred lines of corn (Carter and Poneleit, 1973; Daynard and Kannenberg, 1976).

The results here indicate that maturity measured in days to silking was effective in classifying the inbreds into different maturity groups under the tropical or short-day environment. Planting during cool winter months (1985 and 1987 trials) extended silking date by about 2 weeks over the summer planting season, but thermal units clearly showed that regardless of planting dates, maturity remained basically constant from season to season. This reinforces the practice of using data from different seasons and environments when estimating maturity in terms of calendar days. Either days or heat units may be used when comparing maturity among cultivars within a given environment or by using the means over environments, since the relative order and magnitude were not affected as evidenced by the high correlation (0.999) between days and GDD. Bias occurs when comparison is made between two different cultivars planted in different environments.

It is convenient to express maturity in days, since heat units are still viewed as an abstract unit by most farmers. Weather stations are often operated only by major

research stations to permit accurate estimation of GDD. Growing degree day values from temperate studies are of little value in the tropics because of photoperiod sensitivity (Brewbaker, 1981). One of the objections in using GDD is that it is not an exact figure and can vary from year to year and locations to locations (Baker, 1970). Heat units are no better than calendar days in areas where high cloud cover and monsoon rains are the norm, plus other environmental stresses such as drought and high incidence of pests and diseases.

Inbreds reached silking much later in Iowa than in Korea, about 30% longer in terms of days but was only 7% longer using heat units. These data confirmed the results of Lee (1987) who showed that photoperiod sensitivity, using tassel initiation as an index, increased with increasing daylength. There is no direct evidence linking the effect of temperature on silking delay, but the temperature effect appeared to be independent of photoperiod effect, based on similarities of heat unit values in Iowa and Korea. Photoperiod and temperature effects were reported to be independent (Hunter et al., 1974) and photoperiod sensitivity was the same or less at lower temperature (Breuer et al., 1976 and Stevenson and Goodman, 1972). Some researchers have observed that photoperiod sensitivity is expressed more at lower temperatures (Coligado and Brown, 1975b; Francis, 1972a; Hesketh et al., 1969). It was

apparent that photoperiod effects were considerably greater than temperature effects when comparing data from Iowa, Korea, and Waimanalo. Russell and Stuber (1983) reported greater effect due to photoperiod than to temperature in their phytotron studies which involved seven inbreds.

Previous attempts to identify photoperiod sensitivity in inbreds were made using artificial lights in the field (Lee, 1978; Brewbaker, 1981; Francis, 1970) or under controlled environments inside the phytotron (Russell and Stuber, 1983; Kiniry et al., 1983; Rood and Major, 1980). The main sensitivity index used was delay in days to tassel initiation (which could be done only through destructive sampling), silking and anthesis delay, and leaf number differences. Brewbaker (1981) showed that these indices were highly correlated.

Silking delay measured as the difference in silking between the short daylength of Hawaii and long daylength of Iowa and Korea, provided in vivo performance of these inbreds. This was made possible through collaboration of researchers as part of the Maize Inbred Resistance (MIR) trials initiated by the University of Hawaii (Brewbaker et al., 1989). The use of artificial lights will permit rapid screening in the field, but evaluations in actual long daylength environment are ultimately essential. With the MIR trials, multilocation testings are facilitated. Indeed, the actual silking delay was effective in classifying

photoperiod sensitivity among the 90 inbreds. Thirty-eight of the inbreds were previously screened under lighted field conditions in Hawaii (Brewbaker, 1981). Correlation between the results of this study and that lighted field experiment was high ( $r = 0.80^{**}$ ), a proof of the effectiveness of using artificial lights to evaluate photoperiod sensitivity.

No inbred in the present study could be called strictly day-neutral. Only a small proportion of the total number displayed low sensitivity, more than two-thirds were in the moderate category, and one-fifth were considered highly sensitive. A majority of the inbreds that showed low sensitivity were derived from temperate lines converted in Hawaii such as A619 (Hi), B73 (Hi), and etc., while those that showed high sensitivity originated from the tropics. Moderate types included both tropical and temperate derived inbreds, hence, this does not necessarily mean that all temperate lines are photoperiod insensitive and that all tropical lines are photoperiod sensitive.

One of the key questions that remain largely unanswered is whether or not photoperiod sensitivity is distinct from maturity expressed under short day (Russell and Stuber, 1983). Francis et al. (1969) and Hunter et al. (1974) suggested that a trend exists for increasing photoperiod sensitivity with later maturity genotypes. A wide range of responses were found among early inbreds (Rood and Major, 1980), while among inbreds expressing moderate or late

short day maturity a large range of photoperiod sensitivity occurred (Russell and Stuber, 1983).

When inbreds were lumped together under each SD maturity group, silking delay increased with maturity. Regression analysis proved, however, that this relationship was not strong enough for accurate prediction. The correlation coefficient of 0.46 agreed closely with the  $r$  value (0.42) obtained by Russell and Stuber (1983). A wide range of sensitivity occurred in the moderate groups, and narrower ranges were observed for early and late genotypes. No late inbred exhibited low sensitivity, and only one early inbred (Ant C-S5) was found to be highly sensitive to photoperiod. These observations are in agreement with the results of previous studies. The only way to verify the genetic relationship between SD maturity and photoperiod sensitivity is by employing isolines for maturity. This is difficult to accomplish since maturity is governed by more than one pair genes (Giesbrecht 1960a, 1960b; Mohamed, 1959; and Hallauer, 1965). The second and easy way is to conduct a selection study for maturity and measure the correlated effects on photoperiod sensitivity.

## 5. DIALLEL ANALYSIS

A nine-entry diallel analysis was made for inbreds chosen to represent a wide range of variation in maturity and photoperiod sensitivity. The main objective of the study was to determine combining ability effects for these two traits. Trials were planted in four locations, under both short- and long-day conditions.

### 5.1 Maturity Related Traits

#### 5.1.1 Variation Among Entry Means

Mean numbers of days to anthesis (DTA), days to silking (DTS), anthesis to silking interval (ASI), days to blacklayer formation (BLF), and grain filling period (GFP) are presented in Tables 5.1, 5.2, 5.3, 5.4, and 5.5, respectively. GFP was obtained by subtracting DTS from BLF. Comparisons were made between the short-daylength (SD) environments of Kauai and Waimanalo (Wai1) and the long daylength (LD) environment at Iowa and extended daylength at Waimanalo using artificial lighting in the field (Wai2). BLF and GFP were not measured in Iowa so LD means for these traits were based only on Wai2.

All maturity related traits were affected by longer daylengths. All entries showed delayed anthesis, silking, and BLF, as well as extended ASI under longer daylength in Iowa and Wai2. GFP's (Table 5.5) were shortened, however, under LD in many of the entries. Except for few entries, the changes were small, and among the parents, only

Table 5.1. Number of days to anthesis in four environments.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	49.7	56.0	52.8	74.0	92.8	83.4
B73 (Hi)	47.0	55.0	51.0	53.3	75.5	64.4
Hi29	51.0	57.0	54.0	62.7	84.2	73.4
Hi32	46.7	53.3	50.0	52.3	76.3	64.3
Hi34	57.0	61.0	59.0	77.0	101.7	89.3
Narino 330-S6	57.3	65.3	61.3	74.7	102.5	88.6
Oh43 (Hi)	48.0	53.0	50.5	56.0	77.3	66.7
Tx601 (Hi)	57.3	62.0	59.7	78.3	97.0	87.7
Tzi4	57.7	66.7	62.2	69.0	110.7	89.8
Ant C-S5 x B73 (Hi)	46.0	54.7	50.3	55.3	81.5	68.4
Ant C-S5 x Hi29	49.3	54.7	52.0	62.7	87.0	74.8
Ant C-S5 x Hi32	46.0	54.0	50.0	59.0	82.3	70.7
Ant C-S5 x Hi34	52.3	59.0	55.7	71.7	91.8	81.8
Ant C-S5 x Narino 330-S6	50.7	59.0	54.8	69.0	92.8	80.9
Ant C-S5 x Oh43 (Hi)	44.7	52.3	48.5	57.7	82.2	69.9
Ant C-S5 x Tx601 (Hi)	51.7	58.3	55.0	77.3	95.0	86.2
Ant C-S5 x Tzi4	53.0	59.3	56.2	76.0	105.0	90.5
B73 (Hi) x Hi29	47.7	54.0	50.8	59.3	82.7	71.0
B73 (Hi) x Hi32	45.0	53.0	49.0	52.7	74.0	63.3
B73 (Hi) x Hi34	50.7	56.3	53.5	61.7	83.8	72.8
B73 (Hi) x Narino 330-S6	49.7	57.7	53.7	59.0	83.7	71.3
B73 (Hi) x Oh43 (Hi)	44.7	51.3	48.0	51.3	72.8	62.1
B73 (Hi) x Tx601 (Hi)	51.7	55.7	53.7	62.3	84.0	73.2
B73 (Hi) x Tzi4	51.7	58.0	54.8	63.0	87.8	75.4
Hi29 x Hi32	49.0	53.3	51.2	56.7	77.7	67.2
Hi29 x Hi34	52.3	57.0	54.7	64.0	88.2	76.1
Hi29 x Narino 330-S6	52.3	59.3	55.8	63.3	90.2	76.8
Hi29 x Oh43 (Hi)	46.0	54.7	50.3	56.0	78.5	67.3
Hi29 x Tx601 (Hi)	52.7	59.7	56.2	66.0	87.7	76.8
Hi29 x Tzi4	53.0	60.7	56.8	63.7	95.3	79.5
Hi32 x Hi34	49.3	55.3	52.3	58.7	82.3	70.5
Hi32 x Narino 330 S-6	51.0	56.0	53.5	59.0	84.0	71.5
Hi32 x Oh43 (Hi)	45.7	54.7	50.2	52.3	75.8	64.1
Hi32 x Tx601 (Hi)	51.0	56.7	53.8	62.0	83.7	72.8
Hi32 x Tzi4	51.0	59.0	55.0	63.7	87.0	75.3
Hi34 x Narino 330-S6	53.3	60.0	56.7	68.7	90.0	79.3
Hi34 x Oh43 (Hi)	50.3	54.3	52.3	59.0	82.5	70.8
Hi34 x Tx601 (Hi)	54.3	61.3	57.8	72.0	88.7	80.3
Hi34 x Tzi4	54.3	61.7	58.0	73.7	98.0	85.8
Narino 330-S6 x Oh43 (Hi)	49.0	55.3	52.2	58.3	82.0	70.2
Narino 330-S6 x Tx601 (Hi)	53.3	61.0	57.2	71.3	90.8	81.1
Narino 330-S6 x Tzi4	54.3	62.7	58.5	70.3	102.2	86.3
Oh43 (Hi) x Tx601 (Hi)	51.0	54.0	52.5	59.3	79.5	69.4
Oh43(Hi) x Tzi4	50.3	53.7	52.0	63.3	81.5	72.4
Tx601 (Hi) x Tzi4	57.0	63.0	60.0	77.0	101.3	89.2
Mean	50.8	57.3	54.1	63.9	87.4	75.6
LSD (0.05)	1.3	2.4	1.8	3.0	3.3	3.1



Table 5.2. Number of days to silking in four environments.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	50.7	56.0	53.3	93.0	98.7	95.8
B73 (Hi)	49.3	56.7	53.0	58.7	78.2	68.4
Hi29	53.3	59.3	56.3	68.7	87.5	78.1
Hi32	48.7	55.7	52.2	58.3	78.3	68.3
Hi34	60.0	63.3	61.7	90.0	106.7	98.3
Narino 330-S6	59.3	68.0	63.7	79.0	111.3	95.2
Oh43 (Hi)	50.0	56.0	53.0	61.3	80.0	70.7
Tx601 (Hi)	61.0	64.0	62.5	90.0	105.7	97.8
Tzi4	60.7	68.7	64.7	83.0	139.2	111.1
Ant C-S5 x B73 (Hi)	47.0	56.0	51.5	60.3	84.0	72.2
Ant C-S5 x Hi29	50.7	56.0	53.3	69.3	90.8	80.1
Ant C-S5 x Hi32	48.0	55.7	51.8	65.3	84.8	75.1
Ant C-S5 x Hi34	54.3	61.0	57.7	80.0	98.2	89.1
Ant C-S5 x Narino 330-S6	51.7	59.7	55.7	78.3	98.7	88.5
Ant C-S5 x Oh43 (Hi)	46.7	53.3	50.0	62.3	83.7	73.0
Ant C-S5 x Tx601 (Hi)	53.3	60.0	56.7	97.3	105.0	101.2
Ant C-S5 x Tzi4	54.3	60.7	57.5	94.3	113.5	103.9
B73 (Hi) x Hi29	50.0	56.0	53.0	63.7	85.0	74.3
B73 (Hi) x Hi32	47.3	54.7	51.0	58.0	75.7	66.8
B73 (Hi) x Hi34	52.3	58.0	55.2	68.3	87.7	78.0
B73 (Hi) x Narino 330-S6	52.7	60.0	56.3	65.7	86.2	75.9
B73 (Hi) x Oh43 (Hi)	46.7	52.3	49.5	56.0	74.5	65.3
B73 (Hi) x Tx601 (Hi)	54.0	57.0	55.5	72.3	88.0	80.2
B73 (Hi) x Tzi4	53.7	59.7	56.7	73.0	93.3	83.2
Hi29 x Hi32	51.3	56.0	53.7	62.7	81.3	72.0
Hi29 x Hi34	54.7	60.0	57.3	73.0	92.3	82.7
Hi29 x Narino 330-S6	54.7	62.7	58.7	69.7	94.7	82.2
Hi29 x Oh43 (Hi)	48.0	56.7	52.3	62.3	80.7	71.5
Hi29 x Tx601 (Hi)	55.7	62.0	58.8	74.0	92.3	83.2
Hi29 x Tzi4	55.7	62.7	59.2	70.3	105.8	88.1
Hi32 x Hi34	50.7	57.0	53.8	65.0	85.2	75.1
Hi32 x Narino 330 S-6	52.7	58.7	55.7	65.0	86.2	75.6
Hi32 x Oh43 (Hi)	48.7	57.0	52.8	58.7	77.7	68.2
Hi32 x Tx601 (Hi)	53.3	60.0	56.7	71.3	87.7	79.5
Hi32 x Tzi4	53.7	60.0	56.8	72.7	90.0	81.3
Hi34 x Narino 330-S6	55.7	62.7	59.2	74.7	95.3	85.0
Hi34 x Oh43 (Hi)	52.3	56.0	54.2	65.0	86.0	75.5
Hi34 x Tx601 (Hi)	56.7	63.7	60.2	80.3	92.7	86.5
Hi34 x Tzi4	56.3	64.3	60.3	87.7	103.7	95.7
Narino 330-S6 x Oh43 (Hi)	50.3	56.0	53.2	62.3	84.2	73.3
Narino 330-S6 x Tx601 (Hi)	56.7	63.0	59.8	77.3	95.8	86.6
Narino 330-S6 x Tzi4	56.3	64.3	60.3	76.7	107.0	91.8
Oh43 (Hi) x Tx601 (Hi)	53.3	55.7	54.5	64.0	82.0	73.0
Oh43(Hi) x Tzi4	53.0	54.0	53.5	70.7	84.3	77.5
Tx601 (Hi) x Tzi4	59.3	64.7	62.0	90.7	108.3	99.5
Mean	53.0	59.2	56.1	72.0	92.2	82.1
LSD (0.05)	1.1	2.6	1.9	4.7	5.2	4.9

Table 5.3. Anthesis to silking interval in four environments.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	1.0	0.0	0.5	19.0	5.8	12.4
B73 (Hi)	2.3	1.7	2.0	5.3	2.7	4.0
Hi29	2.3	2.3	2.3	6.0	3.3	4.7
Hi32	2.0	2.3	2.2	6.0	2.0	4.0
Hi34	3.0	2.3	2.7	13.0	5.0	9.0
Narino 330-S6	2.0	2.7	2.3	4.3	8.8	6.6
Oh43 (Hi)	2.0	3.0	2.5	5.3	2.7	4.0
Tx601 (Hi)	3.7	2.0	2.8	11.7	8.7	10.2
Tzi4	3.0	2.0	2.5	14.0	28.5	21.3
Ant C-S5 x B73 (Hi)	1.0	1.3	1.2	5.0	2.5	3.8
Ant C-S5 x Hi29	1.3	1.3	1.3	6.7	3.8	5.3
Ant C-S5 x Hi32	2.0	1.7	1.8	6.3	2.5	4.4
Ant C-S5 x Hi34	2.0	2.0	2.0	8.3	6.3	7.3
Ant C-S5 x Narino 330-S6	1.0	0.7	0.8	9.3	4.0	6.7
Ant C-S5 x Oh43 (Hi)	2.0	1.0	1.5	4.7	1.5	3.1
Ant C-S5 x Tx601 (Hi)	1.7	1.7	1.7	20.0	14.3	17.2
Ant C-S5 x Tzi4	1.3	1.3	1.3	18.3	8.5	13.4
B73 (Hi) x Hi29	2.3	2.0	2.2	4.3	2.3	3.3
B73 (Hi) x Hi32	2.3	1.7	2.0	5.3	1.7	3.5
B73 (Hi) x Hi34	1.7	1.7	1.7	6.7	3.8	5.3
B73 (Hi) x Narino 330-S6	3.0	2.3	2.7	6.7	2.5	4.6
B73 (Hi) x Oh43 (Hi)	2.0	1.0	1.5	4.7	1.7	3.2
B73 (Hi) x Tx601 (Hi)	2.3	1.3	1.8	10.0	4.0	7.0
B73 (Hi) x Tzi4	2.0	1.7	1.8	10.0	5.5	7.8
Hi29 x Hi32	2.3	2.7	2.5	6.0	3.7	4.8
Hi29 x Hi34	2.3	3.0	2.7	9.0	4.2	6.6
Hi29 x Narino 330-S6	2.3	3.3	2.8	6.3	4.5	5.4
Hi29 x Oh43 (Hi)	2.0	2.0	2.0	6.3	2.2	4.3
Hi29 x Tx601 (Hi)	3.0	2.3	2.7	8.0	4.7	6.3
Hi29 x Tzi4	2.7	2.0	2.3	6.7	10.5	8.6
Hi32 x Hi34	1.3	1.7	1.5	6.3	2.8	4.6
Hi32 x Narino 330 S-6	1.7	2.7	2.2	6.0	2.2	4.1
Hi32 x Oh43 (Hi)	3.0	2.3	2.7	6.3	1.8	4.1
Hi32 x Tx601 (Hi)	2.3	3.3	2.8	9.3	4.0	6.7
Hi32 x Tzi4	2.7	1.0	1.8	9.0	3.0	6.0
Hi34 x Narino 330-S6	2.3	2.7	2.5	6.0	5.3	5.7
Hi34 x Oh43 (Hi)	2.0	1.7	1.8	6.0	3.5	4.8
Hi34 x Tx601 (Hi)	2.3	2.3	2.3	8.3	4.0	6.2
Hi34 x Tzi4	2.0	2.7	2.3	14.0	5.7	9.8
Narino 330-S6 x Oh43 (Hi)	1.3	0.7	1.0	4.0	2.2	3.1
Narino 330-S6 x Tx601 (Hi)	3.3	2.0	2.7	6.0	5.0	5.5
Narino 330-S6 x Tzi4	2.0	1.7	1.8	6.3	4.8	5.6
Oh43 (Hi) x Tx601 (Hi)	2.3	1.7	2.0	4.7	2.5	3.6
Oh43(Hi) x Tzi4	2.7	0.3	1.5	7.3	2.8	5.1
Tx601 (Hi) x Tzi4	2.3	1.7	2.0	13.7	7.0	10.3
Mean	2.2	1.9	2.0	8.1	4.9	6.5
LSD (0.05)	1.0	1.6	1.3	3.4	2.6	3.0

Table 5.4. Number of days to BLF in 2 environments.

Entries	SD (Wai1)	LD (Wai2)
Ant C-S5	95.3	120.0
B73 (Hi)	93.4	100.4
Hi29	93.0	111.8
Hi32	90.2	97.2
Hi34	98.2	126.4
Narino 330-S6	97.7	116.9
Oh43 (Hi)	91.8	100.0
Tx601 (Hi)	100.3	123.3
Tzi4	100.4	117.3
Ant C-S5 x B73 (Hi)	90.4	100.1
Ant C-S5 x Hi29	93.8	113.9
Ant C-S5 x Hi32	92.4	108.7
Ant C-S5 x Hi34	93.9	120.4
Ant C-S5 x Narino 330-S6	93.3	116.2
Ant C-S5 x Oh43 (Hi)	90.0	101.7
Ant C-S5 x Tx601 (Hi)	98.0	122.9
Ant C-S5 x Tzi4	94.3	124.0
B73 (Hi) x Hi29	93.8	104.1
B73 (Hi) x Hi32	89.2	97.1
B73 (Hi) x Hi34	97.2	109.3
B73 (Hi) x Narino 330-S6	94.9	105.0
B73 (Hi) x Oh43 (Hi)	87.8	97.3
B73 (Hi) x Tx601 (Hi)	94.8	112.9
B73 (Hi) x Tzi4	94.2	113.3
Hi29 x Hi32	94.9	105.0
Hi29 x Hi34	96.4	114.0
Hi29 x Narino 330-S6	96.0	113.9
Hi29 x Oh43 (Hi)	92.7	103.7
Hi29 x Tx601 (Hi)	96.3	108.1
Hi29 x Tzi4	97.0	116.7
Hi32 x Hi34	93.0	103.3
Hi32 x Narino 330 S-6	95.1	106.0
Hi32 x Oh43 (Hi)	89.2	97.7
Hi32 x Tx601 (Hi)	97.1	111.0
Hi32 x Tzi4	93.2	115.0
Hi34 x Narino 330-S6	94.0	113.7
Hi34 x Oh43 (Hi)	93.0	104.4
Hi34 x Tx601 (Hi)	96.4	118.7
Hi34 x Tzi4	96.1	125.0
Narino 330-S6 x Oh43 (Hi)	92.4	107.8
Narino 330-S6 x Tx601 (Hi)	98.8	120.3
Narino 330-S6 x Tzi4	98.1	118.3
Oh43 (Hi) x Tx601 (Hi)	94.1	104.3
Oh43(Hi) x Tzi4	95.3	112.4
Tx601 (Hi) x Tzi4	98.9	123.9
Mean	94.6	111.2
LSD (0.05)	2.2	4.1

Table 5.5. Grain filling period in two environments.

Entries	SD (Wail)	LD (Wai2)
Ant C-S5	44.7	27.0
B73 (Hi)	44.1	41.8
Hi29	39.7	43.1
Hi32	41.6	38.9
Hi34	38.2	36.4
Narino 330-S6	38.3	37.9
Oh43 (Hi)	41.8	38.7
Tx601 (Hi)	39.3	33.3
Tzi4	39.8	34.3
Ant C-S5 x B73 (Hi)	43.4	39.8
Ant C-S5 x Hi29	43.1	44.6
Ant C-S5 x Hi32	44.4	43.3
Ant C-S5 x Hi34	39.6	40.4
Ant C-S5 x Narino 330-S6	41.7	37.9
Ant C-S5 x Oh43 (Hi)	43.3	39.3
Ant C-S5 x Tx601 (Hi)	44.7	25.6
Ant C-S5 x Tzi4	40.0	29.7
B73 (Hi) x Hi29	43.8	40.4
B73 (Hi) x Hi32	41.9	39.1
B73 (Hi) x Hi34	44.9	41.0
B73 (Hi) x Narino 330-S6	42.2	39.3
B73 (Hi) x Oh43 (Hi)	41.1	41.3
B73 (Hi) x Tx601 (Hi)	40.8	40.6
B73 (Hi) x Tzi4	40.6	40.3
Hi29 x Hi32	43.6	42.3
Hi29 x Hi34	41.8	41.0
Hi29 x Narino 330-S6	41.3	44.2
Hi29 x Oh43 (Hi)	44.7	41.3
Hi29 x Tx601 (Hi)	40.7	34.1
Hi29 x Tzi4	41.3	46.3
Hi32 x Hi34	42.3	38.3
Hi32 x Narino 330 S-6	42.4	41.0
Hi32 x Oh43 (Hi)	40.6	39.0
Hi32 x Tx601 (Hi)	43.8	39.7
Hi32 x Tzi4	39.6	42.3
Hi34 x Narino 330-S6	38.3	39.0
Hi34 x Oh43 (Hi)	40.7	39.4
Hi34 x Tx601 (Hi)	39.8	38.3
Hi34 x Tzi4	39.8	37.3
Narino 330-S6 x Oh43 (Hi)	42.1	45.4
Narino 330-S6 x Tx601 (Hi)	42.1	43.0
Narino 330-S6 x Tzi4	41.8	41.7
Oh43 (Hi) x Tx601 (Hi)	40.8	40.3
Oh43(Hi) x Tzi4	42.3	41.8
Tx601 (Hi) x Tzi4	39.6	33.2
Mean	41.6	39.2
LSD (0.05)	2.4	2.3

inbred Hi29 showed an increase in GFP under LD. Ant C-S5 was rather odd with a large decrease of GFP under LD. It was difficult to measure BLF for this particular inbred, since very few kernels developed under LD condition. Rapid drying resulting in wrinkled kernels was also observed in Ant C-S5, thus confounding GFP measurement. Similar conditions were also observed in Tx601 and Tzi4 and in crosses involving the three late inbreds. Otherwise, most of the hybrids had more or less similar GFP under both daylength regimes.

Accumulated thermal units were computed in order to remove temperature effects from photoperiod effects. Growing degree days (GDD) are listed in Appendices 1, 2, 3, 4, and 5 for anthesis, silking, ASI, BLF, and GFP, respectively. Photoperiod had stronger effects than temperature as evidenced by still higher GDD values in LD than SD. What changed were the relative values between locations within daylength. For example, the overall mean for anthesis and silking at Iowa was much higher than Wai2 trial when calendar days were used, but generally become closer when GDD was used. The same thing happened between Wai1 and Kauai trials. GDD of temperate inbreds such as B73 (Hi), Hi32 (Oh545), and Oh43 (Hi) (Hi) were similar across daylengths. Wide differences among daylengths however were observed for ASI among these inbreds. Correlation between

number of days and GDD were 0.999 for all traits indicating that relative order of entries was virtually unchanged.

Analyses of variance of the five maturity related traits for each of the environments are presented in Appendices 6, 8, 10, and 12 for the number of days and Appendices 7, 9, 11, and 13 for GDD. Highly significant variations among entry means were observed for all the maturity traits in all environments. Subdividing the entry means into three components revealed significant variations for parents, parents vs. crosses, and crosses in all environments, except in Kauai for ASI where the parent vs. crosses component was found to be non-significant. Analyses using the number of days and heat units produced the same results. Further partitioning of crosses into general combining ability (GCA) and specific combining ability (SCA) again revealed significant variations for all traits except ASI in Kauai trial, in which the SCA component was not significant.

All the experiments in four environments had a very low coefficients of variation (CV) for all the traits except ASI which ranged from 27.87 % (Waimanalo) to 51.38% (Kauai). The large CV's for ASI were attributed to the confounding of experimental errors since ASI was a derived data from two measured variables, i. e., anthesis and silking. Otherwise, all the other traits had CV's lower than 5% (Table 5.6). This was reflected also in the high coefficients of

determination shown in Table 5.7. Tasseling, silking, and blacklayer formation had values over 0.90, which indicated that over 90% of the total variation among means for these traits was accounted for by the statistical model. ASI and GFP had relatively lower but generally acceptable values.

Combined analyses of variance are presented in Table 5.8. Highly significant variations were observed among environments as well as the interaction between entries and environments (GxE) for all the maturity related traits studied. Partitioning of the GxE into different components (Table 5.9) showed highly significant interaction between environments and parents, parents vs. crosses, SCA, and GCA. Analyses using heat unit values are presented in Appendices 14 and 15 which showed the same results.

Table 5.10 gave the percent contribution of the GxE interactions to the total variation among means. Anthesis, silking, and BLF were found to have GxE contributing less than 10% of the total variation among means. GxE, however, accounted for 32.7, and 37% of the total variation for GFP and ASI, respectively. For each of the GxE, relative magnitude of the components were also computed. Parents vs. crosses x E accounted for the largest proportion, ranging from 36 to 88.3% for silking. The real genetic x environment interaction, i.e., GCA x E, and SCA x E accounted for only a small segments of the total GxE variation.

Table 5.6. Coefficients of variation for the maturity related traits measured in four environments.

Maturity Traits		Short Daylength Wail	Daylength Kauai	Long Daylength Wai2	Daylength Iowa
Anthesis	Days	1.57	2.55	2.85	2.35
	GDD	1.63	2.82	2.92	3.33
Silking	Days	1.26	2.73	3.99	3.48
	GDD	1.30	2.87	3.90	4.39
ASI	Days	27.87	51.38	25.68	32.38
	GDD	27.80	44.13	24.54	42.66
BLF	Days	1.42	-	1.69	-
	GDD	1.34	-	1.63	-
GFP	Days	3.50	-	3.67	-
	GDD	3.36	-	3.81	-

Table 5.7. Coefficients of determination for the maturity related traits measured in four environments.

Maturity Traits		Short Daylength Wail	Daylength Kauai	Long Daylength Wai2	Daylength Iowa
Anthesis	Days	0.97	0.90	0.96	0.97
	GDD	0.97	0.89	0.96	0.96
Silking	Days	0.98	0.90	0.96	0.96
	GDD	0.98	0.89	0.96	0.96
ASI	Days	0.60	0.48	0.84	0.92
	GDD	0.62	0.48	0.84	0.82
BLF	Days	0.88	-	0.97	-
	GDD	0.86	-	0.97	-
GFP	Days	0.71	-	0.93	-
	GDD	0.77	-	0.93	-



Table 5.8.1. Combined analysis of variance for maturity related traits (days) in four environments.

Source	df	Mean Squares		
		Anthesis	Silking	ASI
Environments (E) ***	3	34249.2 **	40403.7 **	1147.7 **
Reps/E	8	8.4 **	10.7 **	1.4
Entries	44	387.7 **	615.8 **	42.0 **
Entries x E	132	37.4 **	98.7 **	22.2 **
Pooled Error	352	2.6	5.4	2.0

Table 5.8.2. Combined analysis of variance for maturity related traits in two environments.

Source	df	Mean Squares	
		BLF	GFP
Environments (E) ***	1	18595.9 **	394.3 **
Reps/E	4	3.4	5.3 **
Entries	44	179.7 **	35.0 **
Entries x E	44	63.3 **	31.1 **
Pooled Error	176	2.7	2.1

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

\*\*\* Environments were tested against Reps/E.

Table 5.9.1. Combined analysis of variance of parents and crosses for days to anthesis silking and ASI.

Source	df	Mean Squares		
		Anthesis	Silking	ASI
Entries	44	32.3 **	51.3 **	3.5 **
Parents (P)	8	63.2 **	104.3 **	8.1 **
P vs C	1	58.3 **	126.5 **	12.7 **
Crosses (C)	35	24.5 **	37.1 **	2.2 **
GCA	8	102.3 **	148.9 **	5.7 **
SCA	27	1.5	3.9	1.2
Entries x E	132	12.5 **	32.9 **	7.4 **
Parents x E	24	9.2 **	18.4 **	2.7 **
P vs C x E	3	396.5 **	1164.4 **	286.9 **
Crosses x E	105	2.3 **	3.9 **	0.5 **
GCA x E	24	8.6 **	13.7 **	1.0 **
SCA x E	81	0.4 **	1.0 **	0.3 **
Pooled Error	352	0.2	0.4	0.2

Table 5.9.2. Combined analysis of variance of parents and crosses for BLF and GFP.

Source	df	Mean Squares ***	
		BLF	GFP
Entries	44	30.0 **	5.8 **
Parents (P)	8	50.3 **	6.1 **
P vs C	1	16.5 **	27.6 **
Crosses (C)	35	25.7 **	5.2 **
GCA	8	100.3 **	9.1 **
SCA	27	3.6 **	4.0 **
Entries x E	44	21.1 **	10.4 **
Parents x E	8	22.0 **	4.8 **
P vs C x E	1	339.9 **	305.9 **
Crosses x E	35	11.8 **	3.2 **
GCA x E	8	45.0 **	5.2 **
SCA x E	27	1.9 **	2.6 **
Pooled Error	176	0.4	0.3

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

\*\*\* Mean squares were adjusted for the number of reps and environments.

### 5.1.2 GCA/SCA Ratio

These ratios were computed from each of the environments and from data across daylengths. The magnitude of GCA was consistently higher in all environments, with mean GCA/SCA ratio ranging from 2.0 (GFP) to 38.4 (anthesis) under short daylength and 2.0 to 37.8 under long daylength (Table 5.11). Ratios were largely affected by daylengths and by the use of either days or GDD.

### 5.1.3 Heterosis

As indicated in the analyses of variance, parent vs. crosses was significant for all cases suggesting significant differences among parents and crosses which is a measure of heterosis. To determine which parents gave the best prepotencies from their crosses, average heterosis values were computed for all the traits in all environments (Table 5.12). It was noted that heterosis for days to anthesis, silking, ASI, and BLF were negative indicating that their hybrids flowered or matured earlier than the mean of the parents. For anthesis, heterosis ranged from -2.41% (Hi32) to -4.90% (Oh43 (Hi)) under SD and -1.47 (Tzi4) to -7.30% (Hi34) under LD. Similar trend was observed for silking with LD giving higher absolute heterosis. For ASI, the absolute heterosis values were much more variable with SD values ranging from -22.39 (Oh43 (Hi)) to 1.90 (Hi32), and LD values ranging from -12.19 (Hi29) to 36.73 (Tzi4). The considerably higher absolute values in LD were primarily due

Table 5.10. Percent of the total variation among means of maturity related traits due to GxE interaction.

Source	Anthesi	Silking	ASI	BLF	GFP
Total GxE (days)	3.9	8.0	32.7	9.4	37
Parents x E	13.3	10.2	6.6	18.9	8.5
P vs. C x E	72.2	80.5	88.3	36.6	67.1
GCA x E	12.5	7.5	2.4	38.7	9.9
SCA x E	1.9	1.8	2.7	5.6	15.2
Total GxE (GDD)	4.29	6.68	29.59	10.09	29.85
Parents x E	9.19	8.13	5.65	17.74	10.23
P vs. C x E	84.27	86.42	89.78	40.79	63.43
GCA x E	5.06	3.98	1.94	36.13	11.24
SCA x E	1.48	1.46	2.63	5.35	15.10

Table 5.11. GCA/SCA ratio for maturity related traits.

Maturity Traits		Short Daylength			Long Daylength		
		Wail	Kauai	Mean	Wai2	Iowa	Mean
Anthesis	Days	51.6	25.1	38.4	37.7	37.9	37.8
	GDD	48.5	25.0	36.7	38.6	28.1	33.4
Silking	Days	50.1	19.9	35.0	17.4	31.8	24.6
	GDD	50.9	18.8	34.9	18.4	29.6	24.0
ASI	Days	2.5	4.5	3.5	4.5	4.3	4.4
	GDD	2.5	1.6	2.0	4.5	7.9	6.2
BLF	Days	12.2	-	12.2	25.5	-	25.5
	GDD	11.9	-	11.9	24.7	-	24.7
GFP	Days	2.0	-	2.0	2.0	-	2.0
	GDD	4.1	-	4.1	2.3	-	2.3

Table 5.12. Average percent heterosis (mid-parent) of the parents for maturity related traits.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Days to Anthesis						
Ant C-S5	-3.96	-2.03	-2.99	-5.46	-2.27	-3.87
B73 (Hi)	-3.38	-3.59	-3.48	-4.09	-3.30	-3.70
Hi29	-2.89	-2.34	-2.62	-4.86	-2.25	-3.55
Hi32	-2.81	-2.01	-2.41	-3.53	-4.21	-3.87
Hi34	-4.17	-2.75	-3.46	-6.90	-7.70	-7.30
Narino 330-S6	-5.19	-4.53	-4.86	-7.36	-6.76	-7.06
Oh43 (Hi)	-5.51	-4.28	-4.90	-7.34	-6.37	-6.85
Tx601 (Hi)	-3.13	-2.51	-2.82	-4.56	-5.01	-4.78
Tzi4	-2.94	-4.04	-3.49	1.95	-4.88	-1.47
Mean Heterosis	-3.78	-3.12	-3.45	-4.68	-4.75	-4.72
Days to Silking						
Ant C-S5	-4.24	-1.59	-2.92	-9.43	-3.76	-6.60
B73 (Hi)	-3.74	-3.90	-3.82	-5.03	-5.51	-5.27
Hi29	-2.88	-2.00	-2.44	-5.91	-3.26	-4.58
Hi32	-2.65	-2.00	-2.33	-4.56	-6.28	-5.42
Hi34	-5.11	-2.59	-3.85	-9.51	-8.89	-9.20
Narino 330-S6	-5.14	-4.86	-5.00	-7.64	-9.98	-8.81
Oh43 (Hi)	-5.33	-5.99	-5.66	-9.34	-9.04	-9.19
Tx601 (Hi)	-3.81	-2.37	-3.09	-4.59	-7.27	-5.93
Tzi4	-3.55	-4.66	-4.11	0.57	-13.41	-6.42
Mean Heterosis	-4.05	-3.33	-3.69	-6.16	-7.49	-6.82
Anthesis to Silking Interval						
Ant C-S5	-11.07	25.65	7.29	-30.36	-17.47	-23.92
B73 (Hi)	-10.78	-7.39	-9.09	-8.63	-35.01	-21.82
Hi29	-3.10	8.18	2.54	-10.49	-13.89	-12.19
Hi32	3.05	0.76	1.90	-8.12	-29.13	-18.63
Hi34	-23.33	6.84	-8.25	-25.98	-17.67	-21.82
Narino 330-S6	-5.77	-14.37	-10.07	-5.91	-48.77	-27.34
Oh43 (Hi)	0.45	-45.24	-22.39	-21.45	-45.02	-33.24
Tx601 (Hi)	-16.06	5.54	-5.26	-6.47	-22.68	-14.57
Tzi4	-16.04	-18.27	-17.15	-9.20	-64.25	-36.73
Mean Heterosis	-9.18	-4.26	-6.72	-14.07	-32.65	-23.36

Table 5.12 cont.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Days to Blacklayer Formation						
Ant C-S5	-2.31	-	-2.31	-2.13	-	-2.13
B73 (Hi)	-1.98	-	-1.98	-2.21	-	-2.21
Hi29	0.70	-	0.70	-2.01	-	-2.01
Hi32	-0.24	-	-0.24	-0.36	-	-0.36
Hi34	-1.77	-	-1.77	-4.32	-	-4.32
Narino 330-S6	-1.21	-	-1.21	-1.57	-	-1.57
Oh43 (Hi)	-2.25	-	-2.25	-3.12	-	-3.12
Tx601 (Hi)	-0.88	-	-0.88	-1.74	-	-1.74
Tzi4	-1.85	-	-1.85	3.46	-	3.46
Mean Heterosis	-1.31	-	-1.31	-1.56	-	-1.56
Grain Filling Period						
Ant C-S5	0.05	-	0.05	14.98	-	14.98
B73 (Hi)	0.23	-	0.23	3.53	-	3.53
Hi29	5.50	-	5.50	5.99	-	5.99
Hi32	2.92	-	2.92	8.30	-	8.30
Hi34	3.04	-	3.04	7.81	-	7.81
Narino 330-S6	4.47	-	4.47	11.41	-	11.41
Oh43 (Hi)	1.77	-	1.77	9.31	-	9.31
Tx601 (Hi)	3.35	-	3.35	4.08	-	4.08
Tzi4	0.70	-	0.70	8.94	-	8.94
Mean Heterosis	2.45	-	2.45	8.26	-	8.26

to longer interval between tasseling and silking in parents than in hybrids under long daylengths.

Heterosis values for BLF were generally lower indicating that parents and hybrids matured more or less at the same time. Consequently, GFP showed positive values ranging from 0.05 (Ant C-S5) to 5.50 (Hi29) under SD and 3.53 (B73) to 14.98 (Ant C-S5) under LD. The dramatic heterosis increase for Ant C-S5 as well as Narino 330-S6 under LD was not due to the longer GFP of hybrids, but was due to the large decrease of GFP of parents relative to hybrids under LD. For example, mean GFP for Ant C-S5 in SD was 44.7 but reduced to 27.0 under LD.

#### **5.1.4 Correlations Among Maturity Related Traits**

Separate simple phenotypic correlations were derived from mean data collected from short daylength trials (Wai1 and Kauai) and long daylength trials (Wai2 and Iowa) for both days and GDD values (Table 5.13 and 5.14). Very high associations were obtained among silking, anthesis, and BLF in both short and long daylength data, with  $r$  values ranging from 0.85 - 0.99 for day values. Comparable values were obtained using GDD data. Medium but significant negative correlations were obtained for GFP with anthesis and silking. Low correlations for ASI with the rest of the traits was observed under SD but was substantially increased under LD.

