INHERITANCE OF POPPING EXPANSION
AND
AGRONOMIC TRAITS
IN POPCORN

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By

Linda Lou Burnham Larish

Thesis Committee:

James L. Brewbaker, Chairman
Richard M. Manshardt
Catherine G. Cavalleto

We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Horticulture.

THESIS COMMITTEE

James L. Brewbaker

Chairperson

Catherine G. Cavaletto

Richard W. Manshardt

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1. INTRODUCTION

Popcorn belongs to the species Zea mays in the Family Gramineae and the Tribe Maydeae. This tribe includes eight genera; five are native to an area extending from India to Burma through the East Indies and into Australia. These five genera are:

1. Coix (Job's Tears)
2. Schlerachne
3. Polytoca
4. Chinonachne
5. Trilobachne

The two genera native to the Americas are:

1. Zea
2. Tripsacum

According to the taxonomic classification of Iltis and Doebley (1980), the genus Zea includes six taxa, one of which is cultivated maize, designated as Zea mays spp. mays. Cultivated maize has been divided according to its agricultural use into the groups of dent, pop, flour, flint, sweet and waxy corns (Jugenheimer 1976, Russell and Hallauer 1980). Perhaps the most important morphological distinction between popcorn and the other types of corn lie in the characteristics of its kernel which enable it to pop. In fact, Sturtevant placed the popcorns into a group separate from the other types of maize called Zea ervata based on the kernel's ability to evert or turn inside out upon being heated (Sturtevant 1899).

Popcorn originated in the Americas (Brunson 1955, Jugenheimer 1976). Like the dents, flints and flour type corns, popcorn was grown by the people of the ancient Aztec, Maya and Inca civilizations who inhabited the New World for centuries before its discovery by European explorers (Mangelsdorf 1974). Popcorn probably reached its height of popularity in American society during the early 1900's. In 1913, the U.S.D.A. published a Farmer's Bulletin entitled "Popcorn for the Home" in which the virtues of growing popcorn and fixing it in delectable ways are extolled (Hartley.1913).

Today, the popularity of popcorn in America continues. In 1981, 247 thousand acres were planted to popcorn in the United states. This acreage was largely confined to eleven states, and the total production for 1981 was 777 million pounds of shelled popcorn or an average of 3,142 pounds per acre (Anonymous 1982). At the present time, popcorn is not grown commercially in the State of Hawaii. As far as is known, this is the first time that a genetic study has been made of introduced inbreds, varieties and hybrids and their adaptation to the environmental conditions at the Waimanalo Research Station and the Kauai Branch Station.

This study has dealt with three popcorn breeding populations: (1) A diallel involving five inbred popcorns; (2) A diallel involving six varieties; (3) An analysis of the F1, F2 and backcross generations between two inbred popcorns and one inbred dent. Interest has centered around popping expansion, its mode of inheritance and kernel characteristics that are correlated with it. Yield and its relationship to popping expansion has also been examined. A major component of yield, ear length, has been correlated to length of tassel and central spike. An investigation has also been made into the improvement of standing ability, through ratings for root and stalk lodging. From the popcorn breeding material used in this study, the most promising parents and crosses have been identified. It is hoped that this work will generate information that may be of use to commercial growers as well as plant breeders who are interested in developing popcorn for the State of Hawaii.

2. LITERATURE REVIEW

2.1. HISTORY OF POPCORN

Because of both consumer demands and grower demands, a good popcorn has to meet several criteria which include; (1) high popping expansion, (2) good flavor and freedom from hulls, (3) white color, (4) high yield, (5) sturdy stalks that stand until the crop is harvested and (6) freedom from disease (Eldredge and Lyerly 1943). In the Bulletin of the Iowa Agricultural Experiment Station, are listed nine varieties that were popular with growers during the 1940's and which form the genetic basis of the inbreds which are used today. These nine varieties and their descriptions are as follows:

> Japanese Hulless-(Dwarf Rice, White Hulless) The most popular white variety, has a short fat ear with slender, white kernels. It has a medium high popping expansion (20.4) and gives a tender popped kernel free from hulls.
>
> White Rice-Was the most popular popcorn around 1913. Has a low popping expansion (17.2), coarse hulls and a coarse-textured popped kernel without a distinctive flavor. Ear is large and yields are high. Kernel is broad and somewhat flattened with a very sharp pointed crown. Has a wide range of adaptation.
>
> Queen's Golden-Long slender ear with medium-sized, yellow pearl- type kernels, medium tenderness and freedom from hulls. Late maturing, not popular as a commercial popcorn.
>
> Yellow Pearl-A type name for all yellow varieties with pearl-type kernels. The ear is of medium length and pointed, with medium to small kernels that are deep

yellow in color. Has medium high popping expansion (20.4), fairly free from hulls, is earlier than Queen's Golden and more popular.

Supergold-Was developed by Dr. A.M. Brunson, an agronomist with the U.S.D.A. by ear-to-row selection for high popping volume (22.6). Has slightly less pointed ears than Yellow Pearl and larger kernels, which are deep yellow in color. It is free from coarse hulls and has no strong flavor.

South American-(Dynamite, Mushroom) Yellow Pearl type, ears are medium in length, kernels are large, round and when popped have a distinct yellow color. The popped kernel is very large with a coarse, heavy hull and a distinctive flavor which some people like. It is late maturing. Has a low popping volume (17.6).

Superb-(Superb South American)-A yellow pearl type having a medium thick and short ear, with a large pale yellow kernel. Has coarse hulls and a distinctive flavor. Earlier than South American. Stalks tend to break before harvest. Has a low popping volume (19.2).

Spanish or Eight Row-White pearl type with a slender, medium length ear with eight kernel rows and large kernels. Has a poor popping expansion (14.5) and produces a tough popcorn with heavy hulls. Stalks tend to fall over after ears ripen.

Tom Thumb-Name for several distinctly different small-eared types. One type is very early with blunt ears, bearing pearl- type, yellow kernels. The other is extremely late with very small slender ears bearing rice-type, small, yellow kernels. The plant produces many tillers and each tiller bears several ears; the yield is large but difficult to harvest. When popped the kernels produce a small very tender popcorn without hulls and with a flavor that many people like. It has a fairly high popping expansion of 20.1.

Only a few of these nine varieties formed the basis for the breeding work that followed in the popcorn producing states. The first hybrid popcorn was developed from a selection of Japanese Hulless called Michigan Pop. Inbreeding began for the development of this hybrid in 1925 and the single cross hybrid seed was finally released in 1934. At the Purdue University Agricultural Experiment Station, inbred lines were developed from the varieties South American and Supergold between 1938 to 1941 (Brunson and Smith 1945, Brunson 1937). It is these inbred lines which form the basis of the synthetics and hybrids that Purdue produces today (Ashman 1986).

2.2. POPPING EXPANSION

According to Weatherwax and Randolph (1955) popping expansion is conditioned by the proportion of horny endosperm in the kernel, the elastic colloidal material that confines it and the steam pressure that is built up within the kernel until it reaches explosive force. Popcorn pops between 172.8 C to 197.8 C depending upon the moisture content of the kernels; a high moisture sample begins to pop at a lower temperature than a sample with low moisture (Huelsen and Bemis 1954). When the pericarp ruptures, the moisture in the kernel vaporizes, providing the driving force for expansion of the kernel (Hoseney et al. 1983). It has been recognized by all popcorn breeders and even home consumers that much of the ability of popcorn to pop depends upon the kernel moisture content. However, there seems to be a difference of opinion on what that moisture content should be. In the early years of popcorn breeding, from

1913 until 1927, it was reported that the moisture content should be held at 12% for maximum popping expansion (Hartley and Willier 1913, Willier and Brunson 1927). In 1943, Eldredge and Lyerly reported that it should be between 12 and 13%, but after 1952, it was decided that 13.5 +/- 0.5% should be the optimum moisture content (Johnson and Eldredge 1952, Robbins and Ashman 1984).

For making comparison tests of popping expansion, it is critical that all of the samples are tested at the same moisture percentage. The ideal moisture content for field harvesting is approximately 17.4% (Lien and Haugh 1975). Bemis and Huelsen (1959), caution that forced air drying at 110 F is injurious to popcorn with a moisture content above 25%. Ashman (1986) recommends conditioning the popcorn samples on the cob after harvesting in a room with the temperature and humidity kept at 70 F and 70% respectively. The proper grain moisture of 13.5 to 14% should be reached in about 3 weeks. After reaching the correct moisture, the samples can be stored in moisture proof jars until they are popped. It has been shown that rewetting over-dried samples to 14.0% reduces popping expansion but if the samples are rewetted to about 14.5% variations in sample moisture of -1.0% would have much less effect on the popping expansion data than it would if the samples are conditioned to 14.0% (Ashman 1986). Bemis and Huelsen (1955) reported that the amount and severity of endosperm fracturing were directly related to the rate of rehydration but that this fracturing did not impair popping expansion. White et al. (1980) found that endosperm fracturing caused by conditioning reduced popping expansion. Moisture testing is usually done with an electronic type moisture tester such as a Burrows Model 700 or Dickey-John moisture tester (Ashman 1986).

It has also been recognized by all popcorn breeders that those kernels with the least amount of soft starch within a variety give the greatest popping expansion. However, measuring the proportion of soft starch in the endosperm is a very tedious, time-consuming task (Willier and Brunson 1927), so that it is not used as a screening method by popcorn breeders.

In an attempt to determine if any relationship existed between kernel morphology and popping expansion, a number of plant breeders through the years have taken measurements of kernel weight, dimensions and volume. Willier and Brunson (1927) found that the smaller than average kernels gave the greatest popping volume with the correlation of expansion being greatest with the length of the kernel and least with the thickness. Lyerly came to the conclusion that the "smaller, shorter, and narrower kernels " gave the greatest popping expansion (Lyerly 1942). In 1949, another group of researchers came to the similar conclusion that smaller kernels gave a higher popping volume than large kernels

(Crumbaker et al. 1949). Haugh et al. (1976), in a somewhat contradictory study of 12 popcorn hybrids, found that greater kernel weight and specific gravity was positively correlated with higher popping expansion.

The most useful criteria to breeders is that the popping expansion of an inbred gives a reliable index of its expected performance in a hybrid cross (Lyerly 1942). If there is a positive correlation between kernel characteristics for thickness and density and popping expansion, as Lyerly (1942) also indicated, then we may be reasonably confident in selecting inbreds or varieties for a mating scheme on the basis of kernel morphology. However, breeders usually do not predict popping expansion in this manner. Instead, the kernels are actually popped and their popping volume is assessed, based on the units of popped corn obtained from a given volume of unpopped corn. So that, if a sample of 100 cubic centimeters of unpopped corn gives 2,400 cubic centimeters of popped corn, that sample is designated as having a popping expansion of 24 (Brunson 1937, Eldredge and Lyerly 1943). A popping expansion of from 18-20 volumes is considered to be fair, 21-26 volumes is good and 27 volumes or above is considered to be excellent (Brunson and Smith 1945).

Another method used is to measure cubic centimeters of popped corn per gram of unpopped corn. This is useful when samples to be popped are from individual ears, in which case a standard sample of 40 grams is taken from the middle section of each ear and combined with a standard 35 grams of popcorn from a commercial variety to reach the electric popper's minimum requirement of 75 grams (Robbins and Ashman 1984).

Popcorn is usually popped in oil using an electric type popper. Maximum popping expansion is said to be achieved if the popper is plugged into a rheostat that reduces the voltage to 70% of the line voltage (Ashman 1984). The major reason that the microwave oven has not been used for popping experimental samples is that a greater number of unpopped kernels are generated than with a hot oil popper (Ashman 1986). However, if samples are to be popped by microwave, the oven should have a power output of at least 600 watts, because the internal temperature of the kernel has to reach 330 to 410 F before it will pop. In addition, popping must be done in a special microwave bag and at least 20 minutes must be allowed between popping samples for the microwave to "cool down" (Anonymous 1986). Roshdy et al. (1984), reported that using a Presto hot air popper, the mean temperature at the center of the kernels was 191.2 C when 100 grams were popped and 187.0 C when 20 grams were popped.

2.3. DESIRABLE QUALITIES OF POPCORN

2.3.1. Tenderness and Hulls

Tenderness seems to accompany a high popping expansion (Brunson and Smith 1945). In a quality test of the nine varieties listed previously, Japanese Hulless and Tom Thumb were rated as the best for tenderness and freedom from hulls (Eldredge et al. 1945). Richardson (1959) found that the inheritance of thin hulls is controlled by a major dominant gene while a modifier complex controls the inheritance of thick hulls.

2.3.2. Flavor

Flavor of popped corn can range from bland to sweet to strongly disagreeable. According to Brunson and Smith (1945), undesirable flavors can be eliminated from hybrids by selecting inbreds with good flavor.

2.3.3. Popped Kernel Shape

There are two types of popped kernel shape: The mushroom type which puffs up when heated and the more common butterfly type which inverts when heated. The variety of popcorn called South American is known to "mushroom" when it is popped, producing a large popped kernel (Brunson 1937, Brunson and Smith 1945).

2.3.4. Color

When popped, yellow kernels turn a cream color compared to white kernels which turn a chalky white. Although red and blue kernels also turn white when they are popped, their dark colored hulls give the popped corn an appearance that consumers do not like. Kernel color is carried either in the pericarp or the aleurone layer of the kernel (Eldredge and Lyerly 1943, Brunson and Smith 1945).

2.3.5. Yield

Unfortunately, breeders have found that higher yields accompany lower popping expansion. It has been suggested that "the genetic constitution necessary to produce extremely high yields also produces too much soft starch in the centers of the kernels..." (Brunson 1937), so that a compromise must be made between either yield or popping expansion.

2.3.6. Standing Ability

The ability of the crop to stand without lodging until harvest is a very important consideration to the popcorn grower (Brunson and Smith 1945). Most inbred lines and their hybrids have weak stalks and are prone to lodging; it is for this reason that outcrosses to dent and flint corns have been made (Crumbaker et al. 1949, Robbins and Ashman 1984).

2.3.7. Resistance to Disease and Insects

Control of insects and disease is particularly important to the popcorn crop because of their effect on the quality of the popped product. Ear rots and stalk rots are the most serious diseases attacking the crop, while the European corn borer and the corn ear worm are the most important insect pests (Brunson 1937, Brunson and Smith 1945). In Hawaii, resistance to rust (*Puccinia sorghi*) is of major importance (Kim 1974).

2.4. BREEDING METHODS

2.4.1. Mass Selection

In corn, selection of superior ears and seed has been practiced by growers in the U.S. since the 1800s (Jenkins 1936). It has been used as a method to improve varieties without resorting to inbreeding. Mass selection is begun among varieties by selecting a large number of ears from desirable plants and then numbering them for identification. A small, identical amount of seed is taken from each ear to test for popping expansion. Selection is based upon popability, so that from each variety only ears are saved for seed that rank in the top 10-15% in popping expansion. In this way, selection for each variety is based on popping expansion after which the best 50 or more ears are bulked together for planting the next mass selection plot (Brunson 1937).

The advantages of mass selection are that the generation interval is minimized and it makes maximum use of the additive genetic variability present in the population before extracting inbred lines for hybridization. The most serious limitation is that it is based upon phenotypic selection of plants at a single location. Modifications to the procedure to reduce environmental sources of variation would be; to grow each mass selection population in isolation, reduce competition between plants by reducing the number of plants per acre and using a "grid system" of selection (Jugenheimer 1976).

According to Brunson (1937), there is a constant drag of regression toward the mean of the population when selecting for high popping expansion. Therefore, the breeder cannot expect the average popping expansion of the crop produced to be as high as the average of the selected ears from which it was planted. However, mass selection has proved to be effective in improving popping expansion, as was demonstrated by the variety Supergold. Over a six year period, breeders were able to increase its popping expansion from 19 to 26 volumes (Brunson 1937).

2.4.2. Recurrent Selection

There are four different kinds of recurrent selection, the main difference between them being the nature of the test parent. There is simple recurrent selection, recurrent selection for general combining ability, recurrent selection for specific combining ability, and reciprocal recurrent selection. In simple recurrent selection, S1 lines are evaluated and selections are made among them for constituting the next population to be selected (Rao 1983). Recurrent selection for specific combining ability, proposed by Hull (1945), uses a single homozygous line as a tester. Selection of superior lines from the population is based on performance of the topcrossed progenies with the tester. Recurrent selection based on general combining ability relies on the use of a heterozygous population as a tester. The tester may be a variety or a double cross. In the reciprocal recurrent selection method, two heterozygous populations are tested at the same time by testing source A plants against source B plants and source B plants against source A plants (Comstock et al. 1949).

2.4.3. Pedigree or Ear-to-row Selection

Named "ear-to-row', this method is based on the concept of planting one row of corn for each ear and then selecting seed from the most productive rows (Jenkins 1936). This method proved to be disappointing, not only did it require more hand labor but it also introduced a certain amount of inbreeding and offered no advantage over mass selection (Brunson 1937, Jenkins 1936).

2.4.4. Backcrossing to the Recurrent Parent

Most inbred lines of popcorn and their hybrids do not have strong stalks and are vulnerable to lodging. Because of this weakness, it was thought that field corn could be used as the non-recurrent parent in a backcross breeding program to add genes for lodging resistance to popcorn. The success of the program depended on recovery in segregating generations of popcorn quality characteristics such as high popping expansion (Crumbaker et al. 1949, Johnson and Eldredge 1952). This was a very serious concern, because as all popcorn growers know, seed should not be saved for planting from popcorn that has accidentally hybridized with field corn, causing the F1 progeny to give a commercial crop with very reduced popping expansion (Lyerly 1942).

Results of the backcross breeding program for resistance to lodging indicated that it was possible to recover popping volume of the recurrent popcorn parent by the second backcross while improving agronomic traits such as plant vigor, stalk diameter and brace root development. In addition, all of the three-way crosses with recovered popcorn lines were higher in yield than the original parents in the same crosses. This increased yield was attributed to an increase in ear size. The data suggest that genes for combining ability were retained during backcrossing. Even though popping volume of the recovered lines were initially lower than the original popcorn parents, after one and two generations of backcrossing, it was sufficiently recovered to justify the agronomic improvement added through outcrossing to dent corn (Johnson and Eldredge 1952). Usually, effective homozygosity is reached by the sixth or seventh generation of backcrossing to the recurrent parent (Simmonds 1979).

In another backcross breeding program, Robbins and Ashman (1984) compared the progeny of dent x popcorn to flint x popcorn. They hypothesized that since flint corn has endosperm characteristics and popping ability closer to that of popcorn, it should give an advantage over dent corn in recovery of high popping expansion. However, their results showed that flint x pop crosses were not superior to dent x popcorn crosses and it was suggested that agronomic characteristics may be more important than endosperm hardness when selecting a non-popcorn parent for use in a backcross breeding program (Robbins and Ashman 1984).

2.5. HYBRID DEVELOPMENT

The first hybrid popcorn developed was Minhybrid 250. It is a small-eared, small-kerneled hybrid that is reported to have increased in yield by 16% and in popping expansion by 20% over its original progenitor, Japanese Hulless. However, it was limited in adaption to the northern edge of the Corn Belt and in other popcorn producing areas it did not give good yield or standing ability. At the same time that Minhybrid 250 was being developed in Minnesota, breeders at the Kansas Agricultural Experiment Station were testing some inbred lines from a yellow pearl popcorn. At the end of the breeding program in 1931, the resulting hybrids were superior to the foundation material but inferior to the variety Supergold, which had been improved by mass selection. Because of this, the inbred lines were discarded and new ones were started from Supergold and a good strain of South American. Later, six years of severe drought forced the breeding program to move to the Purdue University Agricultural Experiment Station in Lafayette, Indiana. There the program met with success and resulted in the development of four Supergold lines; Sg16, Sg18, Sg30A, Sg32 and one South American line, SA24 (Brunson 1937, Brunson and Smith 1945).

The hybrids that were developed at Purdue and also at the Iowa Agricultural Experiment Station were the result of either single or three-way crosses. At Iowa, it was found that the best hybrid was the result of a three-way cross which gave a 20% increase in yield and a 20% increase in popping expansion over the foundation variety Japanese

Hulless. Single crosses and three-way crosses can be used in popcorn, unlike dent corn, since the inbred lines are more vigorous and easier to propagate than dent inbred lines (Brunson 1936, Brunson and Smith 1945).

As was stated earlier, popping expansion of an inbred line gives a reliable estimate of how it will perform in a hybrid combination. This indicates that general combining ability for popping expansion is the rule, but in some cases an inbred line will exhibit specific combining ability (Brunson 1955). It has also been noted that popcorn hybrids between inbreds from different varieties give the most outstanding increases in yield (Brunson 1937, Brunson and Smith 1945). This example of heterosis is also true for dent corn. As indicated earlier, there is a tendency toward a negative correlation between yield and popping expansion.

2.6. CROSS STERILITY

Many varieties of popcorn will not set seed when pollinated by certain other varieties of popcorn, but the reciprocal crosses are fertile (Brunson 1955). According to Nelson (1953), the genetic basis for this non-reciprocal cross sterility is found on the fourth chromosome. On that chromosome there is a multiple allelic series at the ga locus such that Ga/Ga "cross-sterile" plants will not set seed if pollinated by "normal" ga/ga plants, but will be fertilized by pollen from itself, another "cross-sterile" plant or a "neutral" Ga/Ga plant. When both ga and Ga pollen tubes are competing in ga/Ga styles, only the Ga gametes will fertilize the ovary. Nelson (1951) explains that the mechanism behind this cross-sterility is probably due to a reaction between the diploid style and the haploid pollen tube. That is why the growth of ga pollen tubes in Ga/Ga silks is halted, while in ga/Ga silks it is slowed to the point where it is unable to compete with Ga pollen tubes.

The following is a list of some varieties that were tested for cross-sterility (Brunson 1955):

Cross-sterile Ga /Ga	Neutral Ga/Ga	Normal ga/ga
South American	White Rice	Supergold
Japanese Hulless		Baby Golden-1
Black Beauty		Early Yellow
Ohio Yellow		All sweet corn
Amber Pearl		All dent corn
Yarling Yellow		
Strawberry Pop		
Baby Golden-2		
Tom Thumb		

By backcrossing, Nelson (1952) found it fairly easy to transfer the gene for cross-sterility from one inbred to another. Using this method, it would be easier to produce hybrid seed with a variety like Supergold by barring it from being fertilized by any nearby dent or sweet corn.

2.7. DIALLEL ANALYSIS

The diallel cross is defined as all possible combinations of single crosses among 'n' parents, designated as n squared. As the number of parents increases, the number of single crosses increases rapidly. In a half diallel, designated as [n(n-1)/2], if n=5 there are 10 crosses, but if n=50 there would be 1225 single crosses. Because of this problem, methods of design have been developed which only utilize part of the possible matings in a diallel cross (LeClerg 1965). These designs are known as partial diallels, but for this thesis, we will only be concerned with the half diallel.

The four assumptions underlying the analysis of information from a diallel cross (Griffing 1956) are: (1) the set of parents is a random sample from a population or a chosen or fixed set; (2) the parents are inbred lines derived from a parent population free from forces which change gene frequency; (3) segregation is normal and diploid; and (4) linkage is absent. With these assumptions, Griffing (1956) also designed four different forms of analysis: (1) parents, one set of F1's and reciprocal F1's included; (2) parents, one set of F1's but reciprocal F1's not included; (3) one set of F1's and reciprocal F1's but parents are not included and (4) one set of F1's but neither parents nor reciprocal F1's are included.

Gardner and Eberhart (1966) presented a model for the estimation of genetic effects from the diallel cross of a fixed set of varieties. Their model also assumes arbitrary gene frequencies at all loci, diploid inheritance, two alleles per locus and no epistasis. The Gardner and Eberhart model is designed for parents and one set of F1's. Their analysis partitions variation into Varieties vs. Crosses which reflects average heterosis, and general and specific combining ability. Analysis 3 partitions variation due to heterosis into variation due to average, variety and specific heterosis.

Both the Griffing (1956) and Gardner and Eberhart (1966) models are concerned with the estimation of genetic effects seen in a diallel cross. These effects are partitioned into general and specific combining ability. Sprague and Tatum (1942) have defined general combining ability as the average performance of a line in hybrid combination. While specific combining ability is representative of those cases where a hybrid performs better or worse than expected based on the average performance of the parental lines.

Most critics of diallel analyses conclude that the assumption that genes are independently distributed is untenable. Linkage of genes would violate this assumption (Baker 1978). Hayman (1954b) found that the degree of ydominance may be overestimated due to lack of independence of genes in the parents. When using the Griffing or Gardner and Eberhart diallel analysis, it is also necessary to assume that there is no epistasis. Since this is an unrealistic assumption, interpretation of these analyses should be limited to estimating general and specific combining ability mean squares and effects. Extrapolation of statistical results to include distribution of alleles, dominance and number of genes or in terms of additive and dominance genetic variance is building on false assumptions (Baker 1978).

3. MATERIALS AND METHODS

3.1 PLANTING MATERIALS

Three trials were conducted for this thesis, an inbred diallel, a variety diallel and an analysis of generation means. The inbred diallel involved five inbred popcorn parents which were selected after extensive germplasm screening over previous years at the University of Hawaii's Waimanalo Research Station in Waimanalo, Hawaii. The parents selected and consequently planted with their ten hybrids were as follows:

Line	Origin	Derivation	Seed Type & Color
I28	Minnesota	Japanese Hulless	Yellow pearl pop
Sg18	Indiana	Supergold	Yellow pearl pop
Sg1533	Indiana	Supergold	Yellow pearl pop
R18-1-9	Indiana	Sg18 "recovered"	Yellow pearl pop
KP58K	Kansas	S.A. x SA24	Yellow pearl pop

I28 is an inbred line developed from the open pollinated variety, Japanese Hulless, at the Minnesota Agricultural Experiment Station. Sg18 and Sg1533 are sib-lines derived from the variety Supergold while R18-1-9 is a dent sterile recovery of Sg18 (communication with Dr. Robert B. Ashman, 3-17-89). "Dent sterile recovery" means that an inbred line of Sg18 was outcrossed to an inbred line that was dent or cross sterile, so that it could not be fertilized by pollen from dent, sweet and some types of popcorn. This inbred was then "recovered" by backcrossing to the recurrent parent (Nelson 1952). KP58K is an inbred developed from a cross between the open pollinated variety, South American and one of its inbreds, SA24.

The variety diallel involved six popcorn open pollinated varieties and their 15 hybrids. The parental varieties selected after preliminary screening at the Waimanalo Research Station were as follows:

Line	Origin	Seed Type & Color
Curagua Grande	Chile	White flint
Avati Pichinga	Paraguay	Yellow rice pop
Supergold	Indiana	Yellow pearl pop
Japanese Hulless	Indiana	White hulless pop
Philippine Pop #1	Philippines	Yellow pearl pop
Philippine Pop #6	Philippines	White rice pop

Curagua Grande is an open pollinated variety which originated in Chile and is thought to be a hybrid between Curagua, a popcorn, and Cristalino Chileno, a flint (Timothy et al. 1961). Avati Pichinga is one of the two main races of popcorn used by the Guarani Indians who once occupied parts of northern Argentina, eastern Uraguay, southern Brazil, the Bolivian lowlands and nearly all of Paraguay (Brieger et al. 1958). According to F. G. Brieger, the variety South American, origin of ihbred KP58K, was derived from Avati Pichinga. Supergold is an open pollinated variety which was developed at the Kansas Experiment Station by Dr. Arthur M. Brunson and Japanese Hulless is an old open pollinated variety popular with growers in the 1940's. Both

Philippine Pop numbers 1 and 6 are open-pollinated varieties from the Philippines, bred following the association of Dr. Brunson with the University of the Philippines College of Agriculture at Los Banos.

The generation mean analysis (gma) involved crosses between two popcorn inbreds and a dent inbred, carried out to the F2 and backcross generations. The three inbred lines were as follows:

Line	Origin	Derivation	Seed Type & Color
Hi26	Hawaii	CI21E(=K577CxHy)BC2)	Yellow dent
I28	Minnesota	Japanese Hulless	Yellow pearl pop
Sg18	Indiana	Supergold	Yellow pearl pop

Hi26 is an inbred developed at the Waimanalo Experiment Station from CI21E, using a derived line from India, CM202. The pedigrees of I28 and Sg18 were mentioned previously.

3.2 FIELD PREPARATION AND TRIAL LAYOUT

The sites where the inbred diallel, variety diallel and generation mean analysis (gma) were planted included the Waimanalo Research Station and the Kauai Branch Station in Hawaii and the International Institute of Tropical Agriculture at Ibadan, Nigeria. The Waimanalo Research Station is located on the island of Oahu at an elevation of 20 m and receives approximately 1380 mm of rainfall each year, while the Kauai Branch Station is located on the island of Kauai at an elevation of 200 m and receives a much higher average annual rainfall of 2100 mm. The International Institute of Tropical Agriculture (IITA) is located at an elevation of 150 m. Both IITA and the Waimanalo Research Station conduct irrigated trials while the Kauai Branch Station must depend on adequate rainfall.

The inbred diallel was planted at the Waimanalo Research Station on July 16, 1987 and at the Kauai Branch Station on August 18, 1987. At the Kauai Station, Dr. Ramon de la Pena and Mr. James Oshita coordinated the trial. At both locations, the trial was planted in a randomized complete block design with four replications. Each plot consisted of two rows, 3.7 m long and 76 cm apart, containing approximately 28 plants. At the Kauai Branch Station, 10.7 inches of rain fell between the planting date and flowering. Due to the heavy rainfall and an ensuing blight, the trail was destroyed so that no data was recorded from the Kauai location.

At the Waimanalo Research Station, the trial field was prepared by applying 600 lbs/acre of 16-16-16 together with a supplement of treble superphosphate and Eradicane or Sutan at preplant time. Lasso and Atrazine were applied as preemergent herbicides. Approximately one month after planting, urea was applied as a side dressing at the rate of 300 lbs/acre. At the Kauai Branch Station, 474 lbs/acre of

16-16-16 was applied to the trial field at preplant time and 360 lbs/acre of urea was applied as a side dressing approximately one month later.

The variety diallel was planted at the Waimanalo Research Station on February 3, 1987, at the Kauai Branch Station on June 3, 1987 and at IITA in May, 1987. At all three sites the trial was planted in a randomized complete block design with four replications. At Waimanalo and Kauai the plots consisted of two rows 6.7 m long and 76 cm wide while at IITA, one row plots were planted which were 5 m long. The plots at IITA contained approximately 22 plants while the plots at Waimanalo and Kauai contained approximately 60 plants each.

Field preparation for the variety diallel at the Waimanalo Research Station involved the same procedures used for the inbred diallel except that it was necessary to apply Roundup to control the nutgrass in replication four on February 17, 1987. Unfortunately, this damaged maize in the plots and forced the replanting of replication four in the prepared field next to trial two on March 5, 1987. At the Kauai Branch Station the field was prepared for planting the variety diallel by applying 560 lbs/acre of 16-16-16. A side dressing of urea was applied to the trial one month later at the rate of 426 lbs/acre.

The gma was planted at the Waimanalo Research Station on September 17, 1987 and at the Kauai Branch Station on November 10, 1987. The three parents and their F1, F2 and backcross generations were planted in a randomized complete block design with four replications. Each plot consisted of four rows that were 6.7 m long and 75 cm apart and contained approximately 120 plants. Field preparation for this trial at the Waimanalo Research Station and the Kauai Branch Station was the same as for the other trials at these locations. At the Waimanalo Research Station heavy rainfall and strong winds knocked down some plots before preharvest data was collected. Because of the rain and loss to birds grain yield results were lower than expected.

3.3 PREHARVEST DATA

For the inbred diallel, preharvest data were collected on ten plants chosen at random from the center of each plot. For the variety diallel, preharvest data were recorded from five plants chosen at random from the center of each plot at the Waimanalo and IITA sites, and from ten plants at the Kauai site. For the gma, preharvest data were collected from twenty tagged plants in the center two rows at the Waimanalo site and from twenty five plants at the Kauai site. The same number of measurements were taken for the parents, F1, F2 and backcross progenies at both locations.

Preharvest character measurements for all three trials were as follows:

o Plant height, measured in cm from plant base to top of the tassel.

o Ear height, measured in cm from plant base to node bearing the highest ear.

o Length of the central spike, measured in cm from the uppermost tassel branch to the top of the tassel.

o Tassel length, measured in cm from the lowest branch of the tassel to the top of the tassel.

o Days to silking, taken as the date when at least half of the plants in the plot have silks 2 to 3 cm long.

o Ear number, recorded as the number of silking ears on each plant.

o Tiller number, recorded as the number of axillary stems.

o Stalk lodging, recorded as the number of plants broken on a scale of 1-5, where 1 is no breakage, 2 is broken below tassel, 3 is broken above ear, 4 is broken below ear and 5 is broken and on the ground. Where recorded as a percentage of all plants in the plot, a plant is lodged when it is broken between the ear and the ground.

o Root lodging, recorded as the number of plants leaning on a scale of 1-5, where 1 is no leaning, 2 is 25 leaning, 3 is 45 leaning, 4 is 65 leaning and 5 is on the ground.

o Plant aspect, judged at the brown husk stage on characteristics such as plant and ear height, uniformity, degree of disease and insect damage on a scale of 1 to 5, where 1 is excellent and 5 is poor. Where recorded as the percentage of all plants in the plot, lodged refers to plants that are leaning 45 or more.

o Husk cover, taken as the number of ears in each plot that had any portion of the ear exposed, rated on a scale of 1 to 5.

o Curvularia, taken as the disease resistance rating for each plot on a scale of 1 to 5, where 1 is not susceptible and 5 is very susceptible.

o Rust, taken as the rating of disease resistance to *Puccinia sorghi* Schw. on a scale of 1 to 10, where 1 is not susceptible and 10 is very susceptible.

3.4 POSTHARVEST DATA

After each trial was harvested, data were taken on the following characteristics:

o Ear aspect, recorded after husking on qualities such as disease and insect resistance, ear size, grain fill and uniformity of ear on a scale of 1 to 5.

o Ear rot, incidence of ear and kernel rots caused by *Diplodia spp.*, *Fusarium spp.*, or *Gibberella spp.* on a scale of 1 to 5.

o Ear length, recorded as the grain filled length in cm of each ear.

o Ear diameter, recorded as the grain filled diameter of each ear.

o Kernel row, recorded as the number of kernel rows for each ear.

o Kernel depth, calculated as half the average difference in mm between the ear diameter and cob diameter for ten ears in the diallel analysis and as the length in mm from the crown to the base of an individual kernel in the gma.

o Kernel width, recorded as the maximum distance in mm from one side of a kernel to the other in the diallel analysis and as the distance in mm from the germinal to the abgerminal side of a kernel (same as kernel thickness) in the gma.

o Kernel thickness, recorded as the distance in mm from the germinal to the abgerminal side of a kernel in the diallel analysis.

o Kernel weight, taken as the weight in grams of 100 kernels at 15% moisture x 100 to give 1000 kernel weight.

o Popping expansion, recorded as the volume in cubic centimeters of popped kernels divided by their weight in grams before popping. Corn was popped in a Presto Popcorn Now Plus hot air popper in half cup units which were previously weighed. At the end of popping, the weight of unpopped kernels was subtracted from the kernels' initial weight. Volume of the popped kernels was measured using 2,000 and 1,000 cc graduated cylinders. Prior to popping, popcorn was conditioned to a moisture between 13.0% to 13.6%, as measured by a Burrows 700 Digital Moisture Computer.

o Grain yield, taken as the shelled grain weight per plant in kilograms times the number of plants for each plot, adjusted to 15% moisture and multiplied by a factor based on the plot size and planting density to get kilograms per hectare. For the gma, grain weight for each ear was arrived at by multiplying the weight of 100 kernels times the number of kernels for each ear. Ear grain weight was then multiplied by the ratio of plants per plot to plants per hectare to arrive at kilograms per hectare.

3.5 DATA ANALYSIS

For the inbred diallel, combining ability was analyzed using model 1 of Griffing (1956) in which the genotypes are assumed to be a chosen or fixed set of constants. In model 1, the genotypes constitute a population from which the combining ability of parents can be compared and outstanding hybrid combinations can be identified. Method 2 was used for analysis in which the parents and one set of F1 are included but not the reciprocal F1. This results in $p(p+1)/2$ different genotypes.

For the variety diallel, Gardner and Eberhart's Analysis 3 (1966) was used to arrive at the general and specific combining ability. For the gma, Mather's (1949) model to estimate additive, dominance and error variance was used in the absence of epistasis and the six parameter analysis of Hayman (1958) and Jinks and Jones (1958) was used when there was significant non-allelic interaction.

4. INBRED DIALLEL

4.1 RESULTS

The five popcorn inbred parents and their ten hybrids were planted at the Waimanalo Research Station on July 16, 1987. At the Waimanalo Research Station 3.15 inches of rainfall was recorded between the date of planting and flowering. Also during this period, the mean high temperature was 84.7 F and the mean low was 74.6 F. The daily mean for the index of growing degree days was 29.6. The analysis of variance and Griffing's fixed model, method 2 were done using Lotus 123. The results obtained using Lotus 123 were further validated using MSTAT's Griffing's diallel analysis, and the two-way analysis of variance.

4.2 MEAN VALUES

Array mean values for the 17 characteristics measured are summarized in Tables 4.1 to 4.17 together with the overall means of parents and hybrids, least significant differences (LSD) among parents and hybrids, coefficient of variation (CV) for each character and average heterosis. Average heterosis was calculated between the parents and hybrids excluding crosses between R18-1-9, Sg1533 and Sg18

(1), and only between the parents R18-1-9, Sg1533, Sg18 and their hybrids (2). This was done to compare the heterosis of crosses among sib-lines with crosses that had at least one parent not in common. CV's were very low for grain yield, popping expansion, days to silking, plant height, ear height, ear length, ear diameter, kernel row, kernel depth, tassel length and length of central spike, indicating the uniformity of the experimental field and for popping expansion, the consistency of measurements. For measurements that were not quantitative, but based on scores or percentages, CV's were very high, indicating that these measurements should have been scored on a larger scale (1-10) with smaller increments and percentages should not have been used.

4.2.1. Grain Yield

Hybrids exceeded inbreds in grain yield by 48%. Heterosis was 131%, excluding crosses between sib-lines and only 24% among sib-lines. It is commonly observed that the yield of hybrids among inbreds exceeds the sum of the two parent lines (Hull 1945). The lower yields among the sib-lines reflects the action of inbreeding depression. According to Good and Hallauer (1977), grain yield is reduced by a factor of -.45 q/ha with each sib-mating. Altogether, F1 means ranged from 2875.29 kg/ha to 5367.21 kg/ha. KP58K produced the highest yielding hybrids with a

Table 4.1. Mean values for grain yield (kg/ha) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	1788.13	4907.72	4735.09	4338.88	4866.74	4712.11	CV (%) = 14.27	130.77
KP58K		1247.17	4999.28	5367.21	4737.82	5003.01	LSD(F1) = 32.95	
R18-1-9			2523.66	3060.17	2875.29	3917.46	AVG(F1) =4326.27	
Sg1533				2112.05	3374.45	4035.18	LSD(P) = 30.61	24.30
Sg18					2853.85	3963.58	AVG(P) =2104.97	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.2. Mean values for popping expansion (cc/g) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	24.87	23.39	34.55	29.50	33.00	30.11	CV (%) = 3.39	-3.24
KP58K		34.98	35.27	29.60	32.10	30.09	LSD(F1) = 1.25	
R18-1-9			34.70	31.55	32.75	33.53	AVG(F1) = 31.34	
Sg1533				31.80	31.64	30.57	LSD(P) = 1.64	-4.70
Sg18					34.17	32.37	AVG(P) = 32.1	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.3. Mean values for days to silking of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	47.00	45.25	46.00	45.00	47.00	45.81	CV (%) = 2.74	-6.31
KP58K		47.75	47.25	45.00	46.50	46.00	LSD(F1) = 1.83	
R18-1-9			52.25	48.75	48.75	47.69	AVG(F1) = 46.75	
Sg1533				47.25	48.00	46.69	LSD(P) = 1.93	-3.48
Sg18					51.25	47.56	AVG(P) = 49.1	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

array mean of 5003.01 kg/ha which was 676.74 kg/ha above the F1 average. Crosses of R18-1-9, Sg1533 and Sg18 with I28 averaged 3103.3 kg/ha, while crosses of the sib-lines with KP58K averaged 4857.56 kg/ha. The highest yielding cross occurred between KP58K and Sg1533, resulting in a grain yield of 5367.21 kg/ha. According to 'Popcorn Production and Marketing' (Ziegler et al. 1984) popcorn yields for the years 1977 through 1981 averaged 2846 pounds per acre, which is equivalent to 3187.5 kilograms per hectare. Yields obtained at Hawaii were very good in comparison

4.2.2. Popping Expansion.

F1 means ranged from 23.39 cc/g to 35.27 cc/g with an LSD of 1.25. Heterosis was -3.24% excluding crosses between sib-lines and -4.7% among sib-lines. R18-1-9 had the highest array mean for its hybrids of 33.53 cc/g. In crosses with I28 and KP58K, R18-1-9 showed heterosis of 13.7% with I28 and only 1.3% with KP58K. I28 showed a higher heterosis than KP58K in combination with Sg1533 and Sg18 also. This higher heterotic effect is partly due to its poor popping performance as an inbred. R18-1-9 gave the highest popping expansion in combination with KP58K of 35.27 cc/g, but in combination with Sg1533 and Sg18, popping expansion for R18-1-9 was reduced below its parental volume of 34.7 cc/g. Hybrids between R18-1-9, Sg1533 and Sg18 were below the LSD of 1.25 for F1, because of the close relationship among them. Contrary to the literature, a significant negative correlation between yield and popping expansion was not found.