Table 5.13. Correlation among SD maturity related traits in number of days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.99 **	0.35 *	0.85 **	-0.62 **
Silking	0.99 **		0.23	0.85 **	-0.63 **
ASI	0.33 *	0.45 **		0.36 *	-0.37 *
BLF	0.86 **	0.86 **	0.31		-0.2
GFP	-0.77 **	-0.78 **	-0.44 **	0.42 **	

\* significant at 5% level of probability  
 \*\* significant at 1% level of probability

Table 5.14. Correlation among LD maturity related traits in number of days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.98 **	0.76 *	0.94 **	-0.52 *
Silking	0.99 **		0.87 **	0.91 **	0.60 **
ASI	0.81 **	0.90 **		0.68 **	-0.70 **
BLF	0.92 **	0.91 **	0.76 **		-0.39 **
GFP	-0.57 **	-0.63 **	-0.70 **	-0.43 **	

\* significant at 5% level of probability  
 \*\* significant at 1% level of probability



### 5.1.5 Estimates of Genetic Effects

Anthesis. Genetic parameters estimated using the Gardner-Eberhart (1966) model were listed in Table 5.15. Estimates for each environment and across daylengths were obtained. Mean of the parents ( $M_p$ ) was greater than the mean of the crosses ( $M_c$ ) in all environments reflecting negative heterosis.  $H$  is simply the difference between  $M_p$  and  $M_c$ , and the negative values meant that hybrids flowered earlier than their parents. Parental estimates ranged from -5.81 (Oh43 (Hi)) to 6.56 (Tzi4) under SD and from -14.3 (Hi32) to 11.20 (Tzi4). The higher the value of the estimates, the longer that particular parent took to shed pollen in relation to the population mean. For example, B73 (Hi), Hi29, Hi32, and Oh43 (Hi) are classified as early flowering, while Ant C-S5, Hi34, Narino 330-S6, Tx601 (Hi), and Tzi4 are late flowering. Signs of the estimates were consistent in all four environments, except Ant C-S5, which was considered an early line under SD, but become late under LD. The general combining ability (GCA) estimates ranged from -3.37 for Oh43 (Hi) (Hi) to 3.11 for Tzi4 under SD and from -7.54 to 7.94 under LD for the same lines. LD estimates were generally bigger than their SD estimates reflecting the greater number of days to flower in Iowa and Wai2. Their relative rankings and signs resembled that of the parental estimates. Ant C-S5 was not consistent in all environments, exhibiting earliness in its crosses in short

Table 5.15. Estimates of genetic parameters for the number of days to anthesis.

Genetic Estimates	Short Daylength			Long Daylength			
	Wail	Kauai	Mean	Wai2	Iowa	Mean	
Mean	50.82	57.33	54.08	63.86	87.36	75.61	
Mp	52.41	58.81	55.61	66.37	90.89	78.63	
Mc	50.43	56.96	53.69	63.23	86.48	74.86	
H	-1.98	** -1.85	** -1.92	** -3.14	** -4.41	** -3.77	**
Parental Estimates							
P1	-2.74	** -2.81	** -2.78	** 7.63	** 1.94	** 4.79	**
P2	-5.41	** -3.81	** -4.61	** -13.04	** -15.39	** -14.21	**
P3	-1.41	** -1.81	** -1.61	** -3.70	** -6.72	** -5.21	**
P4	-5.74	** -5.48	** -5.61	** -14.04	** -14.56	** -14.30	**
P5	4.59	** 2.19	** 3.39	** 10.63	** 10.78	** 10.70	**
P6	4.93	** 6.52	** 5.72	** 8.30	** 11.61	** 9.95	**
P7	-4.41	** -5.81	** -5.11	** -10.37	** -13.56	** -11.96	**
P8	4.93	** 3.19	** 4.06	** 11.96	** 6.11	** 9.04	**
P9	5.26	** 7.85	** 6.56	** 2.63	** 19.78	** 11.20	**
GCA Estimates							
g1	-1.39	** -0.62	* -1.01	** 3.26	** 3.69	** 3.47	**
g2	-2.34	** -2.15	** -2.25	** -5.88	** -5.93	** -5.91	**
g3	-0.15	-0.34	-0.25	-2.03	** -0.67	-1.35	*
g4	-2.20	** -1.96	** -2.08	** -5.98	** -6.43	** -6.21	**
g5	1.94	** 1.33	** 1.63	** 3.35	** 1.93	** 2.64	**
g6	1.47	** 2.19	** 1.83	** 1.88	** 3.40	** 2.64	**
g7	-3.11	** -3.62	** -3.37	** -6.93	** -8.15	** -7.54	**
g8	2.75	** 1.99	** 2.37	** 5.93	** 2.69	** 4.31	**
g9	3.04	** 3.19	** 3.11	** 6.40	** 9.47	** 7.94	**
SCA Estimates							
s12	-0.69	0.48	-0.11	-5.27	** -2.74	** -4.01	**
s13	0.45	-1.33	* -0.44	-1.80	* -2.50	* -2.15	*
s14	-0.83	* -0.38	-0.61	-1.51	-1.40	-1.46	
s15	1.36	** 1.33	* 1.35	* 1.82	* -0.26	0.78	
s16	0.17	0.48	0.32	0.63	-0.74	-0.05	
s17	-1.26	** -0.38	-0.82	* -1.89	* 0.14	-0.87	*
s18	-0.12	0.00	-0.06	4.92	** 2.14	* 3.53	**
s19	0.93	* -0.19	0.37	3.11	** 5.36	** 4.23	**
s23	-0.26	-0.48	-0.37	4.01	** 2.79	** 3.40	**
s24	-0.88	* 0.14	-0.37	1.30	-0.12	0.59	
s25	0.64	0.19	0.42	0.96	1.36	1.16	
s26	0.12	0.67	0.39	-0.23	-0.29	-0.26	
s27	-0.31	0.14	-0.08	0.92	0.43	0.67	
s28	0.83	* -1.14	* -0.15	-0.94	0.76	-0.09	
s29	0.55	0.00	0.27	-0.75	-2.19	* -1.47	*
s34	0.93	* -1.33	-0.20	1.44	-1.71	-0.14	
s35	0.12	-0.95	-0.42	-0.56	0.43	-0.07	

Table 5.15 cont.

Genetic Estimates	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
s36	0.60	0.52	0.56	0.25	0.95	0.60
s37	-1.17 **	1.67 *	0.25	1.73	0.83	1.28
s38	-0.36	1.05	0.35	-1.13	-0.83	-0.98
s39	-0.31	0.86	0.27	-3.94 **	0.05	-1.95 *
s45	-0.83 *	-1.00	-0.92 *	-1.94 *	0.36	-0.79
s46	1.31 **	-1.19	0.06	-0.13	0.55	0.21
s47	0.55	3.29 **	1.92 **	2.01 *	3.93 **	2.97 **
s48	0.02	-0.33	-0.15	-1.18	0.93	-0.12
s49	-0.26	0.81	0.27	0.01	-2.52 *	-1.26
s56	-0.50	-0.48	-0.49	0.20	-1.81	-0.80
s57	1.07 **	-0.33	0.37	-0.65	2.24 *	0.79
s58	-0.79	1.05	0.13	-0.51	-2.43 *	-1.47 *
s59	-1.07 **	0.19	-0.44	0.68	0.12	0.40
s67	0.21	-0.19	0.01	0.15	0.26 *	0.21
s68	-1.31 **	-0.14	-0.73 *	0.30	-1.74	-0.72
s69	-0.60	0.33	-0.13	-1.18	2.81 **	0.82
s78	0.93 *	-1.33	-0.20	-2.89 **	-1.52	-2.21 **
s79	-0.02	-2.86 **	-1.44 **	0.63	-6.31 **	-2.84 **
s89	0.79	0.86	0.82	1.44	2.69 *	2.07 *
S.E. gca	0.16	0.30	0.23	0.37	0.42	0.40
S.E. sca	0.40	0.73	0.56	0.91	1.03	0.97

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

daylength and lateness in long daylength. Hi29 can be regarded as neutral combiner since its estimate were small and insignificant, except in Wai2. Except for Hi29 and Ant C-S5, two distinct groups of inbreds based on origin showed opposite general combining abilities, i.e., temperate-derived lines such as B73 (Hi), Hi32, and Oh43 (Hi) (Hi) were early combiners (with negative signs), while tropical-derived lines like Hi34, Narino 330-S6, Tx601, and Tzi4 were late-anthesis combiners.

The specific combining ability (SCA) estimates were generally lower than that of GCA under both daylengths. Only 6 and 13 of the crosses showed significant estimates for SD and LD, respectively. Estimates using GDD are shown in Appendix 16. Relative order and magnitude for all the estimates were basically the same with day values ( $r=0.99$ ).

Silking. The hybrids were much earlier than the parents as evidenced by a high H estimate (-4.19). As in anthesis, parental estimates, are all significant, with the same entries showing negative and positive values, and LD produced large estimates than short daylengths (Table 5.16). Ant C-S5 again showed inconsistent estimates between the two daylengths. Similar trends were observed for GCA where temperate and tropical lines can be easily separated for their prepotencies in their crosses. Oh43 (Hi) would, for example, set back the silking date about 3.63 and 9.94 days in the average of its crosses under SD and LD, respectively.

Table 5.16. Estimates of genetic parameters for the number of days to silking.

Genetic Estimates	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Mean	52.99	59.21	56.10	72.01	92.17	82.09
Mp	54.78	60.85	57.81	75.78	98.39	87.08
Mc	52.55	58.81	55.68	71.06	90.62	80.84
H	-2.23	** -2.05	** -2.14	** -4.71	** -7.77	-6.24 **
<b>Parental Estimates</b>						
P1	-4.11	** -4.85	** -4.48	** 17.22	** 0.28	8.75 **
P2	-5.44	** -4.19	** -4.81	** -17.11	** -20.22	** -18.67 **
P3	-1.44	** -1.52	** -1.48	** -7.11	** -10.89	** -9.00 **
P4	-6.11	** -5.19	** -5.65	** -17.44	** -20.06	** -18.75 **
P5	5.22	** 2.48	** 3.85	** 14.22	** 8.28	** 11.25 **
P6	4.56	** 7.15	** 5.85	** 3.22	** 12.94	** 8.08 **
P7	-4.78	** -4.85	** -4.81	** -14.44	** -18.39	** -16.42 **
P8	6.22	** 3.15	** 4.69	** 14.22	** 7.28	** 10.75 **
P9	5.89	** 7.81	** 6.85	** 7.22	** 40.78	** 24.00 **
<b>GCA Estimates</b>						
g1	-2.05	** -1.16	** -1.61	** 5.54	** 4.82	** 5.18 **
g2	-2.39	** -2.40	** -2.39	** -7.31	** -7.23	** -7.27 **
g3	0.04	0.22	0.13	-3.36	** -0.28	** -1.82 **
g4	-2.10	** -1.63	** -1.87	** -7.12	** -8.06	** -7.59 **
g5	1.80	** 1.75	** 1.78	** 3.64	** 2.30	** 2.97 **
g6	1.47	** 2.37	** 1.92	** 0.16	3.30	** 1.73 **
g7	-3.05	** -4.21	** -3.63	** -9.60	** -10.28	** -9.94 **
g8	3.14	** 2.22	** 2.68	** 8.40	** 3.84	** 6.12 **
g9	3.14	** 2.84	** 2.99	** 9.64	** 11.58	** 10.61 **
<b>SCA Estimates</b>						
s12	-1.11	** 0.75	-0.18	-8.96	** -4.21	* -6.59 **
s13	0.13	-1.87	* -0.87	* -3.92	** -4.33	** -4.12 **
s14	-0.39	-0.35	-0.37	-4.15	** -2.54	-3.35 **
s15	2.04	** 1.61	* 1.82	* -0.25	0.43	0.09
s16	-0.30	-0.35	-0.32	1.56	-0.07	0.75
s17	-0.77	* -0.11	-0.44	-4.68	** -1.49	-3.09 **
s18	-0.30	0.13	-0.08	12.32	** 5.72	** 9.02 **
s19	0.70	* 0.18	0.44	8.08	** 6.48	** 7.28 **
s23	-0.20	-0.63	-0.42	3.27	** 1.89	2.58 **
s24	-0.73	* -0.11	-0.42	1.37	0.34	0.85
s25	0.37	-0.15	0.11	0.94	1.98	1.46
s26	1.04	** 1.23	1.13	** 1.75	-0.52	0.62
s27	-0.44	0.13	-0.15	1.85	1.39	1.62
s28	0.70	* -1.63	* -0.46	0.18	0.77	0.47
s29	0.37	0.42	0.39	-0.39	-1.64	-1.01
s34	0.85	* -1.39	-0.27	2.08	* -0.95	0.57
s35	0.27	-0.77	-0.25	1.65	-0.30	0.68

Table 5.16 cont.

Genetic Estimates	Short Daylength			Long Daylength		
	Wai2	Kauai	Mean	Wai2	Iowa	Mean
s36	0.61	1.27	0.94	1.80	1.03	1.41
s37	-1.54 **	1.85 *	0.15	4.23 **	0.60	2.41 **
s38	-0.06	0.75	0.35	-2.11 *	-1.85	-1.98 *
s39	-0.06	0.80	0.37	-7.01 **	3.91 *	-1.55 *
s45	-1.58 **	-1.92 *	-1.75 **	-2.58	0.32	-1.13
s46	0.75 *	-0.87	-0.06	0.89	0.32	0.60
s47	1.27 **	4.04 **	2.65 **	4.32 **	5.39 **	4.85 **
s48	-0.25	0.61	0.18	-1.01	1.27	0.13
s49	0.08	-0.01	0.04	-0.92	-4.14 *	-2.53 *
s56	-0.15	-0.25	-0.20	-0.20	-0.88	-0.54
s57	1.04 **	-0.35	0.35	-0.11	3.36 *	1.63 *
s58	-0.82 *	0.89	0.04	-2.77	-4.09 *	-3.43 *
s59	-1.15 **	0.94	-0.11	3.32 *	-0.83	1.25
s67	-0.63	-0.96	-0.80	0.70	0.53	0.62
s68	-0.49	-0.39	-0.44	-2.30	-1.92	-2.11
s69	-0.82 *	0.32	-0.25	-4.20 **	1.51	-1.35
s78	0.70 *	-1.15	-0.23	-5.87 **	-2.18	-4.03
s79	0.37	-3.44 **	-1.54 *	-0.44	-7.59 **	-4.01 **
s89	0.51	0.80	0.65	1.56	2.29	1.93
S.E. gca	0.14	0.33	0.24	0.59	0.66	0.63
S.E. sca	0.34	0.81	0.57	1.44	1.60	1.52

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

Conversely, Tzi 4 would add 2.99 and 10.61 days to silking, on the average, to hybrids whenever it was involved as one of the parents under SD and LD. Less than 50% of the total crosses had SCA estimates that significantly differed from zero. Some of the SCA estimates under LD were rather inflated such as the case of Ant C-S5 x B73 (Hi), Ant C-S5 x Tx601 and Ant C-S5 x Tzi4 (Hi), though their values under SD were very small. Genetic estimates using GDD are presented in Appendix 17).

Anthesis to Silking Interval (ASI). Means of parents and crosses had similar ASI as shown by insignificant H's under SD. Under LD, however, ASI became significant indicating the increasing time lag between anthesis and silking. Parental estimates were not consistent as to origin nor daylength regimes as temperate and tropically-adopted inbreds showed both positive and negative estimates (Table 5.17). Only five parents had significant estimates under SD while all were significant under LD.

Most of the SD GCA estimates were either not significant, or if significant they were relatively small. Greater and significant GCA estimates were however obtained under LD. Inbreds such as Tx601 and Tzi4 conferred higher LD ASI in their crosses; inbreds like Hi32 and Oh43 (Hi) (Hi) produced opposite effects. Crosses involving tropical-derived lines lengthened the period between anthesis and silking under long daylengths. Much larger values were

Table 5.17. Estimates of genetic parameters for anthesis to silking interval (days).

Genetic Estimates	Short Daylength			Long Daylength		
	wail	Kauai	Mean	Wai2	Iowa	Mean
Mean	2.17	1.88	2.03	8.15	4.86	6.51
Mp	2.37	2.04	2.20	9.41	7.50	8.45
Mc	2.12	1.84	1.98	7.83	4.20	6.02
H	-0.25 *	-0.19	-0.22	-1.57 **	-3.30 **	-2.44 **
Parental Estimates						
P1	-1.37 **	-2.04 **	-1.70 **	9.59 **	-1.67 **	3.96 **
P2	-0.04	-0.37	-0.20	-4.07 **	-4.83 **	-4.45 **
P3	-0.04	0.30	0.13	-3.41 **	-4.17 **	-3.79 **
P4	-0.37 *	0.30	-0.04	-3.41 **	-5.50 **	-4.45 **
P5	0.63 **	0.30	0.46 **	3.59 **	-2.50 **	0.55 *
P6	-0.37 **	0.63 **	0.13 **	-5.07 **	1.33 **	-1.87 **
P7	-0.37 **	0.96 **	0.30 **	-4.07 **	-4.83 **	-4.45 **
P8	1.30 **	-0.04	0.63	2.26 **	1.17 **	1.71 **
P9	0.63 **	-0.04	0.30 **	4.59 **	21.00 **	12.80 **
GCA Estimates						
g1	-0.66 **	-0.53 **	-0.60 **	2.29 **	1.41 **	1.85 **
g2	-0.04	-0.25	-0.15	-1.43 **	-1.38 **	-1.40 **
g3	0.20	0.56 **	0.38 *	-1.33 **	0.31	-0.51 *
g4	0.10	0.32	0.21	-1.14 **	-1.71 **	-1.43 **
g5	-0.14	0.42 *	0.14	0.29	0.29	0.29
g6	0.01	0.18	0.09	-1.71 **	-0.45	-1.08 **
g7	0.05	-0.58 **	-0.26 **	-2.67 **	-2.21 **	-2.44 **
g8	0.39 **	0.23	0.31 *	2.48 **	1.70 **	2.09 **
g9	0.10	-0.34	-0.12	3.24 **	2.03 **	2.63 **
SCA Estimates						
s12	-0.42	0.27	-0.07	-3.69 **	-1.74 *	-2.71 **
s13	-0.32	-0.54 *	-0.43 *	-2.12 *	-2.10 **	-2.11 **
s14	0.44	0.04	0.24	-2.64 *	-1.40	-2.02 *
s15	0.68 *	0.27 *	0.48 *	-2.07 *	0.43	-0.82
s16	-0.46	-0.82 *	-0.64 *	0.93	-1.17	-0.12
s17	0.49 **	0.27	0.38 *	-2.79 **	-1.90 *	-2.35 **
s18	-0.18	0.13	-0.02	7.40 **	7.02 **	7.21 **
s19	-0.23 *	0.37	0.07	4.98 **	0.86	2.92 **
s23	0.06	-0.15	-0.05	-0.74	-0.81	-0.77
s24	0.15 *	-0.25	-0.05	0.07	0.55	0.31
s25	-0.27	-0.35	-0.31	-0.02	0.71	0.35
s26	0.92 **	0.56	0.74 **	1.98	0.12	1.05
s27	-0.13	-0.01	-0.07	0.93	1.05	0.99
s28	-0.13	-0.49 *	-0.31 *	1.12	-0.52	0.30
s29	-0.18	0.42	0.12	0.36	0.64	0.50
s34	-0.08	-0.06	-0.07	0.64	0.86	0.75
s35	0.15	0.18	0.17	2.21 *	-0.64	0.79



Table 5.17 cont.

Genetic Estimates	Short Daylength			Long Daylength		
	wail	Kauai	Mean	Wai2	Iowa	Mean
s36	0.01	0.75 *	0.38 *	1.55	0.43	0.99
s37	-0.37	0.18	-0.10	2.50 *	-0.14	1.18
s38	0.30	-0.30	0.00	-0.98	-1.55	-1.26
s39	0.25	-0.06	0.10	-3.07 **	3.95 **	0.44
s45	-0.75 *	-0.92 **	-0.83 **	-0.64 *	0.05	-0.30
s46	-0.56	0.32	-0.12	1.02	0.12	0.57
s47	0.73 *	0.75 **	0.74 **	2.31 *	1.55	1.93 *
s48	-0.27	0.94 **	0.33 *	0.17	-0.19	-0.01
s49	0.35	-0.82 **	-0.24	-0.93	-1.52	-1.23
s56	0.35	0.23	0.29	-0.40	1.29	0.44
s57	-0.04	-0.01	-0.02	0.55	1.21	0.88
s58	-0.04	-0.15	-0.10	-2.26 *	-2.19 **	-2.23 **
s59	-0.08	0.75 **	0.33 *	2.64 *	-0.86	0.89
s67	-0.85 **	-0.77 **	-0.81 **	0.55	0.62	0.58
s68	0.82 **	-0.25	0.29 *	-2.60 *	-0.45	-1.52 *
s69	-0.23	-0.01	-0.12	-3.02 **	-0.95	-1.99 *
s78	-0.23	0.18	-0.02	-2.98 **	-1.19	-2.08 *
s79	0.39	-0.58 **	-0.10	-1.07	-1.19	-1.13
s89	-0.27	-0.06	-0.17	0.12	-0.93	-0.40
S.E. gca	0.12	0.20	0.16	0.43	0.32	0.38
S.E. sca	0.30	0.48	0.39	1.05	0.79	0.92

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

found for many SCA estimates, though only one-third of them were actually statistically significant. More than half of the crosses involving Ant C-S5 gave significant SCA estimates under LD particularly with Tx601 where the value (7.21) was much larger than any of the GCA's and SCA's. GDD data are listed in Appendix 18.

Blacklayer Formation (BLF). Entries planted under the light (LD) at Waimanalo matured about 16.5 days later than when planted outside the light (SD) (Table 5.18). Inbred parents reached physiological maturity about 1.2 and 1.7 days later than their hybrids under SD and LD, respectively. Temperate and tropical lines, like in anthesis and silking, showed both negative and positive parental estimates under SD and LD, respectively, with the LD estimates about 3 to 4 times than SD estimates. The same happened with GCA estimates where the latest maturing general combiner under SD was Tzi4, while the earliest was Hi32. Hi34 gave the highest GCA under LD at 13.8. Basically, GCA estimates followed the same trend with anthesis and silking in terms of signs and relative magnitude. This is not surprising since the three traits are highly correlated with each other. Less than half of the SCA estimates were not significant.

Many of the SCA estimates were significant under SD and LD environments and few did exhibit comparable values with GCA. Notable among them were the crosses between Ant C-S5

Table 5.18. Estimates of genetic parameters for the days to blacklayer formation.

Genetic Estimates	Short Daylength Wai1	Long Daylength Wai2
Mean	94.595	111.193
Mp	95.604	112.605
Mc	94.342	110.840
H	-1.261 **	-1.765 **
Parental Estimates		
P1	-0.270	7.395 **
P2	-2.159 **	-12.160 **
P3	-2.604 **	-0.827 *
P4	-5.381 **	-15.383 **
P5	2.619 **	13.840 **
P6	2.063 **	4.284 **
P7	-3.826 **	-12.605 **
P8	4.730 **	10.728 **
P9	4.830 **	4.728 **
GCA Estimates		
g1	-1.217 **	3.025 **
g2	-1.772 **	-6.785 **
g3	0.879 **	-1.055 **
g4	-1.502 **	-6.134 **
g5	0.768 **	3.168 **
g6	1.131 **	2.072 **
g7	-2.883 **	-8.198 **
g8	2.814 **	5.056 **
g9	1.783 **	8.850 **
SCA Estimates		
s12	-0.909	-6.968 **
s13	-0.227	1.079
s14	0.821 *	0.937
s15	-0.004 **	3.413 **
s16	-0.923	0.286
s17	-0.242 **	-4.000 **
s18	2.061 **	3.968 **
s19	-0.576 *	1.286
s23	0.329	1.111
s24	-1.846 **	-0.810
s25	3.885 **	2.111 *
s26	1.188	-1.127
s27	-1.909 **	1.476
s28	-0.606	3.778 **
s29	-0.131	0.429
s34	1.170	1.349
s35	0.456	1.048

Tab 5.18 cont.

Genetic Estimates	Short Daylength Wai1	Long Daylength Wai2
s36	-0.352	2.032 *
s37	0.329	2.079 *
s38	-1.701 *	-6.730 **
s39	-0.004	-1.968 *
s45	-0.608	-4.540 **
s46	1.140	-0.778
s47	-0.735	1.159
s48	1.458 *	1.238
s49	-1.401 *	1.444
s56	-2.241 **	-2.413 *
s57	0.773	-1.365
s58	-1.479 *	-0.397
s59	-0.782	2.143 *
s67	-0.146	3.063 **
s68	0.480	2.365 *
s69	0.854	-3.429 **
s78	-0.162	-3.365 **
s79	2.091 **	0.952
s89	-0.050	-0.857
S.E gca	0.277	0.386
S.E. sca	0.672	0.939

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

and B73 (Hi) and Hi29 and Tx601 (Hi). GDD estimates are presented in Appendix 19.

Grain Filling Period (GFP). Of all the maturity related traits studied only in the GFP where the mean of the hybrids was greater than the mean of the parents as indicated by positive H values in both environments. Tropical lines notably Tzi4, Tx601, and Hi34, had negative parental and GCA estimates, while temperate lines had positive estimates (Table 5.19). This was a complete reversal from what happened to the other traits. Lines such as Ant C-S5 became positive general combiner under LD. This was due to the rapid kernel drying of this inbred and under LD. The rest of the inbreds exhibited the same signs and comparable GCA estimates. Several of the crosses displayed high SCA both under SD and LD. More than half of the crosses had highly significant estimates and about two to three times larger than the GCA estimates. GDD estimates are shown Appendix 20.

#### **5.1.6 Correlations Among GCA Estimates**

Correlation analyses were run among GCA estimates of maturity related traits. Tables 5.20 and 5.21 present correlation coefficients obtained from SD and LD GCA estimates, respectively. Very high genetic correlations were observed among anthesis, silking, and BLF with coefficients of more than ninety percent under both daylengths. Since GCA is a measure of additive genetic

Table 5.19. Estimates of genetic parameters for grain filling period (days).

Genetic Estimates	Short Daylength Wai1	Long Daylength Wai2
Mean	41.602	39.185
Mp	40.826	36.827
Mc	41.796	39.775
H	0.970 **	2.948 **
Parental Estimates		
P1	3.841 **	-9.827 **
P2	3.285 **	4.951 **
P3	-1.159 **	6.284 **
P4	0.730 **	2.062 **
P5	-2.604 **	-0.383
P6	-2.493 **	1.062 **
P7	0.952 **	1.840 **
P8	-1.493 **	-3.494 **
P9	-1.059 **	-2.494 **
GCA Estimates		
g1	0.836 **	-2.520 **
g2	0.614 *	0.527
g3	0.836 **	2.305 **
g4	0.598 *	0.988 **
g5	-1.037 **	-0.473
g6	-0.340	1.908 **
g7	0.170	1.400 **
g8	-0.324	-3.346 **
g9	-1.354 **	-0.790 **
SCA Estimates		
s12	0.198	1.996 *
s13	-0.358	4.996 **
s14	1.214	5.091 **
s15	-2.040 **	3.663 **
s16	-0.626	-1.274
s17	0.531	0.679
s18	2.358 **	-8.353 **
s19	-1.278	-6.798 **
s23	0.531	-2.163 **
s24	-1.119	-2.179 **
s25	3.515 **	1.171
s26	0.152	-2.877 **
s27	-1.469 *	-0.369
s28	-1.308	3.599 **
s29	-0.500	0.821
s34	0.325	-0.734
s35	0.182	-0.607

Table 5.19 cont.

Genetic Estimates	Short Daylength Wai1	Long Daylength Wai2
s36	-0.959	0.234
s37	1.865 *	-2.147 **
s38	-1.642 *	-4.623 **
s39	0.055	5.044 **
s45	0.976	-1.956 **
s46	0.390	-1.671 *
s47	-2.008 **	-3.163 **
s48	1.708 *	2.250 **
s49	-1.485 *	2.361 **
s56	-2.086 **	-2.210 **
s57	-0.262	-1.258
s58	-0.658	2.377 **
s59	0.373	-1.179
s67	0.485	2.361 **
s68	0.968	4.663 **
s69	1.676 *	0.774
s78	-0.864	2.504 **
s79	1.722 *	1.393
s89	-0.562	-2.417 **
S.E. gca	0.299648	0.295666
S.E. sca	0.728228	0.718551

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

Table 5.20. Correlations among GCA estimates of SD maturity traits in number of days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.99 **	0.35	0.94 **	-0.76 *
Silking	0.99 **		0.46	0.97 **	-0.74 **
ASI	0.25	0.34		0.55	-0.15
BLF	0.95 **	0.97 **	0.45		-0.59
GFP	-0.88 **	-0.88 **	-0.22	-0.76 *	

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

Table 5.21. Correlation among GCA estimates of LD maturity traits in number of days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.99 **	0.89 **	0.99 **	-0.57
Silking	0.99 **		0.93 **	0.99 **	-0.63
ASI	0.92 **	0.95 **		0.90 **	-0.80 **
BLF	0.99 **	0.99 **	0.92 **		-0.57
GFP	-0.64 **	-0.70 *	-0.82 **	-0.64	

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.



variance, the high correlations suggest either a common genetic control for these traits or they are closely linked with each other. Low to medium but inverse correlations were observed for GFP with other traits in both daylengths. There was no genetic correlation between ASI and the rest of the traits under SD but there were very high correlations observed under LD.

## 5.2 Photoperiod Sensitivity Traits

### 5.2.1 Variation Among Entry Means

Anthesis Delay. Table 5.22 gave the mean anthesis delay (days) measured in three indices. Index1 is the difference between Wai2 and Wai1; Index2 is between Iowa and Wai2; and Index3 is between the mean of SD (Wai1 and Kauai) and LD (Iowa and Wai2). Presentation of results is centered mostly on index3 unless otherwise indicated. Comparisons are made between index1 and index2 primarily to point out the differential effects of artificial lighting (Index1) relative to actual delay (Index2).

Anthesis delay ranged from 13.4 (B73) to 30.6 days (Ant C-S5) for parents and from 13.9 (Hi32 x Oh43 (Hi)) to 34.3 (Ant C-S5 x Tzi4) days for hybrids. Entry means of for Index2 appeared to be always bigger than Index1 when using calendar days, but when GDD data were used it was the other way around, indicating the stronger effects of artificial lighting in Waimanalo. For example Ant C-S5 had mean delay of 24.3 and 43.2 days for index1 and index2, respectively,

Table 5.22. Anthesis delay (Index1=Wai2-Wai;  
Index2=Iowa-Wai; Index3=LD mean-SD mean).

Entries	Index1	Index2	Index3
Ant C-S5	24.3	43.2	30.6
B73 (Hi)	6.3	28.5	13.4
Hi29	11.7	33.2	19.4
Hi32	5.7	29.7	14.3
Hi34	20.0	44.7	30.3
Narino 330-S6	17.3	45.2	27.3
Oh43 (Hi)	8.0	29.3	16.2
Tx601 (Hi)	21.0	39.7	28.0
Tzi4	11.3	53.0	27.7
Ant C-S5 x B73 (Hi)	9.3	35.5	18.1
Ant C-S5 x Hi29	13.3	37.7	22.8
Ant C-S5 x Hi32	13.0	36.3	20.7
Ant C-S5 x Hi34	19.3	39.5	26.1
Ant C-S5 x Narino 330-S6	18.3	42.2	26.1
Ant C-S5 x Oh43 (Hi)	13.0	37.5	21.4
Ant C-S5 x Tx601 (Hi)	25.7	43.3	31.2
Ant C-S5 x Tzi4	23.0	52.0	34.3
B73 (Hi) x Hi29	11.7	35.0	20.2
B73 (Hi) x Hi32	7.7	29.0	14.3
B73 (Hi) x Hi34	11.0	33.2	19.3
B73 (Hi) x Narino 330-S6	9.3	34.0	17.7
B73 (Hi) x Oh43 (Hi)	6.7	28.2	14.1
B73 (Hi) x Tx601 (Hi)	10.7	32.3	19.5
B73 (Hi) x Tzi4	11.3	36.2	20.6
Hi29 x Hi32	7.7	28.7	16.0
Hi29 x Hi34	11.7	35.8	21.4
Hi29 x Narino 330-S6	11.0	37.8	20.9
Hi29 x Oh43 (Hi)	10.0	32.5	16.9
Hi29 x Tx601 (Hi)	13.3	35.0	20.7
Hi29 x Tzi4	10.7	42.3	22.7
Hi32 x Hi34	9.3	33.0	18.2
Hi32 x Narino 330 S-6	8.0	33.0	18.0
Hi32 x Oh43 (Hi)	6.7	30.2	13.9
Hi32 x Tx601 (Hi)	11.0	32.7	19.0
Hi32 x Tzi4	12.7	36.0	20.3
Hi34 x Narino 330-S6	15.3	36.7	22.7
Hi34 x Oh43 (Hi)	8.7	32.2	18.4
Hi34 x Tx601 (Hi)	17.7	34.3	22.5
Hi34 x Tzi4	19.3	43.7	27.8
Narino 330-S6 x Oh43 (Hi)	9.3	33.0	18.0
Narino 330-S6 x Tx601 (Hi)	18.0	37.5	23.9
Narino 330-S6 x Tzi4	16.0	47.8	27.8
Oh43 (Hi) x Tx601 (Hi)	8.3	28.5	16.9
Oh43(Hi) x Tzi4	13.0	31.2	20.4
Tx601 (Hi) x Tzi4	20.0	44.3	29.2
Mean	13.0	36.5	21.5
LSD (0.05)	3.3	3.7	2.5

but GDD values were 446 and 190, respectively (Appendix 21) Inbreds such as B73 (Hi), Hi32 and Oh43 (Hi), were practically day neutral under Index2 but showed some degree of sensitivity under Index1 if GDD was only considered. Similar observations could also be seen among hybrids. Comparisons among entries would not be affected by using either days or GDD since the two were highly correlated (0.99), hence the relative order of entries were unchanged. Correlations between Index1 and Index2 were 0.61 and 0.81 for inbreds and hybrids, respectively. Ranking of entries according to photoperiod sensitivity did not change from Index1 to Index2, since entries classified as insensitive under Index1 were also classified as sensitive under Index2. This was not important in this study, since the main objective was to determine the combining abilities of the inbreds.

Silking Delay. Silking delay ranged from 15.4 (B73) to 46.4 (Tzi4) for inbreds and from 15.3 (Hi32 x Oh43 (Hi) to 46.4 (Ant C-S5 x Tzi4) for hybrids (Table 5.23). As in anthesis delay, temperate lines such as B73, Hi32 and Oh43 (Hi) were among the least by affected by long daylength as compared to the tropical lines. Ant C-S5, Hi34, and Tzi4 were particularly very sensitive to photoperiod in all of the indices used. Among the hybrids, least sensitive crosses were observed among those involving temperate parents, while those involving tropical line had the most sensitive

Table 5.23. Silking delay (Index1=Wai2-Wail;  
Index2=Iowa-Wail; Index3=LD mean-SD mean).

Entries	Index1	Index2	Index3
Ant C-S5	42.3	48.0	42.5
B73 (Hi)	9.3	28.8	15.4
Hi29	15.3	34.2	21.8
Hi32	9.7	29.7	16.2
Hi34	30.0	46.7	36.7
Narino 330-S6	19.7	52.0	31.5
Oh43 (Hi)	11.3	30.0	17.7
Tx601 (Hi)	29.0	44.7	35.3
Tzi4	22.3	78.5	46.4
Ant C-S5 x B73 (Hi)	13.3	37.0	20.7
Ant C-S5 x Hi29	18.7	40.2	26.7
Ant C-S5 x Hi32	17.3	36.8	23.2
Ant C-S5 x Hi34	25.7	43.8	31.4
Ant C-S5 x Narino 330-S6	26.7	47.0	32.8
Ant C-S5 x Oh43 (Hi)	15.7	37.0	23.0
Ant C-S5 x Tx601 (Hi)	44.0	51.7	44.5
Ant C-S5 x Tzi4	40.0	59.2	46.4
B73 (Hi) x Hi29	13.7	35.0	21.3
B73 (Hi) x Hi32	10.7	28.3	15.8
B73 (Hi) x Hi34	16.0	35.3	22.8
B73 (Hi) x Narino 330-S6	13.0	33.5	19.6
B73 (Hi) x Oh43 (Hi)	9.3	27.8	15.8
B73 (Hi) x Tx601 (Hi)	18.3	34.0	24.7
B73 (Hi) x Tzi4	19.3	39.7	26.5
Hi29 x Hi32	11.3	30.0	18.3
Hi29 x Hi34	18.3	37.7	25.3
Hi29 x Narino 330-S6	15.0	40.0	23.5
Hi29 x Oh43 (Hi)	14.3	32.7	19.2
Hi29 x Tx601 (Hi)	18.3	36.7	24.3
Hi29 x Tzi4	14.7	50.2	28.9
Hi32 x Hi34	14.3	34.5	21.3
Hi32 x Narino 330 S-6	12.3	33.5	19.9
Hi32 x Oh43 (Hi)	10.0	29.0	15.3
Hi32 x Tx601 (Hi)	18.0	34.3	22.8
Hi32 x Tzi4	19.0	36.3	24.5
Hi34 x Narino 330-S6	19.0	39.7	25.8
Hi34 x Oh43 (Hi)	12.7	33.7	21.3
Hi34 x Tx601 (Hi)	23.7	36.0	26.3
Hi34 x Tzi4	31.3	47.3	35.3
Narino 330-S6 x Oh43 (Hi)	12.0	33.8	20.1
Narino 330-S6 x Tx601 (Hi)	20.7	39.2	26.7
Narino 330-S6 x Tzi4	20.3	50.7	31.5
Oh43 (Hi) x Tx601 (Hi)	10.7	28.7	18.5
Oh43(Hi) x Tzi4	17.7	31.3	24.0
Tx601 (Hi) x Tzi4	31.3	49.0	37.5
Mean	19.0	39.2	26.0
LSD (0.05)	4.7	5.5	3.8

reactions. intermediate values were generally the norm between temperate by tropical crosses. Similar trends were observed using GDD values. A number of inbreds had negative GDD delays and were considered day neutral under Index2 but not under Index1 (Appendix 22).

Anthesis to Silking Interval. Lines that showed longer anthesis and silking delays generally increased the time interval between anthesis and silking. Under SD, these lines normally have and ASI of two to three days but were extended to more than 10 days under LD. ASI delay ranged from 1.5 (Oh43 (Hi) to 18.8 days (Tzi4), and from 1.2 (B73 x Hi29) to 15.5 (Ant C-S5 x Tx601) (Table 5.24). Crosses involving Ant C-S5 were more variable compared to other inbreds. ASI delay were quite substantial when a line was crossed with Tx601 (15.5) and Tzi4 (12.1). These ASI are normally unacceptable for hybrids and certainly unpopular among pollinators. It seemed that ASI delay of inbreds was influenced by the origin or maturity under SD, but not for hybrids. Hybrids such as Hi34 x Narino 330-S6, and Ant C-S5 x Hi34 have parents that are tropical and late maturing but their ASI delays were generally low. ASI of crosses between temperate and tropical lines generally were less delayed by LD and were comparable to that of temperate x temperate crosses. GDD data are presented in Appendix 23.

Blacklayer Formation. Results presented in Table 5.25 is for Index1 only. As in anthesis and silking delays, a

Table 5.24. ASI delay (index1=Wai2-Wail;  
Index2=Iowa-Wail; Index3=LD mean-SD mean).

Entries	Index1	Index2	Index3
Ant C-S5	18.0	4.8	11.9
B73 (Hi)	3.0	0.3	2.0
Hi29	3.7	1.0	2.3
Hi32	4.0	0.0	1.8
Hi34	10.0	2.0	6.3
Narino 330-S6	2.3	6.8	4.3
Oh43 (Hi)	3.3	0.7	1.5
Tx601 (Hi)	8.0	5.0	7.3
Tzi4	11.0	25.5	18.8
Ant C-S5 x B73 (Hi)	4.0	1.5	2.6
Ant C-S5 x Hi29	5.3	2.5	3.9
Ant C-S5 x Hi32	4.3	0.5	2.6
Ant C-S5 x Hi34	6.3	4.3	5.3
Ant C-S5 x Narino 330-S6	8.3	3.0	5.8
Ant C-S5 x Oh43 (Hi)	2.7	-0.5	1.6
Ant C-S5 x Tx601 (Hi)	18.3	12.7	15.5
Ant C-S5 x Tzi4	17.0	7.2	12.1
B73 (Hi) x Hi29	2.0	0.0	1.2
B73 (Hi) x Hi32	3.0	-0.7	1.5
B73 (Hi) x Hi34	5.0	2.2	3.6
B73 (Hi) x Narino 330-S6	3.7	-0.5	1.9
B73 (Hi) x Oh43 (Hi)	2.7	-0.3	1.7
B73 (Hi) x Tx601 (Hi)	7.7	1.7	5.2
B73 (Hi) x Tzi4	8.0	3.5	5.9
Hi29 x Hi32	3.7	1.3	2.3
Hi29 x Hi34	6.7	1.8	3.9
Hi29 x Narino 330-S6	4.0	2.2	2.6
Hi29 x Oh43 (Hi)	4.3	0.2	2.3
Hi29 x Tx601 (Hi)	5.0	1.7	3.7
Hi29 x Tzi4	4.0	7.8	6.3
Hi32 x Hi34	5.0	1.5	3.1
Hi32 x Narino 330 S-6	4.3	0.5	1.9
Hi32 x Oh43 (Hi)	3.3	-1.2	1.4
Hi32 x Tx601 (Hi)	7.0	1.7	3.8
Hi32 x Tzi4	6.3	0.3	4.2
Hi34 x Narino 330-S6	3.7	3.0	3.2
Hi34 x Oh43 (Hi)	4.0	1.5	2.9
Hi34 x Tx601 (Hi)	6.0	1.7	3.8
Hi34 x Tzi4	12.0	3.7	7.5
Narino 330-S6 x Oh43 (Hi)	2.7	0.8	2.1
Narino 330-S6 x Tx601 (Hi)	2.7	1.7	2.8
Narino 330-S6 x Tzi4	4.3	2.8	3.7
Oh43 (Hi) x Tx601 (Hi)	2.3	0.2	1.6
Oh43(Hi) x Tzi4	4.7	0.2	3.6
Tx601 (Hi) x Tzi4	11.3	4.7	8.3
Mean	6.0	2.7	4.5
LSD (0.05)	3.6	2.8	2.3

definite pattern occurred for BLF, i.e., tropical lines such as Ant C-S5, Hi34, Tx601, and Tzi4 showed high sensitivity to photoperiod with the temperate lines showing low sensitivity. Most hybrids involving low and high sensitive lines showed intermediate responses with few that were skewed towards the low sensitive parents. Examples were Ant C-S5 x B73 (Hi) (9.7 days), and Oh43 (Hi) x Tx601 (10.2 days). ASI delays in GDD are listed in Appendix 24.