4.2.3. Days to Silking

F1 means ranged from 45 days to 48.75 days with an LSD of 1.83. The F1 average was 2.35 days earlier than the inbred average. Heterosis was -6.31% excluding crosses between sib-lines and -3.48% among sib-lines. Inbreeding is known to cause lengthening in the number of days to silking (Hallauer and Miranda 1981), which is reflected in the more positive heterosis among the sib-lines. According to Good and Hallauer (1977), sib-mating increases the number of days to silking by a factor of .04 with each mating because of the reduction in plant vigor with increased homozygosity. I28 produced hybrids with the shortest number of days to mid-silking of 45.8. The crosses between the sib-lines R18-1-9, Sg1533 and Sg18 were very close, with a range of only 0.75 days.

4.2.4. Plant Height

The F1 means ranged from 199.4 cm to 272.2 cm with an LSD of 19.46. Heterosis was 28.2% excluding crosses between sib-lines and only 4.27 among sib-lines. Again, this reflects inbreeding depression among the sib-lines, when according to Good and Hallauer (1977), plant height is reduced by .53 cm with each sib-mating. KP58K and I28

Table 4.4. Mean values for plant height (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	190.63	264.23	243.70	217.40	249.25	243.65	CV (%) = 5.93	28.22
KP58K		196.00	272.23	254.73	260.95	263.04	LSD(F1) = 19.46	
R18-1-9			201.70	199.40	210.70	231.51	AVG(F1) = 238.31	
Sg1533				184.53	210.50	220.51	LSD(P) = 18.87	4.27
Sg18					208.98	232.85	AVG(P) = 196.37	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.5. Mean values for ear height (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	89.5	128.3	119.9	104.8	123.3	119.1	CV (%) = 8.71	30.86
KP58K		85.4	126.1	120.4	121.0	123.9	LSD(F1) = 13.34	
R18-1-9			98.6	97.7	102.4	111.5	AVG(F1) = 114.44	
Sg1533				84.8	100.6	105.9	LSD(P) = 14.02	5.23
Sg18					102.3	111.8	AVG(P) = 92.11	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.6. Mean values for ear length (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	11.78	16.75	14.18	14.50	13.73	14.79	CV (%) = 4.24	36.84
KP58K		11.78	15.05	15.43	15.63	15.72	LSD(F1) = 0.89	
R18-1-9			10.23	11.20	11.25	12.92	AVG(F1) = 13.91	
Sg1533				9.78	11.38	13.13	LSD(P) = 0.59	7.77
Sg18					11.38	13.00	AVG(P) = 10.99	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

expressed the greatest heterosis, with their array means being 25 and 5 cm respectively above the F1 average.

4.2.5. Ear Height

Mean values for ear height presented in Table 4.5 followed the same pattern as plant height. The F1 ranged from 97.7 cm to 128.3 cm in ear height with an LSD of 13.34. Ear height increased by 19% from the inbred parents to their F1. Heterosis was 31.0% excluding crosses between sib-lines and only 5.2% among sib-lines. According to Good and Hallauer (1977), each cycle of sib-mating reduces ear height by .36 cm. The lowest eared hybrids was produced by Sgl533, with an array mean height of 105.9 cm, while KP58K produced hybrids with the highest set ears with an array mean of 123.9 cm. KP58K and I28 exhibited array mean values 9 and 5 cm respectively above the F1 average while R18-1-9, Sgl533 and Sgl8 had array mean values 3.0, 8.0 and 3.0 cm, respectively, below the F1 average due to the depressed heights in crosses with each other.

4.2.6. Ear Length

F1 means ranged from 11.2 cm to 16.75 cm with an LSD of 0.89. The F1 produced ears 21% longer than their inbred parents. Heterosis was 36.8% excluding crosses between sib-lines and only 7.8% among sib-lines. According to Good and Hallauer (1977), sib-mating reduces ear length by .42 mm with each cycle of mating. KP58K produced hybrids with the longest ears, having an array mean of 15.72 cm. The average of crosses R18-1-9, Sg1533 and Sg18 with I28 was 14.1 cm, while the average with KP58K was 15.4 cm. The crosses of the sib-lines with I28 and KP58K did not differ significantly from each other. The F1 array mean of I28 and KP58K were both 0.8 and 1.8 cm above the F1 average, while those of R18-1-9, Sg1533 and Sg18 were 1.0, 0.8 and 0.9 cm, respectively, below the F1 average. The crosses between R18-1-9, Sg1533 and Sg18 averaged 2.6 cm below the F1 average and did not differ in ear length significantly from each other.

4.2.7. Ear Diameter

The F1 ranged from 2.85 cm to 3.38 cm with an LSD of 0.1. Heterosis was 8.5% excluding crosses between sib-lines, while between sib-lines it was 5.0%. Again, this is in agreement with Good and Hallauer (1977), who observed that each sib-mating reduced ear diameter by .085 mm. KP58K produced the narrowest ears with an array mean for its hybrids of 2.97 cm while I28 produced the widest ears with an array mean of 3.26 cm. The hybrids between R18-1-9, Sg1533 and Sg18 only differed by 0.05 cm.

4.2.8. Ear Number

The F1 average was 2.04 ears per plant with an LSD of 0.33. I28 produced hybrids with the highest number of ear per plant with an array mean of 2.09, however, array means

Table 4.7. Mean values for ear diameter (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	2.94	3.10	3.35	3.38	3.19	3.26	CV (%) = 2.43	8.51
KP58K		2.31	2.95	2.98	2.85	2.97	LSD(F1) = 0.1	
R18-1-9			2.96	3.19	3.21	3.18	AVG(F1) = 3.13	
Sg1533				3.03	3.13	3.17	LSD(P) = 0.13	4.96
Sg18					3.09	3.10	AVG(P) = 2.87	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.8. Mean values for ear number of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	1.70	2.10	2.15	2.05	2.05	2.09	CV (%) = 12.1	5.57
KP58K		2.13	1.98	2.03	2.05	2.04	LSD(F1) = 0.33	
R18-1-9			2.03	2.13	1.98	2.06	AVG(F1) = 2.04	
Sg1533				1.95	1.88	2.02	LSD(P) = 0.37	1.35
Sg18					1.93	1.99	AVG(P) = 1.95	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.9. Mean values for ear aspect of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	4.00	1.50	2.00	2.13	2.50	2.03	CV (%) = 21.58	-55.75
KP58K		4.00	1.75	1.75	2.00	1.75	LSD(F1) = 1.05	
R18-1-9			5.00	3.63	3.50	2.72	AVG(F1) = 2.48	
Sg1533				5.00	4.00	2.88	LSD(P) = 0.7	-20.50
Sg18					4.00	3.00	AVG(P) = 4.4	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

only varied by 0.04 ears. There was only an increase in 0.09 ears from the parental average to the F1 average. Mean square analysis of variance of ear number showed no significance between entries, therefore this characteristic will be dropped from further consideration in this diallel.

4.2.9. Ear Aspect

Ear aspect, which can be seen in Table 4.9, shows a 44% improvement from the parents to their F1. The F1 ranged from 1.5 to 4 and had an LSD of 1.05. KP58K gave the best quality ears with an F1 array mean of 1.75 while Sg18 produced the poorest quality ears with an F1 array mean of 3.0. CV for ear aspect was a high 21.58%, indicating the difficulty in standardizing such an empirical rating. Because of the high CV, this characteristic will not be analyzed further in this section. Analysis of variance and analysis for general and specific combining ability can be seen in Appendix A.

4.2.10. Kernel Row

F1 mean values ranged from 11.2 to 18.1 rows with an LSD of 0.71. Surprisingly, heterosis was higher at 7.5%, for crosses among sib-lines than it was for hybrids excluding between sib crosses. R18-1-9 produced hybrids with the greatest number of kernel rows, having an array mean of 16.3 while KP58K produced hybrids with the fewest number of kernel rows with an array mean of 12.9. The three

Table 4.10. Mean values for kernel row number of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals		H(%)
I28	14.55	13.45	18.15	15.28	17.30	16.05	CV (%) =	3.78	3.73
KP58K		10.50	14.00	11.20	13.00	12.91	LSD(F1) =	0.71	
R18-1-9			16.70	16.50	16.55	16.30	AVG(F1) =	15.12	
Sg1533				13.00	15.80	14.70	LSD(P) =	0.98	7.48
Sg18					15.75	15.66	AVG(P) =	14.1	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.11. Mean values for kernel depth (mm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals		H(%)
I28	4.56	5.19	6.04	5.81	5.06	5.53	CV (%) =	7.37	20.69
KP58K		3.00	4.94	4.88	4.75	4.94	LSD(F1) =	0.51	
R18-1-9			4.75	5.13	5.44	5.38	AVG(F1) =	5.24	
Sg1533				4.31	5.13	5.23	LSD(P) =	0.65	11.06
Sg18					5.06	5.09	AVG(P) =	4.34	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.12. Mean values for tassel length (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals		H(%)
I28	26.80	34.28	34.73	34.78	35.43	34.81	CV (%) =	3.22	18.52
KP58K		32.38	38.53	37.63	38.98	37.36	LSD(F1) =	1.47	
R18-1-9			30.13	33.65	34.10	35.25	AVG(F1) =	35.6	
Sg1533				32.43	33.93	35.00	LSD(P) =	1.87	8.04
Sg18					31.55	35.61	AVG(P) =	30.66	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

related sib-lines, R18-1-9, Sg1533 and Sg18, were significantly different from each other in kernel row number except for R18-1-9 and Sg18 whose difference was below the 0.05 level of significance for LSD. In crosses with I28 and KP58K, R18-1-9 and Sg18, had an average kernel row number of 16.1 and 15.2, respectively, while Sg1533 was much lower with an average of 13.2 kernel rows.

4.2.11. Kernel Depth

Heterosis was 20.7% for hybrids excluding crosses between the sib-lines and only 11.1 among the sib-lines. According to Good and Hallauer (1977), the estimate of inbreeding depression for kernel depth was 0.066 mm for each cycle of sib-mating. F1 mean values for kernel depth ranged from 4.75 mm to 6.04 mm with an LSD of 0.51 mm. I28 increased kernel depth among its hybrids resulting in an F1 mean that was 0.29 mm above the F1 average. KP58K was consistent in reducing kernel depth, producing an F1 mean that was 0.30 mm below the F1 average. Kernel depth was significantly different between the related inbreds Sg1533 and Sg18 being greater than the parental LSD of 0.65. The correlation of kernel depth to popping expansion was found to be non significant.

4.2.12. Tassel Length

Hybrids exceeded inbreds by 14% in tassel length, with 18.5% heterosis in the absence of crosses among sib-lines

Table 4.13. Mean values for length of central spike (cm) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	18.30	24.20	22.90	25.80	23.58	24.12	CV (%) = 3.76	18.05
KP58K		23.33	25.03	27.28	25.65	25.54	LSD(F1) = 1.26	
R18-1-9			18.20	23.05	23.28	23.57	AVG(F1) = 24.43	
Sg1533				24.68	23.55	24.92	LSD(P) = 1.46	9.34
Sg18					21.03	24.02	AVG(P) = 21.11	

(1) Heterosis of I28 & KP58K F1: ((F1-MP)/MPx100)
(2) Heterosis of R18, Sg1533 & Sg18 F1: ((F1-MP)/MPx100)

Table 4.14. Mean values for tiller number of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals	H(%)
I28	0.15	1.18	1.15	1.38	1.03	1.19	CV (%) = 56.61	18.05
KP58K		0.1	0.53	0.73	0.75	0.80	LSD(F1) = 0.46	
R18-1-9			0.03	0.25	0.23	0.54	AVG(F1) = 0.74	
Sg1533				0.65	0.15	0.63	LSD(P) = 0.51	9.34
Sg18					0.4	0.54	AVG(P) = 0.27	

Table 4.15. Mean values for plant aspect of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals
I28	3.75	2.25	2.50	2.75	2.25	2.44	CV (%) = 30.81
KP58K		3.75	1.75	2.00	2.25	2.06	LSD(F1) = 1.25
R18-1-9			1.75	3.50	3.00	2.69	AVG(F1) = 2.45
Sg1533				3.75	2.25	2.63	LSD(P) = 0.97
Sg18					2.50	2.44	AVG(P) = 3.1

and 8.04% heterosis between sib-lines. The F1 ranged from 33.6 cm to 38.98 cm with an LSD of 1.47. KP58K's hybrid array mean were 1.76 cm longer than the F1 average. R18-1-9, Sg1533 and Sg18 produced hybrids between each other which were not significantly different in tassel length. In hybrid combination with I28 and KP58K, sib-line performance did not vary significantly. The correlation of tassel length to ear length, as can be seen in Figure 4.1, was highly significant, with r=0.68. Anderson (1944) suggested that the entire ear might be homologous with the tassel branches fused for the length of the tassel rather than being homologous to the central spike of the tassel only. This preliminary evidence supports that idea.

4.2.13. Length of Central Spike

Mean values for central spike length, presented in Table 4.13, mirrored those for tassel length. Hybrids exceeded inbreds by 14% in tassel length, with heterosis for crosses excluding sib-lines being 18.1% and heterosis among sib-lines being 9.3%. F1 mean values ranged from 22.9cm to 27.28 cm with an LSD of 1.26. KP58K gave the highest F1 array mean which was 1.11 cm longer than the F1 average. The crosses between R18-1-9, Sg1533 and Sg18 were not significantly different from each other and averaged 1.14 cm below the F1 average, even though there was a significant difference in spike length between them. Correlation

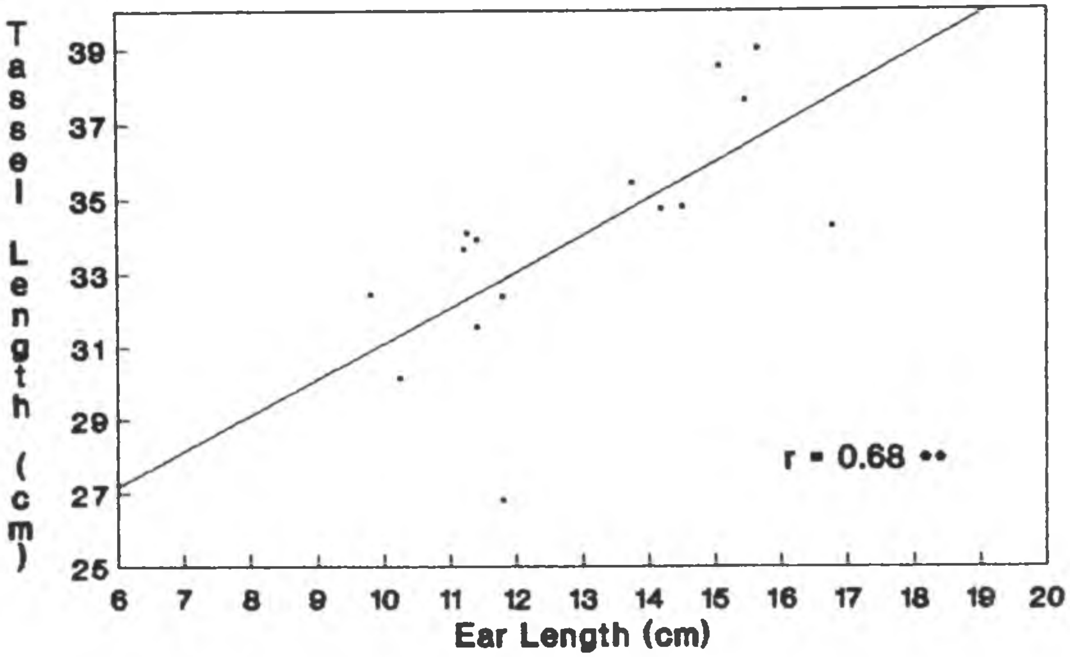


Figure 4.1. Correlation of tassel length to ear length.

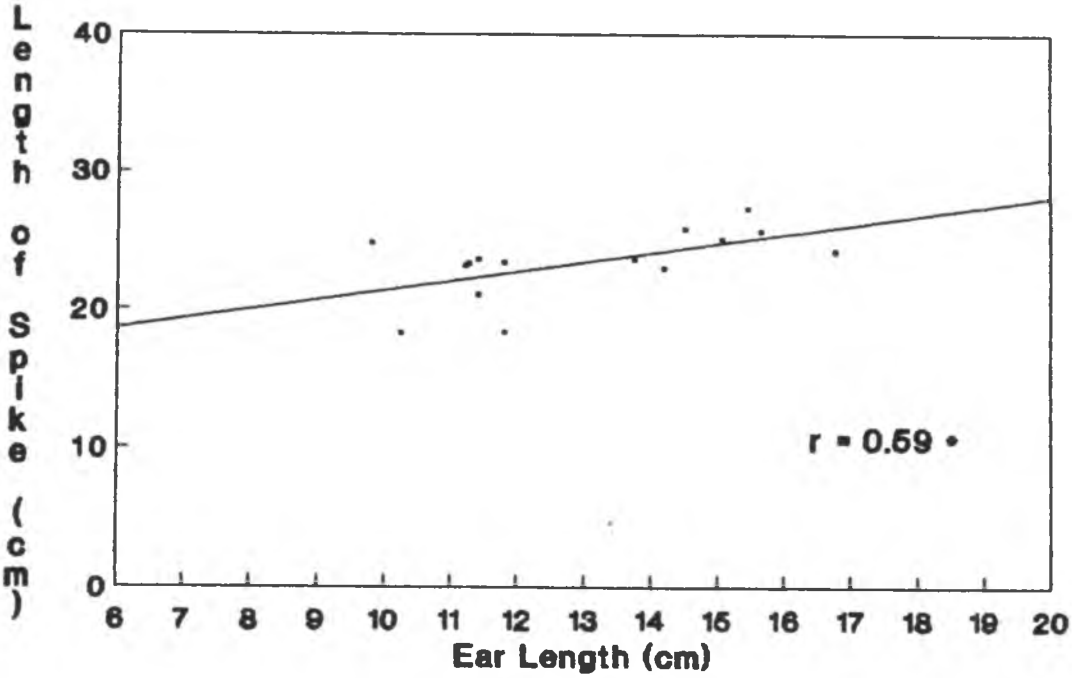


Figure 4.2. Correlation of central spike length to ear length.

between central spike length and ear length was significant at 0.05 level of probability, with r=0.59, as can be seen in Figure 4.2. Central spike length was highly correlated to tassel length, as might be expected, with an r square value of 0.72 significant at 0.01 level of probability.

4.2.14. Tiller Number

Hybrid tiller number ranged from an average of 0.15 tillers per plant to 1.38, with an LSD of 0.46. The number of tillers increased from an inbred average of 0.27 tillers per plant to an F1 average of 0.74 tillers. I28 produced the greatest number of tillers among its hybrids having a F1 mean of 1.19 tillers per plant. However, the CV for this character was 56.6%, indicating that experimental error was unacceptably high because the average number of tillers per plant was either close to 0 or greater than 1. Therefore this character will not be analyzed further in this section. Results of the analysis of variance and analysis of general and specific combining ability can be seen in Appendix A.