Grain Filling Period. Eight of the nine parents showed negative GFP delay indicating that their GFP's were actually shortened by long daylength. Only Hi29 had positive value (3.4 days). Majority of the hybrids had negative values, although most of them were in negligible amount. The parent Ant C-S5 were particularly affected with LD GFP 17.7 days less than SD GFP. Its cross with Tx601 was even worse with -19.1 days (Table 5.25). Appendix 24 showed GFP delay in GDD.

### 5.2.2 Analysis of Variance

Highly significant variation among entry means were detected for all the photoperiod sensitivity traits using the three indices (Table 5.26, 5.27, 5.28, and 5.29). Entry components such as parents, parents vs. crosses and crosses were all significant at 0.01 level of probability, except for BLF where parents vs. crosses was not significant. Further subdivision of crosses revealed that both the GCA and SCA mean squares were highly significant.

Table 5.25. BLF and GFP delays (Index1=Wai2-Wai1).

Entries	BLF		GFP	
	Days	GDD	Days	GDD
AntC5-S5	24.7	425	-17.7	-336
B73 (Hi)	7.0	112	-2.3	-61
Hi 29	18.8	320	3.4	39
Hi 32	7.0	116	-2.7	-63
Hi 34	28.2	483	-1.8	-55
Narino 330 S5	19.2	337	-0.4	-20
Oh 43 (Hi)	8.2	133	-3.1	-80
Tx 601 (Hi)	23.0	403	-6.0	-117
Tzi 4	16.9	299	-5.4	-106
AntC5-S5 x B73 (Hi)	9.7	151	-3.7	-99
AntC5-S5 x Hi 29	20.1	348	1.4	6
AntC5-S5 x Hi 32	16.2	274	-1.1	-48
AntC5-S5 x Hi 34	26.6	449	0.9	-20
AntC5-S5 x Narino 330 S5	22.9	388	-3.8	-101
AntC5-S5 x Oh 43 (hi)	11.7	182	-4.0	-111
AntC5-S5 x Tx 601 (Hi)	24.9	430	-19.1	-350
AntC5-S5 x Tzi 4	29.7	504	-10.3	-212
B73 (Hi) x Hi 29	10.3	171	-3.3	-85
B73 (Hi) x Hi 32	7.9	123	-2.8	-74
B73 (Hi) x Hi 34	12.1	213	-3.9	-81
B73 (Hi) x Narino 330 S5	10.1	173	-2.9	-71
B73 (Hi) x Oh 43 (Hi)	9.6	150	0.2	-22
B73 (Hi) x Tx601 (Hi)	18.1	315	-0.2	-20
B73 (Hi) x Tzi 4	19.1	332	-0.2	-24
Hi 29 x Hi 32	10.1	167	-1.2	-46
Hi 29 x Hi 34	17.6	304	-0.8	-32
Hi 29 x Narino 330 S5	17.9	311	2.9	37
Hi 29 x Oh 43 (Hi)	11.0	176	-3.3	-93
Hi 29 x Tx 601 (Hi)	11.8	204	-6.6	-132
Hi 29 x Tzi 4	19.7	340	5.0	69
Hi 32 x Hi 34	10.3	170	-4.0	-97
Hi 32 x Narino 330 S5	10.9	181	-1.4	-51
Hi 32 x Oh 43 (Hi)	8.4	128	-1.6	-58
Hi 32 x Tx 601 (Hi)	13.9	246	-4.1	-85
Hi 32 x Tzi4	21.8	371	2.8	22
Hi 34 x Narino 330 S5	19.7	335	0.7	-13
Hi 34 x Oh 43 (Hi)	11.4	188	-1.2	-49
Hi 34 x Tx 601 (Hi)	22.2	379	-1.4	-52
Hi 34 x Tzi 4	28.9	494	-2.4	-71
Narino 330 S5 x Oh 43 (Hi)	15.3	262	3.3	37
Narino 330 S5 x Tx 601 (Hi)	21.6	375	0.9	-3
Narino 330 S5 x Tzi 4	20.2	350	-0.1	-23
Oh 43 (Hi) x Tx 601 (Hi)	10.2	171	-0.4	-31
Oh 43 (Hi) x Tzi 4	17.1	293	-0.6	-30
Tx 601 (Hi) x Tzi 4	25.0	433	-6.3	-128
Mean	16.6	282	-2.4	-65
LSD (0.05)	3.8	64	3.2	57



Table 5.26. Analysis of variance of 9 parents and their 36 crosses for anthesis delay.

Source	df	Mean Squares					
		Days			GDD		
		Index1	Index2	Index3	Index1	Index2	Index3
Entries	44	26.42 **	38.67 **	27.33 **	8690 **	37412 **	7383 **
Parents	8	47.46 **	75.79 **	50.33 **	15797 **	73471 **	13320 **
Parents vs Cross	1	9.65 **	42.37 **	24.81 **	2660 **	67228 **	7650 **
Crosses	35	22.08 **	30.08 **	22.15 **	7238 **	28318 **	6018 **
GCA	8	78.87 **	111.48 **	85.62 **	25931 **	103920 **	22707 **
SCA	27	5.26 **	5.96 **	3.341 **	1699 **	5917 **	1074 **
Error	88	1.36	1.70	0.757	420	1328	238
GCA/SCA Ratio		15.00	18.69	25.63	15.26	17.56	21.15
S.E gca		0.17	0.47	0.31002	53.32	12.98	5.50
S.E sca		1.02	1.13	0.75344	314.92	31.55	13.36

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Table 5.27. Analysis of variance of 9 parents and their 36 crosses for silking delay.

Source	df	Mean Squares					
		Days			GDD		
		Index1	Index2	Index3	Index1	Index2	Index3
Entries	44	73.6 **	94.5 **	69.48 **	22749 **	70155 **	17557 **
Parents	8	124.2 **	250.6 **	140.04 **	39000 **	149622 **	31880 **
Parents vs Cross	1	44.3 **	221.1 **	121.28 **	12330 **	168830 **	25718 **
Crosses	35	62.8 **	55.1 **	51.87 **	19332 **	49172 **	14050 **
GCA	8	207.1 **	204.6 **	190.42 **	64299 **	185433 **	51313 **
SCA	27	20.1 **	10.9 **	10.817 **	6009 **	8799 **	3009 **
Error	88	2.8	3.8	1.834	848	2518	507
GCA/SCA Ratio		10.31	18.84	17.60	10.70	21.08	17.05
S.E gca		0.35	0.70	0.48253	10.38	17.88	8.03
S.E sca		2.06	1.70	1.17270	25.22	43.46	19.50

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Table 5.28. Analysis of variance of 9 parents and their 36 crosses for ASI delay.

Source	df	Mean Squares					
		Days			GDD		
		Index1	Index2	Index3	Index1	Index2	Index3
Entries	44	16.32 **	18.98 **	13.98 **	4715 **	4031 **	2862 **
Parents	8	27.29 **	64.26 **	33.63 **	8209 **	9878 **	5675 **
Parents vs Crosse	1	12.62 **	66.82 **	35.26 **	3537 **	12769 **	6038 **
Crosses	35	13.92 **	7.27 **	8.88 **	3951 **	2445 **	2128 **
GCA	8	34.33 **	17.76 **	24.42 **	9716 **	7542 **	6285 **
SCA	27	7.87 **	4.16 **	4.275 **	2242 **	935 *	896 **
Error	88	1.65	0.98	0.671	494	510	204
GCA/SCA Ratio		4.36	4.27	5.71	4.33	8.07	7.01
S.E gca		0.21	0.35	0.29	7.92	10.79	5.09
S.E sca		1.24	0.86	0.71	19.26	26.23	12.37

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Table 5.29. Analysis of variance of 9 parents and their 36 crosses for BLP and GPP delays (Index1).

Source	df	Mean Squares			
		BLP		GPP	
		Days	GDD	Days	GDD
Entries	44	42.20 **	13224 **	20.72 **	6407 **
Parents	8	63.23 **	19770 **	33.90 **	10721 **
Parents vs Crosse	1	1.83	1046	28.15 **	6194 **
Crosses	35	38.54 **	12076 **	17.50 **	5427 **
GCA	8	138.39 **	43577 **	26.18 **	8288 **
SCA	27	8.96 **	2742 **	14.92 **	4579 **
Error	88	1.83	523	1.31	403
GCA/SCA Ratio		15.45	15.89	1.75	1.81
S.E gca		0.23	66.35	0.41	7.16
S.E sca		1.38	391.89	0.99	17.39

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

coefficients of variation were generally acceptable for anthesis, silking, and BLF delays, but were high for ASI and GFP (Table 5.30)

### 5.2.3 GCA/SCA Ratio

For anthesis, silking and BLF delays, the magnitude of GCA was in the order of 10 to 15 times than that of SCA; This was reduced to about four times for ASI and two times for GFP (Table 5.31). As in maturity related traits, additive gene action seemed to be the controlling factor for photoperiod sensitivity traits.

### 5.2.4 Heterosis

Heterosis estimates ranged from -15.98 to 0.77%, -7.86 to -19.16%, -19.72 to -46.59%, -17.11 to 37.09%, and -453.14 to 17.06%, and -453.14 to 13.06% for delays in anthesis, silking, ASI, BF, and GFP, respectively (Table 5.32). The negative values indicated that photoperiod sensitivities of the hybrids were lower than the parental means. Similar values were observed for anthesis and silking delays. Larger reduction in ASI delay were observed, however, among hybrids than their parents. But the greatest absolute heterosis values were estimated from GFP delay with Hi29 leading with -453.14%. Positive heterosis value was found in Tx601 i.e., the hybrids of this parent, on the average, had longer GFP delay than the parental means.

Table 5.30. Coefficients of variation (CV's) for photoperiod sensitivity parameters.

Parameters (delay)		Index1	Index2	Index3
Anthesis	Days	15.50	6.19	6.99
	GDD	14.74	7.08	
Silking	Days	15.11	8.66	9.02
	GDD	14.50	8.97	
ASI	Days	37.20	63.66	31.67
	GDD	36.03	67.51	
BLF	Days	14.14	-	
	GDD	14.02	-	
GFP	Days	82.10	-	
	GDD	53.25	-	

Table 5.31. GCA/SCA ratios for photoperiod sensitivity traits.

Delays		Index1	Index2	Index3
Anthesis	Days	15.0	18.7	25.6
	GDD	15.3	17.6	21.2
Silking	Days	10.3	18.8	17.6
	GDD	10.7	21.1	17.1
ASI	Days	4.4	4.3	5.7
	GDD	4.3	8.1	7.0
BLF	Days	15.4	-	-
	GDD	15.9	-	-
GFP	Days	1.8	-	-
	GDD	1.8	-	-

### 5.2.5 Correlation Among Photoperiod Sensitivity Traits

Delays in anthesis, silking, and BF were highly and positively correlated with each other (Table 5.33). However, GFP delay was negatively correlated with the rest of the traits, albeit from low to medium in magnitude. ASI delay was highly correlated with silking and BLF but not with tasseling delay.

### 5.2.6 Estimates of Genetic Effects

Anthesis Delay. Anthesis delays in crosses were less than for parents resulting in negative H estimate. Strong negative parental effects were observed among temperate inbreds such as B73 (Hi), Hi32, and Oh43 (Hi). These inbreds were good combiners for low sensitivity as shown by their negative GCA estimates. Tropical inbreds such as Ant C-S5, Hi34, Tx601, and Tzi4 were good combiners for high photoperiod sensitivity. All the GCA estimates were significant (Table 5.34). Nine crosses had significant SCA estimates reflecting less importance of SCA relative to GCA. Magnitude of the significant SCA's were, however, comparable to that of GCA's and the large negative and positive signs for these crosses indicated the importance of non-additive genes for low and high photoperiod sensitivity, respectively. GDD estimates are given in Appendix 25.

Silking Delay. The hybrids reduced their silking delay by 4.1 days over their parents as shown by the negative heterosis. All the parental estimates were highly

Table 5.32. Average percent heterosis (mid-parent) of nine parents for photoperiod sensitivity traits.

Entries	Anthesis	Silking	ASI	BLF	GFP
Ant C-S5	-5.34	-12.85	-34.53	-2.63	-56.33
B73 (Hi)	-3.40	-8.03	-27.56	0.75	-106.52
Hi29	-4.59	-7.86	-19.72	-16.48	-453.14
Hi32	-8.01	-12.77	-28.06	2.64	-79.91
Hi34	-15.98	-19.16	-29.93	-17.11	-54.79
Narino 330-S6	-12.18	-17.19	-38.90	-4.08	-67.06
Oh43 (Hi)	-11.87	-16.94	-32.57	-4.35	-353.82
Tx601 (Hi)	-9.67	-12.47	-20.50	-5.77	13.06
Tzi4	0.77	-14.27	-46.59	37.09	-135.10
Mean	-7.81	-13.51	-30.93	-1.10	-143.73

Table 5.33. Correlations among photoperiod sensitivity traits expressed in days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.95 **	0.74 **	0.88 **	-0.53 *
Silking	0.95 **		0.92 **	0.85 **	-0.67 **
ASI	0.73 **	0.91 **		0.68 **	-0.75 **
BLF	0.88 **	0.85 **	0.67 **		-0.18
GFP	-0.52 **	-0.66 **	0.74 **	-0.17	

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

Table 5.32. Average percent heterosis (mid-parent) of nine parents for photoperiod sensitivity traits.

Entries	Anthesis	Silking	ASI	BLF	GFP
Ant C-S5	-5.34	-12.85	-34.53	-2.63	-56.33
B73 (Hi)	-3.40	-8.03	-27.56	0.75	-106.52
Hi29	-4.59	-7.86	-19.72	-16.48	-453.14
Hi32	-8.01	-12.77	-28.06	2.64	-79.91
Hi34	-15.98	-19.16	-29.93	-17.11	-54.79
Narino 330-S6	-12.18	-17.19	-38.90	-4.08	-67.06
Oh43 (Hi)	-11.87	-16.94	-32.57	-4.35	-353.82
Tx601 (Hi)	-9.67	-12.47	-20.50	-5.77	13.06
Tzi4	0.77	-14.27	-46.59	37.09	-135.10
Mean	-7.81	-13.51	-30.93	-1.10	-143.73

Table 5.33. Correlations among photoperiod sensitivity traits expressed in days (upper half) and GDD (lower half).

Maturity Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.95 **	0.74 **	0.88 **	-0.53 *
Silking	0.95 **		0.92 **	0.85 **	-0.67 **
ASI	0.73 **	0.91 **		0.68 **	-0.75 **
BLF	0.88 **	0.85 **	0.67 **		-0.18
GFP	-0.52 **	-0.66 **	0.74 **	-0.17	

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

significant with the same lines showing positive and negative values as in anthesis delay. Highest combiners for low and high sensitivity were Oh43 (Hi) (-6.3) and Tzi4 (7.6), respectively. Significant and large SCA estimates were observed for most of the crosses involving Ant C-S5, especially Ant C-S5 x Tx601 (9.1) and Ant C-S5 x Tzi4 (6.8). These crosses were highly sensitive to photoperiod. More than three-fourths of the remaining crosses had SCA estimates that did not significantly deviate from zero (Table 5.34).

Anthesis to Silking Interval Delay. Parental estimates ranged from -4.7 (Oh43 (Hi) to 12.5 (Tzi4). Narino 330-S6 was found to reduce ASI delay though it tend to increase anthesis and silking delay among its crosses. Inbreds that were good general combiners for low and high photoperiod sensitivity did the same for ASI. Some of the SCA estimates were larger than GCA's especially those hybrids with Ant C-S5 as one of the parents (Table 5.34).

Blacklayer Formation Delay. Average BLF delay in crosses was 16.5 days, about half day less than for the parents. Among the parents Hi34 had the highest parental estimate with 11.2 days delayed followed by Ant C-S5 with 7.7 days. Hi32 and B73 (Hi), however, matured 10 days earlier under long daylength. All estimates were significant except for Tzi4 (Table 5.35).



Table 5.34. Estimates of genetic parameters for anthesis, silking, and ASI delay (index3).

Genetic Parameters	Anthesis	Silking	ASI
Mean	21.533	25.985	4.480
Mp	23.019	29.269	6.250
Mc	21.16203	25.16435	4.037
H	-1.856 **	-4.104 **	-2.213 **
Parental Estimates			
P1	7.565 **	13.231 **	5.667 **
P2	-9.602 **	-13.852 **	-4.250 **
P3	-3.602 **	-7.519 **	-3.917 **
P4	-8.685 **	-13.102 **	-4.417 **
P5	7.315 **	7.398 **	0.083
P6	4.231 **	2.231 **	-2.000 **
P7	-6.852 **	-11.602 **	-4.750 **
P8	4.981 **	6.065 **	1.083 **
P9	4.648 **	17.148 **	12.500 **
GCA Estimates			
g1	4.481 **	6.788 **	2.446 **
g2	-3.661 **	-4.878 **	-1.257 **
g3	-1.102 **	-1.950 **	-0.888 **
g4	-4.126 **	-5.724 **	-1.638 **
g5	1.005 *	1.193 *	0.148
g6	0.815 *	-0.188	-1.173 **
g7	-4.173 **	-6.307 **	-2.173 **
g8	1.934 **	3.443 **	1.779 **
g9	4.827 **	7.622 **	2.755 **
SCA Estimates			
s12	-3.899 **	-6.408 **	-2.643 **
s13	-1.708 *	-3.253 *	-1.679 *
s14	-0.851	-2.979 *	-2.262 **
s15	-0.565	-1.729	-1.298
s16	-0.375	1.068	0.524
s17	-0.054	-2.646 *	-2.726 **
s18	3.589 **	9.104 **	7.238 **
s19	3.863 **	6.842 **	2.845 **
s23	3.768 **	2.997 *	-0.726
s24	0.958	1.271	0.357
s25	0.744	1.354	0.655
s26	-0.649	-0.515	0.310
s27	0.756	1.771	1.060
s28	0.065	0.937	0.607
s29	-1.744 *	-1.408	0.381
s34	0.065	0.842	0.821
s35	0.351	0.926	0.619

Table 5.34 cont.

Genetic Parameters	Anthesis	Silking	ASI
s36	0.042	0.473	0.607
s37	1.030	2.259	1.274
s38	-1.327	-2.324	-1.262
s39	-2.220 *	-1.920	0.345
s45	0.125	0.616	0.535714
s46	0.149	0.664	0.690
s47	1.054	2.199	1.190
s48	0.030	-0.051	-0.345
s49	-1.530	-2.563 *	-0.988
s56	-0.315	-0.336	0.155
s57	0.423	1.283	0.905
s58	-1.601 *	-3.467 **	-2.131 **
s59	0.839	1.354	0.560
s67	0.196	1.414	1.393
s68	0.006	-1.670	-1.810 *
s69	0.946	-1.098	-1.869 *
s78	-2.006 *	-3.801 **	-2.060 **
s79	-1.399	-2.479 *	-1.036
s89	1.244	1.271	-0.238
S.E. gca	0.310025	0.482537	0.291921
S.E. sca	0.753448	1.172700	0.709450

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

Estimates for GCA ranged from -5.3 (Oh43 (Hi)) to 7.1 days (Tzi4). Tropical lines combined well for high sensitivity to photoperiod while temperate lines combined well for low sensitivity. Fourteen SCA estimates were significant with the cross between Ant C-S5 and B73 showing the least with -6.1 days. Estimates in GDD are given in Appendix 26.

Grain Filling Period Delay. Mean of parents and crosses were -3.9 and -2.02 days, respectively. This meant that the grain filling durations were actually longer in SD than in LD. Highly sensitive tropical lines such as Ant C-S5, Tx601 and Tzi4 had all negative parental estimates. Hi29 had the highest positive estimate (7.44). Only five parents had significant GCA estimates with Hi29, Narino 330-S6, and Oh43 (Hi) giving positive GCA estimates; and Ant C-S5 and Tx601 (Hi) showed negative estimates. Half of the SCA estimates were significant with Ant C-S5 x Tx601 having the highest absolute value at -10.7 days (Table 5.35).

#### **5.2.7 Correlation Among GCA Estimates**

Correlation coefficients among GCA estimates are listed in Table 5.36. Delays in anthesis, silking, ASI, and BLF were very highly and positively correlated among each other ( $r > 0.90$ ). This suggests a common additive genetic control for these photoperiod sensitivity traits; and it is expected that directional selection for any one of them is

Table 5.35. Estimates of genetic effects for BLF and GFP delay (Index2).

Genetic Parameters	Blacklayer Foramation	Grain Filling
Mean	16.598	-2.417
Mp	17.001	-3.999
Mc	16.497	-2.021
H	-0.504 **	1.977 **
Parental Estimates		
P1	7.665 **	-13.668 **
P2	-10.001 **	1.665 **
P3	1.777 **	7.443 **
P4	-10.001 **	1.332 **
P5	11.221 **	2.221 **
P6	2.221 **	3.554 **
P7	-8.779 **	0.888 *
P8	5.999 **	-2.001 **
P9	-0.101	-1.435 **
GCA Estimates		
g1	4.241 **	-3.357 **
g2	-5.013 **	-0.087
g3	-1.933 **	1.469 **
g4	-4.632 **	0.389
g5	2.400 **	0.564
g6	0.941	2.248 **
g7	-5.314 **	1.231 **
g8	2.243 **	-3.022 **
g9	7.067 **	0.564
SCA Estimates		
s12	-6.059 **	1.798
s13	1.306	5.354 **
s14	0.115	3.877 **
s15	3.417 **	5.703 **
s16	1.209	-0.648
s17	-3.758 **	0.147
s18	1.908	-10.712 **
s19	1.862	-5.519 **
s23	0.782	-2.694 *
s24	1.036	-1.059
s25	-1.773	-2.345 *
s26	-2.315 *	-3.029 **
s27	3.385 **	1.100
s28	4.384 **	4.908 **
s29	0.560	1.322
s34	0.179	-1.059
s35	0.592	-0.789

Table 5.35 cont.

Genetic Parameters	Blacklayer Foramation	Grain Filling
s36	2.384 *	1.193
s37	1.750	-4.012 **
s38	-5.029 **	-2.981 **
s39	-1.964	4.988 **
s45	-3.932 **	-2.932 **
s46	-1.918	-2.061 *
s47	1.893	-1.154
s48	-0.219	0.542
s49	2.846 *	3.846 **
s56	-0.172	-0.124
s57	-2.138	-0.996
s58	1.082	3.035 **
s59	2.925 *	-1.551
s67	3.209 **	1.876
s68	1.885	3.695 **
s69	-4.283 **	-0.902
s78	-3.204 **	3.368 **
s79	-1.138	-0.329
s89	-0.807	-1.854
S.E gca	0.23	0.41
S.E sca	1.38	0.99

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

accompanied by positive correlated response from others. There was no correlation between GFP with the rest of the photoperiod sensitivity traits.

Table 5.36. Correlations among GCA estimates of photoperiod sensitivity traits expressed in number of days (upper half) and GDD (lower half).

PS Traits	Anthesis	Silking	ASI	BLF	GFP
Anthesis		0.99 **	0.92 **	0.98 **	-0.44
Silking	0.99 **		0.96 **	0.98 **	-0.51
ASI	0.94 **	0.98 **		0.91 **	-0.66
BLF	0.98 **	0.98 **	0.93 **		-0.35
GFP	-0.44 **	-0.50 **	-0.60 **	-0.33	

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

### 5.3 Correlations Between Maturity Traits Under Short Daylength and Photoperiod Sensitivity

Phenotypic and genetic (using GCA estimates)

correlation analyses were made among maturity traits measured under short daylength and photoperiod sensitivity traits (delays). Presented in Table 5.37 and 5.38 are simple phenotypic correlation coefficients for days and GDD, respectively. Highest correlations were observed among anthesis, silking, and BLF in the maturity side and their respective delays in the photoperiod sensitivity side. All  $r$  values were positive and statistically significant. Similar results were obtained for GDD data. Comparable  $r$  values were obtained using GCA estimates, except between anthesis and BLF delay which was slightly increased (Table 5.39 and 5.40). The significant correlations (phenotypic

Table 5.37. Correlations among SD maturity traits and photoperiod sensitivity traits (days).

Maturity Traits	Photoperiod Sensitivity Traits				
	Anthesis Delay	Silking Delay	ASI Delay	BLF Delay	GFP Delay
Anthesis	0.73 **	0.72 **	0.58 **	0.69 **	0.04
Silking	0.66 **	0.65 **	0.52 **	0.64 **	0.01
ASI	-0.13	-0.14	-0.13	-0.09	0.29
BLF	0.62 **	0.63 **	0.56 **	0.56 **	-0.19
GFP	-0.29	-0.25	-0.14	-0.43 **	-0.33

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

Table 5.38. Correlations among SD maturity traits and photoperiod sensitivity traits (GDD).

Maturity Traits	Photoperiod Sensitivity Traits				
	Anthesis Delay	Silking Delay	ASI Delay	BLF Delay	GFP Delay
Anthesis	0.78 **	0.76 **	0.64 **	0.72 **	0.01
Silking	0.73 **	0.71 **	0.58 **	0.66 **	0.04
ASI	-0.05	-0.10	-0.18	-0.09	0.41 **
BLF	0.66 **	0.66 **	0.59 **	0.59 **	-0.13
GFP	-0.48 **	-0.45 **	-0.32	-0.53 **	-0.26

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

Table 5.39. Correlations among GCA estimates of SD maturity traits and photoperiod sensitivity traits (days).

Maturity Traits	Photoperiod Sensitivity Traits				
	Anthesis Delay	Silking Delay	ASI Delay	BLF Delay	GFP Delay
Anthesis	0.76 *	0.74 *	0.64	0.82 **	-0.06
Silking	0.69 *	0.66 *	0.57	0.76 *	-0.01
ASI	-0.24	-0.26	-0.27	-0.17	0.34
BLF	0.64	0.62	0.56	0.68 *	-0.12
GFP	-0.49	-0.47	-0.40	-0.62	-0.18

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.

Table 2.40. Correlations among GCA estimates of SD maturity traits and photoperiod sensitivity traits (GDD).

Maturity Traits	Photoperiod Sensitivity Traits				
	Anthesis Delay	Silking Delay	ASI Delay	BLF Delay	GFP Delay
Anthesis	0.74 *	0.74 *	0.69 *	0.84 **	0.01
Silking	0.68 *	0.68 *	0.64	0.79 **	0.05
ASI	-0.37	-0.38	-0.38	-0.26	0.55
BLF	0.63	0.63	0.61	0.71 *	-0.01
GFP	-0.56	-0.56	-0.53	-0.70 *	-0.15

\* Significant at 5% level of probability.

\*\* Significant at 1% level of probability.



and genotypic) among maturity and photoperiod suggest that it might be possible to predict photoperiod sensitivity in temperate regions based on maturity performance in the tropics.

#### **5.4 Effects of Photoperiod on Morphological and Agronomic Traits**

Morphological Effects. The most obvious effects of photoperiod sensitivity were seen on the physical appearance of the plants. Highly photoperiod sensitive plants were much taller, and produced more leaves than the low photoperiod sensitive plants. Table 5.41 shows the leaf number and plant height for all entries under SD and LD. Entries planted under LD produced four more leaves (19%), and grew 83.2 cm (30.5%) taller than those planted under the SD. Inbreds such as Ant C-S5, Tx601, and Tzi4 were standouts with a LD-SD difference of a meter or more. A majority of the hybrids exhibited dramatic height increase under LD, particularly the highly sensitive ones that reached heights of more than four meters high. One good example is the cross between Tx601 and Tzi4 shown in Figure 5.1. Correlation between leaf number index (LD-SD) with anthesis and silking delays was 0.82. Crosses among low and high photoperiod sensitive inbreds gave noticeably differential results. For example, the cross Ant C-S5 x Hi32 had a 17.9 and 15.9% change for leaf number and plant height, respectively. But the cross Ant C-S5 x Oh43 (Hi)

Table 5.41. Morphological traits under short and long daylengths.

Entries	Leaf Number				Plant Height (cm)			
	SD	LD	Index	%change	SD	LD	Index	%change
Ant C-S5	21.4	26.1	4.7	21.8	197	310	112.3	56.9
B73 (Hi)	18.0	20.9	2.9	16.0	242	276	34.2	14.1
Hi29	22.3	26.2	3.9	17.4	276	339	63.3	23.0
Hi32	17.7	19.9	2.2	12.6	246	268	21.3	8.7
Hi34	21.0	26.5	5.5	26.2	219	281	61.6	28.1
Narino 330-S5	20.3	23.9	3.6	17.5	228	317	88.5	38.8
Oh43 (Hi)	18.0	21.0	3.0	16.7	210	260	50.3	24.0
Tx601 (Hi)	25.7	30.4	4.7	18.4	256	359	103.0	40.3
Txi4	21.4	26.1	4.7	21.8	261	357	95.9	36.7
Ant C-S5 x B73 (Hi)	18.9	22.6	3.7	19.4	251	314	63.2	25.2
Ant C-S5 x Hi29	22.0	26.8	4.8	21.8	288	397	109.1	37.9
Ant C-S5 x Hi32	19.9	23.4	3.6	17.9	262	301	39.5	15.1
Ant C-S5 x Hi34	21.3	27.9	6.6	30.7	250	382	131.8	52.7
Ant C-S5 x Narino 330-S6	20.6	25.1	4.6	22.2	250	376	126.7	50.8
Ant C-S5 x Oh43 (Hi)	19.6	23.7	4.1	21.0	277	364	87.0	31.4
Ant C-S5 x Tx601 (Hi)	23.6	31.9	8.3	35.4	287	425	138.2	48.2
Ant C-S5 x Txi4	23.3	29.7	6.3	27.1	294	433	139.3	47.5
B73 (Hi) x Hi29	21.3	24.2	2.9	13.5	308	360	51.9	16.9
B73 (Hi) x Hi32	18.1	20.6	2.4	13.5	262	305	43.6	16.6
B73 (Hi) x Hi34	20.0	23.8	3.8	18.9	282	342	60.2	21.3
B73 (Hi) x Narino 330-S6	19.8	22.4	2.7	13.5	281	336	54.9	19.5
B73 (Hi) x Oh43 (Hi)	19.0	20.1	1.1	5.8	268	323	54.4	20.3
B73 (Hi) x Tx601 (Hi)	22.4	25.9	3.4	15.2	317	399	82.7	26.1
B73 (Hi) x Txi4	21.7	26.6	5.0	22.9	305	376	71.6	23.5
Hi29 x Hi32	19.2	22.1	2.9	15.0	266	363	96.7	36.3
Hi29 x Hi34	21.6	26.4	4.9	22.7	286	388	101.8	35.6
Hi29 x Narino 330-S6	21.3	25.2	3.9	18.2	301	406	104.1	34.5
Hi29 x Oh43 (Hi)	19.9	22.1	2.2	11.2	267	325	58.0	21.7
Hi29 x Tx601 (Hi)	24.9	28.2	3.3	13.4	300	399	98.7	32.9
Hi29 x Txi4	23.1	26.7	3.6	15.6	290	375	85.2	29.4
Hi32 x Hi34	19.7	25.4	5.7	29.1	269	376	106.8	39.7
Hi32 x Narino 330 S-6	20.8	22.8	2.0	9.6	283	343	59.4	21.0
Hi32 x Oh43 (Hi)	18.1	19.8	1.7	9.2	229	277	48.2	21.1
Hi32 x Tx601 (Hi)	21.6	24.1	2.6	11.9	264	363	99.0	37.5
Hi32 x Txi4	21.8	24.9	3.1	14.3	285	383	98.8	34.7
Hi34 x Narino 330-S6	21.1	25.6	4.4	21.1	272	352	79.9	29.3
Hi34 x Oh43 (Hi)	20.3	24.0	3.7	18.0	282	367	85.0	30.2
Hi34 x Tx601 (Hi)	23.1	29.4	6.3	27.4	304	402	98.6	32.4
Hi34 x Txi4	22.4	28.3	5.9	26.2	286	409	123.2	43.1
Narino 330-S6 x Oh43 (Hi)	19.3	23.2	3.9	20.1	263	337	74.4	28.3
Narino 330-S6 x Tx601 (Hi)	24.7	28.7	4.0	16.2	306	408	101.8	33.3
Narino 330-S6 x Txi4	22.7	26.6	3.9	17.2	291	386	95.8	33.0
Oh43 (Hi) x Tx601 (Hi)	22.2	25.6	3.3	15.0	302	352	50.0	16.5
Oh43(Hi) x Txi4	21.8	26.4	4.7	21.4	283	372	88.6	31.3
Tx601 (Hi) x Txi4	24.6	30.9	6.3	25.8	312	416	104.0	33.3
Mean	21.1	25.2	4.0	19.0	272	356	83.2	30.5



Figure 5.1. A cross between Tx601 (Hi) and Tzi4 grown under short (left) and long (right) daylength in Waimanalo.

had a 21.0 and 31.4% change. The same was observed for crosses Oh43 (Hi) x Tx601 and Oh43 (Hi) x Tzi4. Other observed morphological changes under LD were the excessive production of brace roots (Figure 5.2) and ear tipping or ear tasseling. However, these were very genotype-specific effects.

Yield and Yield Components. Data on total dry matter yield, grain yield, and yield components are listed in Table 5.42. Excessive production of vegetative parts under LD led to the increased above-ground dry matter yield. Remarkable increases were noted for the inbred Ant C-S5 which increased from 9 to 14.9 t/ha or an increase of 64.6%, and for the cross Ant C-S5 x Hi34 which increased from 15.5 to 24.3 t/ha or 56.8% change. Many entries, however, gave lower LD dry matter yield although they appeared taller and had more leaves. This was because their grain yields were drastically reduced under LD, so that whatever increase in vegetative parts were offset by very low grain yield. This was indicated by the negative correlation, although not significant, between dry matter yield and grain yield (Table 5.43).

Grain yield was severely affected by photoperiod with an average reduction of 47.8%. Highly photoperiod sensitive inbreds such as Ant C-S5, Hi34, Tx601, and Tzi4 had more than 50% yield reduction. Low and intermediate photoperiod sensitive lines had differential response. Oh43 (Hi), a low



Figure 5.2. Excessive brace root formation in some of the hybrids. This is a genotype specific response under long daylength in Waimanalo.

Table 5.42. Yield and yield components under short and long daylengths.

Entries	Dry Matter Yield (t/ha)				Grain Yield (t/ha)				Harvest Index			
	SD	LD	Index	%change	SD	LD	Index	%change	SD	LD	Index	%change
Ant C-S5	9.0	14.9	5.8	64.6	3.67	1.46	-2.21	-60.3	0.34	0.09	-0.26	-74.7
B73 (Hi)	10.6	9.7	-0.9	-8.9	5.38	3.34	-2.04	-38.0	0.43	0.29	-0.14	-32.2
Hi29	16.5	16.6	0.1	0.5	6.82	4.40	-2.42	-35.4	0.35	0.22	-0.13	-36.5
Hi32	11.9	7.7	-4.2	-35.1	5.76	2.38	-3.38	-58.6	0.41	0.26	-0.15	-37.5
Hi34	10.7	8.9	-1.9	-17.3	4.21	1.00	-3.21	-76.4	0.33	0.10	-0.23	-69.2
Narino 330-S6	10.5	12.7	2.2	20.6	4.75	1.69	-3.06	-64.5	0.38	0.13	-0.25	-65.8
Oh43 (Hi)	8.8	8.6	-0.1	-1.6	3.70	3.29	-0.42	-11.3	0.36	0.32	-0.04	-9.8
Tx601 (Hi)	10.8	14.1	3.3	30.8	3.97	0.64	-3.33	-84.0	0.31	0.04	-0.27	-86.6
Txi4	16.5	19.8	3.3	20.3	6.90	0.90	-6.00	-87.0	0.35	0.04	-0.31	-88.7
Ant C-S5 x B73 (Hi)	13.2	14.9	1.6	12.3	7.40	4.46	-2.94	-39.8	0.47	0.23	-0.25	-52.3
Ant C-S5 x Hi29	16.9	23.4	6.5	38.5	7.57	5.17	-2.40	-31.7	0.38	0.19	-0.19	-50.7
Ant C-S5 x Hi32	15.7	14.6	-1.0	-6.5	7.93	3.93	-4.00	-50.5	0.43	0.23	-0.20	-47.0
Ant C-S5 x Hi34	15.5	24.3	8.8	56.8	6.86	3.66	-3.20	-46.6	0.38	0.13	-0.25	-65.9
Ant C-S5 x Narino 330-S6	16.3	21.8	5.5	33.4	7.88	3.57	-4.30	-54.6	0.41	0.15	-0.26	-63.9
Ant C-S5 x Oh43 (Hi)	15.7	19.2	3.5	22.3	8.08	5.99	-2.09	-25.8	0.44	0.26	-0.18	-41.1
Ant C-S5 x Tx601 (Hi)	20.3	25.0	4.7	23.2	8.28	1.38	-6.90	-83.4	0.35	0.05	-0.30	-86.4
Ant C-S5 x Txi4	19.7	21.0	1.4	7.0	9.15	0.68	-8.47	-92.6	0.39	0.03	-0.37	-92.8
B73 (Hi) x Hi29	20.6	17.4	-3.2	-15.6	9.41	6.48	-2.93	-31.1	0.39	0.32	-0.07	-17.5
B73 (Hi) x Hi32	15.3	12.7	-2.6	-17.0	8.81	5.74	-3.07	-34.9	0.49	0.38	-0.11	-21.8
B73 (Hi) x Hi34	20.4	17.1	-3.3	-16.2	9.73	5.58	-4.14	-42.6	0.41	0.28	-0.13	-31.5
B73 (Hi) x Narino 330-S6	18.1	18.5	0.4	2.2	9.76	7.18	-2.58	-26.5	0.46	0.33	-0.13	-28.8
B73 (Hi) x Oh43 (Hi)	12.3	11.7	-0.7	-5.3	6.74	4.70	-2.05	-30.4	0.46	0.34	-0.13	-27.2
B73 (Hi) x Tx601 (Hi)	19.5	19.0	-0.5	-2.4	9.71	4.41	-5.30	-54.6	0.42	0.20	-0.23	-53.8
B73 (Hi) x Txi4	19.0	21.0	2.0	10.5	10.06	2.19	-7.87	-78.2	0.45	0.09	-0.36	-79.9
Hi29 x Hi32	17.5	14.5	-3.0	-16.9	8.85	5.69	-3.15	-35.6	0.43	0.33	-0.10	-23.5
Hi29 x Hi34	18.3	18.4	0.1	0.3	9.63	5.56	-4.07	-42.3	0.45	0.26	-0.19	-42.1
Hi29 x Narino 330-S6	19.6	24.5	5.0	25.4	9.45	6.83	-2.62	-27.7	0.41	0.24	-0.17	-42.3
Hi29 x Oh43 (Hi)	14.0	14.0	0.0	0.2	7.37	5.31	-2.06	-28.0	0.45	0.33	-0.12	-27.0
Hi29 x Tx601 (Hi)	16.8	23.0	6.2	37.1	7.24	5.86	-1.38	-19.0	0.37	0.22	-0.14	-38.7
Hi29 x Txi4	23.5	20.5	-3.0	-13.0	10.58	5.45	-5.14	-48.5	0.38	0.24	-0.14	-37.2
Hi32 x Hi34	17.2	22.7	5.5	32.3	9.88	7.18	-2.70	-27.3	0.49	0.27	-0.21	-43.8
Hi32 x Narino 330 S-6	16.3	16.5	0.2	1.0	9.19	6.82	-2.37	-25.8	0.48	0.36	-0.12	-24.8
Hi32 x Oh43 (Hi)	11.2	11.7	0.6	5.0	6.03	4.69	-1.34	-22.2	0.46	0.34	-0.12	-25.6
Hi32 x Tx601 (Hi)	17.3	13.1	-4.2	-24.5	8.07	3.43	-4.64	-57.5	0.40	0.22	-0.18	-44.6
Hi32 x Txi4	18.8	16.1	-2.7	-14.5	10.39	3.49	-6.90	-66.4	0.47	0.19	-0.28	-60.1
Hi34 x Narino 330-S6	18.6	19.6	1.0	5.4	9.59	6.70	-2.89	-30.1	0.44	0.29	-0.15	-33.6
Hi34 x Oh43 (Hi)	17.9	17.3	-0.6	-3.1	9.88	5.82	-4.06	-41.1	0.47	0.28	-0.19	-39.8
Hi34 x Tx601 (Hi)	18.3	27.4	9.0	49.3	9.64	4.30	-5.34	-55.4	0.44	0.14	-0.30	-67.9
Hi34 x Txi4	20.0	25.5	5.4	27.2	9.67	2.05	-7.62	-78.8	0.41	0.07	-0.34	-83.4
Narino 330-S6 x Oh43 (Hi)	18.3	17.9	-0.4	-2.4	9.42	6.17	-3.25	-34.5	0.44	0.27	-0.16	-37.2
Narino 330-S6 x Tx601 (Hi)	23.2	27.8	4.7	20.1	10.36	6.13	-4.23	-40.8	0.38	0.19	-0.19	-49.2
Narino 330-S6 x Txi4	18.1	20.3	2.2	12.2	9.85	2.78	-7.07	-71.8	0.46	0.12	-0.35	-74.8
Oh43 (Hi) x Tx601 (Hi)	19.9	18.2	-1.7	-8.4	10.06	7.48	-2.58	-25.6	0.43	0.35	-0.08	-18.6
Oh43(Hi) x Txi4	20.3	20.8	0.5	2.7	10.27	4.53	-5.74	-55.9	0.43	0.18	-0.25	-57.0
Tx601 (Hi) x Txi4	21.7	30.8	9.0	41.5	10.35	2.24	-8.11	-78.4	0.40	0.06	-0.34	-84.9
Mean	16.7	18.1	1.4	8.6	8.18	4.28	-3.90	-47.8	0.42	0.21	-0.20	-49.28

Table 5.42 cont.

Entries	Ears Per Plant				Bar Length (cm)				Filled Bar Length (cm)			
	SD	LD	Index	%change	SD	LD	Index	%change	SD	LD	Index	%change
Ant C-S5	1.3	0.59	-0.70	-54.4	12.7	11.9	-0.8	-6.3	12.0	10.4	-1.6	-13.3
B73 (Hi)	0.9	0.71	-0.17	-19.0	15.9	17.1	1.2	7.8	14.6	15.1	0.5	3.4
Hi29	1.1	1.12	0.04	3.3	16.9	16.4	-0.6	-3.3	16.0	15.1	-0.85	-5.3
Hi32	1.1	0.80	-0.26	-24.5	18.8	18.5	-0.3	-1.7	17.7	15.9	-1.83	-10.4
Hi34	1.0	0.76	-0.24	-24.0	16.8	15.8	-1.0	-5.8	13.9	12.9	-1	-7.2
Narino 330-S6	1.3	0.67	-0.61	-47.4	12.4	13.8	1.4	11.3	12.2	11.5	-0.7	-5.8
Oh43 (Hi)	0.9	1.03	0.10	10.8	15.8	15.5	-0.3	-1.9	13.9	14.0	0.1	0.7
Tx601 (Hi)	1.0	0.35	-0.62	-63.8	15.0	12.7	-2.3	-15.1	14.0	11.3	-2.73	-19.6
Txi4	1.3	0.54	-0.77	-58.7	16.7	15.8	-0.9	-5.6	15.2	9.8	-5.36	-35.3
Ant C-S5 x B73 (Hi)	1.0	1.05	0.02	1.8	16.5	17.0	0.5	2.8	16.0	14.9	-1.03	-6.5
Ant C-S5 x Hi29	1.1	0.85	-0.25	-22.6	17.1	18.3	1.1	6.6	16.6	16.7	0.1	0.6
Ant C-S5 x Hi32	1.0	0.85	-0.15	-15.3	18.2	18.6	0.4	2.0	17.9	16.7	-1.16	-6.5
Ant C-S5 x Hi34	0.9	0.80	-0.14	-14.8	19.4	20.5	1.1	5.7	17.4	18.0	0.566	3.3
Ant C-S5 x Narino 330-S6	1.2	1.06	-0.16	-12.9	17.7	18.0	0.3	1.8	17.2	15.7	-1.53	-8.9
Ant C-S5 x Oh43 (Hi)	1.0	1.00	-0.03	-3.1	17.5	19.4	1.9	10.9	17.2	18.1	0.933	5.4
Ant C-S5 x Tx601 (Hi)	1.0	0.28	-0.74	-72.6	18.1	17.7	-0.5	-2.6	17.2	14.9	-2.3	-13.4
Ant C-S5 x Txi4	1.1	0.33	-0.79	-70.3	18.6	18.6	0.0	0.1	18.1	10.9	-7.21	-39.9
B73 (Hi) x Hi29	1.1	0.88	-0.19	-17.6	19.1	21.0	1.9	10.1	18.4	20.2	1.753	9.5
B73 (Hi) x Hi32	1.0	0.98	0.02	2.1	18.5	17.0	-1.5	-8.1	17.9	15.4	-2.48	-13.9
B73 (Hi) x Hi34	1.0	0.89	-0.11	-10.8	19.2	19.2	-0.1	-0.3	17.6	17.4	-0.16	-0.9
B73 (Hi) x Narino 330-S6	1.0	0.95	-0.09	-8.6	19.6	20.6	1.0	5.1	18.6	18.8	0.233	1.3
B73 (Hi) x Oh43 (Hi)	0.9	0.88	-0.05	-5.2	16.7	18.5	1.7	10.4	15.1	15.8	0.7	4.6
B73 (Hi) x Tx601 (Hi)	1.1	0.75	-0.30	-28.6	19.0	20.7	1.7	9.0	18.5	18.8	0.266	1.4
B73 (Hi) x Txi4	1.1	0.39	-0.71	-64.3	18.8	20.3	1.5	8.0	17.7	15.8	-1.83	-10.4
Hi29 x Hi32	1.0	0.85	-0.19	-18.2	18.2	20.1	1.9	10.5	17.5	19.2	1.7	9.7
Hi29 x Hi34	1.0	0.98	-0.01	-1.0	19.7	18.3	-1.4	-7.3	19.0	15.7	-3.26	-17.2
Hi29 x Narino 330-S6	1.3	1.00	-0.31	-23.5	19.3	20.5	1.3	6.6	18.6	17.1	-1.46	-7.9
Hi29 x Oh43 (Hi)	1.0	0.84	-0.15	-15.6	16.8	17.5	0.7	4.2	16.5	16.3	-0.21	-1.3
Hi29 x Tx601 (Hi)	1.0	0.94	-0.08	-7.8	17.6	21.9	4.3	24.5	16.3	19.7	3.38	20.7
Hi29 x Txi4	1.3	1.01	-0.27	-21.0	19.2	22.5	3.3	17.1	18.5	19.6	1.146	6.2
Hi32 x Hi34	1.0	1.02	0.03	2.8	22.1	22.0	-0.1	-0.6	20.6	19.1	-1.53	-7.4
Hi32 x Narino 330 S-6	1.0	0.93	-0.09	-8.5	19.3	20.5	1.1	5.9	18.7	18.5	-0.23	-1.2
Hi32 x Oh43 (Hi)	1.0	0.92	-0.12	-11.3	17.3	18.8	1.5	8.6	16.0	17.2	1.2	7.5
Hi32 x Tx601 (Hi)	1.0	0.66	-0.34	-34.1	20.0	21.0	1.0	5.2	18.2	18.1	-0.03	-0.2
Hi32 x Txi4	1.0	0.75	-0.28	-26.9	21.5	17.4	-4.1	-19.2	20.4	15.2	-5.16	-25.4
Hi34 x Narino 330-S6	1.2	0.96	-0.20	-17.2	18.6	23.8	5.2	28.1	17.0	20.7	3.666	21.6
Hi34 x Oh43 (Hi)	1.0	0.92	-0.13	-12.0	19.2	20.2	1.0	5.4	17.9	17.0	-0.83	-4.7
Hi34 x Tx601 (Hi)	1.0	0.84	-0.12	-12.9	18.6	19.8	1.1	6.0	17.0	17.7	0.666	3.9
Hi34 x Txi4	1.1	0.99	-0.07	-6.8	20.5	17.1	-3.4	-16.6	18.3	12.5	-5.83	-31.9
Narino 330-S6 x Oh43 (Hi)	1.0	0.76	-0.20	-20.7	18.8	21.1	2.3	12.3	18.0	18.3	0.266	1.5
Narino 330-S6 x Tx601 (Hi)	1.1	0.86	-0.20	-19.1	19.5	20.5	1.0	5.3	18.5	18.0	-0.53	-2.9
Narino 330-S6 x Txi4	1.1	0.84	-0.31	-26.8	17.8	20.5	2.7	15.4	17.2	15.3	-1.93	-11.2
Oh43 (Hi) x Tx601 (Hi)	1.2	0.88	-0.32	-26.8	19.9	19.3	-0.6	-3.0	19.0	17.5	-1.43	-7.6
Oh43(Hi) x Txi4	1.2	0.92	-0.24	-20.9	20.1	18.1	-2.0	-10.0	18.7	16.0	-2.71	-14.5
Tx601 (Hi) x Txi4	1.2	0.50	-0.68	-57.4	19.1	20.3	1.2	6.5	17.9	16.5	-1.43	-8.0
Mean	1.1	0.82	-0.25	-22.4	18.2	18.8	0.6	3.2	17.1	16.2	-0.91	-5.3

Table 5.42 cont. -

Entries	Percent Ear Fill				Ear Diameter (cm)				Kernel Row Number			
	SD	LD	Index	%change	SD	LD	Index	%change	SD	LD	Index	%change
Ant C-S5	0.95	0.88	-0.07	-7.6	3.71	3.3	-0.40	-10.8	13.1	11.7	-1.3	-0.10
B73 (Hi)	0.92	0.88	-0.04	-4.0	4.65	4.8	0.12	2.6	16.1	16.4	0.3	0.02
Hi29	0.94	0.92	-0.02	-2.4	4.37	3.9	-0.51	-11.8	15.1	12.9	-2.1	-0.14
Hi32	0.94	0.86	-0.08	-8.7	4.49	4.2	-0.31	-7.0	15.5	14.8	-0.7	-0.04
Hi34	0.83	0.81	-0.01	-1.5	4.27	3.3	-0.97	-22.7	12.1	10.5	-1.6	-0.13
Narino 330-S6	0.98	0.83	-0.15	-15.6	3.92	3.4	-0.49	-12.4	13.3	11.5	-1.8	-0.14
Oh43 (Hi)	0.88	0.90	0.02	2.7	4.27	3.9	-0.32	-7.5	13.7	13.9	0.1	0.01
Tx601 (Hi)	0.93	0.88	-0.05	-5.2	4.39	3.5	-0.93	-21.1	14.4	10.9	-3.5	-0.24
Txi4	0.91	0.62	-0.29	-32.3	4.44	3.5	-0.97	-21.9	13.7	10.7	-3.1	-0.22
Ant C-S5 x B73 (Hi)	0.97	0.88	-0.09	-9.4	4.49	4.0	-0.49	-11.0	15.0	14.5	-0.5	-0.03
Ant C-S5 x Hi29	0.97	0.91	-0.05	-5.6	4.19	3.9	-0.29	-6.8	13.2	12.4	-0.8	-0.06
Ant C-S5 x Hi32	0.98	0.90	-0.08	-8.3	4.48	4.2	-0.23	-5.2	14.5	13.9	-0.7	-0.05
Ant C-S5 x Hi34	0.90	0.88	-0.02	-1.8	4.50	4.1	-0.44	-9.8	12.9	12.0	-0.9	-0.07
Ant C-S5 x Narino 330-S6	0.98	0.87	-0.10	-10.5	4.35	3.9	-0.48	-11.0	12.8	12.2	-0.6	-0.05
Ant C-S5 x Oh43 (Hi)	0.98	0.93	-0.05	-4.9	4.56	4.3	-0.23	-5.1	13.9	13.2	-0.7	-0.05
Ant C-S5 x Tx601 (Hi)	0.95	0.84	-0.11	-11.6	4.62	4.1	-0.54	-11.8	13.5	12.7	-0.8	-0.06
Ant C-S5 x Txi4	0.97	0.58	-0.39	-40.1	4.33	3.4	-0.92	-21.3	13.2	12.2	-1.0	-0.07
B73 (Hi) x Hi29	0.96	0.96	-0.00	-0.5	4.63	4.5	-0.10	-2.2	14.5	15.1	0.5	0.04
B73 (Hi) x Hi32	0.96	0.90	-0.06	-6.3	5.13	4.8	-0.33	-6.4	17.7	15.9	-1.9	-0.11
B73 (Hi) x Hi34	0.91	0.91	-0.00	-0.5	4.95	4.6	-0.31	-6.3	15.6	15.5	-0.1	-0.01
B73 (Hi) x Narino 330-S6	0.95	0.92	-0.03	-3.7	4.95	4.7	-0.23	-4.6	16.3	16.1	-0.1	-0.01
B73 (Hi) x Oh43 (Hi)	0.90	0.85	-0.05	-5.5	4.77	4.6	-0.16	-3.4	16.7	16.8	0.1	0.01
B73 (Hi) x Tx601 (Hi)	0.98	0.91	-0.07	-6.9	5.00	4.7	-0.33	-6.7	16.3	16.5	0.3	0.02
B73 (Hi) x Txi4	0.94	0.79	-0.15	-16.2	4.98	4.5	-0.45	-9.0	15.2	15.7	0.5	0.04
Hi29 x Hi32	0.96	0.96	-0.01	-0.7	4.75	4.3	-0.41	-8.7	14.7	15.2	0.5	0.04
Hi29 x Hi34	0.96	0.86	-0.10	-10.8	4.78	4.0	-0.78	-16.3	14.1	12.0	-2.1	-0.15
Hi29 x Narino 330-S6	0.96	0.84	-0.13	-13.4	4.37	4.2	-0.18	-4.1	13.3	14.3	0.9	0.07
Hi29 x Oh43 (Hi)	0.98	0.93	-0.05	-5.2	4.70	4.5	-0.21	-4.4	15.7	15.5	-0.3	-0.02
Hi29 x Tx601 (Hi)	0.93	0.90	-0.03	-3.0	4.63	4.5	-0.16	-3.5	14.5	15.1	0.5	0.04
Hi29 x Txi4	0.96	0.87	-0.09	-9.2	4.68	4.3	-0.37	-7.8	14.7	13.9	-0.8	-0.05
Hi32 x Hi34	0.93	0.87	-0.06	-6.2	4.70	4.4	-0.33	-7.0	14.4	14.0	-0.4	-0.03
Hi32 x Narino 330 S-6	0.97	0.90	-0.07	-6.9	4.67	4.5	-0.20	-4.3	15.5	14.8	-0.7	-0.04
Hi32 x Oh43 (Hi)	0.92	0.91	-0.01	-0.9	4.68	4.2	-0.48	-10.3	15.3	14.1	-1.2	-0.08
Hi32 x Tx601 (Hi)	0.91	0.86	-0.05	-5.1	4.67	4.0	-0.63	-13.6	15.1	13.7	-1.3	-0.09
Hi32 x Txi4	0.95	0.87	-0.08	-8.0	4.93	4.1	-0.83	-16.8	15.3	12.9	-2.4	-0.16
Hi34 x Narino 330-S6	0.91	0.87	-0.05	-5.2	4.63	4.3	-0.30	-6.5	12.9	13.2	0.3	0.02
Hi34 x Oh43 (Hi)	0.93	0.84	-0.09	-9.4	4.79	4.2	-0.62	-13.0	14.0	14.0	0.0	0.00
Hi34 x Tx601 (Hi)	0.91	0.90	-0.01	-1.5	5.17	4.6	-0.59	-11.5	14.3	14.4	0.1	0.01
Hi34 x Txi4	0.89	0.74	-0.15	-17.2	4.83	4.0	-0.85	-17.7	12.8	11.5	-1.3	-0.10
Narino 330-S6 x Oh43 (Hi)	0.96	0.87	-0.09	-9.3	4.73	4.5	-0.25	-5.2	15.3	14.8	-0.5	-0.03
Narino 330-S6 x Tx601 (Hi)	0.95	0.87	-0.08	-8.0	4.85	4.6	-0.25	-5.2	15.7	14.7	-1.1	-0.07
Narino 330-S6 x Txi4	0.97	0.76	-0.21	-21.7	4.57	4.1	-0.51	-11.1	13.7	14.0	0.3	0.02
Oh43 (Hi) x Tx601 (Hi)	0.95	0.91	-0.04	-4.6	4.87	4.5	-0.40	-8.2	15.7	15.2	-0.5	-0.03
Oh43(Hi) x Txi4	0.93	0.89	-0.05	-5.0	4.83	4.4	-0.40	-8.3	14.7	14.4	-0.3	-0.02
Tx601 (Hi) x Txi4	0.94	0.81	-0.13	-13.9	4.83	3.9	-0.90	-18.6	13.7	13.1	-0.7	-0.05
Mean	0.94	0.86	-0.08	-8.3	4.62	4.2	-0.44	-9.7	14.5	13.8	-0.7	-0.05



Table 5.42 cont.

Entries	Kernels Per Row			
	SD	LD	Index	%change
Ant C-S5	20.6	17.3	-3.3	-15.9
B73 (Hi)	33.1	33.2	0.1	0.4
Hi29	32.4	26.9	-5.5	-16.9
Hi32	36.2	30.3	-5.9	-16.2
Hi34	34.3	20.8	-13.4	-39.2
Narino 330-S6	26.1	18.9	-7.2	-27.6
Oh43 (Hi)	29.3	29.2	-0.1	-0.2
Tx601 (Hi)	34.3	15.4	-18.9	-55.1
Txi4	29.8	15.5	-14.3	-48.1
Ant C-S5 x B73 (Hi)	34.7	28.5	-6.2	-18.0
Ant C-S5 x Hi29	32.7	28.7	-3.9	-12.0
Ant C-S5 x Hi32	35.1	30.7	-4.4	-12.5
Ant C-S5 x Hi34	41.5	33.1	-8.4	-20.3
Ant C-S5 x Narino 330-S6	37.3	26.0	-11.3	-30.4
Ant C-S5 x Oh43 (Hi)	33.4	31.4	-2.0	-6.0
Ant C-S5 x Tx601 (Hi)	36.5	27.7	-8.8	-24.1
Ant C-S5 x Txi4	36.5	12.6	-24.0	-65.6
B73 (Hi) x Hi29	40.9	43.5	2.6	6.4
B73 (Hi) x Hi32	41.6	34.3	-7.3	-17.5
B73 (Hi) x Hi34	45.7	41.4	-4.3	-9.3
B73 (Hi) x Narino 330-S6	43.6	42.7	-0.9	-2.0
B73 (Hi) x Oh43 (Hi)	34.0	34.9	0.9	2.5
B73 (Hi) x Tx601 (Hi)	42.9	43.3	0.5	1.1
B73 (Hi) x Txi4	44.7	33.5	-11.1	-24.9
Hi29 x Hi32	38.7	39.3	0.7	1.7
Hi29 x Hi34	44.8	33.4	-11.4	-25.4
Hi29 x Narino 330-S6	39.1	30.0	-9.1	-23.3
Hi29 x Oh43 (Hi)	36.3	35.7	-0.6	-1.7
Hi29 x Tx601 (Hi)	38.9	40.7	1.9	4.8
Hi29 x Txi4	42.3	38.3	-4.0	-9.4
Hi32 x Hi34	48.9	43.5	-5.3	-10.9
Hi32 x Narino 330 S-6	42.5	38.2	-4.3	-10.2
Hi32 x Oh43 (Hi)	33.9	33.3	-0.6	-1.8
Hi32 x Tx601 (Hi)	42.5	36.3	-6.2	-14.6
Hi32 x Txi4	47.0	27.3	-19.7	-41.8
Hi34 x Narino 330-S6	46.8	47.7	0.9	2.0
Hi34 x Oh43 (Hi)	44.9	40.2	-4.7	-10.4
Hi34 x Tx601 (Hi)	45.3	39.2	-6.1	-13.5
Hi34 x Txi4	49.7	22.4	-27.3	-54.9
Narino 330-S6 x Oh43 (Hi)	43.3	38.4	-4.9	-11.2
Narino 330-S6 x Tx601 (Hi)	42.2	37.9	-4.3	-10.3
Narino 330-S6 x Txi4	44.1	26.7	-17.4	-39.4
Oh43 (Hi) x Tx601 (Hi)	44.9	41.9	-2.9	-6.5
Oh43(Hi) x Txi4	43.7	29.5	-14.3	-32.6
Tx601 (Hi) x Txi4	45.7	27.4	-18.3	-40.1
Mean	39.2	32.2	-7.0	-17.8

Table 5.43. Correlations among % LD-SD difference for yield and yield components.

	Grain Yield	Harvest Index	Ears/Plant	Ear Length	Filled Length	% Ear Fill	Ear Diameter	Kernel Rows	Kernels Per Row
DM Yield	-0.16	-0.54 **	-23.00	0.03	-0.08	-0.15	-0.17	-0.10	-0.24
Grain Yield		0.96 **	0.76 **	0.40 **	0.70 **	0.65 **	0.75 **	0.48 **	0.83 **
Harvest Index			0.72 **	0.31 *	0.64 **	0.64 **	0.71 **	0.43 **	0.82 **
Ears/plant				0.12	0.45 **	0.58 **	0.48 **	0.29 *	0.54 **
Ear Length					0.77 **	0.10	0.52 **	0.62 **	0.58 **
Filled Ear Length						0.71 **	0.68 **	0.59 **	0.86 **
% Ear Fill							0.49 **	0.25	0.69 **
Ear Diameter								0.70 **	0.82 **
Kernel Rows									0.60 **

\* Significant at 0.01 level of probability.

\*\* Significant at 0.05 level of probability.

photoperiod sensitive line, showed a more stable yield with only 11.3% reduction. B73 (Hi) and Hi32, both low photoperiod sensitive lines, were much more affected with 38.0 and 58.6% reduction, respectively. Very high yield reductions were observed among crosses having high photoperiod sensitivity, with Ant C-S5 x Tzi4 leading at 92.6% reduction. Crosses among low sensitive lines reduced their grain yields from 22.2 to 34.9%. Few crosses among low and high photoperiod sensitive lines had yield reductions comparable to low x low photoperiod sensitive crosses. This dependent, however, on the specific high parent. For example, when Oh43 (Hi) was crossed with Tx601 (Hi), LD yield reduced by only 25.6%, but reduction was significantly increased to 55.9% when crossed with Tzi4. Similar phenomenon was observed for B73 (Hi) crosses with Tx601 (Hi) and Tzi4.

Large grain yield reductions under LD can be traced to several yield component factors that were measured in this study. Harvest index, number of ears per plant, ear length (base-tip), filled ear length, percent ear filling (filled ear length/ear length), ear diameter, kernel row number, and number of kernels per row are all contributing factors to grain yield. Under favorable growing conditions, grain yield is primarily a function of ear length and diameter, or ear size, and number of ears per plant. Number of kernel rows and kernel per row are in turn influenced by ear

diameter and length. Results showed that reductions in ear length and ear diameter were considered negligible. In fact some entries had increased ear length under LD such as B73 (7.8%), Narino 330-S6 (11.3%); and 75% of the crosses gave positive changes. Filled ear length was more affected as reflected by negative ear filling index, although several hybrids did exhibit no change or even had increased filled ear length. Figure 5.3 illustrates the cross between two highly photoperiod sensitive lines, Tx601 and Tzi4. Under extended daylength, both the parents showed shorter and smaller ears, as well as fewer kernels per ear. The hybrid ear lengths, however, were not affected but still with a lot of missing kernels. Another example is the cross Hi34 x Tzi4 (Figure 5.4). Ear length of the hybrid was reduced but ear filling was not affected. Low x low photoperiod sensitive crosses such as B73 (Hi) x Hi32 (Figure 5.5) were basically unaffected as far ear lengths and diameter were concerned. Low x high photoperiod sensitive cross as illustrated by B73 (Hi) x Tx601 basically gave a stable hybrid (Figure 5.6).

Reductions in kernel row number were negligible (0.05%), but reductions in numbers of kernels per row were considerable, especially among highly photoperiod sensitive inbreds and hybrids with a mean of -17.8%. There was, however, no corresponding reduction in ear filling as should be expected. This is because ear filling was much more



Figure 5.3 Ears of Tx601 (Hi) and Tzi4 and their F1 produced from short (upper row) and long (lower row) daylength in Waimanalo.



Figure 5.4. Ears of Hi34 and Tzi4 and their F1 produced from short (upper row) and long (lower row) in daylength Waimanalo.



Figure 5.5. Ears of B73 (Hi) and Hi32 and their F1 produced from short (upper row) and long (lower row) daylength in Waimanalo.

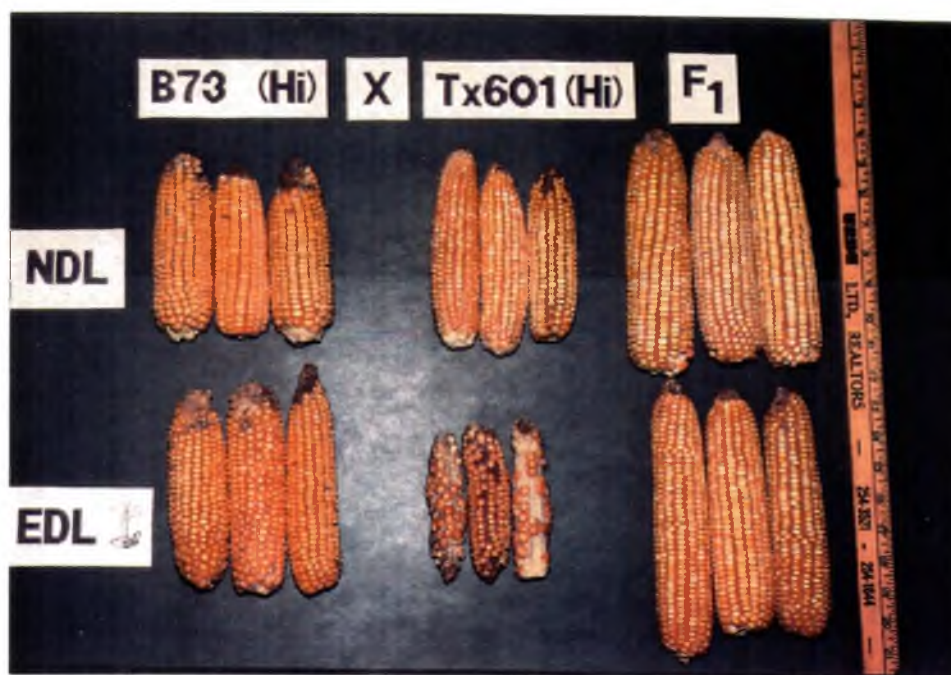


Figure 5.6. Ears of B73 (Hi) and Tx601 (Hi) and their F1 produced from short (upper row) and long (lower row) daylength in Waimanalo.



difficult to measure due to missing kernels in the middle of the ear that could not be accounted in the measurement.

Number of ears per plant is a measure of plant prolificacy and can seriously affect yield under stressful environments. More than half of the plant populations among highly sensitive lines such as Ant C-S5, Tx601 (Hi), produced no ears. This was the main reason for the very low grain yield under LD among these lines. Two inbreds, Hi29 and Oh43, actually had more ears/plant under LD than under SD suggesting more tolerance to LD.

Harvest index is an important physiological trait since it is an indirect measurement of source-sink relationship. It is particularly important in the yield analysis because of the large effects of photoperiod on vegetative parts. Harvest index was reduced from 0.42 to 0.21 (50% reduction), the largest among the yield components. Highest reductions among inbreds were observed in Tx601 (Hi) and Tzi4 with more than 80%. Ant C-S5 x Tzi4 were almost entirely vegetative with 92.8% reduction in harvest index. Correlation analysis (Table 5.43) showed that change in harvest index had the highest correlation with change grain yield (0.96). This suggests that the basic reason for low yield was inability of the plants under LD to provide photosynthates for reproductive part development. There was no doubt that assimilate supply

increased under LD as manifested by larger plants, but most of them were diverted to vegetative parts.

That large grain yield reductions under long daylength was due to negative changes in all of the components measured, with the harvest index exerting the largest influence. A definitive relationship by regression analysis was not attempted because it does not make any sense and is unreliable with the set of genotypes studied. Yield is controlled by complex genetic systems such as inbreeding depression and heterosis which are very specific phenomenon. Accurate prediction equation that can be generated from regression (simple or multiple) should involve isolines, a very difficult mission given the current state of technology for polygenic-inherited traits.

### **5.5 Discussion**

Choice of maturity trait(s) that can accurately and conveniently describe a given genotype is widely disputed, and is one of the complex and frustrating problems confronting maize researchers (Hallauer and Russell, 1962). To a plant physiologist, a corn plant is mature when the maximum dry weight of the kernels has been attained. To a plant breeder, flowering time (anthesis and silking) is usually the most important, since plants that flower at the same time can readily be crossed. Yet, for the farmers grain moisture is probably the most critical measure of maturity (Gunn and Christensen, 1964).



The five maturity related traits described in this study constitute the important phenological stages in maize. The number of days or heat units to anthesis, silking, and BLF (a measure of physiological maturity) are the most commonly used traits to define the relative maturity of the plant. ASI and GFP are generally not highly regarded as maturity traits since they are interval measurements (secondary data), hence subjected to more errors as shown by their higher coefficients of variations relative to the primary traits.

The nine parents used for diallel analysis were carefully selected from more than a hundred elite inbreds collected by the Hawaii Foundation Seed Facility (HFSF). Selection was done so that all maturity and photoperiod sensitivity groups were represented. Sites of trials were chosen to compare the response under short daylength conditions in the tropics as well as in the long daylength conditions in temperate areas. At Waimanalo, daylength was extended to about 16 hours by light supplement in the field. This set-up was found to be effective in screening for photoperiod sensitivity under tropical condition (Brewbaker, 1981; Lee, 1978). The trials in Waimanalo were conducted during summer time in order to minimize the effects of other environmental stresses, such as diseases and pests that complicated the results as experienced by Lee (1978). Pests and disease incidence were basically absent. Even the

dreaded Maize Mosaic Virus and southern rust (Puccinia sorghi) which could wreak havoc during winter planting were negligible.

Maturity differences among parents expressed under SD was wide enough to permit their arbitrary classification; although much earlier or later parents as reported in the literature could have been used. These parents, however, were also selected for their differential responses to photoperiod which were clearly manifested in their wide maturity variations expressed under LD in Iowa and extended daylength in Waimanalo. Maturity expressed under LD was confounded by photoperiod sensitivity, so that maturity classification under SD could not be applied to maturity under LD. This was assuming that the two traits are independent of each other. This seemed to be not the case as there was strong indication of close association between the two variables. Lines that matured earlier under SD also matured relatively earlier under LD as far as anthesis, silking, and BLF were concerned. Parents can also be roughly classified according to their origin. Temperate-derived lines such as B73 (Hi), Hi32, and OH43 (Hi) were all early maturing under short and long daylengths. Conversely, tropical derived lines such as Tx601, Tzi4, Hi34, and Narino 330-S6 were late maturing under both daylengths. Temperate derived lines had undergone a conversion program in Hawaii, i.e., they had been converted for tropical

adaptation especially for disease resistance through backcrossing. Hence, they basically retained their original genotypic make-up.

Earliness of maturity is a favored trait in areas where multiple cropping is practiced (Bradfield, 1972) or where growing season is short, whether limited by cold or drought (Dinkel, 1974; Brawn, 1968, and Goldsworthy, 1974). Hybrid combinations in this study exhibited earliness relative to mid-parent as indicated by negative heterosis for anthesis, silking, and BLF. The large negative heterosis values for maturity traits measured under LD environment were due to larger effects of photoperiod on the parents than on their hybrids.

Variations due to general combining ability (GCA) and specific combining ability (SCA) were statistically significant for all the maturity related traits. The magnitude of GCA was, however, much higher than SCA particularly for anthesis, silking, and BLF as shown by very high GCA/SCA ratios both under short and long daylengths. This indicated a preponderance of additive gene action controlling maturity per se. This was in general agreement with the results reported by Hallauer (1965), and Troyer and Brown, (1972). Specific hybrid combinations did exhibit high SCA estimates suggesting that non-additive type of gene action was more important in the inheritance of these traits. Variation due parents vs. crosses was attributable to non-

additive genetic effects (Gardner and Eberhart, 1966). This actually makes the model better than Griffing's model since heterosis is sorted out. Heterosis (H) estimates were significant and high reflecting larger contribution of dominance or epistatic gene effects. Earlier studies demonstrated the relative importance of dominance gene action for tasseling and silking dates (Giesbrecht, 1960a and 1960b; Jones, 1955; Mohamed, 1959; Hallauer and Russell, 1962). Presence of dominant genes could easily be discerned by the fact that the hybrids always flowered or matured earlier than the mid-parent as indicated by negative heterosis. High GCA/SCA ratios may not necessarily mean that additive gene action was relatively more important than dominance or epistatic gene action since contribution of non-additive effects appeared to be larger when heterosis was included. Furthermore, GCA estimates could be biased upward by the presence of epistasis in the inheritance of flowering as reported by Hallauer and Russell (1962).

The genetics of ASI is virtually unknown and very few workers have studied the inheritance of GFP. ASI of tropical materials was reported to increase under temperate conditions (Hallauer and Sears, 1972; Troyer and Brown, 1976) as well as under drought conditions (Bolanos and Edmeades, 1988). GFP was sensitive to environmental stress (Shaw, 1985; Daynard, 1972). Highly sensitive lines, particularly Ant C-S5, showed extreme shortening of their

GFP, but intermediate and low photoperiod sensitive types were generally unaffected. It was probably due to the rapid drying of grains under stressful conditions of LD resulting in the premature blacklayer formation of kernels, relative to silking date (Shaw, 1985; Daynard and Duncan, 1969; Daynard, 1972). Rensch and Shaw (1972) reported that environments caused a 10 to 20 days difference in the length of GFP within a variety. In the absence of environmental stress, genetic variations in GFP are mostly due to general combining ability effects (Cross (1975). The use of ordinary light bulbs in the field was very effective in eliciting photoperiodic responses among genotypes. The illumination produced from these bulbs was above the 43-45 lux (Faungfufong, 1975; and Francis, 1970), the critical light intensities reported in light studies for corn. One of the advantages in this set up is it allows rapid screening of lines in the tropics for intended use in temperate environments. Photoperiod sensitivity is probably the most important limiting factor in the exchange of germplasm across latitudes (Salmon, 1985; Brown and Goodman, 1977; Brown, 1975). As such, rapid screening for photoperiod insensitivity of tropical cultivars would help alleviate this problem. The use of artificial light in the field allows much larger experimental area, hence more genotypes can be screened, than with the use of phytotrons. Another advantage is the elimination of other environmental

variables that can affect flowering. Foremost among them is the temperature effect. Any genetic study on flowering requires the separation of external factors through controlled experiments (Murfet, 1977). Since photoperiod acts on the timing of plant development, it is important to isolate temperature from photoperiod effects. This was done by planting at the same time in the field and by using accumulated heat units. There is still some disagreement on the interaction of photoperiod and temperature with some workers suggesting that the two variables are independent (Hunter et. al., 1974) while others showed otherwise (Breuer et. al., 1976; Stevenson and Goodman, 1972; Coligado and Brown, 1975b; Francis, 1972a; and Hesketh et al., 1969). By planting experimental materials under the light with controls (unlighted) in an adjacent field, temperature effects could be contained. It is important, however, to compare photoperiod sensitivity using the light experiment with the results from actual planting in long daylength environment (Iowa), i.e., Index1 vs. Index2. Results indicated that correlation between Index1 and Index2 was about 80% for anthesis and silking delay, a figure similar to inbred screening in Chapter 3. This strong correlation was considered high enough to justify the use of artificial lighting to simulate long daylength in the tropics.

The five photoperiod sensitivity parameters (delays) used in this study led to the question of which of them was

the best as far as accuracy and convenience are concerned. Correlation analyses showed that anthesis, silking, and BLF delays were highly associated with each other. Therefore, any of the three could accurately describe photoperiodic responses among genotypes. Anthesis and silking are preferable, however, to BLF since the later is more tedious and laborious to measure than the former. There were arguments that anthesis was better because it was less affected by environmental stresses, particularly pests and diseases, than silking (Lee, 1978). There is, however, one trait that should be given more consideration--the interval between anthesis and silking (ASI). It was clearly shown in this experiment that substantial delays in ASI were observed among lines judged as photoperiod sensitive based on anthesis and silking delay. ASI was more delayed under the light experiment at Waimanalo than in Iowa. This can be explained by the fact that effective daylength under light in Waimanalo (16 hrs) was little longer than in Iowa (15.3 hrs). There was evidence in previous studies indicating that when longer photoperiodic conditions were applied soon after induction of tassel development, the interval between male and female flowering widened (Moss and Harrison, 1968; Faungfupong, 1975; Aitkin, 1980; and Struik, 1982). An ASI delay of more than a week is highly undesirable because it can lead to poor pollination, not to mention the breeders problems in making crosses. Correlation was much more

higher between ASI and silking ( $r=0.92$ ) than between ASI and anthesis ( $r=0.74$ ). This would make silking delay a better photoperiod sensitivity index than anthesis delay because it could take into account ASI delay. Moreover, photoperiod effects on silking would directly affect the most important trait in maize which is the grain yield.

Diallel analysis revealed that the magnitude of GCA was much higher than SCA especially for anthesis, silking, and BLF delays as indicated by high GCA/SCA ratios. Hence additive gene action was more important among these traits. Lee (1978) and Rood and Major (1980) reported the importance of GCA over SCA in the control of photoperiod sensitivity from their diallel studies. Preponderance of additive gene action was also reported by Russell and Stuber (1983) and Spencer (1974). Breeding for photoperiod insensitivity can therefore be accomplished by recurrent selection schemes that can accumulate favorable alleles. For ASI and GFP, the GCA/SCA ratio was closer to unity which suggested the equal importance of additive and non-additive gene effects. Temperate lines such as B73 (Hi), Hi32, and Oh43 (Hi) were found to be good combiners for low photoperiod sensitivity. This could be explained by the fact that were bred and selected under long daylengths of temperate areas. Under these conditions very late genetic materials could be routinely eliminated either by breeders doing artificial selection or by frost acting on natural selection. On the



other hand, tropical lines were good combiners for high photoperiod sensitivity. This was related with their tropical origin where daylengths are short. Several crosses among low and high photoperiod sensitive lines showed little or practically no flowering delay at all when planted in Iowa and when the delay (Index2) was expressed in accumulated heat units. This is a hopeful sign that highly sensitive tropical lines can be directly used in temperate areas by crossing them with adapted local lines. Inbreds such as Hi34, Narino 330-S6, and Tzi4 are excellent sources of resistance to pests and diseases (Brewbaker et al., 1989). These inbreds generally did well in their crosses with Oh43 (Hi) and B73 (Hi) as far as flowering delays were concerned. Their average heterosis for photoperiod sensitivity were among the highest and all negative indicating a reduction of photoperiod sensitivity relative to parental means.

Predicting photoperiod sensitivity on the basis of SD maturity would save a lot of work and time in identifying photoperiod insensitive lines. Early and late maturing lines tended to have low and high photoperiod sensitivity, respectively. Simple phenotypic correlations among days to anthesis, silking, and BLF and their respective delays were all highly significant with an  $r$  values averaging about 0.70. This was much higher than the correlation coefficient obtained by Russell and Stuber (1984) ( $r=0.42$ ) and in

Chapter 3 ( $r=0.46$ ). This was probably due to the type of genetic materials used in the study. The  $r$  values were generated from hybrids while in previous studies  $r$  values were from inbreds which are more unstable than hybrids. Prediction equations from regression analyses however would be of little value since hybrid performance is a product of complex genetic phenomenon such as heterosis and interactions among additive and non-additive genes.

Measures of genetic correlations between SD maturity and photoperiod sensitivity traits were provided by correlating GCA estimates of the parents. This would be a better indicator of relationship since variations to GCA reflects additive genetic component of variation, which was the chief cause of resemblance among relatives; hence the main determinant of the observable genetic properties of the population and of the response to selection (Falconer, 1989). Significant and relatively high correlation suggests that selection for earliness, based on anthesis, silking, or BLF under SD would be accompanied by some reduction in photoperiod sensitivity. This could be verified through selection studies (Chapter 7).

Effects of photoperiod sensitivity on morphological and agronomic traits were very apparent. All inbreds and hybrids, particularly those with high photoperiod sensitivity, planted under long daylength exhibited increased numbers of leaves and increased plant heights, and

consequently an increase in total dry matter yield. Excessive vegetative development coupled with late floral initiation limited utilization of these materials in breeding programs in temperate areas (Eberhart, 1971; and Hallauer and Sears, 1972). Significant increases in leaf numbers and plant heights as a result of delayed flowering had been reported by other workers (Hesketh et. al., 1969, Stevenson and Goodman, 1972; Hunter et. al., 1977; and Spencer, 1974). This may not be too bad if the farmer is after silage yield, since studies have shown the potential of tropical germplasm in silage production in Corn Belt areas (Thompson, 1968; Efron and Everett, 1969). But he would be in big trouble if the crop is harvested for grains. Results indicated a drastic reduction in yield, some as high as 90%, among tropical inbreds and hybrids. Even the low sensitive inbreds and hybrids produced lower yields relative to normal daylength planting, but the amount of reduction depended on the degree of sensitivity. Similar observations were also reported by Lee (1978), and by Ragland et al. (1966). This is critical in view of the increased interest among temperate breeders in using tropical germplasm as source of pests and disease resistance and generally to broaden genetic variability (Lonnquist, 1974 and Brown, 1975). There were, however, some promising temperate x tropical crosses (low x high photoperiod sensitive) with reasonable grain yields under LD that need further study.