4.2.15. Plant Aspect

There was a 26% improvement in plant aspect from the average of the inbreds to the average score of the F1. Array mean values had a range of 0.25 and an average of 2.45, indicating that the F1 were uniform for plant aspect. The range from high score to low for all lines was 2.0, indicating that most ratings were centered around 3.0. CV for plant aspect was 30.81% because of the difficulty in standardizing ratings. Due to the high experimental error, this trait will not be discussed further in this section. Analysis of variance and analysis of general and specific combining ability for plant aspect can be seen in Appendix A.

4.2.16. Stalk Lodging array means ranged from 0.0% to 38.5% with a very high LSD of 19.85%. There was much less stalk lodging among the F1s which showed a 56% improvement over the inbreds, which largely reflected hybrid vigor. I28 had the highest array mean value of 11.56 for the percentage of stalk lodged plants. KP58K, which was the most resistant to stalk lodging as a parent, gave an array mean for its hybrids that was 50% higher than the F1 mean. CV for stalk lodging was 154.36% which indicates that the experimental error was unacceptably high due to the fact that there was such a large statistical difference between plants that showed lodging and those that showed no lodging (0). This trait will not be discussed further in this section, but the analysis of variance and analysis for general and specific combining ability can be seen in Appendix A.

4.2.17. Root Lodging

The percentage of root lodging presented in Table 4.17, indicates that the F1 on the average had a greater number of lodged plants than the inbreds. Array mean values ranged

Table 4.16. Mean values for stalk lodging (%) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals
I28	30.50	38.50	2.25	1.75	3.75	11.56	CV (%) = 154.36
KP58K		0.00	0.00	0.00	0.75	9.81	LSD(F1) = 19.85
R18-1-9			0.75	5.00	11.00	4.56	AVG(F1) = 6.48
Sg1533				29.75	1.75	2.13	LSD(P) = 18.37
Sg18					13.50	4.31	AVG(P) = 14.9

Table 4.17. Mean values for root lodging (%) of inbred diallel.

Parents	I28	KP58K	R18-1-9	Sg1533	Sg18	F1 array mean	Variances and mean totals
I28	0.75	1.75	1.75	5.88	8.50	4.47	CV (%) = 156.57
KP58K		0.00	0.75	6.00	3.25	2.94	LSD(F1) = 8.02
R18-1-9			2.50	0.75	2.00	1.31	AVG(F1) = 3.69
Sg1533				1.75	6.25	4.72	LSD(P) = 7.19
Sg18					8.50	5.00	AVG(P) = 2.7

from 0.75% to 8.5% root lodging with an LSD of 8.02. R18-1-9 had the lowest percentage of root lodging among its hybrids while Sg18 had the highest percentage. Root lodging results were not reliable, however, because of the experiment's high CV of 156.57%, again indicating the difficulty in standardizing this type of data. Analysis of variance for root lodging showed no significant variation between entries, for this reason it will not be considered further.

4.3 ANALYSIS OF VARIANCE

Tables 4.18 and 4.19 summarize analyses of variance for 11 characteristics measured in the inbred diallel. Significant differences at the 0.01 probability level were seen between entries for all traits. The F1 were significantly different from inbreds and there was a significant difference between F1 at the 0.01 probability level for all traits. Inbreds were significantly different at the 0.01 probability level except for ear height which was significant at 0.05 and plant height which showed non-significance.

Table 4.18. Analysis of variance mean squares for grain yield, popping expansion, days to silking, plant height, ear height and ear length.

Source	df	Grain Yield	Popping Expansion	Days to Silking	Plant Height	Ear Height	Ear Length
		Mean Squares					
Entries	14	0.54**	62.31**	17.57**	3561.19 **	896.19 **	19.37**
F1 vs Inbreds	1	0.37**	9.65**	73.63**	23455.64 **	6646.90 **	113.88**
Between Inbreds	4	0.98**	89.66**	24.20**	360.74	251.49 *	3.44**
Between F1	9	0.36**	56.00**	8.39**	2773.11 **	543.76 **	15.96**
Reps	3	0.07		5.29**	109.35	35.53	0.92
Error	42	0.02	1.15(1)	1.69	177.16	86.82	0.30

*,** Significant at the 0.0

(1) Based on sampling error with 59 df.

Table 4.19. Analysis of variance mean squares for ear diameter, kernel row, kernel depth, tassel length and length of central spike.

Source	df	Ear Diameter	Kernel Row	Kernel Depth	Tassel Length	Length of C. Spike
		Mean Squares				
Entries	14	0.254**	19.89**	1.93**	39.91**	25.65**
F1 vs Inbreds	1	0.945**	13.94**	10.74**	326.04**	147.41**
Between Inbreds	4	0.395**	23.85**	2.54**	22.03**	33.99**
Between F1	9	0.114**	18.79**	0.68**	16.06**	8.42**
Reps	3	0.014	0.39	0.18	1.90	0.45
Error	42	0.005	0.31	0.13	1.20	0.77

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

4.4 COMBINING ABILITY

Tables 4.20 through 4.23 present the combining ability mean squares based on Griffing's fixed model method 2 (Griffing 1956) and their estimated variance components and percent values. General combining ability was significant for 10 of the traits at the 0.01 level of probability. Specific combining ability was significant at the 0.01 probability level for all characteristics. The ratio of the mean square GCA to the mean square SCA was greater than 1.0 for popping expansion, days to mid-silking, ear length, ear diameter, kernel row, kernel depth and length of the central spike. Kernel row number gave the highest GCA to SCA ratio, while grain yield gave the lowest. For five of the traits, the greater percent of genetic variance was due to specific combining ability. SCA was more important to genetic variance for grain yield, plant height, ear height, ear length and tassel length. General combining ability made up most of the genetic variance for popping expansion, days to mid-silking, ear diameter, the number of kernel rows, kernel depth and length of central spike. The variance due to error was small for all of the traits.

Two factors probably contributed to the high percentage of SCA: 1) The high heterosis expressed by the F1 in crosses excluding the crosses among sib-lines, 2) The very

Table 4.20. General (GCA) and specific (SCA) combining ability mean squares and their mean square ratios for grain yield, popping expansion, days to silking, plant height and ear height.

		Mean square				
Source	df	Grain yield	Popping expansion	Days to silking	Plant height	Ear height
GCA	4	0.010	23.32**	9.62**	679.36**	116.71**
SCA	10	0.185**	9.02**	2.30**	974.90**	267.01**
ERROR	42	0.005	0.23 (1)	0.42	44.29	21.70
GCA/SCA(2)		0.05	2.59	4.18	0.70	0.44

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

(1) Based on sampling error with 59 df.

(2) Ratio of msGCA/msSCA.

Table 4.21. Estimated variance components and their percent values for grain yield, popping expansion, days to silking, plant height and ear height.

Source	Grain yield	Popping expansion	Days to silking	Plant height	Ear height
GCA	0.002	7.70	3.06	211.69	31.67
%	1.74	62.46	69.23	29.35	17.99
SCA	0.090	4.40	0.94	465.3	122.65
%	92.92	35.69	21.21	64.51	69.68
ERROR	0.005	0.23	0.42	44.29	21.7
%	5.34	1.87	9.56	6.14	12.33

Table 4.22. General (GCA) and specific (SCA) combining ability mean squares and their mean square ratios for ear length, ear diameter, kernel row, kernel depth, tassel length and length of central spike.

		Mean squares					
Source	df	Ear length	Ear diameter	Kernel row	Kernel depth	Tassel length	Length of c. spike
GCA	4	6.16**	0.14**	15.06**	0.73**	8.53**	10.65**
SCA	10	4.31**	0.03**	0.94**	0.38**	10.57**	4.72**
ERROR	42	0.08	0.00	0.08	0.03	0.30	0.19
GCA/SCA(1)		1.43	4.67	16.02	1.92	0.81	2.26

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
(1) Ratio of msGCA/msSCA.

Table 4.23. Estimated variance components and their percent value for ear length, ear diameter, kernel row, kernel depth, tassel length and length of central spike.

Source	Ear length	Ear diameter	Kernel row	Kernel depth	Tassel length	Length of c. spike
GCA	2.03	0.047	4.99	0.23	2.74	3.48
%	48.04	73.00	90.76	52.56	33.55	58.64
SCA	2.12	0.016	0.43	0.17	5.13	2.27
%	50.17	24.86	7.81	39.92	62.78	38.12
ERROR	0.075	0.001	0.078	0.033	0.299	0.19
%	1.78	2.14	1.42	7.52	3.67	3.24

low heterosis expressed between the sib-lines. These two factors lead to the expression of overdominance in the characteristics of grain yield, plant height, ear height, ear length and tassel length. In the characteristics where GCA made up the greatest percentage of genetic variation, such as popping expansion, days to silking, ear diameter, kernel row number, kernel depth and length of central spike, the crosses among sib-lines expressed a heterotic effect that was closer to and in the case of kernel row number, higher than the expression seen among crosses excluding the sib-lines. This supports the theory that the expression of heterosis is caused by overdominance.

4.5 GENERAL AND SPECIFIC COMBINING ABILITY EFFECTS

4.5.1. Grain Yield

Estimates of general and specific combining ability and their standard errors (S.E.) for grain yield are given in Table 4.24. The parents I28, KP58K and Sg18 contributed positively to increased yield with GCA estimates of 0.046, 0.021 and 0.010, respectively. R18-1-9 and Sg1533 decreased yields with GCA effects of -0.026 and -0.050, respectively. It is evident from Table 4.35 that the positive GCA effects of I28 and KP58K were due to the significant SCA effects of individual crosses. However, the GCA effects were not significant, indicating that none of the inbreds performed

Table 4.24. GCA and SCA effects for grain yield of inbred diallel.

	SCA effects				GCA	GCA	SCA
Parents	KP58K	R18-1-9	Sg1533	Sg18	effects	S.E.	S.E.
I28	0.291	0.301	0.232	0.320	0.046	0.038 (3)	0.066 (1)
KP58K		0.362	0.462	0.316	0.021		0.086 (2)
R18-1-9			-0.060	-0.174	-0.026		
Sg1533				-0.008	-0.050		
Sg18					0.010		

(1). S.E (sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.25. GCA and SCA effects for popping expansion of inbred diallel.

	SCA effects				GCA	GCA	SCA
Parents	KP58K	R18-1-9	Sg1533	Sg18	effects	S.E.	S.E.
I28	-5.54	3.73	1.20	2.99	-2.77	0.256 (3)	0.444 (1)
KP58K		1.57	-1.58	-0.78	0.11		0.573 (2)
R18-1-9			-1.51	-2.02	2.00		
Sg1533				-0.61	-0.52		
Sg18					1.18		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.26. GCA and SCA effects for days to silking of inbred diallel.

	SCA effects				GCA	GCA	SCA
Parents	KP58K	R18-1-9	Sg1533	Sg18	effects	S.E.	S.E.
I28	-0.333	-1.833	-0.833	-0.476	-1.136	0.346 (3)	0.600 (1)
KP58K		-0.905	-1.155	-1.298	-0.814		0.775 (2)
R18-1-9			0.345	-1.298	1.436		
Sg1533				-0.048	-0.564		
Sg18					1.079		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

consistently well in all crosses. The negative SCA effects between the hybrids of the sib-lines R18-1-9, Sg1533 and Sg18 reflected their close genetic relationship. I28 and KP58K in hybrid combination with R18-1-9, Sg1533 and Sg18 averaged yields 0.26 units higher than expected on the basis of the parental lines.

4.5.2. Popping Expansion

Estimates of general and specific combining ability and their S.E. for popping expansion are presented in Table 4.25. R18-1-9 was the outstanding general combiner, increasing popping expansion by 2.0, which was significant at the 0.01 level of probability. Sg18 also expressed a high GCA of 1.18, which was significant at the 0.01 level of probability. I28 was notable in its depression of popping expansion with a GCA of -2.77 which was largely due to its poor performance in hybrid combination with KP58K. The crosses between I28 and the sib-lines Sg1533, Sg18 and R18-1-9, increased popping expansion 1.2 to 3.73 units more than expected based on the additive contributions of the parental lines. These increases were significant at the 0.01 and 0.05 probability level as can be seen in Table 4.35. The hybrid KP58K x R18-1-9 exhibited an SCA effect 1.57 units more than expected on the basis of its parental lines, but KP58K x Sg1533 was -1.58 units below expectation based on the parents. Crosses between the sib-lines R18-1-9, Sg1533 and Sg18 performed poorly, reducing popping expansion an average of -1.38 units below the expectation of the additive contributions of the parental lines. These crosses were significantly below parental expectations at the 0.05 and 0.01 level of probability.

4.5.3. Days to Silking

Estimates of general and specific combining ability for days to silking and their S.E. are presented in Table 4.26. I28, KP58K and Sg1533 tended to shorten the number of days to silking, with negative GCA values ranging from -0.564 to -1.136. According to Table 4.35, only GCA effects of I28 and KP58K were significant at the 0.01 and 0.05 probability level, respectively. R18-1-9 and Sg18 tended to lengthen the number of days to silking, with positive GCA values of 1.436 and 1.079 respectively, significant at the 0.01 level of probability. The hybrids averaged 0.78 units earlier in days to silking than expected based on the additive contributions of the parental lines. The hybrid exhibiting the greatest negative SCA effect occurred between I28 and R18-1-9, which was significant at the 0.01 probability level.

4.5.4. Plant Height

Estimates of general and specific combining ability for plant height and their S.E. are presented in Table 4.27. I28, KP58K and Sg18 had positive GCA effects indicating that

Table 4.27. GCA ad SCA effects for plant height of inbred diallel.

Parents	SCA effects KP58K	R18-1-9	Sg1533	Sg18	GCA effects	GCA S.E.	SCA S.E.
I28	24.47	20.32	5.22	23.03	1.41	3.557 (3)	6.161 (1)
KP58K		36.24	29.93	22.11	14.02		7.954 (2)
R18-1-9			-9.01	-11.75	-2.36		
Sg1533				-0.76	-13.55		
Sg18					0.48		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.28. GCA and SCA effects for ear height of inbred diallel.

Parents	SCA effects KP58K	R18-1-9	Sg1533	Sg18	GCA effects	GCA S.E.	SCA S.E.
I28	15.86	10.79	2.94	12.99	1.88	2.490 (3)	4.313 (1)
KP58K		15.41	16.87	9.12	3.51		5.568 (2)
R18-1-9			-2.49	-6.19	0.18		
Sg1533				-0.87	-6.98		
Sg18					1.41		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.29. GCA and SCA effects for ear length of inbred diallel.

Parents	SCA effects KP58K	R18-1-9	Sg1533	Sg18	GCA effects	GCA S.E.	SCA S.E.
I28	1.828	1.298	1.628	0.475	0.729	0.151 (3)	0.262 (1)
KP58K		1.639	2.029	1.846	1.257		0.338 (2)
R18-1-9			-0.161	-0.494	-0.783		
Sg1533				-0.354	-0.793		
Sg18					-0.410		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

they tended to increase plant height. KP58K exhibited the highest positive GCA effect of 14.02, which was significant at the 0.01 level of probability. R18-1-9 and Sg1533 decreased plant height with GCA effects of -2.36 and -13.55 respectively. The three hybrids between the closely related sib-lines R18-1-9, Sg1533 and Sg18 had negative SCA values that ranged from -0.76 to -11.75, indicating that they were much shorter than expected based on the average of their parental GCA effects. The other seven hybrids had SCA effects that ranged from 5.22 to 36.24, reflecting a high degree of heterosis which was significant at the 0.01 and 0.05 level of probability, except for the hybrid I28 x Sg1533.

4.5.5. Ear Height

Estimates of general and specific combining ability and their S.E. for ear height are found in Table 4.28. I28, KP58K, R18-1-9 and Sg18 all contributed to increase ear height with positive GCA effects, while Sg1533 strongly reduced ear height with a GCA effect of -6.98. None of these GCA effects were significant at the 0.05 or 0.01 probability level, indicating that none of the inbreds performed significantly well or poorly over all crosses. The three hybrids between the closely related sib-lines, R18-1-9, Sg1533 and Sg18, gave negative SCA effects, indicating that their ear heights were below the parental expectation. The seven other hybrids showed positive SCA effects that ranged from 2.94 to 16.87, and were significant for four of the hybrids.

4.5.6. Ear Length

Estimates of general and specific combining ability and their S.E. for ear length are presented in Table 4.29. GCA effects were significant for all parental lines at the 0.01 probability level. The best general combiners were I28 and KP58K, which increased ear length by 0.729 and 1.257, respectively. R18-1-9, Sg1533 and Sg18 significantly decreased ear length, with GCA effects that had an average value of -0.662. Crosses of the sib-lines to I28 and KP58K were all significant at the 0.01 level of probability, except for the cross I28 x Sg18. The three hybrids among the closely related sib-lines, R18-1-9, Sg1533 and Sg18, had ear lengths below the expectation of the parental lines.

4.5.7. Ear Diameter

Estimates of general and specific combining ability and their S.E. for ear diameter can be found in Table 4.30. All of the parents except for KP58K gave positive values for GCA, indicating that they tended to increase ear diameter in hybrid combination. KP58K tended to decrease ear diameter resulting in a GCA of -0.252, which was significant at the 0.01 probability level. SCA was only significant for the crosses I28 x KP58K and I28 x Sg1533 at the 0.05 probability

Table 4.30. GCA and SCA effects for ear diameter of inbred diallel.

	SCA effects				GCA effects	GCA S.E.	SCA S.E.
Parents	KP58K	R18-1-9	Sg1533	Sg18			
I28	0.217	0.164	0.177	0.013	0.091	0.038 (3)	0.065 (1)
KP58K		0.107	0.120	0.016	-0.252		0.085 (2)
R18-1-9			0.027	0.073	0.051		
Sg1533				-0.024	0.068		
Sg18					0.042		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.31. GCA and SCA effects for kernel row of inbred diallel.

	SCA effects				GCA effects	GCA S.E.	SCA S.E.
Parents	KP58K	R18-1-9	Sg1533	Sg18			
I28	0.304	1.297	0.401	1.083	0.655	0.151 (3)	0.262 (1)
KP58K		0.094	-0.731	-0.270	-2.292		0.338 (2)
R18-1-9			0.861	-0.427	1.415		
Sg1533				0.797	-0.559		
Sg18					0.780		

(1). S.E (sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.32. GCA and SCA effects for kernel depth of inbred diallel.

	SCA effects				GCA effects	GCA S.E.	SCA S.E.
Parents	KP58K	R18-1-9	Sg1533	Sg18			
I28	0.574	0.669	0.654	-0.230	0.230	0.093 (3)	0.160 (1)
KP58K		0.351	0.499	0.240	-0.552		0.207 (2)
R18-1-9			-0.007	0.172	0.203		
Sg1533				0.070	-0.008		
Sg18					0.126		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

level. These combining ability results reflect the low heterosis for this character, which was 8.5% excluding sib-lines and 5.0% among sib-lines. Low heterosis was partly due to the lack of diversity in ear diameter between the inbred lines.

4.5.8. Kernel Row

Estimates of general and specific combining ability and their S.E. for the number of kernel rows is given in Table 4.31. GCA effects were significant for inbreds at the 0.01 level of probability. KP58K and Sg1533 were consistent in decreasing the number of kernel rows in their hybrids, with GCA values of -2.292 and -0.559, respectively. GCA effects were positive, increasing the number of kernel rows, for R18-1-9, Sg18 and I28 in descending order. It is interesting to note that crosses between I28 and R18-1-9 and I28 and Sg18, where the parental lines tended to increase the number of kernel rows, resulted in hybrids with significant positive SCA effects. While a cross between KP58K and Sg1533, which both tended to decrease the number of kernel rows, resulted in a hybrid with a significant negative SCA effect. Crosses between Sg1533, which significantly decreased the number of kernel rows and R18-1-9 and Sg18, which both significantly increased the number of kernel rows resulted in hybrids which showed heterotic effects at the 0.05 probability level.

4.5.9. Kernel Depth

Estimates of general and specific combining ability and their S.E. for kernel depth are presented in Table 4.32. The parents I28, R18-1-9 and Sg18 tended to increase kernel depth, with GCA values of 0.230, 0.203 and 0.126, respectively. The GCA effects of I28 and R18-1-9 were significant at the 0.05 level of probability. KP58K and Sg1533 tended to decrease kernel depth, with GCA values of -2.292 and -0.559, respectively. The GCA effect of KP58K were significant at the 0.01 level of probability, while that of Sg1533 was non-significant. Only three of the hybrids with I28, showed significant positive SCA effects at the 0.01 probability level. The cross between I28 and R18-1-9 expressed a high degree of heterosis. The same cross showed the greatest positive heterosis for popping expansion as well. Hybrids between the three related sib-lines gave surprisingly different SCA values. Sg18 X R18-1-9 and Sg18 X Sg1533 resulted in increased kernel depth over either parent, while R18-1-9 X Sg1533 resulted in decreased kernel depth.

4.5.10. Tassel Length

Estimates of general and specific combining ability for tassel length and their S.E. are summarized in Table 4.33. I28 and R18-1-9 shortened tassel length resulting in negative GCA effects, while KP58K, Sg1533 and Sg18 tended to

Table 4.33. GCA and SCA effects for tassel length of inbred diallel.

	SCA effects				GCA	GCA	SCA
Parents	KP58K	R18-1-9	Sg1533	Sg18	effects	S.E.	S.E.
I28	0.391	2.685	2.224	2.775	-1.559	0.293 (3)	0.507 (1)
KP58K		3.434	2.022	3.274	1.493		0.655 (2)
R18-1-9			-0.113	0.238	-0.352		
Sg1533				-0.443	0.160		
Sg18					0.258		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

Table 4.34. GCA and SCA effects for length of central spike of inbred diallel.

	SCA effects				GCA	GCA	SCA
Parents	KP58K	R18-1-9	Sg1533	Sg18	effects	S.E.	S.E.
I28	0.589	1.883	2.157	1.497	-0.981	0.233 (3)	0.404 (1)
KP58K		1.764	1.389	1.319	1.268		0.521 (2)
R18-1-9			-0.247	1.543	-1.326		
Sg1533				-0.813	1.299		
Sg18					-0.261		

(1). S.E.(sii-sjj) all parents in common.
(2). S.E. (sij-skl) no parents in common.
(3). S.E. (gi-gj) between GCA effects.

increase tassel length resulting in positive GCA values. Only the GCA effects of I28 and KP58K were significant at the 0.01 level of probability. Crosses of the sib-lines with I28 and KP58K showed significant SCA effects at the 0.01 level of probability. Crosses between the sib-lines R18-1-9, Sg1533 and Sg18 did not show significant SCA.

4.5.11. Comparison of Tassel Length to Ear Length

Because of the high correlation between tassel length and ear length (r=0.68**), it is interesting to compare their genetic variances and genetic effects. The greatest component of variance for both traits was SCA, being 50.17% for ear length and 62.78% for tassel length. Looking at Table 4.35 and 4.36, the GCA effects for KP58K were both significant and positive for both traits. The three sister lines, R18-1-9, Sg18 and Sg1533 gave significantly negative GCA effects for ear length but did not contribute significantly in either direction for tassel length. SCA was significantly positive for four of the same hybrids between ear length and tassel length. In addition, crosses between the three sister lines showed SCA that was non-significant and usually negative for both traits.

4.5.12. Length of Central Spike

Estimates of general and specific combining ability and their S.E. for length of central spike is presented in Table 4.34. I28 and R18-1-9, showed negative GCA effects which were significant at 0.01 level of probability. KP58K and Sg1533 significantly increased spike length over all crosses at the 0.01 level of probability. All of the hybrids expressed heterosis except for Sg1533 x R18-1-9 and Sg1533 x Sg18, which was the same result as for tassel length. A significant heterotic effect was seen between R18-1-9 and Sg18, both of which gave negative GCA effects. In all other traits except ear diameter, kernel depth and tassel length, the hybrid between these two inbreds performed below the expectation of the parents.

Table 4.35. Significance of GCA and SCA effects for six characteristics.

	Grain yield	Popping expansion	Days to silking	Plant height	Ear height	Ear length
			GCA Effects			
I28	0.046	-2.77 **	-1.14 **	1.41	1.88	0.73 **
KP58K	0.021	0.11	-0.81 *	14.02 **	3.51	1.26 **
R18-1-9	-0.026	2.00 **	1.44 **	-2.36	0.18	-0.78 **
Sg1533	-0.050	-0.52 *	-0.56	-13.55 **	-6.99	-0.79 **
Sg18	0.010	1.18 **	1.08 **	0.48	1.41	-0.41 **
			SCA Effects			
I28xKP58K	0.291 **	-5.54 **	-0.33	24.47 **	15.86 **	1.83 **
I28xR18-1-9	0.301 **	3.73 **	-1.83 *	20.32 *	10.80	1.30 **
I28xSg1533	0.232 *	1.20 *	-0.83	5.22	2.94	1.63 **
I28xSg18	0.320 **	2.99 **	-0.48	23.03 **	13.00 *	0.47
KP58KxR18-1-9	0.362 **	1.57 **	-0.90	36.24 **	15.41 **	1.64 **
KP58KxSg1533	0.462 **	-1.58 **	-1.15	29.93 **	16.87 **	2.03 **
KP58KxSg18	0.316 **	-0.78	-1.30	22.11 **	9.11	1.85 **
R18-1-9xSg1533	-0.060	-1.51 *	0.35	-9.01	-2.49	-0.16
R18-1-9xSg18	-0.174	-2.02 **	-1.30	-11.75	-6.19	-0.49
Sg1533xSg18	-0.008	-0.61	-0.05	-0.76	-0.87	-0.35

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 4.36. Significance of GCA and SCA effects for five characteristics.

	Ear diameter	Kernel row	Kernel depth	Tassel length	Length of c. spike
	GCA Effects				
I28	0.091 *	0.66 **	0.230 *	-1.56 **	-0.98 **
KP58K	-0.252 **	-2.29 **	-0.552 **	1.49 **	1.27 **
R18-1-9	0.051	1.42 **	0.203 *	-0.35	-1.33 **
Sg1533	0.068	-0.56 **	-0.008	0.16	1.30 **
Sg18	0.042	0.78 **	0.126	0.26	-0.26
	SCA Effects				
I28xKP58K	0.217 *	0.30	0.574 **	0.39	0.59
I28xR18-1-9	0.164	1.30 **	0.669 **	2.69 **	1.88 **
I28xSg1533	0.177 *	0.40	0.654 **	2.22 **	2.16 **
I28xSg18	0.013	1.08 **	-0.230	2.78 **	1.50 **
KP58KxR18-1-9	0.107	0.09	0.351	3.43 **	1.76 **
KP58KxSg1533	0.120	-0.73 *	0.499 *	2.02 **	1.39 *
KP58KxSg18	0.016	-0.27	0.240	3.27 **	1.32 *
R18-1-9xSg1533	0.027	0.86 *	-0.007	-0.11	-0.25
R18-1-9xSg18	0.073	-0.43	0.172	0.24	1.54 **
Sg1533xSg18	-0.024	0.80 *	0.070	-0.44	-0.81

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

4.6. DISCUSSION

The results of the inbred diallel have been greatly affected by the relationship between the three sister lines, R-18-1-9, Sg1533 and Sg18. General combining ability, which is a measure of average performance (Sprague and Tatum 1942) was reduced due to the poor performance of the sib-lines with each other. Specific combining ability became more important because I28 and KP58K served as "test crosses" for the three sister lines. The three sib-lines in crosses with I28 and KP58K gave positive SCA effects for grain yield, plant height, ear height, ear length, tassel length, length of central spike and tiller number (see Appendix A). Results of this trial also indicated that for traits where heterosis is low, such as popping expansion, days to silking, ear diameter and kernel row number, GCA effects are revealed. Kernel depth showed high heterosis, but it was average over all of the hybrids, even the three sister lines exhibited some heterosis in crosses between them. Length of central spike, which had the same average heterosis as tassel length, showed a greater variance due to GCA than SCA because of the contribution of R18-1-9 and Sg1533 to GCA. Stalk lodging (see Appendix A) expressed high negative heterosis from the parents to F1, which may have resulted from improved plant vigor. This resulted in a high percentage of SCA (40.65%) which was only significantly expressed in one cross. Tiller number and ear aspect (see Appendix A) also showed a preponderance of SCA (56.85% and 60.19%, respectively). The parent which contributed most to increasing the number of tillers was I28.

The effects of inbreeding are (1) vigor and yield are reduced as the traits become more fixed and (2) differences among lines increase, while variability within lines decrease (Hallauer and Miranda 1981). This tendency is commonly referred to as inbreeding depression. Among the three sib-lines, R18-1-9, Sg1533 and Sg18 the approach to homozygosity must have "fixed" alleles for some traits in the same way, so that crosses between them resulted in low heterosis and negative SCA effects. The other side to the coin are the heterotic effects expressed in crosses of R18-1-9, Sg1533 and Sg18 to I28 and KP58K. All crosses with I28 and KP58K performed better than both parents involved in the cross. These two lines were of diverse genetic origin, both from each other and also from the sib-lines derived from Supergold. According to Johnson and Hays (1940), diversity in genetic origin is prerequisite to the maximum expression of hybrid vigor. The three crosses which performed the best for both yield and popping expansion were, R18-1-9 x KP58K, R18-1-9 x I28 and Sg18 x I28. For these three crosses the average grain yield was 4867.04 kg/ha and the average popping expansion was 34.3 cc/g.

The two main hypotheses proposed to account for hybrid vigor or heterosis are (1) allelic interaction or overdominance and (2) dominant favorable growth factors (Hallauer and Miranda 1981). Hull (1945) favored the theory of overdominance and designed a recurrent selection breeding program around it. Specific combining ability is largely dependent upon dominant and epistatic effects (Sprague and Tatum 1942), therefore, significant SCA must be a direct indication of hybrid vigor. If this vigor is to be kept intact, it is advisable to derive triple cross hybrids from this diallel. A three way cross is preferable over a single cross because (1) the number of combinations is much greater than obtainable with single crosses, (2) unique dominance or epistatic effects can be preserved, and (3) a three way cross would have greater stability over environments (Hallauer and Miranda 1981). With this in mind, R18-1-9 should be selected as representative of the three sib-lines because of its high positive GCA for popping expansion and combined with I28 and KP58K. This would result in three possible hybrids: (I28xKP58K)xR18-1-9, (I28xR18-1-9)xKP58K and (KP58KxR18-1-9)xI28. Single crosses between these inbreds gave high and significant SCA effects for grain yield and popping expansion, with the exception of I28 x KP58K which had a high negative SCA for popping expansion. It is hoped that the high GCA of R18-1-9 will be able to overcome this negative effect between the two other inbreds.

5. VARIETY DIALLEL

5.1. INTRODUCTION

A diallel cross of six popcorn varieties was planted and the data recorded at Waimanalo, Oahu (5.2), Kapaa, Kauai (5.3) and Ibaden, Nigeria (5.4). In the following text and tables, the varieties are referred to by their abbreviations; AP (Avati Pichinga), CG (Curagua Grande), JH (Japanese Hulless), PP#1 (Philippine Pop #1), PP#6 (Philippine Pop #6) and S (Supergold). AP x JH for example, would be a cross between Avati Pichinga and Japanese Hulless.

The data recorded at Waimanalo included a study of the relationship between popping expansion and kernel measurements such as thickness, depth, width, weight and volume. The diallel was also rated for its resistance to Puccinia sorghi, referred to as rust rating in the tables and text. A study was also made of the diallel's resistance to seed weevil attack by means of average kernel weight loss, taken after 8 months of weevil infestation, and rating on a scale of 1-9 of weevil damage.

General and specific combining ability for this trial was analyzed using Gardner and Eberhart's model which assumes a fixed set of varieties, with diploid inheritance, two alleles at each locus and no epistasis. Analysis 3 of the model was used, which allows an estimate of general and specific combining ability and the average heterosis of varieties vs crosses (Gardner and Eberhart 1966). The estimation of sum of squares for model 3 is as follows:

Source	df	Sum of Squares
Varieties	n-1	S'1'
Varieties vs Crosses	1	S'2'
Crosses	[n(n-1)/2]-1	S'3'
GCA	n-1	S'31'
SCA	n(n-3)/2	S'32'

5.2. VARIETY DIALLEL-WAIMANALO

5.2.1. Results

The six popcorn varieties and their fifteen hybrids were planted at the Waimanalo Research Station on February 3, 1987. Between the date of planting and the flowering date, 6.27 inches of rainfall was recorded. The mean high temperature was 76.5 F and the mean low was 64.8 F. The total number of growing degree days from planting to the average flowering date for the first three replications was 1362.5. Replication four was replanted on March 5, 1987 due an infestation of nutgrass. Between the planting date and the flowering date of replication four, 6.56 inches of rainfall was recorded. Also during this time the mean high temperature was 77.0 F and the mean low was 67.0 F. The mean number of growing degree days from planting to flowering was 22.

5.2.2. Mean Values

Array mean values for the 20 characters measured are summarized in Tables 5.1 to 5.20 together with statistics for overall means of the parents and F1, the least significant difference (LSD) of all entries, percentage coefficient of variation (CV) and average percentage of heterosis (H). CV ranged from a low of 2.08% to 24.23% for all of the traits measured. Heterosis was observed for all characteristics except ear number, tassel type and average kernel weight loss due to weevil infestation. Physiological characteristics and components of grain yield showed significant increases in size from the parents to the F1. The number of days to silking was shortened as a result of heterosis, while tiller number increased from the parents to the F1. Popping expansion, kernel thickness and the number of kernel rows showed negative heterosis between the parents and their hybrids. The number of ears, tassel type and average kernel weight loss due to weevil damage showed no change from the parents to the F1. Ratings for rust and kernel damage due to weevils were lower among the F1 than the parental varieties.

Yield Mean values for grain yield and their array means are presented in Table 5.1. Average heterosis between parents and hybrids was 86.1%. F1 means ranged from 2269.04 kg/ha to 4415.56 kg/ha with an average yield of 3306.02 kg/ha. The high yielding parent was Avati Pichinga with an array mean for its hybrids that exceeded the F1 average by 335.01 kg/ha. The average heterosis of AP over the mean of all parents was 106%, which is more like the performance of an inbred than a variety. The two high yielding hybrids were AP X PP#1 and AP X S with yields of 4415.56 and 4172.0 kg/ha, respectively. The cross between PP#1 and PP#6, which

Table 5.1. Mean values for grain yield (kg/ha).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	959.11	3216.13	3266.46	4415.56	3134.98	4172.00	3641.03	CV (%) = 16.42
CG		1286.13	2269.04	3466.95	2637.98	3540.04	3026.02	AVG(P) = 1776.45
JH			437.46	2995.93	2526.32	3364.20	2884.39	AVG(F1) = 3306.02
PP#1				3149.07	3763.04	2967.93	3521.88	LSD = 666.38
PP#6					2505.09	3853.82	3183.23	AVG H(%)= 86.10
S						2321.81	3579.60	

Table 5.2. Mean values for popping expansion (cc/g).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	30.40	28.30	36.50	35.85	31.77	37.67	34.02	CV (%) = 2.48
CG		18.61	26.36	18.40	24.32	27.47	24.97	AVG(P) = 30.10
JH			40.12	17.28	24.68	36.76	28.32	AVG(F1) = 28.35
PP#1				25.89	16.38	32.09	24.00	LSD = 0.88
PP#6					25.56	31.51	25.73	AVG H(%)= -5.81
S						40.01	33.10	

Table 5.3. Mean values for kernel thickness (mm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	3.38	3.52	3.55	3.60	3.40	3.61	3.54	CV (%) = 10.68
CG		3.98	3.34	3.91	3.95	3.62	3.67	AVG(P) = 3.79
JH			3.66	3.67	3.88	3.60	3.61	AVG(F1) = 3.64
PP#1				3.71	3.55	3.66	3.68	LSD = 0.34
PP#6					3.99	3.79	3.71	AVG H(%)= -3.96
S						4.04	3.66	

Table 5.4. Mean values for kernel width (mm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	4.24	5.57	4.72	5.53	5.26	4.66	5.15	CV (%) = 9.80
CG		5.47	5.44	6.86	6.38	5.34	5.92	AVG(P) = 5.13
JH			4.38	6.01	5.78	5.10	5.41	AVG(F1) = 5.62
PP#1				5.43	6.40	5.71	6.10	LSD = 0.47
PP#6					6.64	5.64	5.89	AVG H(%)= 9.55
S						4.61	5.29	

may be closely related, expressed heterosis of only 33.3% over the midparent.

Popping expansion Mean values for popping expansion are given in Table 5.2 with their array means. F1 means ranged from 16.38 to 36.76 cc/g with an average of 28.35 cc/g. Average heterosis between the parents and their hybrids was -5.8%. Verma and Singh (1980) reported the expression of heterosis for 28 F1 hybrids over the better parent for popping expansion. The average heterosis over all hybrids was a very low -14.1%. For this trial, the outstanding varieties were Avati Pichinga and Supergold with array mean values of 34.02 and 33.1 cc/g respectively. Hybrids showing superior popping expansion were AP X S, JH X S and AP X JH with popping expansions of 37.67, 36.76 and 36.5 cc/g, respectively. The cross between PP#1 and PP#6 showed a depressed heterosis of -36.3%, again pointing to their probable genetic similarity.

Kernel thickness Mean values for kernel thickness and their array means are given in Table 5.3. Average heterosis between parents and their hybrids was -4.0%. Total means for the parental varieties and the F1 varied by 0.15 which is not significant. The F1 means ranged from 3.4 to 3.95 mm with an average of 3.64 mm. Array mean values for kernel thickness were not significantly different from the F1 average. Regression analysis of kernel thickness to popping expansion showed r=-0.20, which was not significant.

Kernel width Mean values for kernel width and their array means are given in Table 5.4. Average heterosis was 9.6%. Hybrid means ranged from 4.66 to 6.86 mm with an average of 5.62 mm. The hybrids AP X S, AP X JH and JH X S had kernel widths that were 0.96, 0.9 and 0.52 mm below the Fl average. As can be seen in Table 5.2, these 3 hybrids also had the highest popping expansions, averaging 23% above the Fl average. The hybrids CG X PP#1, PP#1 X PP#6 and JH X PP#1 had kernel widths that were 1.24, 0.78 and 0.39 mm above the Fl average; their popping expansion averaged 38% below the Fl average. Regression analysis indicated that kernel width is highly correlated to popping expansion at P=0.001 level of significance with r=-0.75, as can be seen in Figure 5.1. Lyerly (1942) reported a correlation of -0.50 for kernel width to popping expansion, significant at 0.01 probability level. Willier (1927) also found a negative correlation of kernel width to popping expansion of -0.29

Kernel depth Mean values for kernel depth is presented in Table 5.5. Average heterosis between varieties and their hybrids was 13.8%. Hybrid means ranged from 7.68 to 10.23 mm with an average of 9.08. Avati Pichinga had an array mean value of 6.26 mm, tending to reduce kernel depth and

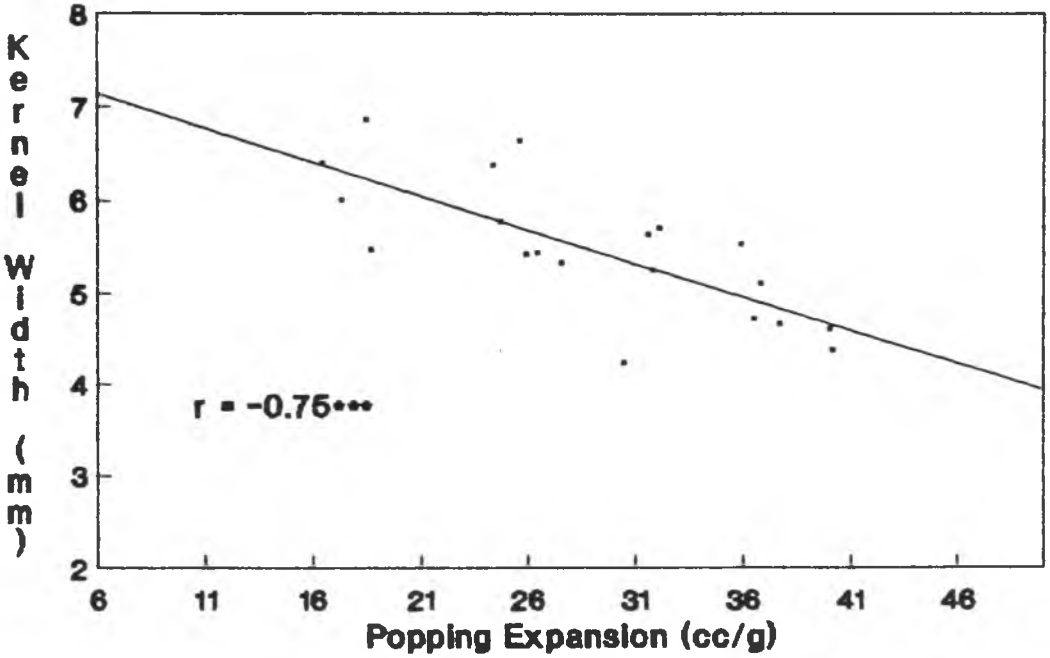


Figure 5.1. Correlation of kernel width to popping expansion.