The large reduction in grain yield among photoperiod sensitive entries were traced to be the result of combination of negative changes in different yield components notably ear filling, number of ears per plant, and harvest index. Ear size, i.e., ear length and diameter, were basically unaffected, and in some cases even increased as reported by Lee (1978). The effects of pests and diseases were ruled out as mentioned earlier. Poor pollination would result in low ear filling among the very late genotypes. However, low ear filling was also observed among early and medium maturing genotypes that could certainly be not attributed to poor pollination because of the abundance of pollen grains at their silking stage. These findings were in sharp contrast with Lee's (1978) study where he attributed low grain yields primarily to poor pollination and diseases, but not daylength effects. Further analyses revealed that the very low harvest index was the main cause for the low grain yield. Harvest index is the ratio between grain yield and above ground parts (stover), an indirect measure of source-sink relationship (Tollenaar, 1977). A low ratio suggests that majority of the photosynthates goes to the vegetative parts instead of the reproductive parts. This was not difficult to see considering the gigantic increases in plant size with drastic grain yield reductions among sensitive genotypes under LD. Faungfupong (1976) reported similar reductions in

grain/stover ratio in his studies in Iowa. It was also highly possible that the missing kernels or low ear filling were not really due to poor pollination, but rather to the inability of the ovules to completely develop because of the lack of assimilate supply. This is consistent with Ragland's et al. (1966) suggestion that the unfilled ear length was already pollinated but failed to develop into mature kernels. Low yield under long daylength could therefore be mainly attributed to photoperiod effects.

## 6. GENERATION MEAN ANALYSIS

The main objectives of this study were: a) to estimate additive, dominance, and epistatic gene effects for maturity and photoperiod sensitivity; b) to determine heritabilities; and c) to estimate the number of genes controlling maturity and photoperiod sensitivity. Six generation-populations were evaluated in Waimanalo (SD), Kauai, and under extended daylength in Waimanalo (LD). Silking delay (LD-SD) was the main photoperiod sensitivity index.

### 6.1 Variation Among Generation Means and Scaling Tests

Number of days to silking. Parental inbreds used in this study were selected both for earliness and lateness as well as for sensitivity to photoperiod. However, as noted earlier, it was difficult to find early genotypes that were photoperiod sensitive, and late maturing genotypes that are photoperiod insensitive. Only Ant C-S5 seemed to fit the class of relatively early but highly sensitive lines. Oh43 (Hi) was considered as early maturing with low photoperiod sensitivity, while Hi34 and Tx601 (Hi) were late maturing and also highly photoperiod sensitive.

Average number of days to silking for the six population means (P1, P2, F1, F2, BP1, and BP2) evaluated in three environments are presented in Table 6.1. In general, the four inbreds exhibited the expected relative days to silking in the three environments, with Oh43 (Hi) silked the earliest and Tx601 (Hi) the latest in three environments.

Table 6.1. Average number of days to silking for the parents, F1's, F2's and backcrosses to both parents in three environments.

Cross	P1	P2	F1	F2	BP1	BP2
-----						
Waimanalo (short daylength)						
Ant C5-S5 x Hi34	55.7	61.2	56.6	56.7	53.8	56.0
Ant C5-S5 x Oh43 (Hi)	55.7	51.4	48.4	51.0	50.8	48.7
Ant C5-S5 x Tx601 (Hi)	55.7	62.8	54.8	56.9	54.1	58.0
Hi34 x Oh43 (Hi)	61.2	51.4	51.5	54.6	54.2	50.9
Hi34 x Tx601 (Hi)	61.2	62.8	57.4	61.3	59.6	61.7
Oh43 (Hi) x Tx601 (Hi)	51.4	62.8	54.7	55.4	53.0	58.0
Kauai (short daylength)						
Ant C5-S5 x Hi34	62.0	66.2	63.3	63.2	60.8	63.0
Ant C5-S5 x Oh43 (Hi)	62.0	60.3	57.7	57.0	57.5	56.7
Ant C5-S5 x Tx601 (Hi)	62.0	69.0	64.0	63.8	62.7	64.7
Hi34 x Oh43 (Hi)	66.2	60.3	60.2	60.6	58.3	57.2
Hi34 x Tx601 (Hi)	66.2	69.0	67.2	67.5	66.8	67.8
Oh43 (Hi) x Tx601 (Hi)	60.3	69.0	59.3	63.2	59.3	62.3
Waimanalo (long daylength)						
Ant C5-S5 x Hi34	91.9	89.5	86.6	86.9	90.2	86.3
Ant C5-S5 x Oh43 (Hi)	91.9	62.1	65.4	66.8	77.0	61.0
Ant C5-S5 x Tx601 (Hi)	91.9	91.5	93.8	90.8	91.7	93.1
Hi34 x Oh43 (Hi)	89.5	62.1	68.4	72.3	74.0	61.6
Hi34 x Tx601 (Hi)	89.5	91.5	87.9	85.6	86.2	89.3
Oh43 (Hi) x Tx601 (Hi)	62.1	91.5	72.1	71.2	67.8	81.6
-----						

The cross between Oh43 (Hi) and Tx601 (Hi) showed the largest difference between the two parents both in short and long days. However, the difference under long daylength was about 30 days or three times as much as under short daylengths. This was due to the confounding effect of photoperiod sensitivity on flowering. Similar response was observed for the cross between Oh43 (Hi) and Hi34. It was noted that silking date for Ant C-S5 was similar to Tx601, and even higher than Hi34 under long daylength which was a complete reversal under the short daylength. This was due to the fact that Ant C-S5 is a unique inbred that it is relatively early maturing, but highly photoperiod sensitive.

All F1 hybrids were early silking than the midparent values under short daylength, and even earlier than the early parents in crosses such as Ant C-S5 x Oh43 (Hi), Ant C-S5 x Tx601 (Hi), Hi34 x Oh43 (Hi), and Oh43 (Hi) x Tx601 (Hi). Under long daylength, however, the F1's among sensitive and insensitive inbreds were lower than the midparent values, but none were earlier than the low parent. In contrast, the F1's among sensitive inbreds silked later than the midparent values and even later than the high parent such as in the cross between Ant C-S5 and Tx601 (Hi). The F2's generally silked later than the F1's, although they did not differ much from the early parents. F2's of crosses such as Ant C-S5 x Oh43 (Hi) (short daylengths in Waimanalo and Kauai), Hi34 x Oh43 (Hi), and Oh43 (Hi) x Tx601 (Hi)



(both in Kauai) had silking dates lower than the lower parents indicating transgressive segregants for earliness.

Means of backcross progenies, in all cases, showed a shift toward the recurrent parents. However, a number of backcrosses usually involving Oh43 (Hi) as a recurrent parent showed earlier silking date than the early parent, but in no case was there a backcross to the late parents which showed later silking dates than the late parents. This held true both in short and long daylengths.

Frequency distributions for the six populations from the cross Oh43 (Hi) x Tx601 (Hi) and Oh43 (Hi) x Hi34 under 12-hour and 16-hour daylengths are illustrated in Figures 6.1, 6.2., 6.3, and 6.4. In each case, the two parents were well separated from each other satisfying one of the requirements for GMA, i.e. the parents must possess opposing traits. The narrow distributions of both parents and their F1 hybrid were indicative of the uniformity of populations. In GMA, the parents are assumed to be homozygous, and as such, they should not have exhibited variation among individuals. Variations observed here were attributed to environmental effects. Under short daylength, the F1 for Oh43 (Hi) x Tx601 (Hi) was inclined more to Oh43 (Hi) suggesting partial dominance of early silking to late silking, while the F1 for Oh43 (Hi) x Hi 34 was almost the same as the P1 suggesting a complete dominance. Under long daylength, F1's likewise

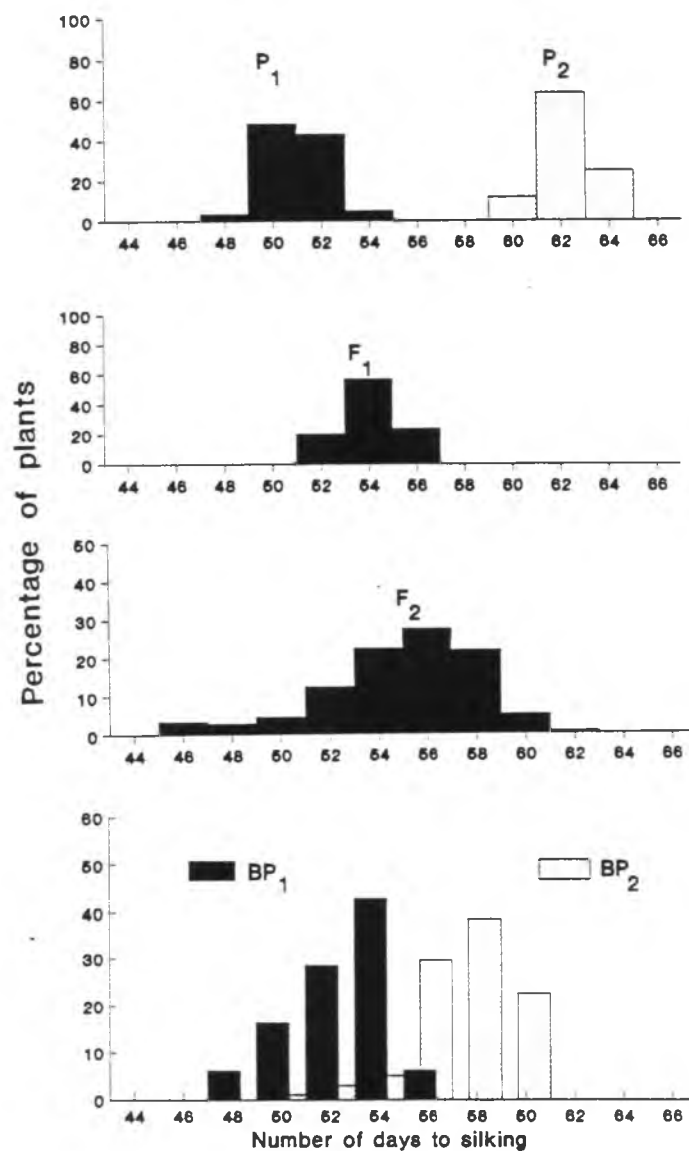


Figure 6.1. Frequency distributions for OH43 (P<sub>1</sub>), Tx601 (P<sub>2</sub>), their F<sub>1</sub>, F<sub>2</sub>, and backcrosses for number of days to silking under short daylength in Hawaii.

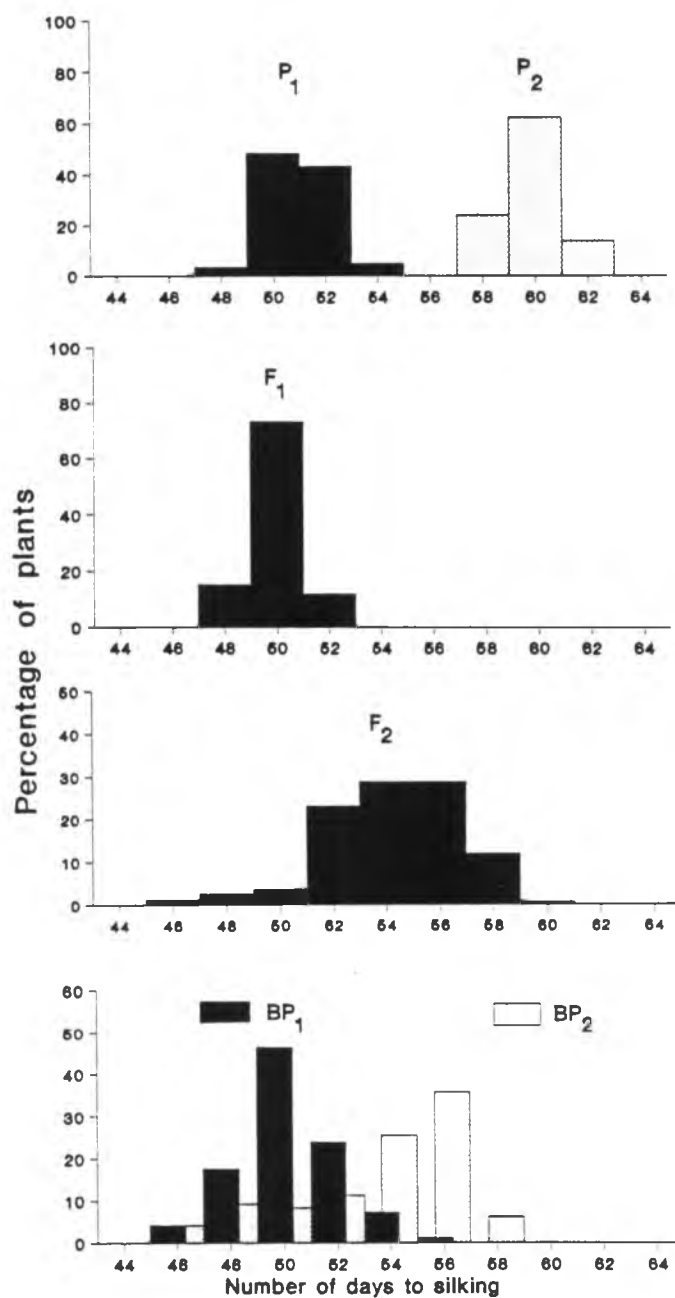


Figure 6.2. Frequency distributions for OH43 (P<sub>1</sub>), Hi34 (P<sub>2</sub>), their F<sub>1</sub>, F<sub>2</sub>, and backcrosses for number of days to silking under short daylength in Hawaii.

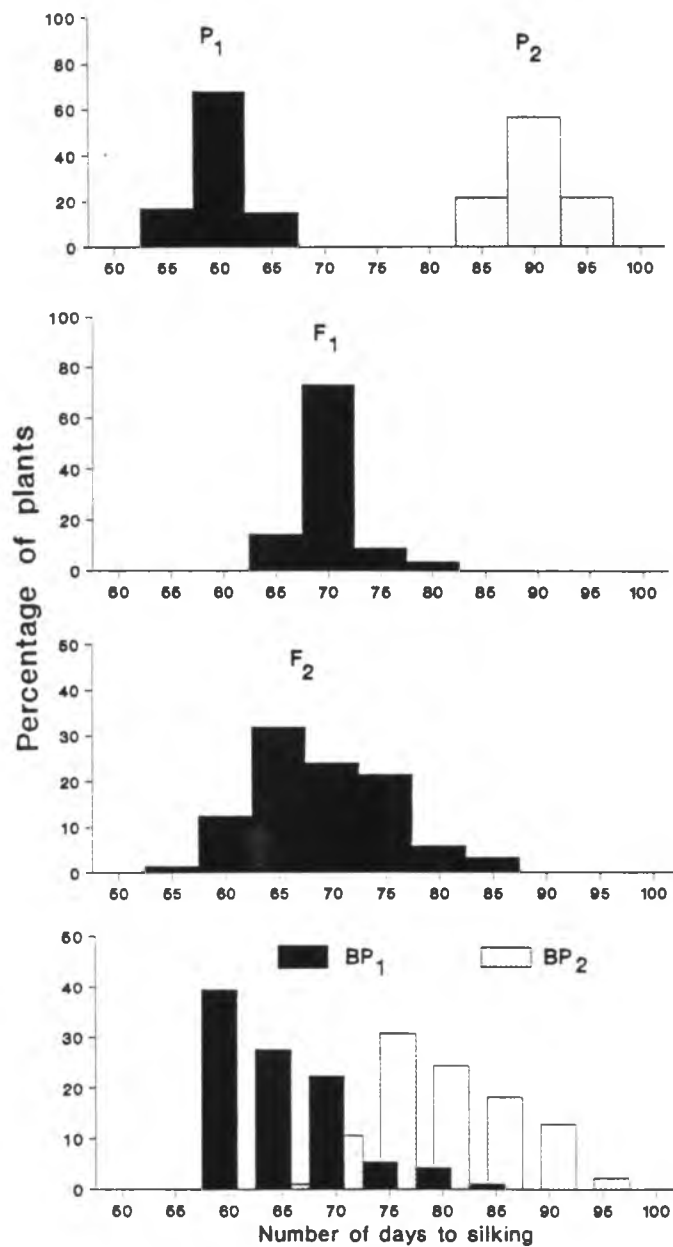


Figure 6.3. Frequency distributions for OH43 (P<sub>1</sub>), Tx601 (P<sub>2</sub>), their F<sub>1</sub>, F<sub>2</sub>, and backcrosses for number of days to silking under long daylength in Hawaii.

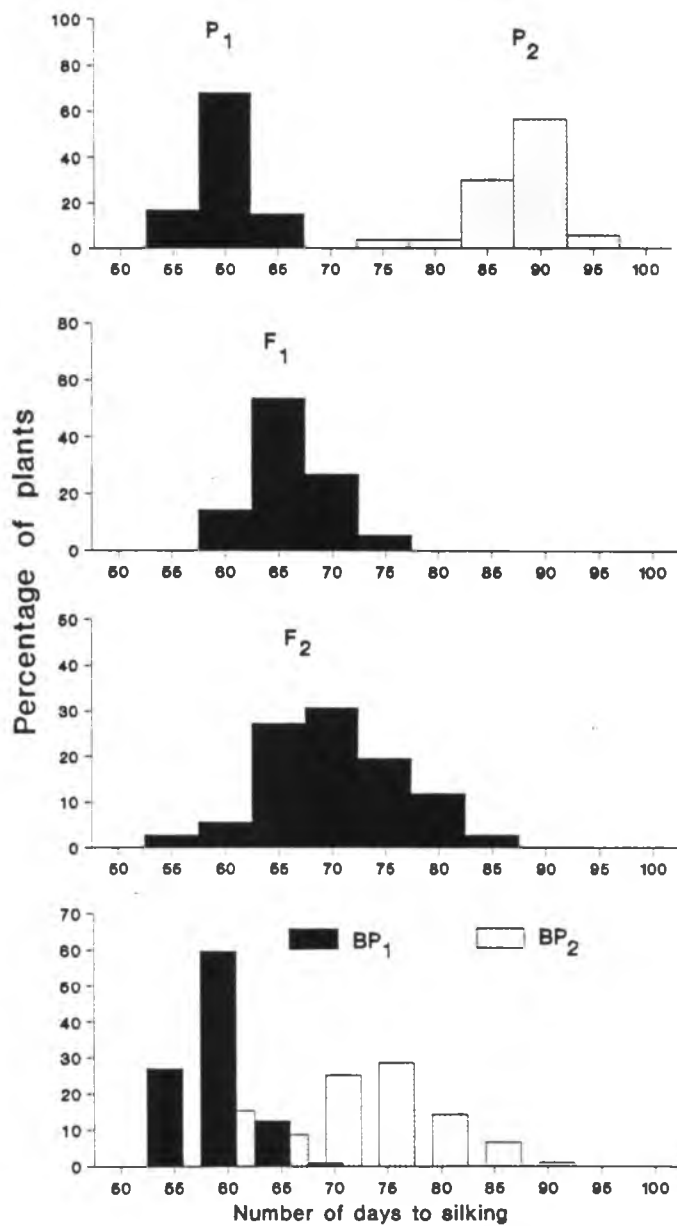


Figure 6.4. Frequency distributions for OH43 (P<sub>1</sub>), Hi34 (P<sub>2</sub>), their F<sub>1</sub>, F<sub>2</sub>, and backcrosses for number of days to silking under long daylength in Hawaii.

indicated the presence of partial dominance genes for earliness.

F2 populations for both crosses were widely distributed from 46 to 62 days under short days and from 55 to 85 days under long days. Wider variation under long days was due to the fact that sensitive parents flowered much more later than in the short daylength. It is clear however that wider segregation occurred within the range of the early parent (Oh43 (Hi)) under both daylengths, and only a very small proportion of the F2 individuals were in the late parent range. Consequently, F2 means were lower than the midparent values, again indicating the dominance of early over late silking. A small proportion of F2 individuals in both crosses were transgressive segregants.

Distribution for backcross progenies were wide but not as dispersed as the F2's. Backcrosses were skewed more towards the early parent than towards the late parents. In the cross Oh43 (Hi) x Hi34, the backcross to Oh43 (Hi) produced progenies that silked earlier than OH43 (Hi), a clear manifestation of transgressive segregation. On the other hand, backcross to Hi34 did not move many of the progenies toward late silking.

Scaling tests were conducted to determine the additivity of gene effects and the independence of heritable components from non-heritable ones (Table 6.2). In all crosses, except that of Hi34 x Tx601 (Kauai), one or more of

Table 6.2. Tests of scale effects for six crosses in three environments.

Cross	A	B	C	D
Waimanalo (12-hr. daylength)				
Ant C5-S5 x Hi34	-4.74 **	-5.87 **	-3.40 **	3.61 **
Ant C5-S5 x Oh43 (Hi)	-2.52 **	-2.35 **	0.24	2.55 **
Ant C5-S5 x Tx601 (Hi)	-2.20 **	-1.55 **	-0.38	1.68 **
Hi34 x Oh43 (Hi)	-4.39 **	-1.26 **	2.77 **	4.21 **
Hi34 x Tx601 (Hi)	0.59	3.25 **	6.60 **	1.38 **
Oh43 (Hi) x Tx601 (Hi)	-0.07	-1.57 **	-1.86	-0.11
Kauai (12-hr daylength)				
Ant C5-S5 x Hi34	-3.67 **	-3.50	-2.17	2.50 *
Ant C5-S5 x Oh43 (Hi)	-4.67 *	-4.67 **	-9.67 *	-0.17
Ant C5-S5 x Tx601 (Hi)	-0.67	-3.67 **	-3.67 **	0.33
Hi34 x Oh43 (Hi)	-9.67 **	-6.17 **	-4.43	5.70 **
Hi34 x Tx601 (Hi)	0.33	-0.50	0.50	0.33
Oh43 (Hi) x Tx601 (Hi)	-1.00	-3.67	4.67	4.67 **
Waimanalo (16-hr-daylength)				
Ant C5-S5 x Hi34	1.85	-3.48 **	-7.12 **	-2.74 **
Ant C5-S5 x Oh43 (Hi)	-3.25	-5.44 **	-17.42 **	-4.37 **
Ant C5-S5 x Tx601 (Hi)	-2.38	0.94	-7.99 **	-3.28 **
Hi34 x Oh43 (Hi)	-9.95 **	-7.21 **	0.70	8.92 **
Hi34 x Tx601 (Hi)	-5.07 **	-0.80	-14.41 **	-4.27 **
Oh43 (Hi) x Tx601 (Hi)	1.38	-0.39	-12.90 **	-6.94 **

\* Significant at 0.01 level of probability.

\*\* Significant at 0.05 level of probability.

the quantities A, B, C, and D (see Chapter 3) differ significantly from zero within the limits of their respective sampling error. This suggests that the additive-dominance model was not adequate to describe days to silking, and that non-allelic interactions (epistasis) are present among the genetic materials studied.

Significant C and D values provided evidence for the presence of additive x additive and dominance x dominance type of interactions, respectively.

Photoperiod Sensitivity. Silking delays as a measure of photoperiod sensitivity is presented in Table 6.3. Among the four inbreds, Oh43 (Hi) was least affected by daylength.

Table 6.3. Average silking delay (days) of the parents, F1's, F2's, and backcrosses to both parents.

Cross	P1	P2	F1	F2	BP1	BP2
Ant C-S5 x Hi34	36.2	28.3	30.0	30.2	36.4	30.4
Ant C-S5 x Oh43 (Hi)	36.2	10.7	17.0	15.8	26.2	12.3
Ant C-S5 x Tx601 (Hi)	36.2	28.6	39.0	33.8	37.6	35.1
Hi34 x Oh43 (Hi)	28.3	10.7	16.8	17.7	19.8	10.8
Hi34 x Tx601 (Hi)	28.3	28.6	30.6	24.3	26.6	27.6
Oh43 (Hi) x Tx601 (Hi)	10.7	28.6	17.5	15.8	14.8	23.6

The rest were highly sensitive to long daylength particularly Ant C-S5 and Tx601 (Hi) with silking delay of 36.24 and 28.64 days, respectively. Hi34 closely followed with 28.33 days. F1's involving Oh43 (Hi) were moderately sensitive with mean values lower than the midparent values suggesting partial dominance for low photoperiod sensitivity. F2's differed little from the F1 values;



backcross progenies were skewed towards the recurrent parent, although more shifting of the mean was observed when the recurrent parent was Oh43 (Hi). Of particular interest was the backcross (Hi34 x Oh43 (Hi)) x Oh43 (Hi) where the mean silking delay of the progenies was almost equal to that of the OH43 (Hi), strong evidence of major gene controlling the trait.

Scaling tests were not conducted, since silking delay was a derived or secondary data, hence no individual data could be recorded among the segregating populations and variance among means within a large number of progenies could not be computed. Frequency distributions, likewise, could not be illustrated.

## 6.2 Estimates of Genetic Effects

Number of days to silking. Since epistasis was detected in the scaling test, a six parameter model (Hayman, 1958) and Jinks and Jones (1958) was used to estimate the different gene effects. The notations used here were the same as Gamble's (1962a, 1962b).

The six parameters, namely, mean ( $m$ ), additive effect ( $a$ ), dominance effect ( $d$ ), additive x additive effect ( $aa$ ), additive x dominance effects ( $ad$ ), and dominance x dominance effect ( $dd$ ) obtained from three environments are given in Table 6.4. Means of all crosses were highly significant in three environments. Additive gene effects were significant, except for Ant C-S5 x Oh43 (Hi) (Kauai), and Ant C-S5 x

Table 6.4. Estimates of genetic effects from six-parameter model for the number of days to silking in three environments.

Cross	m	a	d	aa	ad	dd
-----						
Waimanalo (12-hr. daylength)						
Ant C5-S5 x Hi34	56.69 **	-2.19 **	-9.03 **	-7.22 **	0.56	17.84 **
Ant C5-S5 x Oh43 (Hi)	51.04 **	2.04 **	-10.27 **	-5.11 **	-0.09	9.98 **
Ant C5-S5 x Tx601 (Hi)	56.92 **	-3.90 **	-7.85 **	-3.36 **	-0.32	7.11 **
Hi34 x Oh43 (Hi)	54.62 **	3.32 **	-13.21 **	-8.42 **	-1.57 **	14.07 **
Hi34 x Tx601 (Hi)	61.33 **	-2.14 **	-7.43 **	-2.76 **	-1.33 **	-1.07
Oh43 (Hi) x Tx601 (Hi)	55.43 **	-4.95 **	-2.27 **	0.21	0.75 **	1.43
Kauai (12-hr daylength)						
Ant C5-S5 x Hi34	63.17 **	-2.17 *	-5.75 *	-5.00 *	-0.08	12.17 **
Ant C5-S5 x Oh43 (Hi)	57.00 **	0.83	-3.17	0.33	0.00	9.00
Ant C5-S5 x Tx601 (Hi)	63.83 **	-2.00 **	-2.17	-0.67	1.50 **	5.00 *
Hi34 x Oh43 (Hi)	60.60 **	1.17 **	-14.48 **	-11.40	-1.75 **	27.23 **
Hi34 x Tx601 (Hi)	67.50 **	-1.00 *	-1.08	-0.67	0.42	0.83
Oh43 (Hi) x Tx601 (Hi)	63.17 **	-3.00 **	-14.67 **	-9.33 **	1.33	14.00 **
Waimanalo (16-hr-daylength)						
Ant C5-S5 x Hi34	86.90 **	3.86 **	1.38	5.48 **	2.67 **	-3.85
Ant C5-S5 x Oh43 (Hi)	66.84 **	15.98 **	-2.93	8.74 **	1.09	-0.06
Ant C5-S5 x Tx601 (Hi)	90.76 **	-1.44	8.67 **	6.55 *	-1.66	-5.12
Hi34 x Oh43 (Hi)	72.27 **	12.32 **	-25.33 **	-17.85 **	-1.37	35.00 **
Hi34 x Tx601 (Hi)	85.62 **	-3.11 **	5.97 **	8.53 **	-2.14 **	-2.66
Oh43 (Hi) x Tx601 (Hi)	71.23 **	-13.78 **	9.19 **	13.89 **	0.88	-14.87 **

\* Significant at 0.01 level of probability.

\*\* Significant at 0.05 level of probability.

m = mean

a = additive gene effects

d = dominance gene effects

aa = additive x additive epistasis

ad = additive x dominance epistasis

dd = dominance x dominance epistasis

Tx601 (Hi) (12-hr daylength, Waimanalo). Dominance gene effects were significant for all crosses in Waimanalo (12-hr), but not for Ant C-S5 x Hi34 (16-hr), Ant C-S5 x Oh43 (Kauai, and Waimanalo, 16-hr), Ant C-S5 x Tx601 (Hi) (Kauai), and Hi34 x Tx601 (Hi) (Kauai). Additive x additive types of epistasis were significant for most of the crosses in Waimanalo (12- and 16-hr), but only for Ant C-S5 x Hi34 and Oh43 (Hi) x Tx601 (Hi) on Kauai. Few crosses had significant additive x dominance interaction, while more than half of the crosses in Waimanalo (12-hr) and Kauai showed significant dominance x dominance interaction. The signs of additive and additive x dominance effects depended on whether or not particular parents were P1 or P2 in the cross. Thus, the additive gene effect for Hi34 x Oh43 was negative while in Oh43 x Tx601, it was positive.

The relative magnitude of the different gene effects changed with the type of crosses and the environment in which they were evaluated. For example, in the cross Oh43 (Hi) x Tx601 (Hi), additive was larger than dominance gene effects in both trials in Waimanalo, but it was reversed for Kauai trial. Likewise, in the cross between Hi34 and Oh43 (Hi), dominance was much bigger than additive gene effects in all environments. In most of the crosses, it was apparent, however, that dominance gene effects were greater in magnitude. Under short daylengths in Waimanalo and Kauai, all dominance gene effects had a negative sign

Table 6.5. Estimates of genetic effects from three-parameter model for days to silking in three environments.

Cross	m	a	d
-----			
Waimanalo (12-hr. daylength)			
Ant C5-S5 x Hi34	65.66 **	-2.76 **	-26.87 **
Ant C5-S5 x Oh43 (Hi)	58.67 **	2.12 **	-20.25 **
Ant C5-S5 x Tx601 (Hi)	62.62 **	-3.58 **	-14.96 **
Hi34 x Oh43 (Hi)	64.74 **	4.88 **	-27.28 **
Hi34 x Tx601 (Hi)	64.78 **	-0.82 **	-6.36 **
Oh43 (Hi) x Tx601 (Hi)	56.92 **	-5.70 **	-3.69
Kauai (12-hr daylength)			
Ant C5-S5 x Hi34	69.08 **	-2.08 **	-17.92 **
Ant C5-S5 x Oh43 (Hi)	60.83 **	0.83 **	-12.17
Ant C5-S5 x Tx601 (Hi)	66.17 **	-3.50 **	-7.17 *
Hi34 x Oh43 (Hi)	74.65 **	2.92 **	-41.72 **
Hi34 x Tx601 (Hi)	68.25 **	-1.42 **	-1.92
Oh43 (Hi) x Tx601 (Hi)	74.00 **	-4.33 **	-28.67 **
Waimanalo (16-hr-daylength)			
Ant C5-S5 x Hi34	85.24 **	1.20	5.23
Ant C5-S5 x Oh43 (Hi)	68.29 **	14.89 **	-2.87
Ant C5-S5 x Tx601 (Hi)	85.14 **	0.22	13.79 *
Hi34 x Oh43 (Hi)	93.69 **	13.69 **	-60.34 **
Hi34 x Tx601 (Hi)	81.97 **	-0.97	8.62
Oh43 (Hi) x Tx601 (Hi)	62.92 **	-14.66 **	24.06 **
-----			

\* Significant at 0.01 level of probability.

\*\* Significant at 0.05 level of probability.

m = mean

a = additive gene effects

d = dominance gene effects

indicating dominance of early over late silking. This corroborated the trends in the frequency distributions.

Of the three epistatic effects, **dd** had bigger magnitude in most of the crosses, followed by **ad**, with **aa** being the least important. This was not necessarily the order for all crosses. In most cases, **dd** and **aa** had opposite signs, resulting in the canceling of these epistatic effects. This was referred to as duplicate type of epistasis.

Although scaling tests revealed the presence of epistasis, the three-parameter model advanced by Jinks and Jones (1958) was nevertheless fitted. Results (Table 6.5) showed that estimates for additive gene effects in the three-parameter model were comparable in magnitude with the six-parameter model. Estimates of dominance gene effects were much more biased upward in magnitude compared to the additive effects estimates from the six-parameter model.

Photoperiod sensitivity. Estimates of gene effects are listed in Table 6.6. Test of significance, however, could not be performed because no individual data were recorded.

Table 6.6. Estimates of genetic effects from six-parameter model for photoperiod sensitivity (silking delay).

Cross	m	a	d	aa	ad	dd
Ant C-S5 x Hi34	30.2	6.1	10.4	12.7	2.1	-21.7
Ant C-S5 x Oh43 (Hi)	15.8	13.9	7.3	13.9	1.2	-10.0
Ant C-S5 x Tx601 (Hi)	33.8	2.5	16.5	9.9	-1.3	-12.2
Hi34 x Oh43 (Hi)	17.7	9.0	-12.1	-9.4	0.2	20.9
Hi34 x Tx601 (Hi)	24.3	-1.0	13.4	11.3	-0.8	-1.6
Oh43 (Hi) x Tx601 (Hi)	15.8	-8.8	11.5	13.7	0.1	-16.3

Estimates of dominance gene effects were larger than estimates of additive gene effects in all crosses, except in Ant C-S5 x Oh43 (Hi). Photoperiod insensitivity appeared dominant in the cross Hi34 x Oh43, but recessive in others. Estimates for **aa** and **dd** were large but canceled each other as indicated by their opposing signs. Estimates for **ad** were small and considered negligible.

Estimates of additive effects were mostly not affected by employing the three parameter model (Table 6.7). An overestimate of the dominance effects however were realized due to the presence of epistasis.

Table 6.7. Estimates of genetic effects from 3-parameter model for photoperiod sensitivity.

Cross	m	a	d
Ant C-S5 x Hi34	19.58	3.96	32.11
Ant C-S5 x Oh43 (Hi)	9.62	12.76	17.38
Ant C-S5 x Tx601 (Hi)	22.52	3.80	28.75
Hi34 x Oh43 (Hi)	28.95	8.81	-33.06
Hi34 x Tx601 (Hi)	17.90	-0.16	14.98
Oh43 (Hi) x Tx601 (Hi)	6.01	-8.96	27.75

### 6.3 Heritability and Numbers of Genes

Following the model of Mather (1949), environmental as well as genetic variances were estimated. Variance components would only be valid in the absence of epistasis, which was indicated by the previous scaling test for the traits under consideration. Nevertheless, variance components were computed to determine the extent of the effects of epistasis on the genetic variance as well as on

the heritability estimates and minimum number of genetic factors that could be derived from the variance components.

Table 6.8 shows the estimates of variance components, heritability estimates and minimum number of gene factors for days to silking under short and long daylengths at Waimanalo. Variance components could not be computed from Kauai since individual plant data were not recorded. Environmental as well as genetic variances were generally smaller in the short daylength than in long daylength. In most cases, environmental variances (E) were small relative to genetic variances. Dominance variances were generally higher than the additive variances. Two crosses exhibited negative sign for additive variance, and were considered zero (variance are always positive) in the computation for heritability estimates.

Narrow sense heritability (nh) estimates ranging from 0.00 to 0.61 and 0.00 to 0.73 under short and daylength, respectively. Broad sense heritability (bh) ranged from 0.87 to 0.94, and 0.07 to 0.94 under the short and long daylength, respectively. Number of genes governing days to silking varied depending on both types of crosses and environments. Using Castle-Wright formula, gene number ranged from <1-2 and <1-14 under short and long daylength, respectively. In general, more genes were revealed under long than under short daylength environment. The formula attributed to Sewall Wright produced similar results. For

Table 6.8. Genetic variances, heritability estimates, and gene numbers for days to silking under short and long daylengths.

Cross	VE	VA	VD	nh	bh	nl	n2
Waimanalo (short daylength)							
Ant C5-S5 x Hi34	1.37	-0.50	10.89	0.00	0.89	1.4	1.7
Ant C5-S5 x Oh43 (Hi)	1.35	0.62	8.47	0.06	0.87	0.8	3.3
Ant C5-S5 x Tx601 (Hi)	1.21	6.74	3.13	0.61	0.89	1.4	2.5
Hi34 x Oh43 (Hi)	1.27	-0.33	20.43	0.00	0.94	2.3	3.4
Hi34 x Tx601 (Hi)	1.42	3.65	7.56	0.29	0.89	0.1	1.6
Oh43 (Hi) x Tx601 (Hi)	1.38	13.76	7.58	0.61	0.94	1.9	2.1
Waimanalo (long daylength)							
Ant C5-S5 x Hi34	29.5	2.2	-23.4	0.07	0.07	0.1	0.4
Ant C5-S5 x Oh43 (Hi)	29.0	-22.7	69.6	0.00	0.71	14.9	19.5
Ant C5-S5 x Tx601 (Hi)	32.2	38.6	-17.7	0.55	0.55	0.0	0.1
Hi34 x Oh43 (Hi)	13.9	21.4	66.7	0.21	0.86	3.1	3.5
Hi34 x Tx601 (Hi)	16.8	2.1	28.6	0.04	0.65	0.0	0.2
Oh43 (Hi) x Tx601 (Hi)	9.8	-24.9	148.4	0.00	0.94	4.5	4.8

VE = environmental variance  
 VA = additive variance  
 VD = dominance variance  
 nh = narrow-sense heritability  
 nb = broad-sense heritability  
 nl = gene number (Castle-Wright)  
 n2 = gene number (Sewall-Wright)



the crosses with opposing traits, gene numbers ranged from 2-3 and 3-4 under the short and long daylength, respectively. Hi34 and Tx601 (Hi) were considered genetically identical (as far as maturity loci were concerned) because they both differed from Oh43 (Hi) by the same number of genes. The cross Ant C-S5 x Hi34, which have the same background, gave different SD maturity performance, hence the gene number estimates were valid; but under LD environment they were both highly sensitive as reflected by the absence of gene differences.

#### 6.4 Discussion

Maturity, here defined as the time from planting to silk emergence, and photoperiod sensitivity, as the difference between LD and SD maturity, were main criteria for the choice of parents. It is unfortunate at this point in time that no definite relationship has been established between the two traits, so that interpretation of results for maturity per se could be restricted only at short day environments for tropical materials. Difficulty in interpretation arises when these genetic materials are evaluated under different daylengths since maturity is confounded by photoperiod sensitivity. Thus selection of maize genotypes for genetic studies should take into account this problem.

In this GMA study, maturity expressed under short day of Waimanalo (Wail) and Kauai, should be free of any

confounding effect of photoperiod. Inbreds used were tropical in origin, except for Oh43 (Hi). This inbred, however, had been converted for tropical adaptation in Hawaii. Estimates of genetic effects for SD maturity from Waimanalo and Kauai should not be biased by genetic effects for photoperiod sensitivity. Maturity expressed under the extended daylength in Waimanalo (Wai2) was no doubt affected by photoperiod. Subtracting SD values from LD values was the only way of estimating photoperiodic response for genetic analysis.

Except for Hi34 x Tx601 (Kauai), maturity data failed to fit a non-epistatic or reduced (three-parameter) model, which indicated that six-parameter or epistatic model should be fitted. Majority of the main genetic effects, i.e., additive (**a**) and dominance (**d**), were significant at 1% level of probability which reflected a rather small standard errors of the estimates. Digenic epistatic effects (**aa**, **ad**, **dd**) were inconsistent among crosses with some having significant estimates in one location but not in the other, but the relative magnitude of the effects was readily observed. Among the six crosses, only two adequately fulfilled one of the requirements for GMA of SD maturity, that is the two parents should have opposite phenotypic expression. Only the cross Oh43 (Hi) x Hi34 and Oh43 (Hi) x Tx601 (Hi) met this requirement. The rest of the crosses had observed variations but were not wide enough to generate significant

variations in late generations. They are useful, however in detecting canceling of gene effects since all crosses were made (diallel) among the four parents (Hallauer and Miranda, 1981).

Both additive and dominance gene effects controlled the expression of SD as well as LD maturity. But dominance gene effects were more important as indicated by their higher magnitude than additive gene effects. The negative dominance effect estimates are also a sign that earliness is dominant over lateness. This relationship could easily be discerned among F1 and F2 distributions where the progenies shifted more to the early parent. Transgressive segregants in the F2's occurred only in the early side. Epistasis played a significant role in the inheritance of maturity with dominance x dominance exerting the greatest effects among the three digenic epistasis. This interaction (**dd**) tended to bias maturity upward while **aa** and **ad** tended to bias it downward as indicated by their negative estimates. Consequently, the three epistatic effects would cancel each other in the overall expression of the trait. Estimates of main genetic effects might also be confounded by the presence of epistasis (Hallauer and Russell, 1962).

Scaling tests for photoperiod sensitivity was not considered valid because variance could not be computed due to the nature of the data. There was no way of identifying individual genotypes among advanced segregating (F2 and

backcross) generations planted under SD that corresponded to individuals planted under LD. Silking delay was, therefore computed as the difference among means, not among individuals. Hence, neither statistical tests nor estimation of genetic variances were made. Comparisons could be made, however, as far as relative magnitudes of gene effects were concerned. Dominance appeared to be more important than additive gene effects in two of the three crosses that met the GMA requirement for opposing traits. Photoperiod sensitivity was also over insensitivity in these crosses, while in the other cross, photoperiod insensitivity was dominant over photoperiod sensitivity. This confirmed the suggestion of Russell and Stuber (1983) that sensitivity to photoperiod may be dominant in some loci but recessive at others. Estimates for **aa** and **dd** were large, but estimates for **ad** effects were generally small. Epistatic effects tended to accentuate or suppress photoperiod sensitivity depending on the cross.

Partitioning of the measured variation assumed that the genetic effects must be additive, that is, there should be no interloci interaction or epistasis (Mather, 1949). Results clearly showed the presence of significant digenic epistasis, so that extreme caution is necessary in the interpretation of the estimated variances. Although the computed variances might be confounded, they were included because of the relative importance of the dominance to

additive gene effects and the relative importance of dominance that had been reported (Hallauer and Russell (1962); Giesbrecht, 1960a and 1960b; Jones; 1955; Mohamed, 1959).

Absolute values of genetic variances were higher under LD than under SD because of the exaggerating effects of photoperiod. In most cases, however, dominance variances (H) were greater than additive variances (D) under both daylengths. Some estimates for D and H were negative, but they were presumably estimates of zero or some small positive values, since variances are the result of squared deviations.

Heritabilities were higher under SD than under LD presumably because of the large environmental effects caused by long daylength. Maturity was found to be highly heritable (broad sense) but would be of less significance to the plant breeder since dominance accounted for most of the genetic variance. Narrow sense heritability would be a better measure of heritability since it indicates the amount of genetic variation relative to the total variation, thus it is useful in predicting progress due to selection. Additive genetic variance is the component of variation useful to breeders in selection program because it is fixable (Hallauer and Miranda, 1981). The low narrow sense heritability observed in this study would not preclude rapid genetic advance to due to selection since heritability

changed with environments and genetic materials (Ayala, 1982). Even the simple backcross technique might be very effective as shown by significant shifting of the progenies towards the recurrent parent.

Maturity appeared to be controlled by a few genes, from two to three under SD, and from three to fourteen under LD. Recent molecular techniques using restriction fragment length polymorphisms (RFLP) mapping identified different numbers of loci that controlled anthesis, silking, silking delay depending on the materials under study (Grant et al., 1989). For example, they had identified two, three, and nine loci among the four populations assayed for silking. As of now a total of 10 and 11 loci have been mapped for silking and silking delay, respectively. This means that the expression of the trait is variable depending on the number of loci present in the genotype. This probably explained why the magnitude of additive and dominance effects changed with the type of parents used. This is probably the reason why different workers found different number of gene pairs controlling maturity: four genes were reported by Giesbrecht (1960), two to eleven by Jones (1955), and two or three by Mohamed (1959) and Hallauer (1965). Others using teosinte x maize crosses reported single-gene control (Galinat, 1966; and Langham, 1940), and no simple genetic control of maturity (Mangelsdorf, 1947; and Rogers, 1950). There is however a general agreement

about the importance of both additive and dominance effects, with earliness showing partial dominance.

Photoperiod sensitivity has been hypothesized to be controlled by few (two or three) loci (Spencer, 1974; Lee, 1978; and Francis, 1972c). These hypotheses were based upon data from early generations which could be misleading (Russell and Stuber, 1983), and by the constraint of finding inbreds that differed only in photoperiod sensitivity. This difficulty of separating maturity from photoperiod was the main reason for inconclusive results (Lee, 1978). In this study, this problem was circumvented by using silking delay (LD-SD), but in the process lost the ability to compute for population variance needed for estimation of heritability and gene number as well as statistical testing. It is in this area that molecular genetic techniques should be applied.

## 7. DIVERGENT MASS SELECTION FOR SILKING DATE

Selection for early and late silking was initiated in two maize composites developed at UH. Three cycles were completed and evaluated for progress due to selection in Waimanalo (SD), on Kauai, and under extended daylength in Waimanalo (LD). Correlated responses to selection were also measured for photoperiod sensitivity, plant height, leaf number and grain yield. An important objective was to determine relationship between maturity expressed under short daylength and photoperiod sensitivity.

### 7.1 Response Due to Selection

Mean number of days to silking for each of the four environments are presented in Table 7.1. Means from short daylength (SD) environments were taken from Waimanalo (Wai1) and Kauai trials; means for long daylength (LD) environment were measured from the extended daylength in Waimanalo (Wai2). Base populations (C0) of MIRSYN 1 and HIC 4g generally gave comparable silking dates in the three environments. As expected for both populations, silking was much more delayed under the LD trial. Three cycles of selection for early silking in both populations brought about a significant reduction in silking date from the base populations. Selection for late silking significantly increased the silking date for both populations in the three evaluation trials. Mean number of days to silking under short and long daylengths at Waimanalo for the different



Table 7.1. Mean number of days to silking of MIRSYN1 and HIC 4g in three environments\*.

Population	SD		LD
	Wail	Kauai	Wai2
MIRSYN 1			
C0	55.7 c	62.5 bc	83.3 b
Early C1	53.9 b	60.4 b	82.4 b
Early C2	49.8 a	55.8 a	74.9 a
Early C3	49.3 a	55.7 a	74.0 a
Late C1	56.2 cd	62.9 cd	83.3 b
Late C2	56.6 d	64.4 de	84.9 b
Late C3	59.2 e	66.0 e	91.3 c
Mean	54.4	61.1	82.0
HIC 4g			
C0	55.6 c	60.4 cd	80.2 b
Early C1	54.0 b	60.1 c	79.6 b
Early C2	52.6 a	56.8 b	75.1 a
Early C3	51.7 a	54.8 a	74.3 a
Late C1	56.3 c	62.2 de	84.0 c
Late C2	57.6 d	62.6 e	85.2 cd
Late C3	58.7 e	65.2 f	86.3 d
Mean	55.2	60.3	80.7

\* means with common letter within a population are not statistically significant at 5% level of probability.

selection cycles of early and late silking for MIRSYN 1 and HIC 4g are illustrated in Figure 7.1 and 7.2, respectively. There was a clear-cut trend of response for MIRSYN 1 in both directions but a plateau appeared to occur earlier in the late direction for HIC 4g. Divergent mass selection definitely resulted in distinct separation of means between early and late silking.

Analyses of variance (Table 7.2) for each environment revealed significant differences between the two populations and among cycles of selection. Interaction between

Table 7.2. Analyses of variance for number of days to silking in four environments.

Source	df	Mean Squares		
		Wail	Kauai	Wai2
Reps	2	4.6 *	12.7 *	5.8
Entries	13	28.1 **	40.4 **	79.6 **
Populations	1	7.1 *	5.5	23.1
Cycles	6	57.1 **	85.0 **	158.9 **
Pop'n x cycles	6	2.6 *	1.6	9.6
Error	26	0.40	3.00	6.21

populations and cycles of selection was significant only at Wail and represented a very small proportion of the total variation among. Combined analysis of variance across locations (Table 7.3) showed significant variation for all the sources of variation except populations x cycles interaction. Variations among cycles of selection accounted for over 90 percent of the total variation among entry means indicating effectiveness of divergent selection in both populations.

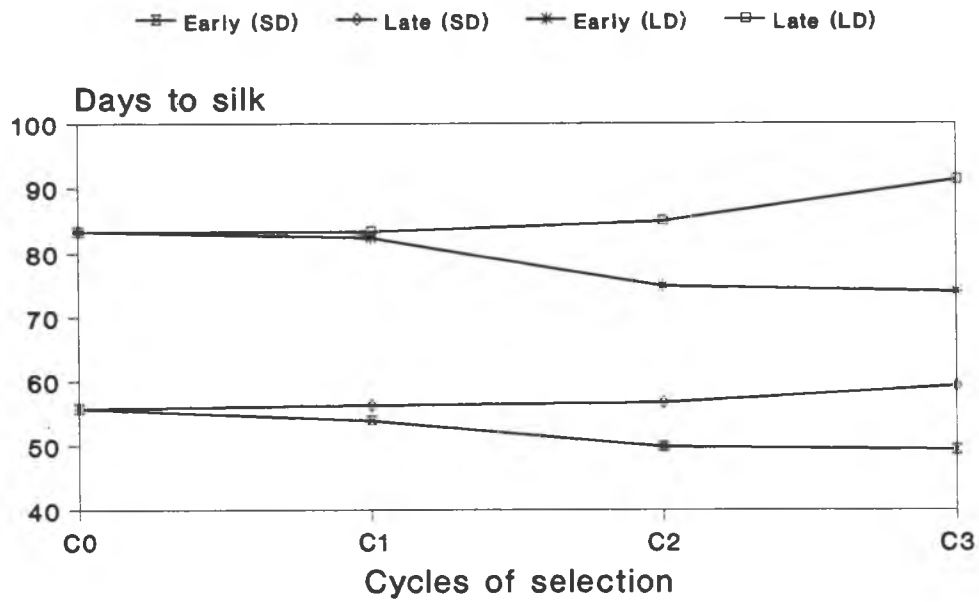


Figure 7.1. Number of days to silking from three cycles of divergent selection of MIRSYN 1.

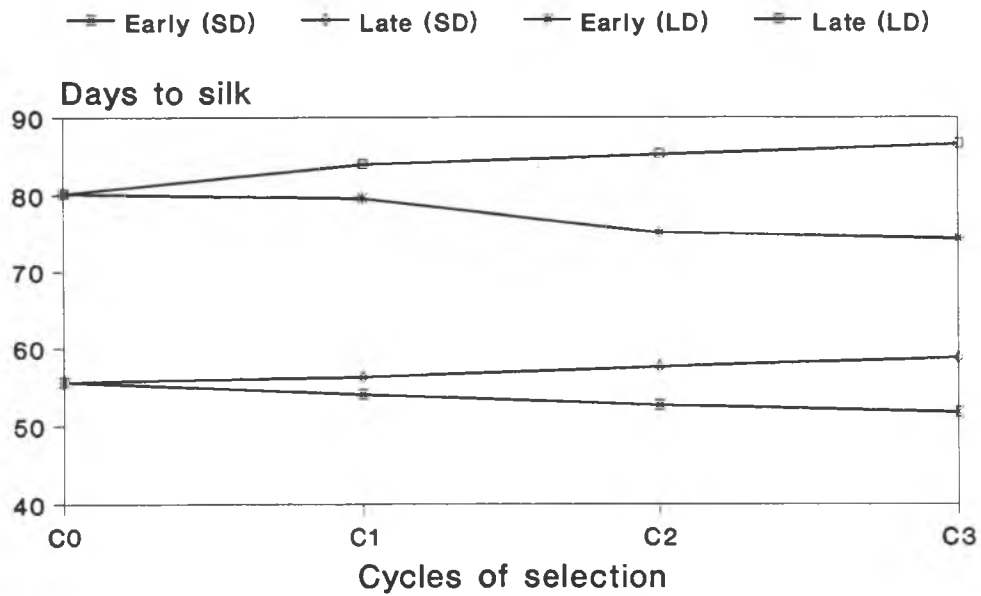


Figure 7.2. Number of days to silking from three cycles of divergent selection of HIC 4g.

Table 7.3. Combined analysis of variance for number of days to silking across four environments.

Source	df	MS
Environment (E)	2	8118.8 **
Reps/E	6	7.7 *
Entries	13	136.8 **
Populations (P)	1	91.4 **
Cycles (C)	6	275.6 **
P x C	6	5.3 ns
Entries x E	26	5.7 *
Pooled Error	78	3.2

Progress due to selection was computed from the mean of each of the environments (Table 7.4). Genetic advance

Table 7.4. Percent gain from selection for the number of days to silking in three environments

Population		SD		LD
		Wail	Kauai	Wai2
MIRSYN 1	Early	-3.84	-3.63	-3.72
	Late	2.08	1.87	3.20
HIC 4g	Early	-2.29	-3.08	-2.43
	Late	1.88	2.67	2.54

resulting from selection for early silking ranged from -3.63 (2.3 days) at Kauai to -3.84% (2.1 days) at Wail per cycle for MIRSYN 1; and from -2.29 (1.3 days) at Wail to -3.08% (1.9 days) at Kauai per cycle for HIC 4g. Selection for late silking resulted in a genetic gain of 1.87 (1.2 days) at Kauai to 3.20% (2.7 days) at Wai2 per cycle for MIRSYN 1; and from 1.88 (1 day) at Wail to 2.67% (1.6 days) at Kauai per cycle for HIC 4g. In general more progress were realized for earliness than for lateness when

evaluations were made under SD (Wai1 and Kauai), but became more or less comparable under LD of Wai2. Averaged over daylengths, greater progress was realized when selecting for earliness than for lateness in both populations.

## 7.2 Realized Heritability Estimates

Realized heritability for number of days to silking is basically similar to narrow-sense heritability, since it is based on the amount of genetic advance which in turned is influenced by the magnitude of additive genetic variance in a population. As shown in Table 7.5, realized heritability

Table 7.5. Realized heritability averaged over three cycles.

Population	Wai1	Wai2
MIRSYN 1	0.92	0.40
HIC 4g	0.58	0.21

for MIRSYN 1 was 0.92 when evaluated under short daylength (Wai1) and was reduced to 0.40 when evaluated under long daylength (Wai2). For HIC 4g it was 0.58 and 0.21, respectively. Higher estimates were obtained in Wai1 because selection was conducted under the stable short-day environment, while in Wai2 the confounding effect of photoperiod sensitivity tended to bias upward the contribution of the environmental variance to the total phenotypic variance, thus reducing heritability. The higher heritability suggested greater additive genetic variance for maturity in this population.

### 7.3 Correlated Effects of Selection for Silking Date

Effects on Photoperiod Sensitivity. Photoperiod sensitivity expressed as silking delay for the different selection cycles is given in Table 7.6. This photoperiod

Table 7.6. Photoperiod sensitivity of different cycles of selection for MIRSYN 1 and HIC 4g.

Population	Silk Delay	% change from C0	Silk Delay	% change from C0
	MIRSYN 1		HIC 4g	
C0	27.6	0.00	24.6	0.00
Early C1	28.5	3.26	25.6	3.93
Early C2	25.1	-8.84	22.5	-8.69
Early C3	24.7	-10.39	22.6	-8.28
Late C1	27.1	-1.70	27.7	12.30
Late C2	28.4	2.93	27.7	12.25
Late C3	32.1	16.38	27.6	12.01
Mean	27.6		25.5	

sensitivity index was obtained by subtracting silking date of Wai1 from Wai2. Photoperiod sensitivity decreased with selection for early silking, from 27.6 at C0 (base population) to 24.7 days at C3 for MIRSYN 1 and from 24.6 at C0 to 22.6 days at C3 (third cycle) for HIC 4g. This was translated into a sensitivity reduction of 10.4 and 8.3% from C0 to C3 for MIRSYN 1 and HIC 4g, respectively. Conversely, selection for late silking resulted in the increase of sensitivity from 27.6 to 32.1 days at C3 for MIRSYN 1 and from 24.6 to 27.6 days at C3 for HIC 4g; or an increase from C0 of 16.3 to 12.0%, respectively. Correlated gains per cycle for MIRSYN 1 and HIC 4g were

-3.46 and -2.76% for early silking selection and 5.46 and 2.61% for late silking selection (Table 7.7).

Table 7.7. Correlated gain (%) in photoperiod sensitivity per cycle of selection.

Populations		% Gain
MIRSYN 1	Early	-3.46
	Late	5.46
HIC 4g	Early	-2.76
	Late	4.07

As illustrated in Figure 7.3 and 7.4, significant reduction in photoperiod sensitivity occurred at cycle 2 of early selection (EC2) for both populations. Increased sensitivity due to late selection was gradual in MIRSYN1 and showed increasing response, but in HIC 4g the increase was sudden and seemed to reached some plateau at the second cycle (LC2). Absolute percent change from C0 were generally larger when selecting for late silking than selecting for early silking. These data suggested that photoperiod sensitivity was associated with SD maturity, but late maturity was more strongly associated with high photoperiod sensitivity than early maturity was with low photoperiod sensitivity. Correlation coefficients between the two traits were 0.89 and 0.90 for MIRSYN 1 and HIC 4g, respectively.

The number of days to silking under short daylength for different cycles of selection were regressed on photoperiod sensitivity (as silking delay in days) to determine

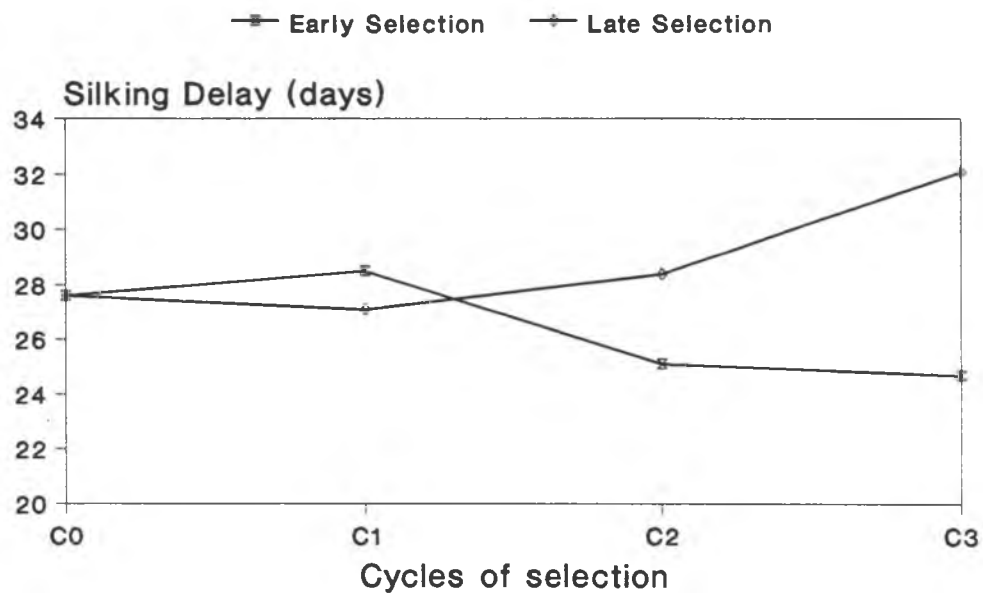


Figure 7.3. Photoperiod sensitivity of MIRSYN 1 divergently selected for silking date.

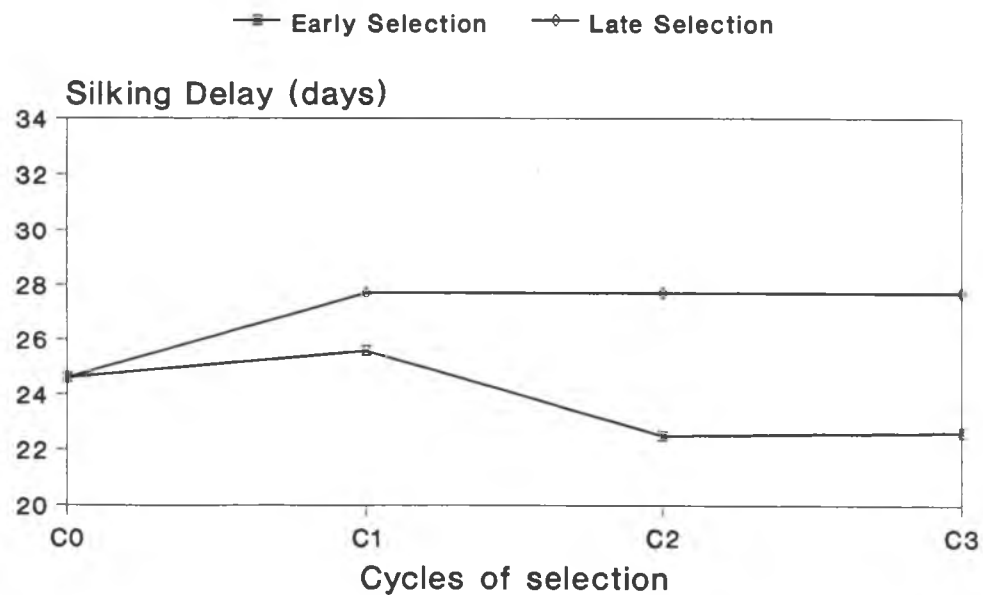


Figure 7.4. Photoperiod sensitivity of HIC 4g divergently selected for silking date.



relationship between the two traits. For MIRSYN 1 (Figure 7.5), the regression coefficient ( $b$ ) was 0.60, i.e., for every day increase of silking date under short daylength, there was a corresponding 0.6 day increase in silking delay. Coefficient of determination was ( $r^2=0.79$ ). For HIC 4g,  $b$  was comparable at 0.82 with an  $r^2$  of 0.82. This represented a strong relationship since about 80% of the total variation in silking delay could be accounted for by the variation in silking date under short daylength. This suggested that recurrent selection for earliness of tropical populations conducted under short day environments, i.e., in the tropics would result in lowering of photoperiod sensitivity when these populations are planted in long day environments, i.e., in the temperate growing zones.

Plant Height. Divergent selection affected plant height in the same manner as it affected silking date. Populations that silked earlier were shorter; ones that silked later were taller than the original population. This happened in both composites (Table 7.8) at two daylengths. One of the most striking effects of photoperiod on sensitive corn plants was the enormous increase in plant height. MIRSYN 1 populations, on an average, grew 97.7 cm (37.9%) more under LD than under SD. HIC 4g had a mean difference of 83.6 cm (31.1%). In MIRSYN 1 there was no apparent plant height index (LD-SD) trend among selection cycles, while in HIC 4g, as selection for earliness and lateness advanced,

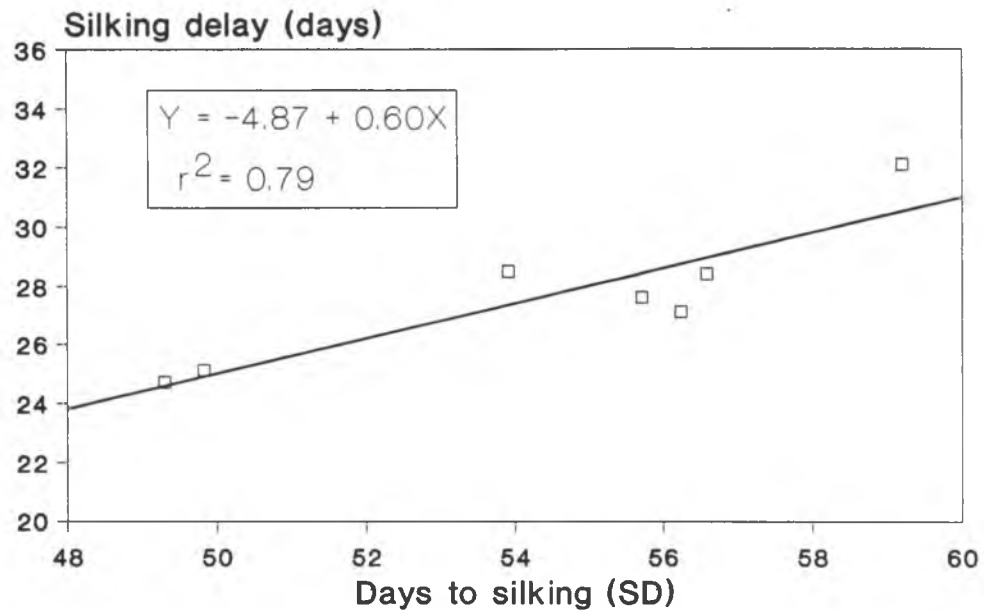


Figure 7.5. Relationship between silking date under short daylength and photoperiod sensitivity of MIRSYN 1.

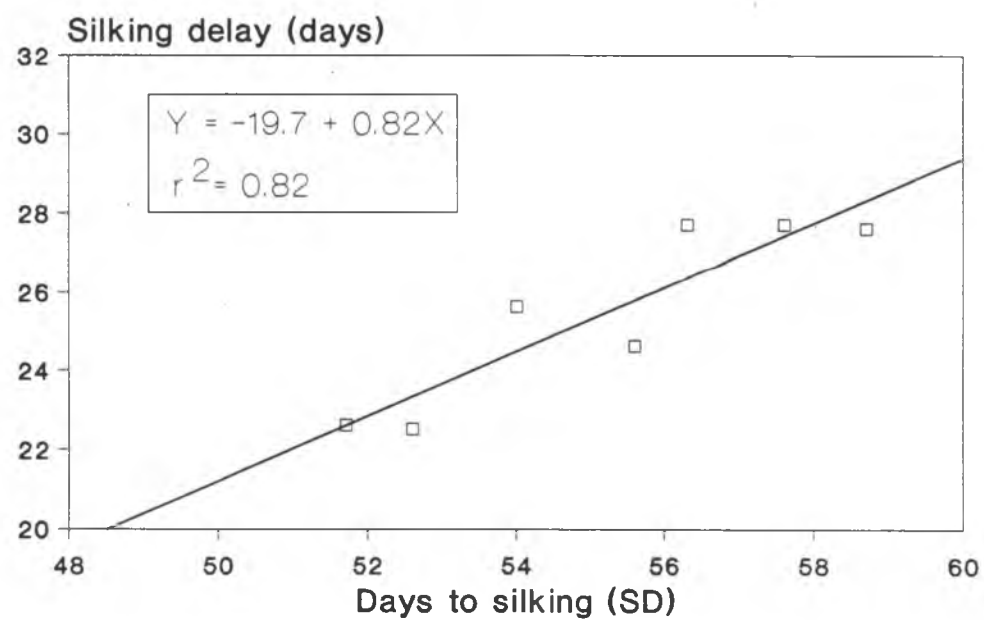


Figure 7.6. Relationship between silking date under short daylength and photoperiod sensitivity of HIC 4g.

Table 7.8. Plant height (cm) measured under short and long daylength.

Population	SD	LD	Index (LD-SD)	Percent Change
-----				
MIRSYN 1				
C0	264.2	356.7	92.4	35.0
Early C1	255.0	343.3	88.3	34.6
Early C2	238.5	326.7	88.2	37.0
Early C3	224.6	326.7	102.1	45.5
Late C1	270.8	368.3	97.5	36.0
Late C2	277.5	395.0	117.5	42.3
Late C3	282.3	380.0	97.7	34.6
Mean	259.0	356.7	97.7	37.9
HIC 4g				
C0	260.8	351.7	90.8	34.8
Early C1	263.3	326.7	63.3	24.1
Early C2	250.0	323.3	73.3	29.3
Early C3	256.5	308.3	51.8	20.2
Late C1	274.4	367.5	93.1	33.9
Late C2	280.3	390.0	109.7	39.1
Late C3	285.2	388.3	103.2	36.2
Mean	267.2	350.8	83.6	31.1
-----				

plant height index appeared to decrease and increase, respectively.

Plant height was highly and significantly correlated with days to silking in both daylengths (Table 7.9). Figures 7.7 and 7.8 illustrate the relationship between number of days to silking under SD and plant height for MIRSYN 1 and HIC 4g, respectively. Plant height increased at the rate of 5.64 cm (MIRSYN 1) and 4.72 cm (HIC 4g) per day increase of silking date. Coefficients of determination were 0.96 and 0.87, respectively.

When silking delay was regressed on plant height index, practically no relationship was detected for

Table 7.9. Correlations among number of days to silking and agronomic traits.

Population	Days to Silk	
	SD	LD
MIRSYN 1		
Plant Height	0.98 **	0.85 *
Leaf Number	0.95 **	0.95 **
Grain Yield	0.57	-0.82 *
HIC 4g		
Plant Height	0.93 **	0.96 **
Leaf Number	0.96 **	0.98 **
Grain Yield	0.27	-0.20

MIRSYN 1, and very weak relationship for HIC 4g (Figures 7.9 and 7.10). This meant that plant height index would be a poor substitute for silking delay as a photoperiod sensitivity index.

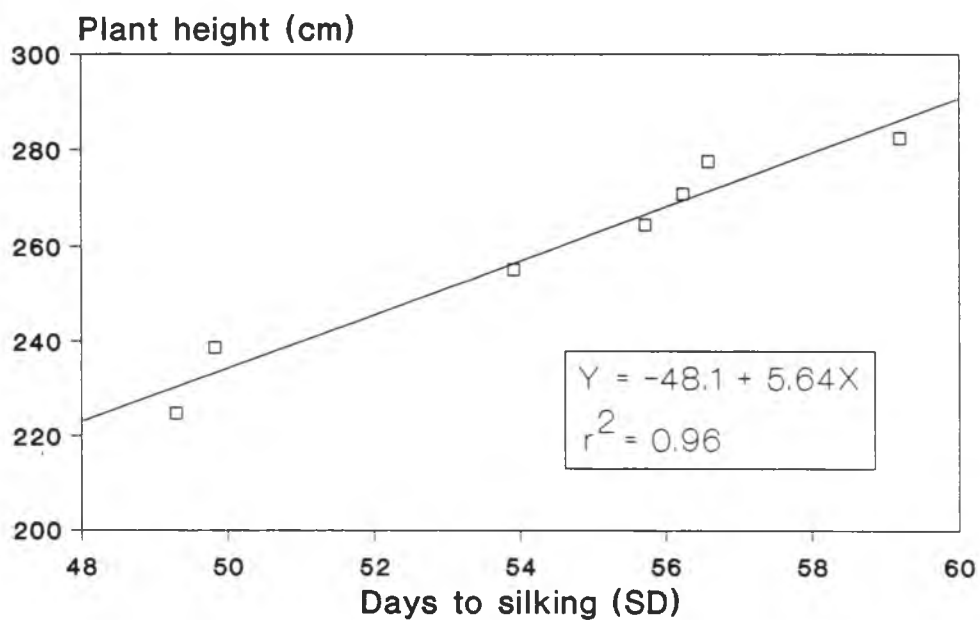


Figure 7.7. Relationship between silking date under short daylength and plant height of MIRSYN 1.

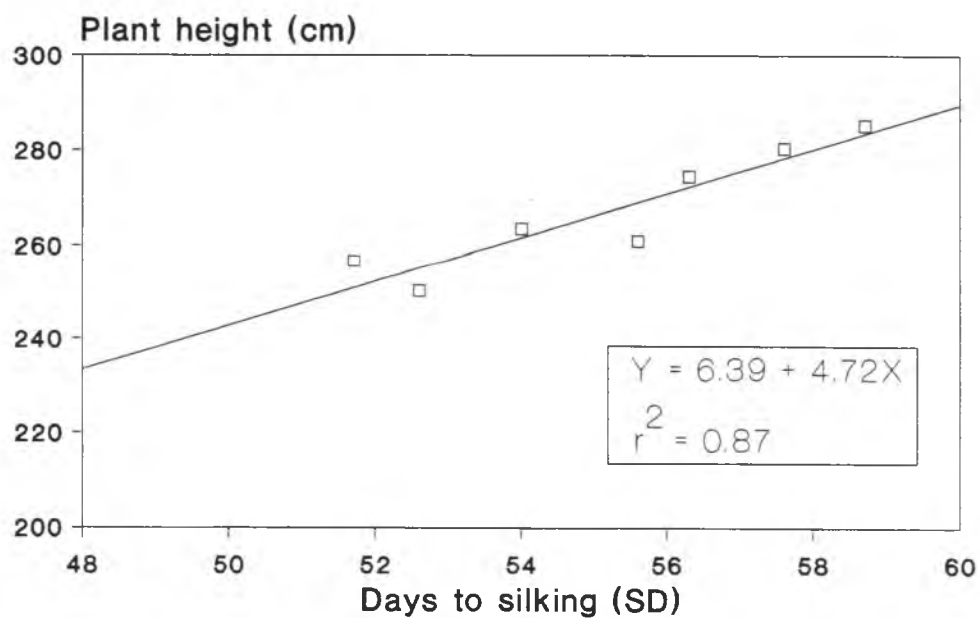


Figure 7.8. Relationship between silking date under short daylength and plant height of HIC 4g.

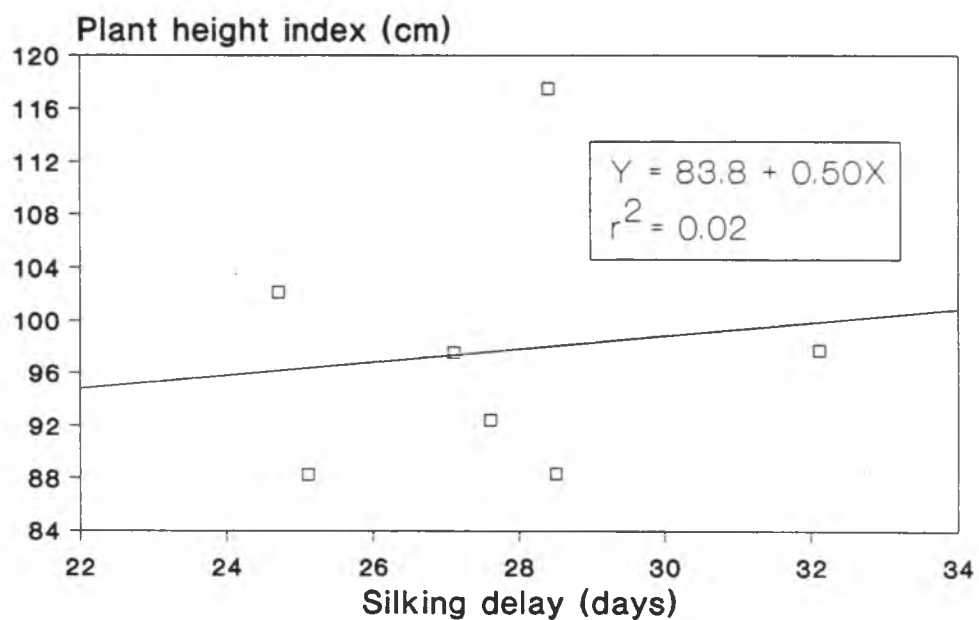


Figure 7.9. Relationship between photoperiod sensitivity and plant height index (LD-SD) of MIRSYN 1.

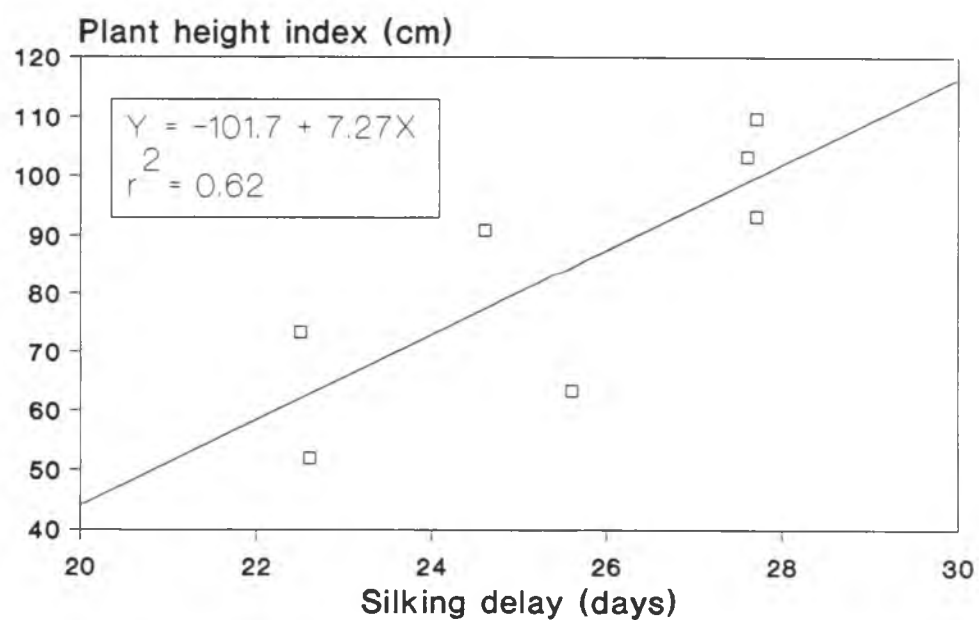


Figure 7.10. Relationship between photoperiod sensitivity and plant height index (LD-SD) of HIC 4g.

Number of Leaves per Plant. Populations planted under long daylength produced, on an average, six more leaves than under short daylength. The two composites gave comparable leaf number in both daylengths. Leaf number index (LD-SD) was 6.3 and 5.6 at CO for MIRSYN 1 and HIC 4g, respectively. This was reduced to 3.8 and 4.4 leaves, respectively, at the third cycle of selection for earliness. Conversely, leaf number index was increased to 8.8 and 7.2, respectively at the third cycle of selection for lateness (Table 7.10). Correlations between leaf number and days to silking were in the high 0.90's in both daylengths.

Regression analysis indicated a positive and strong relationship between number of days to silking and leaf number under SD (Figure 7.11 and 7.12). Leaf number increased at the rate of 0.24 (MIRSYN 1) and 0.31 (HIC 4g) for every day increase in silking date with an  $r^2$  of 0.90 and 0.93, respectively.

Prediction equations between silking delay and leaf number index (difference in leaf number between LD and SD) also showed a strong linear relationship for both populations (Figure 7.13 and 7.14) with an  $r^2$  value of 0.77 (MIRSYN 1) and 0.91 (HIC 4g). Leaf number index is thus a good alternative to silking delay as a photoperiod sensitivity index.

Grain Yield. Grain yield under SD appeared to decrease as selection for early silking progressed and

Table 7.10. Number of leaves per plant under short and long daylength.

Population	SD	LD	Index (LD-SD)	Percent Change
-----				
MIRSYN 1				
C0	21.0	27.3	6.3	30.0
Early C1	20.8	25.7	4.8	23.2
Early C2	20.0	24.0	4.0	20.0
Early C3	19.8	23.7	3.8	19.3
Late C1	21.3	27.7	6.4	29.9
Late C2	22.2	29.7	7.5	33.8
Late C3	22.2	31.0	8.8	39.6
Mean	21.1	27.0	5.9	28.0
HIC 4g				
C0	21.4	27.0	5.6	26.2
Early C1	21.2	26.3	5.2	24.4
Early C2	20.9	24.7	3.8	18.2
Early C3	20.3	24.7	4.4	21.7
Late C1	21.5	28.3	6.8	31.8
Late C2	22.1	29.7	7.6	34.4
Late C3	22.8	30.0	7.2	31.4
Mean	21.4	27.2	5.8	26.9
-----				



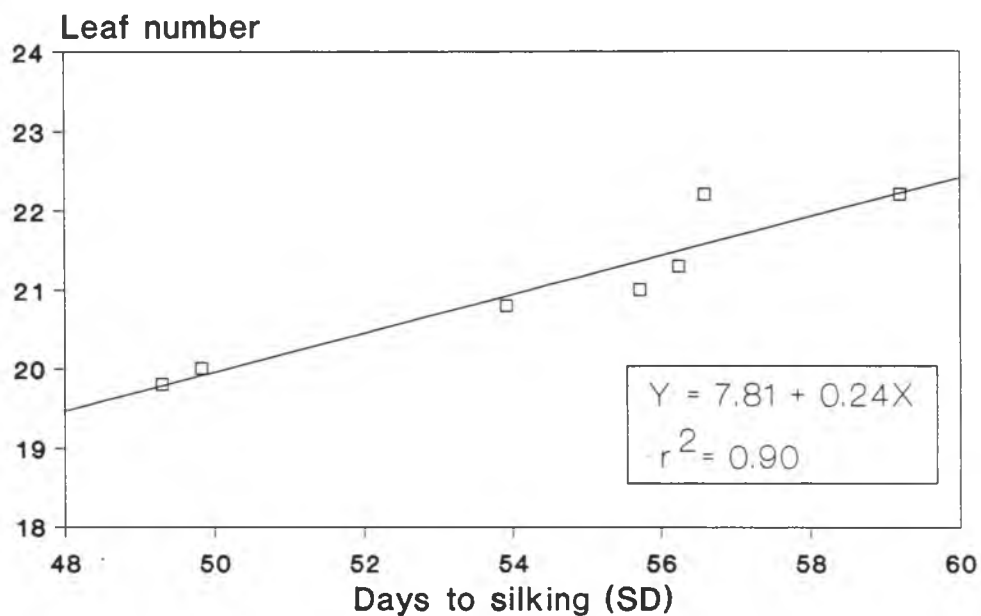


Figure 7.11. Relationship between silking date under short daylength and leaf number of MIRSYN 1.

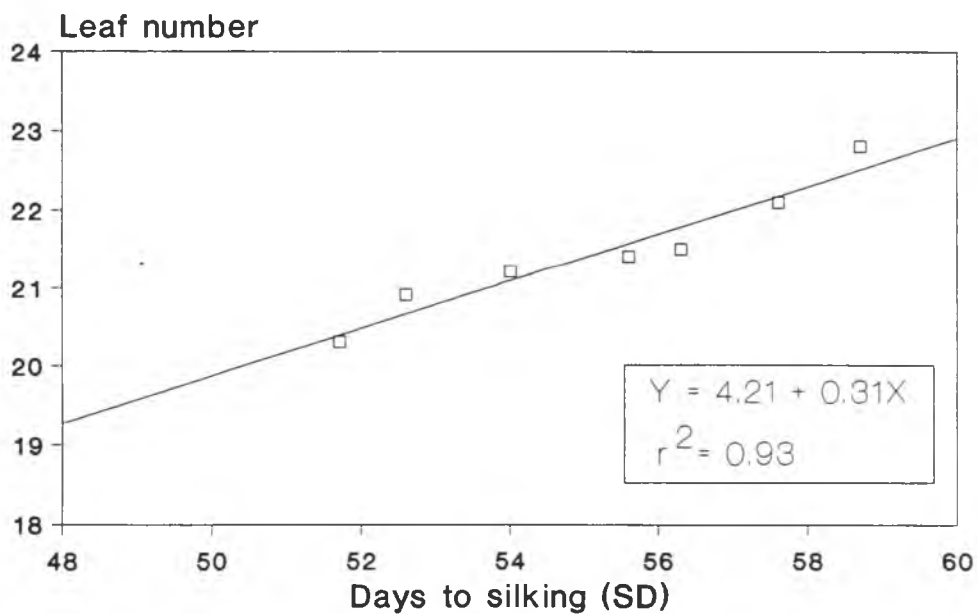


Figure 7.12. Relationship between silking date under short daylength and leaf number of HIC 4g.