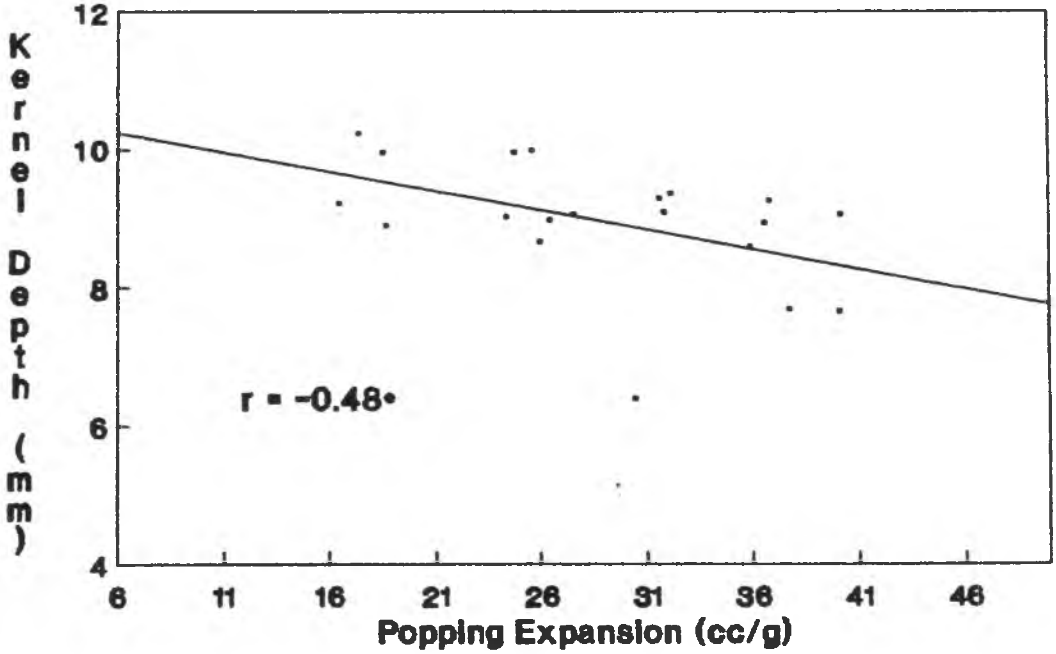


Figure 5.2. Correlation of kernel depth to popping expansion.

Table 5.5. Mean values for kernel depth (mm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	6.39	7.92	8.91	8.57	9.06	7.68	8.43	CV (%) = 13.06
CG		8.88	8.95	9.94	9.00	9.04	8.97	AVG(P) = 7.98
JH			9.03	10.23	9.95	9.04	9.42	AVG(F1) = 9.08
PP#1				8.65	9.21	9.34	9.46	LSD = 1.00
PP#6					9.98	9.26	9.30	AVG H(%)= 13.78
S						7.64	8.87	

Table 5.6. Mean values for 1000 kernel weight (g).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	66.17	111.20	107.69	121.05	116.88	100.28	111.42	CV (%) = 3.00
CG		126.90	100.97	186.70	164.32	147.26	142.09	AVG(P) = 107.82
JH			64.42	148.09	126.61	113.46	119.36	AVG(F1) = 133.56
PP#1				121.16	158.95	144.70	151.90	LSD = 4.01
PP#6					166.47	155.22	144.40	AVG H(%)= 23.87
S						101.82	132.18	

Table 5.7. Mean values for 1000 kernel volume (ml).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	89.8	145.1	134.8	148.7	143.2	122.9	138.94	CV (%) = 2.99
CG		172.5	144.6	247.2	218.4	193.3	189.72	AVG(P) = 146.50
JH			97.2	195.8	173.6	154.0	160.56	AVG(F1) = 175.00
PP#1				155.0	212.0	184.2	197.58	LSD = 6.27
PP#6					233.6	208.0	191.04	AVG H(%)= 19.45
S						130.9	172.48	

Table 5.8. Mean values for days to silking.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	77.0	67.0	69.8	66.0	66.3	67.0	67.2	CV (%) = 2.08
CG		63.8	63.5	60.0	61.0	61.3	62.6	AVG(P) = 67.42
JH			70.5	63.0	62.3	63.3	64.4	AVG(F1) = 63.65
PP#1				64.8	59.5	63.0	62.3	LSD = 1.91
PP#6					62.0	62.0	62.2	AVG H(%)= -5.59
S						66.5	63.3	

this differed significantly from the array mean value of 9.46 mm for Philippine Pop #1. The cross between PP#1 and PP#6 show a heterosis of -1.2%, which suggests their genetic similarity. Regression analysis indicates that kernel depth is negatively correlated to high popping expansion at P=0.05 level of significance with a coefficient of -0.48, as can be seen in Figure 5.2. Lyerly (1942) found a correlation between popping expansion and kernel depth of -0.60, significant at 0.01 level of probability. Willier (1927) reported a negative correlation of -0.44.

<u>Kernel weight</u> Mean values for 1000 kernel weight and their array means are given in Table 5.6. Average heterosis was 23.8% from parents to their hybrids. Verma and Singh (1980) found heterosis of F1 hybrids over the better popcorn variety for kernel weight had an average value of -0.3%. The hybrids ranged from 100.3 to 186.7 g with an average of 133.6 g. Avati Pichinga had an array mean value for its hybrids that was 22.1 g below the F1 average while Philippine Pop #1 had an array mean value that was 18.3 g above the F1 average. The cross between PP#1 and PP#6, however, only had a heterotic effect of 9.1%. Regression analysis, in Figure 5.3, shows that 1000 kernel weight is negatively correlated to high popping expansion at P=0.01 level of significance, with a coefficient of -0.64. Lyerly (1942) reported a correlation coefficient of -0.44,

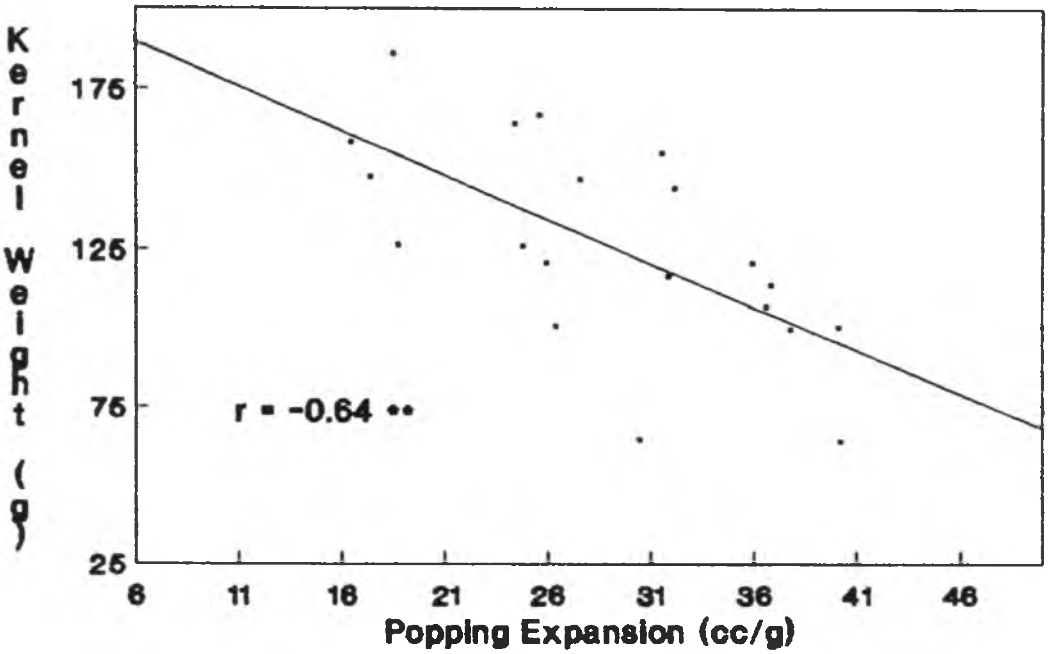


Figure 5.3. Correlation of kernel weight to popping expansion.

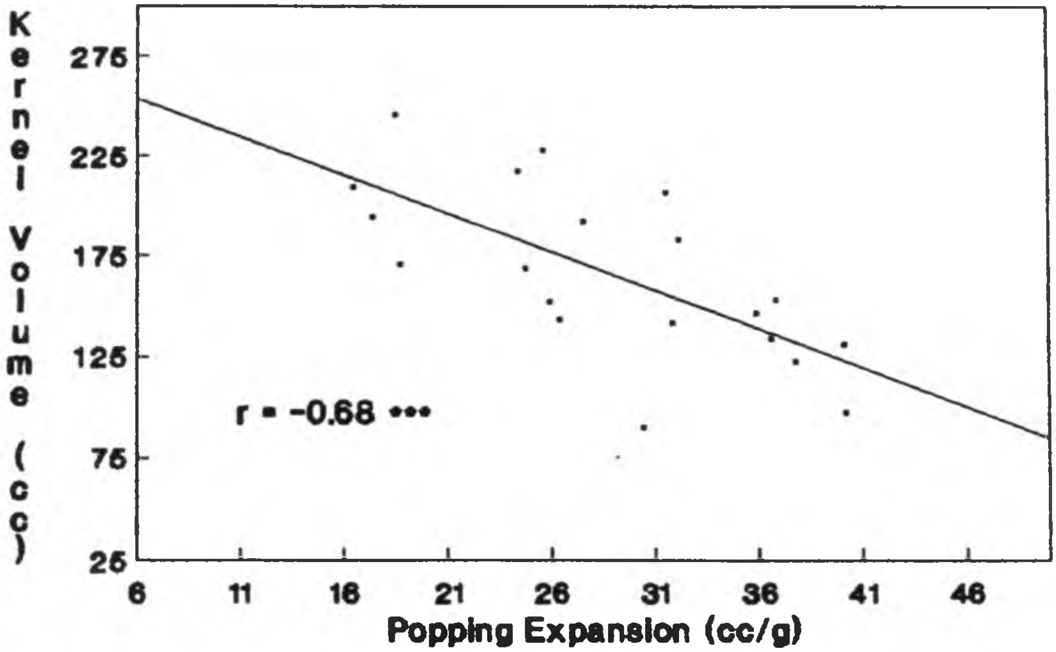


Figure 5.4. Correlation of kernel volume to popping expansion.

significant at 0.01, while Willier (1927) found a correlation of -0.31 for kernel weight.

Kernel volume Mean values for 1000 kernel volume is presented in Table 5.7. Average heterosis of the hybrids over the parents was 19.5%. Kernel volume results were similar as those for kernel weight. The hybrid AP X S, which had the lowest kernel weight, also had the lowest volume of 122.9 ml. The hybrid with the heaviest kernels, CG X PP#1, also had the greatest volume for 1000 kernels of 247.2 ml. Array mean values gave similar results, with Avati Pichinga having the lowest volume for its hybrids of 138.9 ml, while Philippine Pop #1 gave the highest volume of 197.6 ml. The cross between PP#1 and PP#6 only exhibited a heterosis of 9.1%. Regression analysis, seen in Figure 5.4, shows that volume of 1000 kernels is negatively correlated to high popping expansion with a coefficient of 0.68, at P=0.001 level of significance. Willier (1927) reported a positive correlation for kernel volume of 0.38, which does not agree with the present findings.

Days to silking Mean values for days to silking are presented in Table 5.8. Average heterosis was -5.6, reflecting the increased vigor of the hybrids over their parents. Hybrids were an average of 3.8 days earlier to flower than the parental varieties, and ranged from 60.0 to 69.8 days with an average of 63.65 days. Avati Pichinga was the latest variety and had an array mean value for its hybrids that was 3.6 days above the F1 average.

Plant height Mean values for plant height and array means are given in Table 5.9. Average heterosis between the parents and their hybrids was 16.5%. Hybrids ranged from 192.1 to 229.2 cm in height with an average of 209.6. Avati Pichinga and Japanese Hulless tended to increase plant height with array mean values for their hybrids of 216.2 and 217.4 cm respectively. Philippine Pop #6 tended to bring down plant height with an array mean value for its hybrids of 198.4 cm. PP#1 x PP#6 only had a heterosis of -1.13 below the midparent, indicating a close genetic relationship.

Ear height Mean values for ear height are presented in Table 5.10. Average heterosis of the hybrids over parents was 19.1%. Hybrids ranged from 80.4 to 111.4 cm in ear height with an average of 94.7 cm. Japanese Hulless had the highest array mean value of 100.5 cm for ear height because it produced the tallest hybrids, as was seen in Table 5.9. The variety with the lowest array mean value for plant height, Philippine Pop #6, also gave the lowest array mean value for ear height of 85.64 cm. The cross PP#1 x PP#6 showed no heterosis, with a value of -1.2%.

Table 5.9. Mean values for plant height (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	144.5	214.3	232.2	216.8	202.0	215.9	216.2	CV (%) =	5.39
CG		183.5	212.4	208.8	195.1	210.3	208.2	AVG(P) =	179.9
JH			176.4	209.0	204.1	229.3	217.4	AVG(F1) =	209.6
PP#1				208.7	192.1	202.9	205.9	LSD =	15.34
PP#6					179.8	199.1	198.4	AVG H(%)=	16.51
S						186.6	211.5		

Table 5.10. Mean values for ear height (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	68.3	94.7	111.1	98.8	90.7	99.3	98.9	CV (%) =	8.55
CG		85.9	98.5	94.1	83.8	98.4	93.9	AVG(P) =	79.5
JH			77.1	94.9	86.8	111.4	100.5	AVG(F1) =	94.7
PP#1				92.1	80.4	91.4	91.9	LSD =	10.93
PP#6					70.6	86.6	85.6	AVG H(%)=	19.12
S						83.5	97.4		

Table 5.11. Mean values for ear length (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	12.1	16.9	15.1	17.2	16.4	16.6	16.4	CV (%) =	4.70
CG		14.0	13.6	15.5	16.6	16.1	15.7	AVG(P) =	13.00
JH			7.8	13.9	13.7	13.9	14.0	AVG(F1) =	15.40
PP#1				16.6	14.8	15.5	15.4	LSD =	0.98
PP#6					14.9	15.8	15.5	AVG H(%)=	18.46
S						12.6	15.6		

Table 5.12. Mean values for ear diameter (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	2.23	3.20	3.51	3.10	3.18	3.00	3.20	CV (%) =	2.92
CG		3.55	4.05	3.55	3.65	3.44	3.58	AVG(P) =	3.22
JH			3.74	3.95	4.04	3.65	3.84	AVG(F1) =	3.50
PP#1				3.19	3.49	3.33	3.48	LSD =	0.14
PP#6					3.45	3.38	3.55	AVG H(%)=	8.70
S						3.19	3.36		

Ear length Mean values for ear length and array means are given in Table 5.11. Average heterosis of hybrids over their parents was 18.5%. Hybrid ear length increased by 2.4 cm over the average length for parental varieties. The hybrids ranged from 13.6 to 17.2 cm with an average of 15.4. Avati Pichinga increased ear length among its hybrids 1.02 cm over the F1 average. Japanese Hulless produced hybrids with the shortest ears, 1.35 cm less than the F1 average. There was no heterosis expressed for PP#1 x PP#6, infact it was depressed by -6.3%.

Ear diameter Mean values for ear diameter and array means are given in Table 5.12. Average heterosis of hybrids over parents was 8.7%. Ear diameter among hybrids ranged from 3.0 to 4.05 cm with an average of 3.5 cm. The array mean value for the hybrids of Avati Pichinga was 0.3 cm below the F1 average, which was significant. Hybrids of Japanese Hulless were 0.34 cm wider than the F1 average.

Ear number Mean values for ear number are presented in Table 5.13. There was no change in the average number of ears from the parental varieties to the F1 so that no heterosis was expressed. There was also no significant difference among array mean values, the greatest being 0.37. Hybrids ranged from 1.25 ears per plant to 2.0 ears.

Table 5.13. Mean values for ear number.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	2.0	1.9	1.7	1.8	1.8	2.0	1.8	CV (%) = 15.41
CG		1.5	1.7	1.6	1.3	1.8	1.6	AVG(P) = 1.70
JH			1.3	1.6	1.4	2.2	1.7	AVG(F1) = 1.70
PP#1				1.9	1.7	2.0	1.7	LSD = 0.37
PP#6					1.6	1.6	1.5	AVG H(%)= 0.00
S						1.8	1.9	

Table 5.14. Mean values for kernel row number.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	12.8	14.3	19.0	13.8	15.0	15.7	15.5	CV (%) = 4.19
CG		15.6	19.6	13.6	15.0	14.7	15.4	AVG(P) = 16.65
JH			23.8	17.4	20.0	20.3	19.2	AVG(F1) = 16.32
PP#1				14.1	15.0	15.8	15.1	LSD = 0.97
PP#6					14.2	16.0	16.2	AVG H(%)= -1.98
S						19.5	16.5	

Table 5.15. Mean values for length of central spike (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	28.7	32.3	34.1	31.4	31.8	30.4	32.0	CV (%) = 6.44
CG		20.4	23.8	23.9	24.9	22.2	25.4	AVG(P) = 24.92
JH			22.2	26.1	30.4	24.0	27.7	AVG(F1) = 27.43
PP#1				29.7	26.7	23.4	26.3	LSD = 2.43
PP#6					29.4	26.6	28.1	AVG H(%)= 10.07
S						19.2	25.3	

Table 5.16. Mean values for tassel type.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics
AP	5.0	3.0	2.0	3.3	3.3	4.0	3.1	CV (%) = 21.05
CG		1.0	1.3	2.0	1.8	2.3	2.1	AVG(P) = 2.21
JH			1.0	1.5	1.0	1.3	1.4	AVG(F1) = 2.18
PP#1				2.8	2.3	2.0	2.2	LSD = 0.65
PP#6					1.5	2.0	2.1	AVG H(%)= -1.36
S						2.0	2.3	

Kernel row Mean values for the number of kernel rows and array means are given in Table 5.14. There was no significant difference between the F1 average and the parental variety average for the number of kernel rows. Average heterosis between hybrids and parents was -2.0%. Hybrids ranged from 13.55 to 20.0 row with an average of 16.32. Japanese Hulless clearly tended to increase the number of kernel rows among its hybrids with an array mean that was 2.92 rows above the F1 average. The cross between PP#1 and PP#6 showed a heterotic effect of 6.0% above the midparent.

Length of central spike Mean values and array means for length of the central spike are given in Table 5.15. Average heterosis was 10.1%. Hybrids ranged from a central spike length of 22.15 to 34.05 cm with an average of 27.43 cm. Avati Pichinga tended to increase central spike length with an array mean for its hybrids of 31.96 cm. Regression analysis, seen in Figure 5.5, indicated that central spike length was positively correlated to increased ear length at 0.05 level of significance with a coefficient of 0.44.