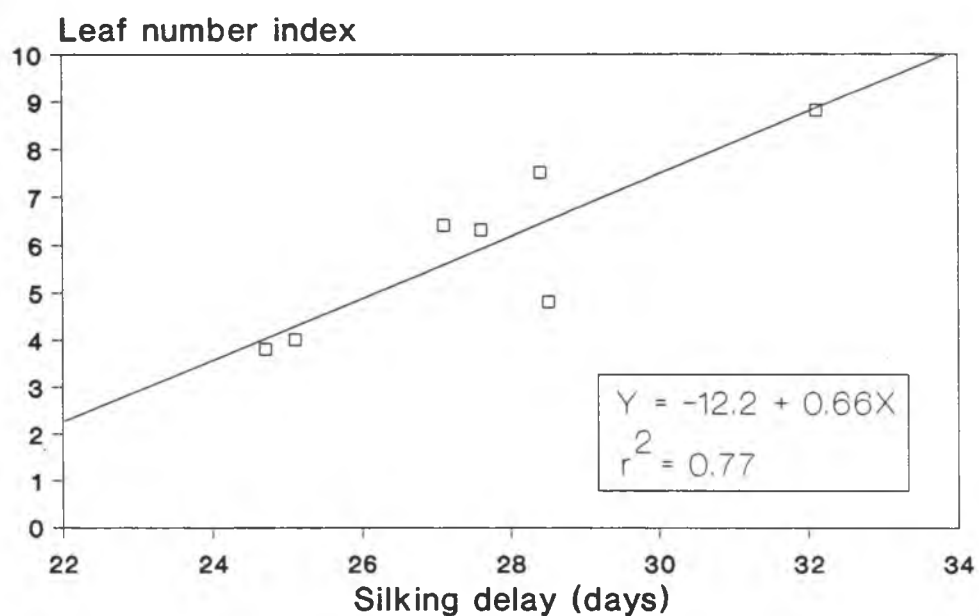


Figure 7.13. Relationship between photoperiod sensitivity and leaf number index (LD-SD) of MIRSYN 1.

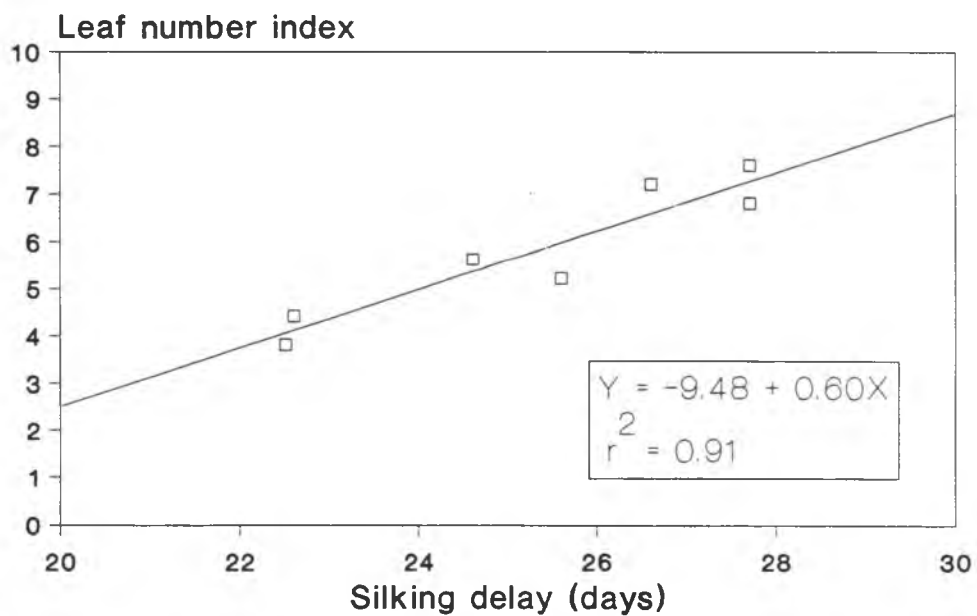


Figure 7.14. Relationship between photoperiod sensitivity and leaf number index (LD-SD) of HIC 4g.

increased with selection for late silking for MIRSYN 1 (Table 7.11). However, regression analysis indicated a weak relationship with an  $r^2$  of only 0.46 (Figure 7.15). There was practically no relationship between silking date and grain yield under SD in HIC 4g as illustrated Table 7.11 and Figure 7.16.

There were large yield reductions when both populations were planted under LD conditions. All MIRSYN 1 and HIC 4g populations reduced their yield on the average by 6.4 t/ha or 81.3% and 75.7%, respectively. The yield index decreased with selection for earliness in MIRSYN 1 but not in HIC 4g; but increased with selection for lateness in both populations. The effect of silking delay on yield index in MIRSYN 1 as illustrated in Figure 7.17 was negative (since the index was negative) and linear with an  $r^2=0.81$ . Yield index was not significantly affected by silking delay in HIC 4g (Figure 4.18). The severe grain yield reductions under LD in all cycles of selection in both directions, and coupled by their high silking delay (even after three cycles of selection) would make these composites highly undesirable. There is evidence suggesting that it probably will take several more cycles of early selection to achieve acceptable photoperiod tolerance and yield.

#### 7.4 Discussion

Selection for early flowering in corn had been employed not only to bring down maturity of late maturing

Table 7.11. Grain yield (t/ha) under short and long daylength.

Populations	SD	LD	Index (LD-SD)	Percent Change
-----				
MIRSYN 1				
C0	8.130	2.243	-5.9	-72.4
Early C1	7.716	1.366	-6.3	-82.3
Early C2	7.479	1.938	-5.5	-74.1
Early C3	7.425	2.031	-5.4	-72.6
Late C1	7.371	0.923	-6.4	-87.5
Late C2	8.562	1.190	-7.4	-86.1
Late C3	8.272	0.487	-7.8	-94.1
Mean	7.851	1.454	-6.4	-81.3
HIC 4g				
C0	8.173	2.718	-5.5	-66.7
Early C1	8.639	1.626	-7.0	-81.2
Early C2	9.215	2.333	-6.9	-74.7
Early C3	8.559	1.664	-6.9	-80.6
Late C1	7.086	1.616	-5.5	-77.2
Late C2	8.813	2.393	-6.4	-72.9
Late C3	8.926	2.051	-6.9	-77.0
Mean	8.487	2.057	-6.4	-75.7
-----				

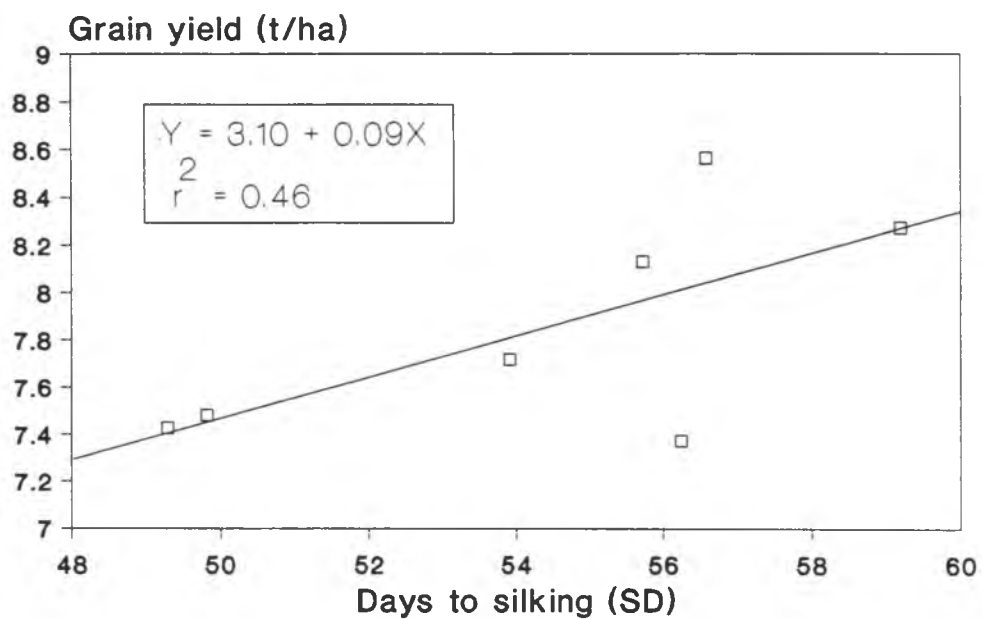


Figure 7.15. Relationship between silking date under short daylength and grain yield of MIRSYN 1.

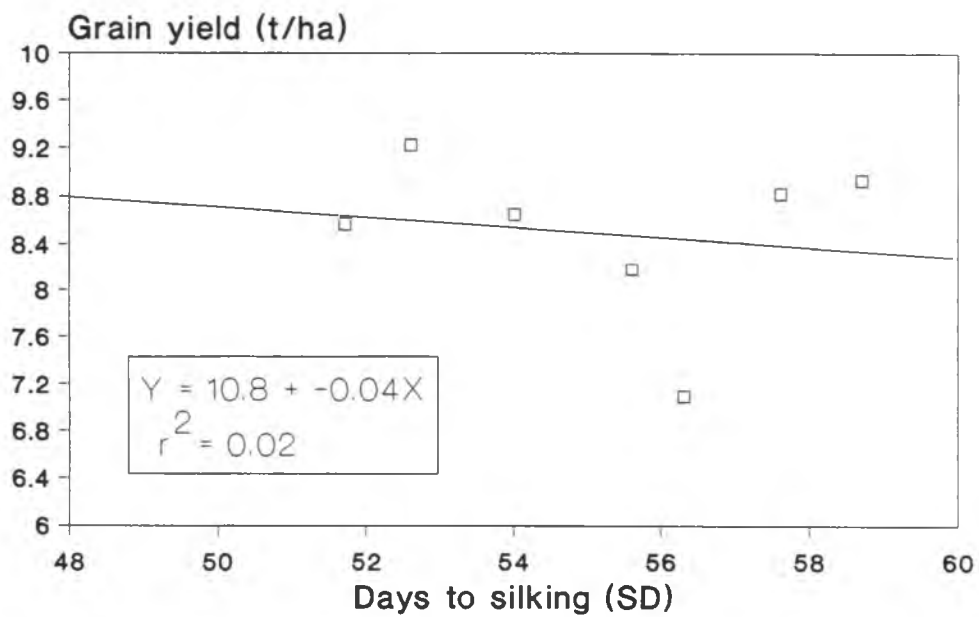


Figure 7.16. Relationship between silking date under short daylength and grain yield of HIC 4g.

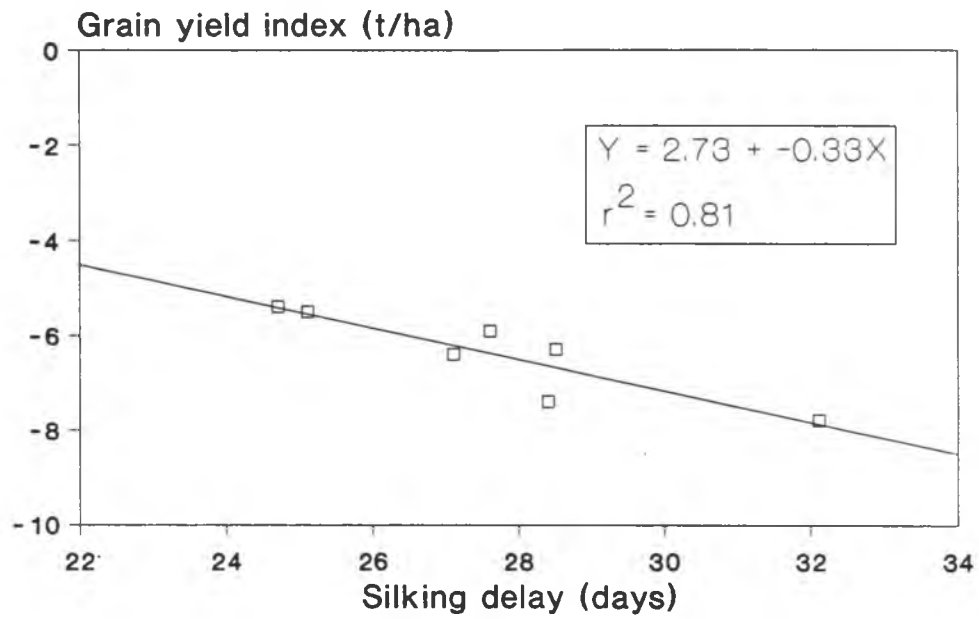


Figure 7.17. Relationship between photoperiod sensitivity and grain yield index (LD-SD) of MIRSYN 1.

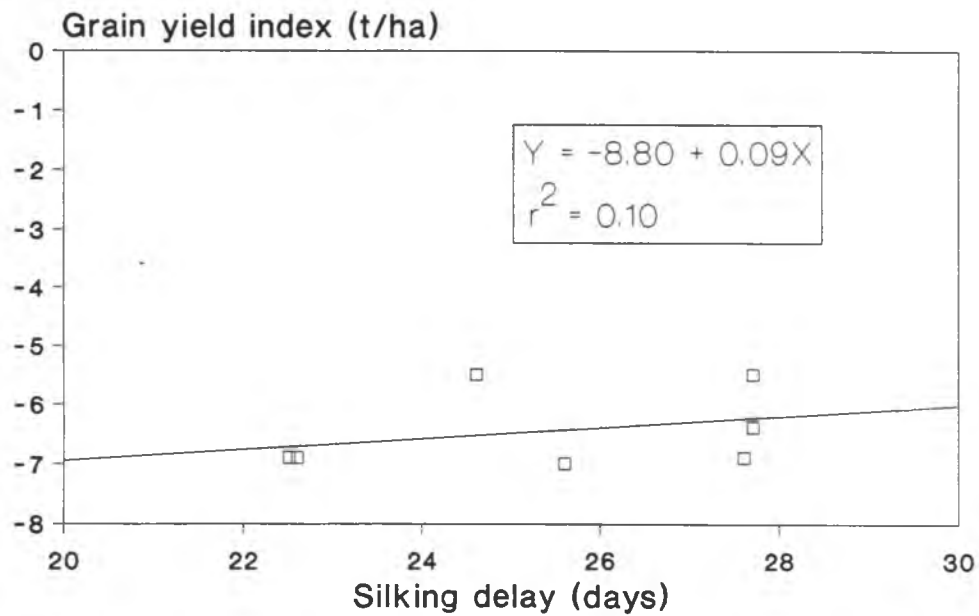


Figure 7.18. Relationship between photoperiod sensitivity and grain yield index (LD-SD) of HIC 4g.

adapted lines but also as means of integrating exotic germplasm into adapted cultivars (Hallauer and Sears, 1972; Troyer and Brown, 1972 and 1976; Troyer and Larkins, 1985). Good genetic progress due to selection were reported among exotic tropical populations grown under long days which could be attributed mainly to the high genetic variability of these populations (Goodman, 1965). Flowering (anthesis and silking) as a selection trait had relatively high heritability and was much easier to measure than other maturity related traits.

In this study, selection for early and late silking was effective in diverging silking dates of the two composite populations. This supported previous studies that divergent selection for maturity and other quantitative traits had been successful in maize (Cross et al., 1987; Odhiambo and Compton, 1987; Cortez-Mendoza and Hallauer, 1979; Teyker et al., 1989) as well as in other crops (Reith and Baltensperger, 1987; Watson and McLean, 1987; McLean and Watson, 1989). Progress due to selection realized for the two populations was generally comparable to the ones reported by Troyer and Larkins (1985), and Troyer and Brown (1976). Slightly greater gains were observed in early selection than in late selection in both populations when evaluations were done under SD environments of Wail and Kauai. This can be attributed to the observation that early silking plants were easier to tag in the field than late

silking plants. Plants tended to delay their flowering when subjected to environmental stress, particularly nutrient deficiencies, so that late silking plants were not necessarily genotypically late, thus confounding selection for lateness. This problem was minimized, however, by stratifying selection plots into small grids.

Response to divergent selection evaluated under LD environment in Wai2 showed a substantial increase in percent gain per cycle for lateness, but not for earliness, particularly in MIRSYN. This was probably due to confounding effects of photoperiod on flowering in which late maturing genotypes were affected by photoperiod more than early maturing ones as reported in Chapter 4 and by a number of workers (Brewbaker, 1981; Hunter et al., 1974; Francis, 1972c).

In general, better response to selection was observed in MIRSYN1 than in HIC 4g. MIRSYN 1 was a relatively new synthetic and has never been subjected to any systematic selection schemes. In contrast, HIC 4g had been advanced through seven generations of mass selection, largely for pest and disease resistance, although not for maturity. In effect, MIRSYN 1 would probably have more genetic variability than HIC 4g. Response to selection is largely dependent on the amount of genetic variability present in the population (Allard, 1960; Hallauer and Miranda, 1981). The presumed high genetic variability in MIRSYN1 relative to



HIC 4g was also reflected in the higher realized heritability in MIRSYN 1.

One of the most important objectives of this study was to determine the correlated responses of selection on photoperiod sensitivity. This was made possible by evaluating the materials under LD environment in Wai2. Results indicated that selection for early and late silking resulted in a corresponding decrease and increase of photoperiod sensitivity, respectively. Correlated responses from cycle to cycle, however, were not consistent between the two populations and there was some evidence of leveling off (plateau) of response in HIC 4g. This possibly corroborates the suggestion that HIC 4g has less genetic variability for maturity than MIRSYN 1. This could not be ascertained unless selection was advanced through several more cycles.

Selection for late silking elicited greater response (increasing photoperiod sensitivity) than did selection for early silking on lowering photoperiod sensitivity. This was shown by the larger correlated gain for high photoperiod sensitivity than gain for low photoperiod insensitivity per cycle of selection in both populations. These results support the previous findings that photoperiod had a stronger effect on late maturing lines. In Chapter 4, it was clearly demonstrated that all late maturing inbreds were highly sensitive to photoperiod, whereas much more variation

occurred among early and medium maturing inbreds. This suggested that the genetic control of SD maturity and photoperiod are related and that the effects of SD maturity on photoperiod sensitivity is threshold in nature.

The correlated response to selection confirmed the high additive genetic correlation between SD maturity and photoperiod sensitivity noted in the diallel analysis. A high degree of genetic association between two traits would indicate that they are either controlled by the same genes (pleiotropy) or they are controlled by different genes but are linked in the same chromosome (linkage) (Falconer, 1989, Hallauer and Miranda, 1981; and Hedrick, 1983). The relationship between SD maturity and photoperiod sensitivity was examined by regression analysis. It was pointed out in Chapter 4 and Chapter 5 (diallel analysis) that regressing photoperiod sensitivity on SD maturity was of little value because of the nature of the materials involved, that is, genetic variations among inbreds and hybrids in other traits, aside from maturity and photoperiod sensitivity, would preclude establishment of meaningful relationship between the two variables.

In this case however, variations among maturity and photoperiod sensitivity were the result of gene accumulations by selection under a common genetic background. Although open-pollinated populations are genetically heterogeneous, the use of recurrent selection

would not change the original genetic background from one cycle of selection to another and the amount of genetic variability of the trait under consideration would basically remain constant (Hallauer and Miranda, 1981; Falconer, 1989). Of course, the only way to guarantee that a certain set of genotypes differ only in maturity is through the use isolines, which is probably impossible to attain because maturity is controlled by more than one gene. In the absence of isolines, selection experiments such as this study would be a better avenue in resolving the issue of whether genes for SD maturity are related to the genes controlling photoperiod sensitivity.

Results from regression analysis revealed a strong linear relationship between the number of days to silking and silking delay (days). For both populations about 80 percent of the total variation in photoperiod sensitivity could be accounted for by the variation in SD maturity. The correlation coefficient of about 0.90 was a much higher values obtained than from inbreds (0.42) and hybrids (0.70). This relationship would provide a reasonably high prediction accuracy. The issue of whether the genes were pleiotropic or linked would be difficult to resolve. It could be surmised, however, that this relationship is due more to pleiotropic effects than linkage because the base populations used for selection are considered random-mating populations and as such, linkage equilibrium should have

been reached (Hedrick, 1983; Li, 1955). MIRSYN 1 and HIC 4g had undergone recombination at least seven and ten times, respectively (including selection cycles) which should have broken linkage blocks. Hallauer and Miranda (1981) explained that the amount of linkage disequilibrium in maize tends to be dissipated over generations of random mating populations. One of the characteristics of pleiotropism is that it should be repeatable and predictable (Hedrick, 1983). By repeating selection using other random mating populations or by continuing the selection of the same populations through several more cycles should determine whether or not pleiotropic effects are really involved.

Correlated response on plant height and leaf number were linear and highly predictable. These traits were strongly and positively associated with silking date morphologically and ontogenetically because internode formation stops at floral initiation (Troyer and Larkins, 1985). Further analysis showed that leaf number is much better than plant height as an alternative to silking delay as a photoperiod sensitivity index. A number of workers prefer leaf number as an index (Stevenson and Goodman, 1972; Russell and Stuber, 1985; Hunter et al., 1977; Tollenaar and Hunter, 1983). However, some complications are foreseen using this index because of its dependence on temperature (Hanway, 1963; Hesketh et al., 1969; Colligado and Brown, 1975b; Francis, 1972a; Lee, 1978). Brewbaker (1981)

reported that anthesis, silking and leaf number as indices were highly correlated. Silking delay was preferred in this study because it was relatively easy to measure than leaf number, especially when thousands of plants were involved.

There was no clear-cut trend on the effects of maturity on grain yield under SD. Although highest yields were observed in the later maturing populations (cycles), there was evidence that yield increased also with selection for earliness. A reason why selection for earliness is a popular avenue for population improvement lies on the fact that selection for earliness could also result in yield improvement (Troyer, 1978; Troyer and Larkins 1985). Besides, early maturing cultivars fit better in multiple cropping systems (Bradfield, 1972), and in areas where growing period is limited by drought or cold (Dinkel, 1974; Brawn, 1968; Goldsworthy, 1974).

## 8. SUMMARY AND CONCLUSION

The growing interest among temperate maize breeders for new genetic resources has spurred research on local adaptation of exotic cultivars. Introduced genotypes usually possess undesirable traits, such as susceptibility to biotic and environmental stresses in the area. Effects of photoperiod on maturity of corn is one of the most important limiting factors in the rapid integration of tropical materials into temperate breeding programs and vice versa. Clear understanding of the genetic behavior affecting maturity per se and photoperiodic response is imperative if rapid progress in the exchange of germplasm is desired.

Studies were conducted to evaluate tropical-adapted maize inbreds for maturity and photoperiod sensitivity. These were elite inbreds that were screened for general resistance to the most important pests and diseases of corn and are therefore very valuable to any corn breeder in the world. Three trials in Waimanalo, Hawaii (day-neutral environment) showed their relative short day maturity measured as days to silking. Growing degree days (GDD) were also computed. Genotypic variations in maturity were rather wide and should present a broad pool for breeders looking for lines that will fit in specific growing conditions. A trial in Iowa and Korea provided information on their response to long daylength expressed as silking

delay when compared to Hawaii trials. Unlike inside controlled laboratory conditions, this procedure of estimating photoperiod sensitivity is susceptible to other environmental factor which affect silking, like temperature. Results indicated, however that photoperiod effects were much stronger than temperature effects, thus actual silking delay should be a fairly accurate estimate of photoperiod sensitivity. Results also confirmed the day-neutrality of Waimanalo where variations in daylengths did not elicit corresponding variations in maturity. Temperature, however, influenced maturity variations at different times of the year in Waimanalo.

There was no single inbred that could be called strictly day-neutral. Only a small proportion exhibited low sensitivity, and they were mostly temperate in origin. A majority of the inbreds fell into an intermediate category; about 20 percent were identified as highly sensitive (exclusively tropical-derived). There was evidence that short day maturity is positively associated with photoperiod sensitivity, since early and late maturing lines generally showed low and high photoperiod sensitivity, respectively. However, very wide variations were observed among the intermediate types that confused this relationship. The absence of insensitive types among late maturing lines confirmed previous reports that photoperiod exerts greater effects on late maturing genotypes.

A nine-entry diallel analysis was made to determine combining ability estimates of inbreds chosen to represent a wide variation for maturity and photoperiod sensitivity. Trials were conducted under short daylength (SD) environment in Waimanalo and Kauai, and under long daylength (LD) environment in Iowa and extended daylength in Waimanalo. Artificial light was added to extend the daylength in Waimanalo to 16 hours. Maturity related traits evaluated included days to anthesis and silking, anthesis to silking interval (ASI), days to blacklayer formation (BLF), and grain filling period (GFP). Differences among LD and SD means for these traits represented a measure of photoperiod sensitivity. Morphological and agronomic traits were also recorded.

Using the Gardner-Eberhart model (Analysis III), variations among general combining ability (GCA) estimates were found to be much larger than variations among specific combining (SCA) ability estimates for days to anthesis, silking, and BLF expressed under SD conditions. GCA and SCA variations contributed more or less equally to the expression of ASI and GFP. Temperate-derived inbreds such as B73 (Hi), Hi32, and Oh43 (Hi) exhibited significantly large but negative estimates indicating that they were high combiners for early maturity. Tropical-derived inbreds such as Hi34, Tx601 (Hi), and Tzi4 were high combiners for late maturity. Relatively high GCA estimates suggested the



preponderance of additive genetic variations for these traits. Significant and large SCA estimates were obtained from several crosses, suggesting that they made use of non-additive genetic variation (dominance and epistasis). Estimates for heterosis, in most cases, were high. Heterosis was entirely attributable to non-additive genetic variation and the negative estimates proved that earliness was dominant over lateness. Therefore, the high GCA/SCA ratio did not necessarily indicate that non-additive genetic action was less important in the inheritance of these traits.

The use of artificial light to extend daylength in Waimanalo was effective in eliciting photoperiodic response among entries. An advantage of this system was a better control of temperature effects since the control (unlighted) and treated plants were exposed to the same temperature fluctuations. Photoperiod sensitivity index obtained from light studies was highly correlated with the index obtained from actual flowering delay (Iowa vs. Hawaii). The magnitude of the delay (using GDD), however, was generally greater under light experiment than actual delay. This was attributed to the fact that average effective daylength under light in Waimanalo was longer than in Iowa by about an hour. Besides, the plants were exposed to a constant daylength from planting to flower initiation in Waimanalo, while in Iowa, daylength was relatively shorter at early

stages and gradually increased to about 16 hours. A better system that will closely simulate Corn Belt daylength would require a much larger space and expenses.

Photoperiod sensitivity indices expressed as delays to anthesis, silking, and BLF turned out to be highly correlated and any of them could be effectively used as an index. However, silking delay was regarded a better index because it accounted for the delay in the period between anthesis and silking (ASI) which was highly affected by daylength. Moreover, silking date was much easier to measure than blacklayer formation. GFP delay was not a good index because as a derived datum it was more susceptible to measurement errors.

Variations due to GCA effects were higher than SCA effects for all of the sensitivity traits studied. Temperate-derived lines were high combiners for low photoperiod sensitivity, while the tropical-derived lines were high combiners for high photoperiod sensitivity. Most of the temperate x tropical crosses showed intermediate responses, and in some cases, more to the low side as exhibited by high negative SCA estimates. Heterosis estimates were highly significant and indicated the dominance of insensitivity. GCA estimates for maturity and photoperiod sensitivity were highly correlated which suggested a common genetic control. Since GCA reflects additive genetic variation, selection for maturity per se

was predicted to result in lowering of photoperiod sensitivity.

Plants grown under long days produced enormous amount of biomass. Highly sensitive lines grew very tall and showed excessive leafiness. There was, however, no corresponding increase in grain yield as most of the photosynthates were diverted to vegetative parts as evidenced by large reduction in harvest index. It was postulated that photoperiod affected assimilate supply (source) more than the sink.

Generation mean analyses (GMA) were conducted to estimate the relative contribution of main genetic effects (additive and dominance) and digenic epistatic effects for maturity expressed as days to silking and photoperiod sensitivity expressed as silking delay. Scaling tests revealed the presence of epistatic effects, so that a six-parameter model was fitted. Additive and dominance effects were highly significant in a majority of the crosses. Magnitude of the estimates varied with type of cross. In general, dominance effects had greater magnitude than additive effects for the two traits. Significant amounts of interloci (epistasis) interaction particularly additive x additive and dominance x dominance were detected and thought to bias the estimates of the main genetic effects. However, the three epistatic effects seemed to cancel each other in majority of the crosses.

Genetic variance components were computed for maturity and heritability estimates were high for broad sense but low for narrow sense. They could not be computed for photoperiod sensitivity, since silking delay was a derived datum and no individual plant measurement was possible. Heritability values reflected the high dominance genetic variance relative to additive genetic variance. Gene number varied with the types of crosses and environments and ranged from one to three under SD and one to 19 under LD. Two to four genes seemed to be the mode among the important crosses. These gene numbers fall within the range of loci number identified for silking recently reported using RFLP mapping (Grant et al., 1989).

Divergent mass selection for silking date was initiated in two maize population (MIRSYN 1 and HIC 4g) developed by UH. Selection was effective in changing silking date in both directions after three cycles. Selection for early silking resulted in silking date reduction of about two days per cycle while selection for late silking resulted in silking date increase of a little less than two days per cycle. Earliness and lateness were accompanied by corresponding decrease and increase of plant height, respectively. Leaf number was highly and positively correlated with silking date.

An important objective of the study was to determine the correlated effects on photoperiod sensitivity. Results

indicated that selection for early and late silking resulted in corresponding decrease and increase of photoperiod sensitivity. Selection for late silking, however, elicited greater response (increasing photoperiod sensitivity) than did selection for early silking on lowering photoperiod sensitivity. This supported previous observations that photoperiod appeared to have stronger effects on late maturing genotypes. A corollary suggestion was that genetic control of SD maturity and photoperiod sensitivity were related and this relationship was threshold in nature. Regression analysis predicted a 0.60 day reduction in photoperiod sensitivity (silking delay) for every day reduction in SD maturity (silking date). Accuracy of this prediction is about 80%.

The following conclusions were arrived at based on the foregoing findings:

- a) Extensive genotypic variation for maturity and photoperiod sensitivity were found among tropical-adapted maize inbreds. Sources for photoperiod tolerance were found mostly among temperate-derived lines; there were practically no tropical-derived lines insensitive to photoperiod.
- b) High GCA/SCA ratios may not necessarily mean that additive gene action was relatively more important than non-additive gene action, since heterosis

(entirely attributable to non-additive gene action) estimates were large.

- c) There were significant amounts of additive and dominance genetic variations determined from generation mean analysis. In most cases, however, estimates of dominance gene effects were larger than additive gene effects. Large amounts of epistatic gene effects were detected, but since they canceled each other, dominance gene effects were deemed to be the main contributors to the inheritance of maturity and photoperiod sensitivity.
- d) Maturity and photoperiod sensitivity appeared to be controlled by few genes (between two and four).
- e) Maturity expressed under short daylength conditions and photoperiod sensitivity appeared to be under the same genetic control. Pleiotropism was most likely behind this relationship.

## Appendix 1. Growing degree days (GDD) to anthesis.

Entries	Short Daylength			Long Daylength		
	Wai2	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	881	818	850	1327	1072	1200
B73 (Hi)	832	802	817	948	835	892
Hi29	906	833	870	1125	934	1029
Hi32	826	775	800	930	844	887
Hi34	1017	895	956	1383	1234	1308
Narino 330-S6	1023	961	992	1340	1243	1292
Oh43 (Hi)	851	770	810	997	853	925
Tx601 (Hi)	1023	909	966	1407	1148	1277
Tzi4	1029	981	1005	1236	1344	1290
Ant C-S5 x B73 (Hi)	813	797	805	985	907	946
Ant C-S5 x Hi29	875	797	836	1125	975	1050
Ant C-S5 x Hi32	813	786	800	1055	917	986
Ant C-S5 x Hi34	931	865	898	1283	1062	1172
Ant C-S5 x Narino 330-S6	900	865	882	1236	1077	1157
Ant C-S5 x Oh43 (Hi)	788	759	774	1029	912	971
Ant C-S5 x Tx601 (Hi)	919	854	886	1388	1114	1251
Ant C-S5 x Tzi4	942	870	906	1364	1274	1319
B73 (Hi) x Hi29	844	786	815	1061	922	992
B73 (Hi) x Hi32	794	770	782	936	812	874
B73 (Hi) x Hi34	900	823	862	1107	929	1018
B73 (Hi) x Narino 330-S6	881	844	863	1055	929	992
B73 (Hi) x Oh43 (Hi)	788	743	766	913	794	853
B73 (Hi) x Tx601 (Hi)	919	813	866	1119	932	1026
B73 (Hi) x Tzi4	919	849	884	1132	997	1064
Hi29 x Hi32	869	775	822	1010	867	939
Hi29 x Hi34	931	834	882	1150	996	1073
Hi29 x Narino 330-S6	931	870	900	1138	1028	1083
Hi29 x Oh43 (Hi)	813	797	805	998	872	935
Hi29 x Tx601 (Hi)	936	875	906	1185	992	1089
Hi29 x Tzi4	942	890	916	1141	1121	1131
Hi32 x Hi34	875	807	841	1049	915	982
Hi32 x Narino 330 S-6	906	818	862	1055	934	994
Hi32 x Oh43 (Hi)	807	797	802	930	848	889
Hi32 x Tx601 (Hi)	906	828	867	1113	929	1021
Hi32 x Tzi4	906	865	886	1144	981	1062
Hi34 x Narino 330-S6	948	880	914	1230	1028	1129
Hi34 x Oh43 (Hi)	894	791	843	1055	915	985
Hi34 x Tx601 (Hi)	966	900	933	1288	1007	1148
Hi34 x Tzi4	966	905	936	1321	1167	1244
Narino 330-S6 x Oh43 (Hi)	869	807	838	1042	912	977
Narino 330-S6 x Tx601 (Hi)	948	895	921	1279	1039	1159
Narino 330-S6 x Tzi4	966	920	943	1258	1238	1248
Oh43 (Hi) x Tx601 (Hi)	906	786	846	1061	881	971
Oh43(Hi) x Tzi4	894	781	837	1138	907	1022
Tx601 (Hi) x Tzi4	1017	924	970	1382	1222	1302
Mean	902	838	870	1143	997	1070
LSD (0.05)	24	38	31	54	54	54

## Appendix 2. Growing degree days (GDD) to silking.

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	900	818	859	1661	1177	1419
B73 (Hi)	875	828	852	1049	867	958
Hi29	948	870	909	1230	986	1108
Hi32	863	813	838	1042	867	954
Hi34	1074	929	1001	1613	1299	1456
Narino 330-S6	1061	1003	1032	1418	1353	1386
Oh43 (Hi)	888	818	853	1100	896	998
Tx601 (Hi)	1094	940	1017	1615	1281	1448
Tzi4	1087	1014	1051	1492	1615	1554
Ant C-S5 x B73 (Hi)	832	818	825	1081	935	1008
Ant C-S5 x Hi29	900	818	859	1242	1047	1144
Ant C-S5 x Hi32	851	813	832	1172	944	1058
Ant C-S5 x Hi34	966	895	930	1435	1167	1301
Ant C-S5 x Narino 330-S6	919	895	907	1407	1167	1287
Ant C-S5 x Oh43 (Hi)	826	797	811	1119	926	1023
Ant C-S5 x Tx601 (Hi)	948	879	914	1728	1260	1494
Ant C-S5 x Tzi4	966	889	927	1682	1382	1532
B73 (Hi) x Hi29	888	818	853	1144	944	1044
B73 (Hi) x Hi32	838	797	817	1036	830	933
B73 (Hi) x Hi34	931	849	890	1224	986	1105
B73 (Hi) x Narino 330-S6	936	880	908	1180	964	1072
B73 (Hi) x Oh43 (Hi)	826	759	792	998	812	905
B73 (Hi) x Tx601 (Hi)	960	834	897	1295	991	1143
B73 (Hi) x Tzi4	954	875	914	1310	1078	1194
Hi29 x Hi32	913	818	865	1126	903	1014
Hi29 x Hi34	972	879	925	1308	1067	1187
Hi29 x Narino 330-S6	972	919	945	1246	1106	1176
Hi29 x Oh43 (Hi)	851	828	839	1119	894	1006
Hi29 x Tx601 (Hi)	991	909	950	1327	1062	1195
Hi29 x Tzi4	991	919	955	1262	1277	1270
Hi32 x Hi34	900	834	867	1167	949	1058
Hi32 x Narino 330 S-6	936	860	898	1168	959	1064
Hi32 x Oh43 (Hi)	863	834	848	1049	861	955
Hi32 x Tx601 (Hi)	948	880	914	1278	991	1135
Hi32 x Tzi4	954	880	917	1303	1028	1165
Hi34 x Narino 330-S6	991	919	955	1340	1117	1229
Hi34 x Oh43 (Hi)	931	818	874	1168	959	1064
Hi34 x Tx601 (Hi)	1010	934	972	1441	1073	1257
Hi34 x Tzi4	1004	944	974	1570	1254	1412
Narino 330-S6 x Oh43 (Hi)	894	818	856	1119	929	1024
Narino 330-S6 x Tx601 (Hi)	1010	924	967	1388	1124	1256
Narino 330-S6 x Tzi4	1004	944	974	1377	1297	1337
Oh43 (Hi) x Tx601 (Hi)	948	813	880	1150	914	1032
Oh43(Hi) x Tzi4	942	786	864	1265	940	1103
Tx601 (Hi) x Tzi4	1061	950	1005	1622	1314	1468
Mean	943	868	905	1290	1912	1253
LSD (0.05)	20	40	30	82	76	79



## Appendix 3. Anthesis to silking interval (GDD).

Entries	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Ant C-S5	19	0	9	334	190	262
B73 (Hi)	43	26	35	100	57	79
Hi29	42	36	39	105	96	100
Hi32	37	21	29	112	42	77
Hi34	58	33	46	230	119	174
Narino 330-S5	38	43	41	78	199	138
Oh43 (Hi)	37	48	43	103	78	90
Tx601 (Hi)	71	30	51	208	241	224
Tzi4	58	33	46	256	489	373
Ant C-S5 x B73 (Hi)	19	21	20	96	51	73
Ant C-S5 x Hi29	25	21	23	117	129	123
Ant C-S5 x Hi32	38	27	32	117	50	84
Ant C-S5 x Hi34	35	30	33	153	190	171
Ant C-S5 x Narino 330-S6	19	31	25	171	162	166
Ant C-S5 x Oh43 (Hi)	38	48	43	90	25	58
Ant C-S5 x Tx601 (Hi)	29	11	20	340	263	302
Ant C-S5 x Tzi4	24	24	24	317	195	256
B73 (Hi) x Hi29	44	32	38	82	39	61
B73 (Hi) x Hi32	44	27	35	100	33	66
B73 (Hi) x Hi34	31	26	28	118	102	110
B73 (Hi) x Narino 330-S6	55	36	45	125	63	94
B73 (Hi) x Oh43 (Hi)	38	22	30	85	33	59
B73 (Hi) x Tx601 (Hi)	41	32	36	176	107	141
B73 (Hi) x Tzi4	35	26	30	178	146	162
Hi29 x Hi32	44	43	43	115	66	91
Hi29 x Hi34	41	45	43	158	128	143
Hi29 x Narino 330-S6	42	48	45	108	140	124
Hi29 x Oh43 (Hi)	38	32	35	121	39	80
Hi29 x Tx601 (Hi)	55	34	44	142	126	134
Hi29 x Tzi4	49	39	44	121	282	202
Hi32 x Hi34	25	27	26	118	61	90
Hi32 x Narino 330 S-6	31	42	36	113	46	80
Hi32 x Oh43 (Hi)	56	37	47	119	23	71
Hi32 x Tx601 (Hi)	41	52	47	166	112	139
Hi32 x Tzi4	47	20	34	159	85	122
Hi34 x Narino 330-S6	43	40	41	110	161	135
Hi34 x Oh43 (Hi)	37	27	32	113	80	96
Hi34 x Tx601 (Hi)	44	34	39	153	120	136
Hi34 x Tzi4	38	39	39	249	156	203
Narino 330-S6 x Oh43 (Hi)	25	32	28	78	31	54
Narino 330-S6 x Tx601 (Hi)	63	29	46	110	153	131
Narino 330-S6 x Tzi4	38	25	31	119	108	113
Oh43 (Hi) x Tx601 (Hi)	42	27	34	89	59	74
Oh43(Hi) x Tzi4	48	5	27	128	60	94
Tx601 (Hi) x Tzi4	45	36	40	240	166	203
Mean	40	31	36	147	118	132
LSD (0.05)	18	22	20	58	45	52

## Appendix 4. Growing degree days (GDD) to BLF.

Entries	SD (Wail)	LD (Wai2)
Ant C-S5	1693	2118
B73 (Hi)	1665	1777
Hi29	1660	1981
Hi32	1613	1729
Hi34	1743	2226
Narino 330-S5	1733	2070
Oh43 (Hi)	1638	1771
Tx601 (Hi)	1771	2175
Tzi4	1777	2076
Ant C-S5 x B73 (Hi)	1621	1772
Ant C-S5 x Hi29	1671	2019
Ant C-S5 x Hi32	1654	1928
Ant C-S5 x Hi34	1676	2125
Ant C-S5 x Narino 330-S6	1670	2058
Ant C-S5 x Oh43 (Hi)	1618	1801
Ant C-S5 x Tx601 (Hi)	1738	2168
Ant C-S5 x Tzi4	1682	2185
B73 (Hi) x Hi29	1671	1842
B73 (Hi) x Hi32	1602	1725
B73 (Hi) x Hi34	1728	1941
B73 (Hi) x Narino 330-S6	1688	1861
B73 (Hi) x Oh43 (Hi)	1579	1729
B73 (Hi) x Tx601 (Hi)	1687	2002
B73 (Hi) x Tzi4	1676	2008
Hi29 x Hi32	1694	1861
Hi29 x Hi34	1715	2018
Hi29 x Narino 330-S6	1708	2019
Hi29 x Oh43 (Hi)	1660	1836
Hi29 x Tx601 (Hi)	1714	1918
Hi29 x Tzi4	1724	2064
Hi32 x Hi34	1660	1830
Hi32 x Narino 330 S-6	1699	1879
Hi32 x Oh43 (Hi)	1605	1733
Hi32 x Tx601 (Hi)	1723	1969
Hi32 x Tzi4	1665	2036
Hi34 x Narino 330-S6	1678	2013
Hi34 x Oh43 (Hi)	1660	1848
Hi34 x Tx601 (Hi)	1720	2099
Hi34 x Tzi4	1709	2203
Narino 330-S6 x Oh43 (Hi)	1649	1911
Narino 330-S6 x Tx601 (Hi)	1750	2125
Narino 330-S6 x Tzi4	1743	2093
Oh43 (Hi) x Tx601 (Hi)	1677	1848
Oh43(Hi) x Tzi4	1698	1991
Tx601 (Hi) x Tzi4	1749	2182
Mean	1686	1968
LSD (0.05)	36	52