Tassel type Mean values for tassel type are given in Table 5.16. Among the parents, Avati Pichinga had a flopped over tassel that was rated 5, while Japanese Hulless and Curagua Grande had perfectly erect tassels that were rated 1. There was no difference between the average tassel score

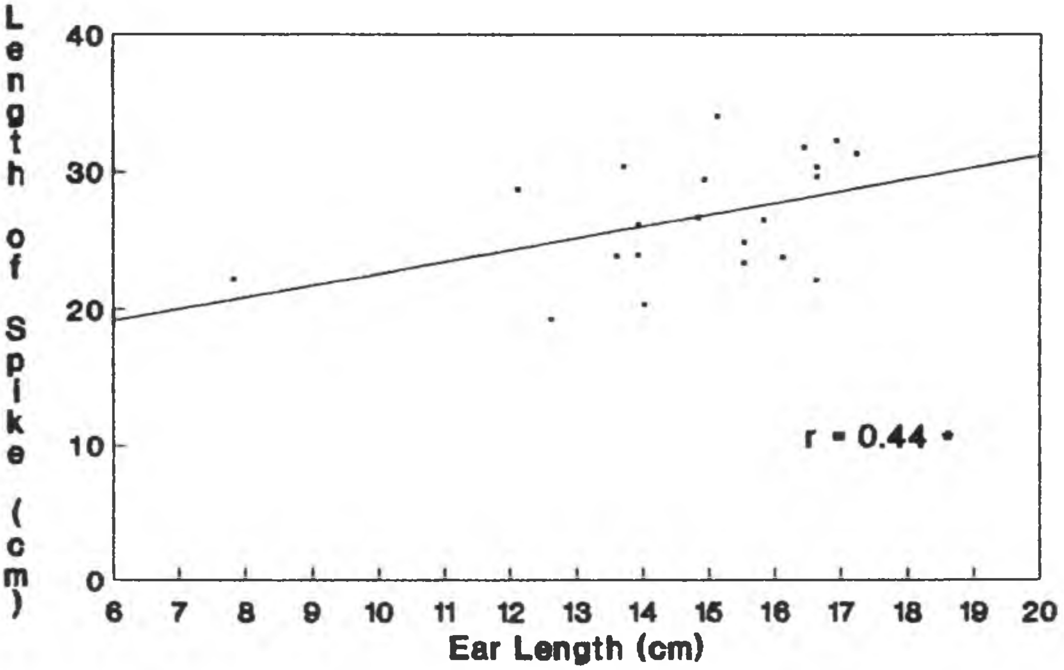


Figure 5.5. Correlation of central spike length to ear length.

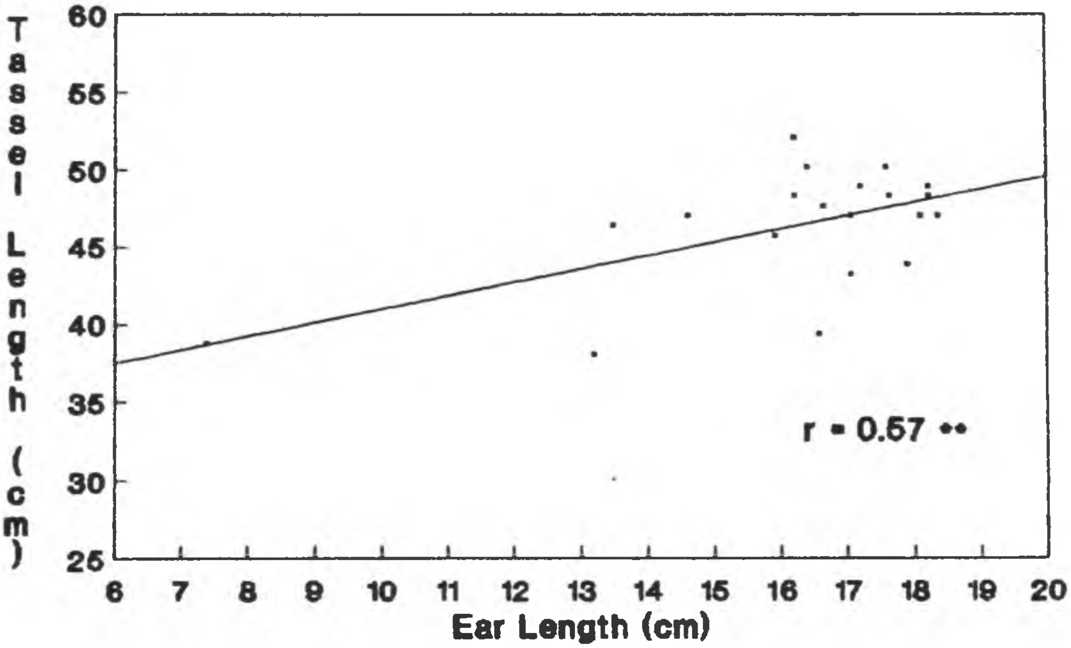


Figure 5.6. Correlation of tassel length to ear length.

of the parents and the F1, which resulted in average heterosis of -1.4%. Avati Pichinga's array mean of 3.1 points was significantly different from the other array means reflecting the tendency of its hybrids to exhibit the floppy tassel characteristic. CV for this trait was high, 21.05 %, indicating the difficulty in standardizing such an empirical rating.

Stem number Mean values and array means for the total stem number are given in Table 5.17. Average heterosis between the parents and hybrids was 34.1%. Hybrids ranged from 1.01 to 2.05 stems with a mean of 1.69 stems. Array mean values were not significantly different from each other indicating that there was not one parent that markedly increased the number of tillers among its F1. The data of Troyer and Hallauer (1968) was found to have an average heterosis of 15.4% for the number of tillers. This was taken from data that reported the average tiller number of varieties and hybrids grown at two different dates and under two different population densities. CV for this trait was high, indicating the difficulty in standardizing a rating of 1-5.

Rust rating Mean values for rust rating on a scale of from 1 to 9 are presented in Table 5.18. Heterosis between parents and hybrids was -12.5%, indicating that hybrids showed more average resistance than parents. Kim (1974)

Table 5.17. Mean values for total number of stems.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	1.3	1.1	2.1	1.7	2.0	1.6	1.7	CV (%) =	24.23
CG		1.3	1.9	1.4	1.3	2.1	1.5	AVG(P) =	1.26
JH			1.6	1.7	2.0	2.0	1.9	AVG(F1) =	1.69
PP#1				1.3	1.8	1.3	1.6	LSD =	0.54
PP#6					1.2	1.7	1.7	AVG H(%)=	34.13
S						1.1	1.7		

Table 5.18. Mean values for rust rating (1-9).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	6.3	4.3	5.5	3.6	6.9	5.7	5.2	CV (%) =	10.48
CG		8.1	8.5	5.8	7.8	5.9	6.5	AVG(P) =	7.2
JH			8.9	7.7	7.9	7.5	7.4	AVG(F1) =	6.3
PP#1				5.7	5.7	5.9	5.8	LSD =	0.98
PP#6					8.1	6.4	6.9	AVG H(%)=	-12.50
S						6.3	6.3		

Table 5.19. Mean values for average kernel weight loss due to weevil damage.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	29.9	34.1	29.7	26.1	26.4	27.7	28.8	CV (%) =	15.21
CG		29.3	43.4	57.6	34.8	26.9	39.4	AVG(P) =	35.33
JH			40.2	53.4	34.5	29.4	38.1	AVG(F1) =	35.15
PP#1				27.0	31.4	33.4	40.4	LSD =	11.17
PP#6					58.7	38.5	33.1	AVG H(%)=	-0.51
S						26.8	31.2		

Table 5.20. Mean values for kernel weevil damage rating (1-9).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistics	
AP	7.0	7.0	4.5	6.0	6.0	6.5	6.0	CV (%) =	14.47
CG		7.0	9.0	8.0	5.5	4.5	6.8	AVG(P) =	7.16
JH			8.0	8.0	8.0	6.5	7.2	AVG(F1) =	6.43
PP#1				5.5	5.5	5.0	6.5	LSD =	2.00
PP#6					8.5	6.5	6.3	AVG H(%)=	-10.20
S						7.0	5.8		

reported an average heterotic effect of 2.3% between nine parents and 36 F1s. Hybrid scores ranged from 3.6 to 8.47 with an average of 6.3 points. The hybrid exhibiting the lowest rust infection was AP X PP#1 with a score of 3.6. Avati Pichinga tended to reduce rust infection among its hybrids with an array mean value of 5.19, while Japanese Hulless had the most infected hybrids with an array mean value of 7.41. CV was only 10.48%, which indicates the superiority of a rating scale of 1-9 over 1-5.

Kernel weight loss Mean values for the average kernel weight loss due to weevil damage is presented in Table 5.19. There was no difference in the average performance of the parents and the F1 making heterotic effects negligible. Hybrids ranged from an average loss of 26.13 mg to 57.61 mg with a mean weight loss of 35.15 mg. Avati Pichinga produced hybrids with the lowest kernel weight loss of 28.8 mg, while Philippine Pop #1 had the highest array mean weight loss of 40.39 mg.

Weevil damage rating Mean values for the amount of weevil damage to kernels on a scale from 1 to 9 is given in Table 5.20. Average heterosis between parents and hybrids was -10.2, indicating that hybrids showed an average higher resistance to weevil attack than parents. Hybrid scores ranged from 4.5 to 9 points with an average score of 6.43. The array mean values were not significantly different indicating that varieties performed similarly in hybrid combination.

5.2.3. ANOV and Combining Ability Mean Square

The analysis of variance and combining ability mean squares for the six varieties and their 15 variety crosses grown at the Waimanalo Research Station are presented in Tables 5.21 to 5.23. Entries differed at P= .01 level of significance for all 20 characteristics measured. Varieties vs Fl gives an indication of the presence of significant heterosis between varieties and Fl. There was significant heterosis at P=0.01 for grain yield, kernel width, kernel depth, 1000 kernel weight, 1000 kernel volume, days to silking, plant height, ear height, ear length, ear diameter, length of central spike, and rust rating. At P= 0.05, heterosis was significant for kernel thickness and weevil rating. There was no significant difference between Fl and the varietal parents for popping expansion, ear number, kernel row, tassel type and average kernel weight loss from weevil damage. As reported earlier, these trait showed no significant heterotic effects in the positive or negative direction. There were significant differences among parental varieties at P=0.01 for all of the traits except weevil rating. Fl differed significantly at P=0.01 for all characteristics except kernel thickness, which was significant at P=0.05.

Table 5.21. Analysis of variance and general (GCA) and specific (SCA) combining ability mean squares for grain yield, popping expansion, kernel thickness, kernel width, kernel depth, kernel weight and kernel volume.

		Mean squares						
Source	df	Grain yield	Popping expansion	Kernel thicknesss	Kernel width	Kernel depth	Weight of 1000 seeds	Volume of 1000 seeds
Reps	3	0.02	(1)	(2)	(2)	(2)	(3)	(4)
Entries	20	0.13**	267.52**	0.439**	5.17**	8.58**	7037.4**	9103.4**
Varieties vs F1	1	1.31**	1.24	0.994*	10.73**	51.83**	19867.9**	17444.1**
Varieties	5	0.14**	310.75**	0.668**	8.21**	10.84**	10690.9**	14219.2**
Between F1	14	0.05**	274.71**	0.318*	3.69**	4.68**	4816.0**	6680.6**
GCA	5	0.02**	114.89**	0.026	0.960**	0.986**	1524.69**	3123.39**
SCA	9	0.007**	15.67**	0.035*	0.040	0.180	223.03**	343.30**
ERROR	60	0.11	0.08	0.015	0.029	0.131	2.05	4.98
MS GCA/SCA		2.86	7.33	0.74	24.00	5.48	6.84	9.10

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
(1)df for sampling error is 76. (2)df for sampling error is 189.
(3)df for sampling error is 126. (4)df for sampling error is 84.

Table 5.22. Analysis of variance and general (GCA) and specific combining ability mean squares for days to silking, plant height, ear height, ear length, ear diameter, ear number and kernel row.

		Mean squares						
Source	df	Days to Silking	Plant Height	Ear Height	Ear Length	Ear Diameter	Ear Number	Kernel Row
Reps	3	240.71**	759.7	106.7	0.58	0.07	0.18	0.97
Entries	20	66.77**	1552.4**	500.1**	18.24**	0.65**	0.22**	32.62**
Varieties vs F1	1	243.22**	15170.8**	3937.3**	102.13**	1.32**	0.05	1.83
Varieties	5	121.67**	1721.4**	341.9**	36.05**	1.14**	0.25**	70.11**
Between F1	14	34.56**	519.3**	311.1**	5.88**	0.43**	0.22**	21.43**
GCA	5	23.00**	315.49**	133.47**	3.76**	0.294**	0.108**	14.37**
SCA	9	0.70	26.74	46.82**	0.20	0.003	0.026	0.35**
ERROR	60	0.45	29.42	14.92	0.12	0.002	0.017	0.12
MS GCA/SCA		32.9	11.80	2.85	18.80	98.00	4.15	41.06

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5.23. Analysis of variance and general (GCA) and specific (SCA) combining ability mean squares for length of central spike, tassel type, stem number, rust rating, weevil rating and kernel weight loss.

		Mean squares					
Source	df	Length of c. spike	Tassel type	Tot.stem number	Rust(5) rating	Weevil(6) rating	Avg.kernel wt.loss(6)
Reps	3	18.91	0.413	0.97	4.22	0.02	264.42
Entries	20	71.05**	4.348**	0.46**	5.76**	3.36**	205.52**
Varieties vs F1	1	108.58**	0.011	3.19**	10.26**	4.61	0.27
Varieties	5	94.19**	9.242**	0.14	5.02**	2.13	310.39**
Between F1	14	60.10**	2.91**	0.38**	5.7**	3.7**	182.73**
GCA	5	36.19**	1.9**	0.12*	4.0**	1.7**	142.27**
SCA	9	3.26**	0.1	0.09*	0.8**	2.0**	63.05**
ERROR	60	0.74	0.05	0.04	0.16	0.46	14.33
MS GCA/SCA		11.10	19.0	1.33	5.0	0.9	2.26

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
(5)df for error is 40, df for reps is 2. (6)df for error is 20, df for reps is 1.

Combining ability mean squares based on Gardner and Eberhart's model 3 (Gardner and Eberhart 1966) are presented in Tables 5.21 to 5.23. General combining ability was significant for 18 of the 19 traits at P=0.01, while specific combining ability was significant for 10 of the traits at P=0.01. The mean squares ratio of GCA to SCA ranged from 0.74 to 98.00. Kernel thickness and weevil rating had sum of squares GCA to SCA ratios less than 1.0 indicating that for these traits most of the genetic variation was due to specific crosses. For the other 16 traits, most of the genetic variation was due to general combining ability.

For popping expansion, kernel thickness, kernel width, kernel depth, weight of 1000 seeds and volume of 1000 seeds in Table 5.21, no figures were given for replications. For these traits, sample means were measured instead of replication means. Grain yield, popping expansion, weight of 1000 seeds and volume of 1000 seeds resulted in a high level of significance for GCA and SCA indicating that variation was due to the performance of specific crosses as well as the performance of parents over many crosses. Kernel width and kernel depth only showed genetic variation due to general combining ability, with kernel width having a high GCA to SCA ratio.

5.2.4. General and Specific Combining Ability Effects

The effects of general and specific combining ability are presented for 19 traits of the six varieties and their 15 varietal crosses in Tables 5.24 through 5.28. Estimates of general and specific combining ability effects for grain yield, ear length, ear diameter and kernel row are presented in Table 5.24.

Avati Pichinga contributed to increased yields with a GCA effect of 0.07, despite its relatively poor yield as a variety. As a variety it significantly increased ear length, decreased ear diameter and decreased the number of kernel rows among its hybrids. Curagua Grande was significantly effective at P=0.01 at decreasing grain yield and the number of kernel rows and increasing ear diameter. It was effective at P=0.05 increasing ear length. Japanese Hulless was significant at P=0.01 at decreasing grain yield and ear length while increasing ear diameter and the number of kernel rows. The highest yielding variety, Philippine Pop #1, contributed to increased grain yield with a GCA effect of 0.05, but this was only significant at P=0.05. Its effect on ear length and diameter were not significant but its reduction of kernel rows was significant. Supergold contributed to increased yields with a GCA effect of 0.06 and to reducing ear diameter which was significant at P=0.01. Philippine Pop #6 had no significant effect on

Table 5.24. Estimates of general and specific combining ability effects for grain yield (Y), ear length (EL), ear diameter (ED) and the number of kernel rows (KR).

	SCA Effects					GCA	Trait
Parents	CG	JH	PP#1	PP#6	S	Effects	
AP	-0.03	0.01	0.08 *	-0.08 *	0.02	0.07 **	Y (t/ha)
	-0.16	0.14	0.58 *	-0.31	-0.24	1.24 **	EL (cm)
	-0.02	-0.03	0.00	0.00	0.06	-0.38 **	ED (cm)
	0.10	0.01	-0.07	-0.18	0.14	-0.98 **	KR
CG		-0.03	0.05	-0.03	0.04	-0.06 **	Y (t/ha)
		-0.43	-0.25	0.75 **	0.10	0.37 *	EL (cm)
		0.03	-0.03	0.00	0.02	0.10 **	ED (cm)
		0.72 **	-0.10	-0.02	-0.70 **	-1.14 **	KR
JH			-0.01	-0.02	0.05	-0.10 **	Y (t/ha)
			0.27	0.01	0.01	-1.73 **	EL (cm)
			0.05	0.06	-0.10 *	0.42 **	ED (cm)
			-1.04 **	0.20	0.11	3.65 **	KR
PP#1				0.06	-0.17 **	0.05 *	Y (t/ha)
				-0.59 *	-0.01	-0.05	EL (cm)
				-0.05	0.03	-0.02	ED (cm)
				0.37	0.84 **	-1.53 **	KR
PP#6					0.07	-0.03	Y (t/ha)
					0.14	0.03	EL (cm)
					0.00	0.06 *	ED (cm)
					-0.38	-0.17	KR
S						0.06 **	Y (t/ha)
						0.15	EL (cm)
						-0.18 **	ED (cm)
						0.17	KR

anything except ear diameter at P=0.05. The highest yielding hybrid, AP X PP#1, exceeded the expectation of either parent by 0.08 units for grain yield and 0.58 for ear length, both of which were significant at P=0.05. The Cross between PP#1 and PP#6 showed a non-significant or negative SCA effect for all four traits, suggesting the hybrid depression between them.

Estimates of general and specific combining ability effects for popping expansion, kernel width, weight of 1000 seeds and the volume of 1000 seeds are given in Table 5.25. This data clearly supports individual correlation results between popping expansion and kernel width, kernel weight and kernel volume. All kernel measurements together correlate to popping expansion at r=0.79, which is significant at 0.001 level of probability. The varieties Curagua Grande, Philippine Pop #1 and Philippine Pop #6 which showed significant negative GCA effects for popping expansion, gave correspondingly significant positive effects for kernel weight, kernel volume and kernel width. While Avati Pichinga and Supergold which showed significant positive GCA effects for popping expansion also gave significant negative GCA effects for kernel weight, kernel volume and kernel width. The variety which contributed the most to popping expansion over all of its hybrids was Avati Pichinga, with a GCA effect of 7.08. This variety

Table 5.25. Estimates of general and specific combining ability effects for popping expansion (PE), kernel width (KW), weight of 1000 seeds (Wt/1000s) and volume of 1000 seeds (Vol/1000s).

	SCA Effects					GCA	Trait
Parents	CG	JH	PP#1	PP#6	S	Effects	
AP	-2.90 **	1.12 **	5.86 **	-0.38	-3.69 **	7.08 **	PE (g/cc)
	0.20	-0.04	-0.10	-0.10	0.05	-0.59 **	KW (mm)
	-5.35 **	19.55 **	-7.76 **	-2.55 *	-3.89 **	-27.67 **	Wt./1000s
	-3.14	23.05 **	-9.42 **	-6.68 **	-3.81 *	-45.13 **	Vol./1000s
CG		2.29 **	-0.28	3.48 **	-2.58 **	-4.23 **	PE (g/cc)
		-0.29 *	0.27 *	0.05	-0.24	0.37 **	KW (mm)
		-25.51 **	19.55 **	6.55 **	4.75 **	10.66 **	Wt./1000s
		-30.68 **	25.69 **	5.02 **	3.12	18.33 **	Vol./1000s
JH			-5.58 **	-0.35	2.52 **	-0.05	PE (g/cc)
			0.06	0.10	0.17	-0.27 **	KW (mm)
			9.35 **	-2.75 *	-0.64	-17.74 **	Wt./1000s
			10.72 **	-3.37	0.28	-18.12 **	Vol./1000s
PP#1				-3.25 **	3.25 **	-5.45 **	PE (g/cc)
				-0.15	-0.09	0.59 **	KW (mm)
				-11.08 **	-10.06 **	22.92 **	Wt./1000s
				-11.18 **	-15.81 **	28.16 **	Vol./1000s
PP#6					0.50 *	-3.28 **	PE (g/cc)
					0.11	0.33 **	KW (mm)
					9.83 **	13.55 **	Wt./1000s
					16.22 **	20.00 **	Vol./1000s
S						5.93 **	PE (g/cc)
						-0.42 **	KW (mm)
						-1.72 **	Wt./1000s
						-3.23 **	Vol./1000s

significantly reduced kernel size among its hybrids by reducing kernel width, kernel volume and kernel weight. Supergold significantly increased popping expansion among its hybrids with a GCA effect of 5.93. Supergold also significantly reduced kernel size among its hybrids but not as markedly as Avati Pichinga. Supergold and Avati Pichinga were clearly the best general combiners for popping expansion. Japanese Hulless had a significant effect on reducing kernel size, yet it did not have a positive effect on increasing popping expansion among its F1. This result may be because the sample of Japanese Hulless used for popping was not of the same seed source used in this diallel and may have given a greater popping expansion.