## Appendix 5. Growing degree days (GDD) for GFP.

Entries	SD (Wail)	LD (Wai2)
Ant C-S5	793	457
B73 (Hi)	790	728
Hi29	712	751
Hi32	750	687
Hi34	669	613
Narino 330-S5	672	653
Oh43 (Hi)	751	671
Tx601 (Hi)	677	560
Tzi4	690	584
Ant C-S5 x B73 (Hi)	789	691
Ant C-S5 x Hi29	771	777
Ant C-S5 x Hi32	804	756
Ant C-S5 x Hi34	710	690
Ant C-S5 x Narino 330-S6	751	651
Ant C-S5 x Oh43 (Hi)	792	681
Ant C-S5 x Tx601 (Hi)	790	439
Ant C-S5 x Tzi4	716	504
B73 (Hi) x Hi29	783	698
B73 (Hi) x Hi32	764	689
B73 (Hi) x Hi34	798	717
B73 (Hi) x Narino 330-S6	751	681
B73 (Hi) x Oh43 (Hi)	754	732
B73 (Hi) x Tx601 (Hi)	727	707
B73 (Hi) x Tzi4	722	698
Hi29 x Hi32	781	735
Hi29 x Hi34	743	710
Hi29 x Narino 330-S6	736	773
Hi29 x Oh43 (Hi)	810	717
Hi29 x Tx601 (Hi)	723	591
Hi29 x Tzi4	733	802
Hi32 x Hi34	759	663
Hi32 x Narino 330 S-6	763	711
Hi32 x Oh43 (Hi)	743	685
Hi32 x Tx601 (Hi)	775	690
Hi32 x Tzi4	711	733
Hi34 x Narino 330-S6	687	673
Hi34 x Oh43 (Hi)	729	680
Hi34 x Tx601 (Hi)	710	658
Hi34 x Tzi4	705	633
Narino 330-S6 x Oh43 (Hi)	755	792
Narino 330-S6 x Tx601 (Hi)	740	737
Narino 330-S6 x Tzi4	739	716
Oh43 (Hi) x Tx601 (Hi)	729	698
Oh43(Hi) x Tzi4	756	726
Tx601 (Hi) x Tzi4	688	559
Mean	743	678
LSD (0.05)	41	42

Appendix 6. Analysis of variance of 9 parents and their 36 crosses for the days to anthesis in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	12.49	**13.02	** 60.41	** 80.75
Parents	8	23.55	**26.09	**109.79	**170.11
Parents vs Crosses	1	28.27	**24.69	** 70.94	**139.86
Crosses	35	9.51	** 9.70	** 48.82	** 58.64
GCA	8	39.07	**37.41	**196.02	**235.54
SCA	27	0.76	** 1.49	** 5.20	** 6.22
Error	88	0.21	0.71	1.11	1.40
GCA/SCA Ratio		51.64	25.09	37.67	37.86
S.E gca		0.16	0.30	0.37	0.42
S.E sca		0.40	0.73	0.91	1.03

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 7. Analysis of variance of 9 parents and their 36 crosses for GDD to anthesis in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	4264	** 3130	** 20131	** 33513
Parents	8	8040	** 6195	** 36841	** 69333
Parents vs Crosses	1	9793	** 5725	** 22659	** 71299
Crosses	35	3243	** 2355	** 16239	** 24246
GCA	8	13264	** 9076	** 65339	** 94704
SCA	27	273	** 364	* 1690	** 3370
Error	88	72	186	372	662
GCA/SCA Ratio		48.51	24.97	38.65	28.10
S.E gca		9.20	4.86	6.87	7
S.E sca		54.34	11.80	16.70	17

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 8. Analyses of variance of 9 parents and their 36 crosses for days to silking in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	14.3 **	14.9 **	119.3 **	155.4 **
Parents	8	28.8 **	27.8 **	202.5 **	402.5 **
Presents vs Crosses	1	35.9 **	30.1 **	159.9 **	435.0 **
Crosses	35	10.4 **	11.5 **	99.1 **	91.0 **
GCA	8	42.7 **	43.0 **	363.3 **	359.8 **
SCA	27	0.9 **	2.2 **	20.9 **	11.3 **
Error	88	0.15	0.87	2.75	3.43
GCA/SCA Ratio		50.07	19.87	17.40	31.79
S.E gca		0.14	0.33	0.59	0.66
S.E sca		0.34	0.81	1.44	1.60

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 9. Analyses of variance of 9 parents and their 36 crosses for GDD to silking in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	4932 **	3441 **	37868 **	56488 **
Parents	8	10066 **	6599 **	65340 **	123748 **
Presents vs Crosses	1	13187 **	6786 **	51020 **	153548 **
Crosses	35	3523 **	2624 **	31213 **	38341 **
GCA	8	14454 **	9732 **	115410 **	150563 **
SCA	27	284 **	518 **	6266 **	5090 **
Error	88	50	207	845	1307
GCA/SCA Ratio		50.93	18.80	18.42	29.58
S.E gca		6.39	5.12	10.36	9.60
S.E sca		37.72	12.45	25.18	23.34

\* significant at 0.05 level of probability

\*\* significant at 0.01 level of probability

Appendix 10. Analyses of variance of 9 parents and their  
36 crosses for ASI (days) in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	0.37 **	0.55 *	15.59 **	19.66 **
Parents	8	0.60 **	0.73 **	26.66 **	68.44 **
Presents vs Crosses	1	0.45 **	0.27	17.84 **	78.23 **
Crosses	35	0.31 **	0.52 *	12.99 **	6.84 **
GCA	8	0.59 **	1.30 **	32.46 **	16.68 **
SCA	27	0.23 *	0.29	7.23 **	3.92 **
Error	88	0.12	0.31	1.46	0.83
GCA/SCA Ratio		2.53	4.53	4.49	4.25
S.E gca		0.02	0.20	0.43	0.32
S.E sca		0.09	0.48	1.05	0.79

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 11. Analyses of variance of 9 parents and their  
36 crosses for ASI (GDD) in 4 environments.

Source	df	Mean Squares			
		Wai 1	Kauai	Wai 2	Iowa
Entries	44	133 **	115 **	4481 **	4178 **
Parents	8	235 **	193 **	8097 **	10694 **
Presents vs Crosses	1	252 **	8	5677 **	15583 **
Crosses	35	106 **	100 *	3620 **	2363 **
GCA	8	197 **	140 *	9047 **	7248 **
SCA	27	79 *	88	2012 **	916 *
Error	88	42	62	434	468
GCA/SCA Ratio		2.50	1.58	4.50	7.91
S.E gca		5.27	2.81	7.42	5.75
S.E sca		31.1	6.83	18.04	13.96

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 12. Analyses of variance of 9 parents and their  
for BLF and GFP (days) in 2 environments.

Source	df	Mean Squares				
		BLF		GFP		
		Wai 1	Wai 2	Wai 1	Wai 2	
Entries	44	8.7 **	72.3 **	3.4 **	18.6 **	
Parents	8	14.0 **	118.3 **	5.6 **	23.5 **	
Parents vs Crosses	1	11.5 **	22.4 **	6.8 **	62.6 **	
Crosses	35	7.4 **	63.3 **	2.8 **	16.2 **	
	GCA	8	25.3 **	244.4 **	4.6 **	26.7 **
	SCA	27	2.1 **	9.6 **	2.3 **	13.1 **
Error	88	0.60	1.18	0.71	0.69	
GCA/SCA Ratio		12.2	25.5	2.0	2.0	
S.E gca		0.28	0.39	0.30	0.30	
S.E sca		0.67	0.94	0.73	0.72	

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 13. Analyses of variance of 9 parents and their  
for BLF and GFP(days) in 2 environments.

Source	df	Mean Squares				
		BLK		GFP		
		Wai 1	Wai 2	Wai 1	Wai 2	
Entries	44	2099 **	21581 **	1388 **	6241 **	
Parents	8	3524 **	35181 **	2458 **	8354 **	
Parents vs Crosses	1	2136 **	6171 **	4709 **	21704 **	
Crosses	35	1773 **	18912 **	1049 **	5316 **	
	GCA	8	6045 **	72781 **	2507 **	9373 **
	SCA	27	507 **	2951 **	617 **	4114 **
Error	88	169	342	208	222	
GCA/SCA Ratio		11.9	24.7	4.1	2.3	
S.E gca		4.6	6.6	26.4	5.3	
S.E sca		10.6	16.0	19.9	12.9	

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 14. Combined analyses of variance for maturity traits (expressed in GDD)  
in 4 environments.

Source	df	Mean Squares								
		Anthesis	Silking	ASI	df	BLF	GPP			
Environments (E)	3	25728227	**30597946	**443528	**	1	5384337	**287980	**	
Reps/Envi	8	2432	**	4584	1145	4	917	1951	**	
Entries	44	176575	**	273380	**	44	51204	**	13277	**
Entries x E	132	28990	**	56792	**	44	19836	**	9610	**
Pooled Error	352	1367		2591	1035	176	767		645	

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

Appendix 15. Analysis of variance of parents and crosses for maturity traits  
(expressed in GDD) in 4 environments.

Source	df	Mean Squares										
		Anthesis	Silking	ASI	df	BLF	GPP					
Entries	44	14715	**	22782	**	1201	**	44	8534	**	2213	**
Parents	8	29106	**	44904	**	2608	**	8	14410	**	2726	**
Parents vs Crosses	1	29189	**	56265	**	4090	**	1	3892	**	11658	**
Crosses	35	11011	**	16769	**	797	**	35	7323	**	1826	**
GCA	8	45363	**	67317	**	2407	**		28519	**	3868	**
SCA	27	833	**	1791	**	320	**	2	1043	**	1221	**
Entries x E	132	9663	**	18931	**	2481	**	44	6612	**	3203	**
Parents x E	24	4885	**	8465	**	771	**	8	6451	**	1802	**
P vs C x E	3	358303	**	719875	**	98026	**	1	118663	**	89401	**
Crosses x E	105	794	**	1296	**	142	**	35	3447	**	1061	**
GCA x E	24	2688	**	4148	**	265	**		13138	**	1980	**
SCA x E	81	233	**	451	**	106	*	2	576	**	788	**
Pooled Error	352	114		216		86		176	128		108	

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.



Appendix 16. Estimates of genetic parameters for  
anthesis (GDD) in 4 environments.

Genetic Parameters	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Mean	902	838	870	1143	997	1070
Mp	932	861	896	1188	1056	1122
Mc	895	832	864	1132	982	1057
H	-37 **	-28 **	-33 **	-56 **	-74 *	-65 **
Parental Estimates						
P1	-50 **	-43 **	-46 **	139 **	16 *	77 **
P2	-100 **	-59 **	-79 **	-240 **	-221 **	-230 **
P3	-26 **	-27 **	-26 **	-63 **	-123 **	-93 **
P4	-106 **	-85 **	-96 **	-258 **	-213 **	-235 **
P5	85 **	35 **	60 **	195 **	178 **	186 **
P6	91 **	100 **	95 **	152 **	187 **	169 **
P7	-81 **	-91 **	-86 **	-191 **	-204 **	-197 **
P8	91 **	49 **	70 **	218 **	92 **	155 **
P9	97 **	121 **	109 **	48 **	287 **	168 **
GCA Estimates						
g1	-26 **	-10	-18 *	58 **	55 **	56 **
g2	-43 **	-33 **	-38 **	-107 **	-91 **	-99 **
g3	-3	-5	-4	-35 **	-12 **	-24 **
g4	-41 **	-30 **	-35 **	-109 **	-93 **	-101 **
g5	36 **	21 **	28 **	61 **	23 **	42 **
g6	27 **	34 **	31 **	34 **	47 **	40 **
g7	-57 **	-57 **	-57 **	-127 **	-116 **	-122 **
g8	51 **	31 **	41 **	108 **	37 **	73 **
g9	56 **	49 **	53 **	118 **	150 **	134 **
SCA Estimates						
s12	-13	7	-3	-98 **	-39 *	-69 **
s13	9	-21	-6	-30	-49 *	-40 *
s14	-16 *	-6	-11	-26	-27	-26
s15	26 **	21 *	23 *	31	2	17
s16	4	8	6	12	-6	3
s17	-24 **	-7	-15	-34 *	-8	-21
s18	-1	0	-1	89 **	40 *	65 **
s19	16 *	-2	7	56 **	87 **	72 **
s23	-5	-8	-6	72 **	42 *	57 **
s24	-17 *	2	-8	20	14	17
s25	12	3	8	21	15	18
s26	3	11	7	-4	-9	-7
s27	-7	1	-3	15	19	17
s28	16 *	-17 *	-1	-14	3	-6
s29	11	1	6	-11	-45 **	-28
s34	17 *	-22	-2	23	-10	7
s35	3	-15	-6	-7	2	-3

## Appendix 16 cont.

Genetic Parameters	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
s36	11	9	10	8	11	9
s37	-22 **	26 *	2	29	19	24
s38	-7	17	5	-20	-15	-18
s39	-6	13	4	-73 **	0	-36 *
s45	-15 *	-16	-15	-35 *	3	-16
s46	24 **	-19	3	-2	-2	-2
s47	9	52 **	31 **	34 *	76 **	55 **
s48	1	-5	-2	-18	3	-8
s49	-4	14	5	4	-58 **	-27
s56	-10	-8	-9	4	-24	-10
s57	21 **	-5	8	-11	26	8
s58	-16 *	16	0	-13	-36 *	-24
s59	-21 **	3	-9	10	12	11
s67	5	-2	1	3	-1	1
s68	-25 **	-2	-14	4	-27	-11
s69	-12	4	-4	-25	59 **	17
s78	18 *	-20	-1	-52 **	-22	-37 *
s79	0	-44 **	-22 *	15	-109 **	-47 **
s89	15 *	12	13	24	53 **	38 *
S.E. gca	3	5	4	7	7	7
S.E. sca	7	12	10	17	17	17

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

- 1 = Ant C-S5
- 2 = B73 (Hi)
- 3 = Hi29
- 4 = Hi32
- 5 = Hi34
- 6 = Narino 330-S6
- 7 = Oh43 (Hi)
- 8 = Tx601 (Hi)
- 9 = Tzi4

Appendix 17. Estimates of genetic parameters for silking (GDD) in 4 environments.

Genetic Parameters	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Mean	943	868	905	1290	1062	1176
Mp	977	892	935	1358	1149	1253
Mc	934	862	898	1274	1040	1157
H	-43 **	-31 *	-37 **	-84 **	-109 **	-97 **

Parental Estimates

P1	-77 **	-74 **	-76 **	303 **	28 **	166 **
P2	-102 **	-64 **	-83 **	-309 **	-282 **	-296 **
P3	-29 **	-23 *	-26 **	-128 **	-163 **	-145 **
P4	-114 **	-80 **	-97 **	-316 **	-282 **	-299 **
P5	98 **	36 *	67 **	255 **	150 **	203 **
P6	85 **	111 **	98 **	60 **	204 **	132 **
P7	-89 **	-74 **	-82 **	-258 **	-254 **	-256 **
P8	117 **	47 **	82 **	257 **	132 **	194 **
P9	111 **	122 **	116 **	134 **	466 **	300 **

GCA Estimates

g1	-38 **	-13 *	-25 **	97 **	72 **	85 **
g2	-44 **	-38 **	-41 **	-132 **	-112 **	-122 **
g3	1	2	1	-59 **	-3 **	-31 **
g4	-39 **	-26 **	-32 **	-127 **	-122 **	-125 **
g5	33 **	25 **	29 **	66 **	36 **	51 **
g6	27 **	38 **	32 **	5	49 **	27 *
g7	-56 **	-63 **	-60 **	-171 **	-155 **	-163 **
g8	58 **	33 **	45 **	149 **	58 **	104
g9	58 **	42 **	50 **	172 **	178 **	175

SCA Estimates

s12	-20 **	7	-7	-158 **	-66 **	-112 **
s13	3	-33 **	-15	-69 **	-63 **	-66 *
s14	-7	-10	-9	-72 **	-46	-59 *
s15	37 **	20	28 **	-2	19	9
s16	-4	9	2	31	6	18
s17	-15 *	11	-2	-80 **	-31	-55 *
s18	-6	-2	-4	209 **	89 **	149 **
s19	12	-2	5	140 **	91 **	115 **
s23	-3	-8	-5	61 *	19	40
s24	-13 *	-2	-7	21	24	23
s25	8	0	4	16	22	19
s26	19 **	18	19 *	33	-13	10
s27	-8	-2	-5	27	39	33
s28	12	-23 *	-5	4	4	4
s29	6	9	8	-4	-29	-17
s34	16 **	-20	-2	38	-11	14
s35	4	-10	-3	27	-6	11

## Appendix 17 cont.

Genetic Parameters	Short Daylength			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
s36	10	17	14	27	20	23
s37	-28 **	27 *	0	76 **	12	44
s38	-2	13	6	-36	-33	-35
s39	-1	14	6	-124 **	62 **	-31
s45	-28 **	-28 *	-28 **	-46	-5	-25
s46	14 *	-14	0	16	-8	4
s47	24 **	61 **	42 **	74 **	98 **	86 **
s48	-5	11	3	-17	15	-1
s49	1	2	1	-15	-68 **	-42
s56	-3	-6	-5	-6	-7	-6
s57	20 **	-6	7	0	38	19
s58	-15 *	14	0	-48	-61 *	-54 *
s59	-21 **	15	-3	58 *	0	29
s67	-11	-18	-15	12	-5	4
s68	-9	-8	-8	-40	-23	-31
s69	-15 *	3	-6	-74 *	30	-22
s78	12 *	-19	-3	-101 **	-29	-65 *
s79	7	-55 **	-24 *	-9	-123 **	-66 *
s89	12	13	13	28	38	33
S.E. gca	3	5	4	10	10	10
S.E. sca	6	12	9	25	23	24

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

Appendix 18. Estimates of genetic parameters for ASI (GDD) in 4 environments.

Genetic Parameters	ShortKauai			Long Daylength		
	Wail	Kauai	Mean	Wai2	Iowa	Mean
Mean	40	31	36	147	65	106
Mp	45	30	37	170	93	131
Mc	39	31	35	141	59	100
H	-6 *	1	-2	-28 **	-35 *	-31 **
						0
Parental Estimates						0
P1	-26 **	-30 **	-28 **	164 **	13 *	88 **
P2	-1	-4	-3	-69 **	-62 **	-65 **
P3	-3	6 *	2	-65 **	-40 **	-52 **
P4	-7 **	-9 **	-8 *	-58 **	-70 **	-64 **
P5	13 **	3	8 *	61 **	-27 **	17 **
P6	-6 **	13 **	3	-92 **	17 **	-37 **
P7	-8 **	18 **	5	-67 **	-50 **	-58 **
P8	26 **	0	13 **	38 **	40 **	39 **
P9	13 **	3	8 *	87 **	179 **	133 **
GCA Estimates						
g1	-12 **	-5	-9 **	38 **	18 **	28 **
g2	-1	-4	-3	-25 **	-21 **	-23 **
g3	4	6 *	5	-24 **	8	-8
g4	2	3	3	-18 *	-29 **	-23 **
g5	-2	2	0	6	12 *	9
g6	0	5	2	-28 **	2	-13
g7	1	-3	-1	-44 **	-39 **	-42 **
g8	7 **	1	4	40 **	21 **	31 **
g9	2	-5	-2	54 **	28 **	41 **
SCA Estimates						
s12	-7	-1	-4	-59 **	-27	-43 *
s13	-5	-11 *	-8	-39 *	-13	-26
s14	9	-3	3	-45 *	-19	-32
s15	11	1 *	6	-33	17	-8
s16	-8	0	-4	19	12	16
s17	10	25 **	17 **	-46 *	-23	-34 *
s18	-4	-16 *	-10	120 **	49 **	85 **
s19	-4	3	0	83 **	4	44 *
s23	2	-1	0	-11	-24	-17
s24	4	-4	0	1	10	5
s25	-5	-3	-4	-4	7	1
s26	16 **	4	10	37 *	-4	16
s27	-2	-3	-2	12	20	16
s28	-4	4 *	0	18	1	10
s29	-5	4	-1	7	16	11
s34	-1	2	0	15	-1	7
s35	1	5	3	35	-8	13

## Appendix 18 cont.

Genetic Parameters	ShortKauai Wail	Kauai	Mean	Long Wai2	Iowa Iowa	Across Mean
s36	-1	6	2	19	9	14
s37	-6	-3 *	-5	48 *	-6	21
s38	6	-4	1	-16	-18	-17
s39	5	7	6	-51 **	61 **	5
s45	-14 *	-11	-12	-11	-8	-9
s46	-11	3	-4	18	-6	6
s47	14 *	5	10	39 *	23	31
s48	-6	17 *	5	1	12	7
s49	5	-9	-2	-19	-10	-15
s56	6	1	4	-9	17	4
s57	-1	-4	-3	10	13	11
s58	1	0	0	-35	-25	-30
s59	0	11	5	48 **	-12	18
s67	-16 **	-1	-8	9	-4	2
s68	16 **	-7	4	-44 *	4	-20
s69	-3	-6	-5	-48 **	-29 *	-39 *
s78	-5	-2	-4	-49 **	-8	-28
s79	6	-18 *	-6	-24	-14	-19
s89	-3	9	3	4	-15	-6
S.E. gca	2	3	3	7	6	7
S.E. sca	6	7	6	18	14	16

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

Appendix 19. Estimates of genetic parameters  
for BLF (GDD) in 2 environments.

Genetic Parameters	SD Wai1	LD Wai2
Mean	1686	1968
Mp	1699	1992
Mc	1682	1962
H	-17 **	-29 **
Parental Estimates		
P1	-6	127 **
P2	-35 **	-214 **
P3	-39 **	-11
P4	-86 **	-262 **
P5	44 **	235 **
P6	34 **	79 **
P7	-61 **	-220 **
P8	72 **	183 **
P9	78 **	84 **
GCA Estimates		
g1	-18 **	51 **
g2	-29 **	-117 **
g3	14 **	-17 *
g4	-22 **	-105 **
g5	12 *	54 **
g6	18 **	37 *
g7	-44 **	-143 **
g8	43 **	87 **
g9	27 **	152 **
SCA Estimates		
s12	-14	-125 **
s13	-7	23
s14	13	20
s15	0	58 **
s16	-12	7
s17	-1	-70 **
s18	31 **	67 **
s19	-9	20
s23	4	14
s24	-29 *	-15
s25	63 **	42 *
s26	17	-22
s27	-29 *	27
s28	-9	69 **
s29	-4	10
s34	20	21
s35	6	19

## Appendix 19 cont.

Genetic Parameters	SD Wai1	LD Wai2
s36	-6	37 *
s37	8	34 *
s38	-25 *	-115 **
s39	1	-33 *
s45	-13	-81 **
s46	21	-15
s47	-10	19
s48	20	24
s49	-22	27
s56	-35 **	-41 *
s57	9	-26
s58	-17	-5
s59	-13	34 *
s67	-7	55 **
s68	7	38 *
s69	16	-59 **
s78	-4	-59 **
s79	33 **	20
s89	-3	-20
S.E. gca	5	7
S.E. sca	11	16

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4



Appendix 20. Estimates of genetic parameters  
for GFP (GDD) in 2 environments.

Genetic Parameters	SD Wai1	LD Wai2
Mean	743.1	677.8
Mp	722.6	633.8
Mc	748.2	688.7
H	25.6 **	54.9 **
Parental Estimates		
P1	70.2 **	-176.8 **
P2	67.0 **	94.6 **
P3	-10.4 *	117.0 **
P4	27.5 **	53.4 **
P5	-53.9 **	-20.5 **
P6	-50.5 **	18.7 **
P7	28.2 **	37.5 **
P8	-45.2 **	-73.6 **
P9	-33.0 **	-50.1 **
GCA Estimates		
g1	19.6 **	-45.9 **
g2	14.7 **	14.7 **
g3	13.3 *	41.9 **
g4	16.3 **	21.9 **
g5	-20.8 **	-12.3 *
g6	-9.0	32.1 **
g7	11.6 *	28.7 **
g8	-15.0 **	-61.4 **
g9	-30.8 **	-19.6 **
SCA Estimates		
s12	6.6	32.9 *
s13	-10.5	92.4 **
s14	19.6	91.4 **
s15	-36.7 **	59.4 **
s16	-7.4	-24.1
s17	13.0	9.7
s18	36.7 **	-142.2 **
s19	-21.3	-119.6 **
s23	6.9	-46.9 **
s24	-15.5	-35.9 **
s25	55.6 **	25.6 *
s26	-2.5	-54.9 **
s27	-20.7	-0.3
s28	-20.6	65.2 **
s29	-9.7	14.3
s34	3.1	-17.6
s35	2.0	-8.0

## Appendix 20 cont.

Genetic Parameters	SD Wai1	LD Wai2
s36	-16.5	10.1
s37	36.5 **	-42.6 **
s38	-24.0	-78.6 **
s39	2.4	91.3 **
s45	15.7	-35.6 **
s46	7.3	-31.3 *
s47	-33.6 **	-54.4 **
s48	25.8 *	41.3 **
s49	-22.5	42.2 **
s56	-31.8 *	-35.2 **
s57	-10.2	-25.3
s58	-2.7	42.6 **
s59	8.1	-23.4
s67	4.2	42.5 **
s68	15.8	78.0 **
s69	31.0 *	15.1
s78	-16.1	42.0 **
s79	26.9 *	28.4 *
s89	-14.9	-48.2 **
S.E. gca	5.14	5.31
S.E. sca	12.48	12.91

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

## Appendix 21. Anthesis delay in GDD.

Entries	Index1	Index2	Index3
Ant C-S5	446	190	350
B73 (Hi)	116	3	75
Hi29	219	27	159
Hi32	105	18	86
Hi34	366	217	352
Narino 330-S6	317	220	300
Oh43 (Hi)	147	2	115
Tx601 (Hi)	384	125	311
Tzi4	207	314	284
Ant C-S5 x B73 (Hi)	172	94	141
Ant C-S5 x Hi29	249	100	214
Ant C-S5 x Hi32	242	103	186
Ant C-S5 x Hi34	352	131	275
Ant C-S5 x Narino 330-S6	336	177	274
Ant C-S5 x Oh43 (Hi)	241	124	197
Ant C-S5 x Tx601 (Hi)	469	195	365
Ant C-S5 x Tzi4	423	331	413
B73 (Hi) x Hi29	217	78	177
B73 (Hi) x Hi32	142	18	92
B73 (Hi) x Hi34	206	29	156
B73 (Hi) x Narino 330-S6	173	48	129
B73 (Hi) x Oh43 (Hi)	125	6	88
B73 (Hi) x Tx601 (Hi)	201	12	160
B73 (Hi) x Tzi4	213	77	180
Hi29 x Hi32	141	-2	116
Hi29 x Hi34	219	65	191
Hi29 x Narino 330-S6	207	97	182
Hi29 x Oh43 (Hi)	185	59	130
Hi29 x Tx601 (Hi)	249	55	183
Hi29 x Tzi4	199	178	215
Hi32 x Hi34	173	39	140
Hi32 x Narino 330 S-6	149	28	133
Hi32 x Oh43 (Hi)	123	41	87
Hi32 x Tx601 (Hi)	206	23	154
Hi32 x Tzi4	237	74	177
Hi34 x Narino 330-S6	283	80	215
Hi34 x Oh43 (Hi)	161	21	142
Hi34 x Tx601 (Hi)	323	41	214
Hi34 x Tzi4	355	201	308
Narino 330-S6 x Oh43 (Hi)	173	43	139
Narino 330-S6 x Tx601 (Hi)	331	91	237
Narino 330-S6 x Tzi4	292	272	305
Oh43 (Hi) x Tx601 (Hi)	155	-26	125
Oh43(Hi) x Tzi4	244	13	185
Tx601 (Hi) x Tzi4	365	205	332
Mean	241	94	200
LSD (0.05)	58	23	43

## Appendix 22. Silking delay in GDD.

Entries	Index1	Index2	Index3
Ant C-S5	761	277	560
B73 (Hi)	173	-9	106
Hi29	282	38	199
Hi32	179	4	117
Hi34	539	225	455
Narino 330-S6	357	292	353
Oh43 (Hi)	212	8	145
Tx601 (Hi)	521	187	431
Tzi4	405	528	503
Ant C-S5 x B73 (Hi)	249	103	183
Ant C-S5 x Hi29	342	146	285
Ant C-S5 x Hi32	321	94	226
Ant C-S5 x Hi34	469	202	371
Ant C-S5 x Narino 330-S6	488	248	380
Ant C-S5 x Oh43 (Hi)	294	101	212
Ant C-S5 x Tx601 (Hi)	780	312	581
Ant C-S5 x Tzi4	716	416	604
B73 (Hi) x Hi29	256	56	191
B73 (Hi) x Hi32	198	-8	116
B73 (Hi) x Hi34	294	55	215
B73 (Hi) x Narino 330-S6	244	28	164
B73 (Hi) x Oh43 (Hi)	172	-13	112
B73 (Hi) x Tx601 (Hi)	335	31	246
B73 (Hi) x Tzi4	356	124	279
Hi29 x Hi32	213	-9	149
Hi29 x Hi34	336	95	262
Hi29 x Narino 330-S6	274	133	231
Hi29 x Oh43 (Hi)	269	43	167
Hi29 x Tx601 (Hi)	336	71	244
Hi29 x Tzi4	271	286	314
Hi32 x Hi34	267	49	191
Hi32 x Narino 330 S-6	232	23	166
Hi32 x Oh43 (Hi)	186	-2	107
Hi32 x Tx601 (Hi)	331	44	221
Hi32 x Tzi4	349	74	249
Hi34 x Narino 330-S6	349	126	273
Hi34 x Oh43 (Hi)	237	28	189
Hi34 x Tx601 (Hi)	431	63	285
Hi34 x Tzi4	566	250	438
Narino 330-S6 x Oh43 (Hi)	225	35	168
Narino 330-S6 x Tx601 (Hi)	378	114	289
Narino 330-S6 x Tzi4	373	293	363
Oh43 (Hi) x Tx601 (Hi)	202	-34	151
Oh43(Hi) x Tzi4	323	-2	239
Tx601 (Hi) x Tzi4	561	253	463
Mean	348	119	271
LSD (0.05)	82	28	63

## Appendix 23. ASI delay in GDD.

Entries	Index1	Index2	Index3
Ant C-S5	315	172	253
B73 (Hi)	57	13	44
Hi29	63	54	61
Hi32	74	5	48
Hi34	172	61	129
Narino 330-S6	39	160	98
Oh43 (Hi)	66	41	48
Tx601 (Hi)	137	170	174
Tzi4	198	431	327
Ant C-S5 x B73 (Hi)	77	32	53
Ant C-S5 x Hi29	92	104	100
Ant C-S5 x Hi32	79	13	51
Ant C-S5 x Hi34	118	155	139
Ant C-S5 x Narino 330-S6	152	143	141
Ant C-S5 x Oh43 (Hi)	52	-12	15
Ant C-S5 x Tx601 (Hi)	311	234	282
Ant C-S5 x Tzi4	293	171	232
B73 (Hi) x Hi29	39	-4	23
B73 (Hi) x Hi32	56	-11	31
B73 (Hi) x Hi34	87	71	81
B73 (Hi) x Narino 330-S6	70	8	49
B73 (Hi) x Oh43 (Hi)	47	-4	30
B73 (Hi) x Tx601 (Hi)	135	66	105
B73 (Hi) x Tzi4	143	112	132
Hi29 x Hi32	72	22	47
Hi29 x Hi34	117	87	100
Hi29 x Narino 330-S6	67	99	79
Hi29 x Oh43 (Hi)	84	1	45
Hi29 x Tx601 (Hi)	87	71	90
Hi29 x Tzi4	72	233	157
Hi32 x Hi34	93	36	64
Hi32 x Narino 330 S-6	83	15	43
Hi32 x Oh43 (Hi)	63	-33	24
Hi32 x Tx601 (Hi)	124	71	92
Hi32 x Tzi4	112	38	89
Hi34 x Narino 330-S6	66	117	94
Hi34 x Oh43 (Hi)	76	43	65
Hi34 x Tx601 (Hi)	108	75	97
Hi34 x Tzi4	211	118	164
Narino 330-S6 x Oh43 (Hi)	53	6	26
Narino 330-S6 x Tx601 (Hi)	47	91	86
Narino 330-S6 x Tzi4	81	70	82
Oh43 (Hi) x Tx601 (Hi)	47	17	40
Oh43(Hi) x Tzi4	79	12	67
Tx601 (Hi) x Tzi4	196	121	163
Mean	107	78	97
LSD (0.05)	63	45	40

## Appendix 24. BLF and GFP delays in GDD.

Entries	BLF	GFP
Ant C-S5	425	-336
B73 (Hi)	112	-61
Hi29	320	39
Hi32	116	-63
Hi34	483	-55
Narino 330-S6	337	-20
Oh43 (Hi)	133	-80
Tx601 (Hi)	403	-117
Tzi4	299	-106
Ant C-S5 x B73 (Hi)	151	-99
Ant C-S5 x Hi29	348	6
Ant C-S5 x Hi32	274	-48
Ant C-S5 x Hi34	449	-20
Ant C-S5 x Narino 330-S6	388	-101
Ant C-S5 x Oh43 (Hi)	182	-111
Ant C-S5 x Tx601 (Hi)	430	-350
Ant C-S5 x Tzi4	504	-212
B73 (Hi) x Hi29	171	-85
B73 (Hi) x Hi32	123	-74
B73 (Hi) x Hi34	213	-81
B73 (Hi) x Narino 330-S6	173	-71
B73 (Hi) x Oh43 (Hi)	150	-22
B73 (Hi) x Tx601 (Hi)	315	-20
B73 (Hi) x Tzi4	332	-24
Hi29 x Hi32	167	-46
Hi29 x Hi34	304	-32
Hi29 x Narino 330-S6	311	37
Hi29 x Oh43 (Hi)	176	-93
Hi29 x Tx601 (Hi)	204	-132
Hi29 x Tzi4	340	69
Hi32 x Hi34	170	-97
Hi32 x Narino 330 S-6	181	-51
Hi32 x Oh43 (Hi)	128	-58
Hi32 x Tx601 (Hi)	246	-85
Hi32 x Tzi4	371	22
Hi34 x Narino 330-S6	335	-13
Hi34 x Oh43 (Hi)	188	-49
Hi34 x Tx601 (Hi)	379	-52
Hi34 x Tzi4	494	-71
Narino 330-S6 x Oh43 (Hi)	262	37
Narino 330-S6 x Tx601 (Hi)	375	-3
Narino 330-S6 x Tzi4	350	-23
Oh43 (Hi) x Tx601 (Hi)	171	-31
Oh43(Hi) x Tzi4	293	-30
Tx601 (Hi) x Tzi4	433	-128
Mean	282	-65
LSD (0.05)	64	57

Appendix 25. Estimates of genetic parameters  
for anthesis, silking and ASI delay (GDD).

Genetic Parameters	Anthesis (Index3)	Silking (Index3)	ASI (Index3)
Mean	199.7	271.0	70.7
Mp	225.8	318.8	93.9
Mc	193.2	259.0	64.9
H	-32.6 **	-59.8	-29.0
Parental Estimates			
P1	124.0 **	241.4 **	116.5 **
P2	-151.1 **	-212.9 **	-62.7 **
P3	-66.5 **	-119.5 **	-53.9 **
P4	-139.4 **	-202.0 **	-55.5 **
P5	126.5 **	136.0 **	8.7
P6	73.9 **	34.5 **	-40.4 **
P7	-111.2 **	-173.8 **	-63.5 **
P8	85.2 **	112.4 **	26.4 **
P9	58.6 **	183.9 **	124.4 **
GCA Estimates			
g1	74.1 **	110.0 **	36.8 **
g2	-60.5 **	-80.8 **	-20.4 **
g3	-19.7 *	-32.7 **	-12.6 *
g4	-65.8 **	-92.6 **	-26.1 **
g5	13.8 *	21.7 *	9.0
g6	9.9	-5.5	-15.9 *
g7	-64.7 **	-103.8 **	-40.8 **
g8	31.9 **	58.4 **	27.0 **
g9	81.2 **	125.2 **	42.9 **
SCA Estimates			
s12	-65.7 **	-105.1 **	-39.3 **
s13	-33.7 *	-51.2 *	-17.8
s14	-15.3	-50.1 *	-35.4 **
s15	-6.5	-19.6	-14.1
s16	-3.0	16.3	19.6
s17	-5.6	-53.6 *	-51.7 **
s18	65.3 **	153.4 **	94.6 **
s19	64.5 **	109.9 **	44.1 **
s23	63.5 **	45.3 *	-17.6
s24	25.1	30.0	5.3
s25	9.7	15.1	5.4
s26	-13.4	-8.8	6.1
s27	19.6	38.1	18.5
s28	-4.9	9.6	9.7
s29	-33.9 *	-24.2	11.9
s34	8.7	15.3	6.6
s35	3.4	13.9	10.0

## Appendix 25 cont.

Genetic Parameters	Anthesis (Index3)	Silking (Index3)	ASI (Index3)
s36	-0.8	9.7	11.7
s37	21.6	44.6 *	25.2
s38	-22.6	-40.4 *	-17.7
s39	-40.1 **	-37.2	-0.5
s45	-0.7	2.8	2.7
s46	-4.7	4.7	10.2
s47	24.6	44.0 *	21.2
s48	-5.6	-3.7	1.5
s49	-32.0 *	-43.0	-12.1
s56	-1.4	-1.9	0.0
s57	-0.1	12.3	13.9
s58	-24.4	-54.2 **	-30.5 *
s59	20.1	31.6	12.5
s67	0.2	18.5	10.8
s68	2.4	-22.9	-24.4
s69	20.8	-15.7	-33.9 *
s78	-35.5 *	-62.0 **	-24.6
s79	-24.8	-41.8 *	-13.3
s89	25.3	20.2	-8.6
S.E. gca	5.5	8.0	5.1
S.E. sca	13.4	19.5	12.4

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4



Appendix 26. estimates of genetic parameters  
for BLF and GFP delay (GDD).

Genetic Parameters	BLF	Index1	GFP
Mean	282.4		-65.3
Mp	292.1		-88.8
Mc	280.0		-59.5
H	-12.1 **		29.3 **
Parental Estimates			
P1	133.0 **		-247.0 **
P2	-180.0 **		27.6 **
P3	28.2 **		127.4 **
P4	-175.9 **		25.8 **
P5	191.1 **		33.3 **
P6	44.8 **		69.2 **
P7	-159.2 **		9.2
P8	111.4 **		-28.4 **
P9	6.5		-17.2 *
GCA Estimates			
g1	69.3 **		-65.5 **
g2	-87.5 **		0.0
g3	-31.4 **		28.5 **
g4	-82.9 **		5.6
g5	41.8 **		8.5
g6	19.2 *		41.1 **
g7	-98.4 **		17.0 *
g8	44.7 **		-46.5 **
g9	125.3 **		11.1
SCA Estimates			
s12	-111.1 **		26.3
s13	30.2		102.9 **
s14	7.2		71.8 **
s15	58.0 **		96.1 **
s16	19.1		-16.7
s17	-68.4 **		-3.3
s18	36.0		-178.8 **
s19	29.1		-98.3 **
s23	10.0		-53.8 **
s24	13.8		-20.3
s25	-21.4		-30.0
s26	-38.8		-52.4 **
s27	55.8 **		20.4
s28	78.1 **		85.8 **
s29	13.8		24.1
s34	1.2		-20.7
s35	13.2		-10.0

## Appendix 26 cont.

Genetic Parameters	Index1	
	BLF	GFP
s36	42.9 *	26.6
s37	25.5	-79.1 **
s38	-89.2 **	-54.6 **
s39	-33.8	88.8 **
s45	-68.7 **	-51.4 **
s46	-35.8	-38.7 *
s47	29.3	-20.9
s48	4.0	15.5
s49	49.0 *	64.6 **
s56	-5.6	-3.4
s57	-35.0	-15.1
s58	12.2	45.3 *
s59	47.3 *	-31.5
s67	61.6 **	38.3 *
s68	31.3	62.2 **
s69	-74.6 **	-15.9
s78	-55.2 **	58.1 **
s79	-13.6	1.6
s89	-17.2	-33.4
S.E. gca	8.64	7.59
S.E. sca	19.8	17.39

\* Significant at 0.05 level of probability.

\*\* Significant at 0.01 level of probability.

1 = Ant C-S5

2 = B73 (Hi)

3 = Hi29

4 = Hi32

5 = Hi34

6 = Narino 330-S6

7 = Oh43 (Hi)

8 = Tx601 (Hi)

9 = Tzi4

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