The hybrid with the greatest popping volume was AP X S (Table 5.2), but the significant SCA effect of this hybrid was 3.69 units below the expectation of both parents. The hybrid which performed the best in popping expansion compared to both parents was AP X PP#1 with a significant SCA of 5.86. It is interesting to note that the parents PP#1 and PP#6 tended to increase kernel size among hybrids with high GCA effects for kernel width, weight and volume of 1000 seeds, yet in hybrid combination with each other, weight and volume of 1000 seeds were significantly reduced below expectation.

Table 5.26. Estimates of general and specific combining ability effects for days to silking (DTS), plant height (PH), ear height (EH) and ear number (EN).

		SCA EfEffects				GCA	Trait
Parents	CG	JH	PP#1	PP#6	S	Effects	
AP	0.29	0.79	-0.40	-0.03	-0.65	4.44 **	DTS
	-1.91	5.06	3.41	-2.09	-4.46	8.41 **	PH (cm)
	-4.23	3.88	2.32	-0.69	-1.28	5.22 **	EH (cm)
	0.17	-0.15	-0.06	0.15	-0.11	0.13 *	EN
CG		0.35	-0.59	0.54	-0.59	-1.38 **	DTS
		-5.26	5.69	1.28	0.21	-1.87	PH (cm)
		-2.47	3.92	-1.29	4.07	-1.03	EH (cm)
		0.08	-0.04	-0.12	-0.08	-0.10	EN
JH			0.16	-0.46	-0.84	0.88 **	DTS
			-5.84	-1.44	7.48	9.86 **	PH (cm)
			-3.57	-6.63 *	8.78 **	7.25 **	EH (cm)
			-0.10	-0.08	0.25 *	-0.04	EN
PP#1				-0.65	1.47 **	-1.69 **	DTS
				-5.84	-1.44	-4.69	PH (cm)
				8.76 **	-11.43 **	-3.48	EH (cm)
				0.15	0.04	0.03	EN
PP#6					0.60	-1.81 **	DTS
					1.13	-13.99 **	PH (cm)
					-0.14	-8.57 **	EH (cm)
					-0.10	-0.24 **	EN
S						-0.44	DTS
						2.28	PH (cm)
						0.62	EH (cm)
						0.22 **	EN

Estimates of general and specific combining abilities for days to silking, plant height, ear height and ear number are presented in Table 5.26. Avati Pichinga had the greatest effect among the varieties for increasing the number of days to silking among its crosses with a GCA of 4.44. As a parent, it also significantly increased plant height, ear height and the number of ears per plant at P= 0.01 and 0.05. Japanese Hulless significantly increased plant height, ear height and the number of days to silking among its F1 with a GCA of 9.86, 7.25 and 0.88, respectively. Philippine Pop #6 significantly reduced plant height, ear height, the number of days to silking and ear number among its crosses with GCAs of -13.99, -8.57, -1.81 and -0.24, respectively. Supergold increased the number of ears among its F1 with a general combining ability of 0.22 that was significant at P=0.01.

Estimates of general and specific combining ability effects for length of central spike, total number of stems, kernel thickness and kernel depth are given in Table 5.27. Avati Pichinga significantly increased central spike length among its F1 with a GCA of 5.66. As was seen in Table 5.24, Avati Pichinga also significantly increased ear length with a GCA effect of 1.24. This supports the positive correlation between ear length and length of central spike reported earlier. However, Curagua Grande, Philippine Pop

Table 5.27. Estimates of general and specific combining ability effects fo length of central spike (LCS), total stem number (Tot.Stem), kernel thickness (KT), and kernel depth (KD).

	SCA Effects					GCA	Trait
Parents	CG	JH	PP#1	PP#6	S	Effects	
AP	1.71 *	0.67	-0.55	-1.37 *	-0.46	5.66 **	LCS (cm)
	-0.40 **	0.12	0.17	0.24	-0.13	-0.02	Tot.Stem
	-0.03	0.09	0.05	-0.21 *	0.09	-0.14 *	KT (mm)
	-0.18	0.19	-0.16	0.53	-0.37	-0.82 **	KD (mm)
CG		-1.31	1.21	-2.81 **	1.20	-2.55 **	LCS (cm)
		0.09	0.04	-0.28	0.55 **	-0.19 *	Tot.Stem
		-0.29 **	0.19 *	0.19 *	-0.07	0.03	KT (mm)
		-0.46	0.53	-0.21	0.31	-0.14	KD (mm)
JH			-0.42	2.55 **	-1.49 *	0.28	LCS (cm)
			-0.13	-0.05	-0.03	0.28 **	Tot.Stem
			0.02	0.20 *	-0.02	-0.04	KT (mm)
			0.22	0.15	-0.10	0.46 **	KD (mm)
PP#1				0.33	-0.56	-1.19 **	LCS (cm)
				0.20	-0.28	-0.17	Tot.Stem
				-0.22 *	-0.05	0.05	KT (mm)
				-0.60 *	0.01	0.46 **	KD (mm)
PP#6					1.31	0.08	LCS (cm)
					-0.11	0.06	Tot.Stem
					0.04	0.09	KT (mm)
					0.14	0.26	KD (mm)
S						-2.28 **	LCS (cm)
						0.03	Tot.Stem
						0.02	KT (mm)
						-0.22	KD (mm)

#1 and Supergold had significantly negative effects as parents on the length of central spike yet they did not have significantly negative effects on ear length.

Also in Table 5.27, Avati Pichinga significantly decreased kernel depth at P=0.01, while Japanese Hulless and Philippine Pop #1 significantly increased kernel depth. As can be seen in Table 5.26, Avati Pichinga significantly raised popping expansion while Philippine Pop #1 significantly lowered popping expansion and Japanese Hulless lowered it but not significantly. This supports the correlation between ear length and central spike length, significant at 0.05 level of probability. The total number of stems was significantly increased at P=0.01 by Japanese Hulless and reduced at P=0.05 level of significance by Curagua Grande.

Estimates of general and specific combining ability effects for tassel type, rust rating, weevil rating and average kernel weight loss due to weevil damage are given in Table 5.28. Avati Pichinga significantly increased the tassel floppiness among its hybrids while Japanese Hulless significantly increased tassel erectness. Philippine Pop #1 significantly decreased the amount of rust infection among its hybrids with a GCA of -1.57. Avati Pichinga also performed very well with a GCA for rust rating of -1.44. Varieties that showed a lower weevil rating (more resistant)

Table 5.28 Estimates of general and specific combining ability effects for tassel type (TT), rust rating (RR), weevil rating (WR) and average kernel weight loss from weevil damage (Avg.Wt.).

	SCA Effects					GCA	Trait
Parents	CG	JH	PP#1	PP#6	S	Effects	
AP	-0.16	-0.35	-0.10	0.09	0.52 **	1.15 **	TT
	-0.79 *	-0.76 *	-0.57	1.23 **	0.90 **	-1.44 **	RR
	0.65	-2.35 **	0.03	0.28	1.40 *	-0.54	WR
	1.63	-1.19	-7.64 *	1.72	5.49	-7.94 **	Avg.Wt.
CG		0.21	-0.04	-0.10	0.09	-0.17	TT
		0.63 *	0.06	0.59	-0.50	0.16	RR
		1.15 *	1.03	-1.23 *	-1.60 **	0.46	WR
		-0.64	10.65 **	-3.10	-8.54 **	5.25 **	Avg.Wt.
JH			0.28	-0.04	-0.10	-0.98 **	TT
			0.79 *	-0.51	-0.41	1.33 **	RR
			0.52	0.78	-0.10	0.96 **	WR
			8.03 *	-1.73	-4.47	3.63 *	Avg.Wt.
PP#1				0.21	-0.35	0.02	TT
				-0.66 *	0.39	-0.73 **	RR
				-0.85	-0.72	0.08	WR
				-7.73 *	-3.31	6.56 **	Avg.Wt.
PP#6					-0.16	-0.17	TT
					-0.65 *	0.74 **	RR
					1.03	-0.17	WR
					10.84 **	-2.56	Avg.Wt.
S						0.15	TT
						-0.67	RR
						-0.79 *	WR
						-4.95 **	Avg.Wt.

also had a lower average weight loss due to weevil attack. Correspondingly, those varieties that had a higher weevil rating (more susceptible) also lost more weight due to weevil attack. Avati Pichinga and Supergold significantly reduced the amount of kernel weight loss due to weevil damage among their hybrids, with GCAs of -7.94 and -4.95, respectively. Supergold also had a significantly low weevil attack rating at P=0.05. Philippine Pop #1, Curagua Grande and Japanese Hulless all had significantly high average kernel weight loss due to weevil damage at P=0.01 and P= 0.05. Japanese Hulless also had a significantly high rating for weevil damage at P=0.01.

5.2.5. Discussion

There was a highly significant correlation between kernel measurements and popping expansion. Kernel width was most highly correlated to popping expansion with r=-0.74, significant at 0.001 probability level. The next most significant measurement was kernel volume, with r=-0.68 significant at 0.001 probability level. Kernel weight had an r=-0.64, which was significant at 0.01 probability level. Kernel depth was correlated by r=-0.48, significant at 0.05 level of probability and kernel thickness only had an r=-0.20 so that it was not correlated to popping expansion. Lyerly (1942) reported that kernel depth was most highly correlated to popping expansion, followed by kernel width and kernel weight, all significant at the 0.01 probability level. Kernel thickness was correlated at r=0.26, significant at 0.05 probability level. Willier and Brunson (1927) also found kernel depth to be most highly correlated to popping expansion, with kernel volume and kernel weight following in that order. Kernel width only had an r=-0.29 while kernel thickness had an r=-0.17. Kernel thickness was negatively correlated to popping expansion in this data and Lyerly's but positively correlated in Willier and Brunson's.

One reason for the differences in results is that both Lyerly and Willier and Brunson were only measuring Yellow Pearl hybrids while the measurements taken in this study included varieties and hybrids of very different kernel types. Curagua Grande, Philippine Pop 1 and 6 were very large kerneled popcorns, almost flinty in kernel type. Japanese Hulless was a very long narrow kerneled popcorn, while Supergold and Avati Pichinga had more small, round kernels.

There was a negative heterotic value for popping expansion which was confirmed by the non-significant mean square of varieties vs hybrids. Verma and Singh (1980) reported an average heterosis for popping expansion over the better parent of -14.1 for 28 hybrids. Observing the heterosis for kernel width, kernel depth, kernel volume and kernel weight in this trial and their negative correlation to popping expansion, it may be that the heterotic effect which increases kernel size from parents to their hybrids may reduce popping expansion. Brunson (1937) reported the difficulty in increasing yield of hybrids while increasing popping expansion. That trend was not seen in this data, Avati Pichinga and Supergold which gave the highest array means for popping expansion also had the highest array means for grain yield. Mean square GCA to SCA ratio was high for both grain yield and popping expansion, indicating that they are both controlled by additive genetic effects and can be selected for by recurrent or mass selection.

There was a significant correlation between length of the central spike and ear length, significant at 0.05 level of probability. Avati Pichinga and Japanese Hulless best exemplified this correlation with Avati Pichinga having positive GCA effects for central spike and ear length, while Japanese Hulless showed negative effects for both characters. GCA to SCA mean square ratio was high for both traits, indicating additive genetic effects governing both traits.

Heterosis for rust rating was high and negative. Kim (1974) reported a positive heterotic effect for 36 hybrids. A GCA to SCA mean square ratio of 5.0 was reported for rust rating, indicating the importance of additive genetic effects for this trait. Resistance can probably be improved by recurrent or mass selection.

5.3. VARIETY DIALLEL-KAUAI

5.3.1. Results

The six varieties and 14 of their hybrids were planted at the Kauai Branch Station on June 3, 1987. From the date of planting to the flowering date, 12.91 inches of rain was recorded. Also during this period, the mean high temperature was 85.2 F and the mean low was 66.0 F. The total number of growing degree days to the average flowering date was 1431.9.

Because the hybrid Avati Pichinga x Curagua Grande was missing from the trial at Kauai, in order to analyze the combining ability using Gardner and Eberhart's Analysis 3, a value for the cross was estimated for ten of the traits based on their average relative performance at the Waimanalo Research Station. For the eleventh trait, tassel length, a value midway between both parents involved in the cross was substituted. In the presented mean values, the calculated values are underlined. In addition, the calculated values were used for obtaining GCA and SCA estimates using Gardner and Eberhart's model and for the combined ANOV of Waimanalo and Kauai.

5.3.2. Mean Values

Array mean values for the 11 characteristics measured at the Kauai Branch Station are summarized in Tables 5.29 to 5.39 together with the statistics for overall means of the parents and F1, LSD, percentage CV and average percentage of heterosis for each trait. As expected, the heterotic effect is seen in the F1 for plant height, ear height, ear length, ear diameter, kernel depth, tassel length and length of central spike. These characters increased in size from the parents to the F1 generation. As a result of the increase in ear and kernel size, grain yield increased from the parents to the F1. The number of days to silking shortened as a result of heterosis. The number of tillers per plant increased from the parents to the F1 due to increased plant vigor. CV was generally higher for this trial at Kauai than at Waimanalo, indicating that there was more variation in the field. CV for grain yield was especially high at 20.86, compared to only 16.42 at Waimanalo.

Grain yield Mean values and array means for grain yield are presented in Table 5.29. Average heterosis between hybrids and varieties was 79.1%. Hybrid mean grain yields ranged from 2386.18 to 4588.1 kg/ha. Philippine Pop #6 and Philippine Pop #1 produced the highest yielding hybrids with array mean values of 3711.53 and 3669.99 kg/ha, respectively. The highest yielding hybrid occurred in the

Table 5.29 Mean values for grain yield (kg/ha).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic
AP	1501.02	3157.74	1541.71	3185.50	3333.88	2459.21	2735.61	CV (%) = 20.24
CG		1349.77	2386.18	4116.54	3309.41	3171.71	3228.32	AVG(P) = 1808.65
JH			169.92	3103.07	3328.57	3597.08	2791.32	AVG(F1) = 3239.21
PP#1				2938.15	4588.10	3311.73	3660.99	LSD = 857.10
PP#6					3973.77	3997.69	3711.53	AVG H(%)= 79.10
S						919.27	3307.48	

Table 5.30 Mean values for days to silking.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic
AP	61.5	59.0	63.0	58.5	61.5	60.3	60.5	CV (%) = 2.77
CG		53.3	53.3	50.8	53.3	54.0	53.4	AVG(P) = 57.13
JH			62.8	54.0	53.8	54.5	55.7	AVG(F1) = 55.72
PP#1				54.3	51.8	54.3	53.9	LSD = 2.19
PP#6					53.5	54.0	54.9	AVG H(%)= -2.47
S						57.5	55.4	

Table 5.31 Mean values for plant height (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic
AP	266.7	280.0	291.5	269.2	281.3	266.7	277.7	CV (%) = 3.82
CG		252.1	288.9	277.5	273.7	265.4	277.1	AVG(P) = 255.36
JH			247.6	271.2	262.9	277.5	278.4	AVG(F1) = 271.73
PP#1				259.1	258.4	250.2	265.3	LSD = 14.63
PP#6					258.4	261.6	267.6	AVG H(%)= 6.41
S						231.1	264.3	

Table 5.32 Mean values for ear height (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic
AP	106.0	112.9	132.1	114.3	115.6	123.8	119.7	CV (%) = 9.53
CG		104.1	120.6	103.5	103.5	104.2	108.9	AVG(P) = 107.30
JH			123.2	119.4	103.5	116.2	118.4	AVG(F1) = 111.53
PP#1				109.2	99.7	99.1	107.2	LSD = 14.87
PP#6					104.8	104.8	105.4	AVG H(%)= 3.93
S						96.5	109.6	

cross between Philippine Pop #1 and Philippine Pop #6. The array mean of Japanese Hulless, Avati Pichinga and Curagua Grande were 447.89, 503.6 and 67.5 kg/ha below the F1 average for grain yield, while the array mean values of Philippine Pop #6, Philippine Pop #1 and Supergold were 472.32, 421.78 and 68.27 kg/ha above the F1 average. Avati Pichinga yielded nearly twice as much at Kauai than at Waimanalo, yet the array mean of its hybrids was 26% lower at Kauai. The cross between PP#1 and PP#6 only expressed a heterotic effect of 31.7%, suggesting their close relationship as varieties.

Days to silking Mean values for days to silking are given in Table 5.30. Average heterosis of hybrids was -2.5%. F1 means ranged from 50.8 days to 63.0 days with a mean of 55.72 days. Avati Pichinga produced hybrids with the greatest number of days to silking with an array mean value of 60.5 days. The average number of days to silking for all entries was 9 days earlier at Kauai than at Waimanalo.

Plant height Mean values for plant height and array means are presented in Table 5.31. Average heterosis of hybrids was 6.4%, which is much lower than the average at Waimanalo of 16.5%. F1 means ranged from 250.2 cm to 291.5 cm with a mean of 271.7 cm. Japanese Hulless, Curagua Grande and Avati Pichinga produced the tallest hybrids with array mean values that were 6.65 cm, 5.38 cm and 6.00 cm above the average F1 height. Avati Pichinga's height was 122 cm higher than at Waimanalo, where it was the shortest of all varieties. This leads to the suspicion that some contamination with hybrids was in the seeds. PP#1 x PP#6 did not express any heterosis above the midparent mean.

<u>Ear height</u> Mean values for ear height are presented in Table 5.32. Average heterosis between hybrids and parents was 3.9%, again much lower than the average heterosis of 19.1% at Waimanalo. F1 means ranged from 99.1 cm to 132.1 cm with a mean of 111.53 cm. Avati Pichinga and Japanese Hulless produced hybrids that had ear heights above the F1 average with array means of 119.72 cm and 118.35 respectively. Array means for the other varieties were below the F1 average. Ear height was 38 cm higher for Avati Pichinga at Kauai than at Waimanalo. The cross between PP#1 and PP#6 was depressed, giving a value of -6.8% for heterosis.

<u>Ear length</u> Mean values for ear length are given in Table 5.33. Average heterosis was 14.4% between hybrids and parents. F1 means ranged from 13.5 cm to 18.5 cm with a mean of 16.89 cm. Avati Pichinga, Curagua Grande, Philippine Pop #6 and Supergold produced hybrids that were an average of 0.44 cm longer than the F1 mean. Japanese Hulless and Philippine Pop #1 had array means that were 1.58

Table 5.33 Mean values for ear length (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	18.4	18.5	15.9	18.1	17.2	17.1	17.33	CV (%) =	7.10
CG		16.6	14.6	17.9	18.2	18.2	17.47	AVG(P) =	14.77
JH			7.4	13.5	16.4	16.2	15.31	AVG(F1) =	16.89
PP#1				17.0	17.6	16.6	16.74	LSD =	1.64
PP#6					16.2	17.6	17.39	AVG H(%)=	14.36
S						13.2	17.13		

Table 5.34 Mean values for ear diameter (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	3.0	3.3	3.5	3.1	3.1	2.9	3.17	CV (%) =	6.07
CG		3.8	4.1	3.7	3.7	3.5	3.65	AVG(P) =	3.32
JH			3.3	4.0	4.1	3.7	3.90	AVG(F1) =	3.55
PP#1				3.3	3.7	3.3	3.56	LSD =	0.30
PP#6					3.5	3.6	3.64	AVG H(%)=	6.93
S						3.0	3.41		

Table 5.35 Mean values for kernel row number.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	15.5	15.1	19.8	16.0	15.3	16.0	16.42	CV (%) =	5.44
CG		20.0	19.5	15.5	15.8	15.5	16.27	AVG(P) =	18.00
JH			24.8	18.5	19.5	20.0	19.45	AVG(F1) =	17.04
PP#1				15.5	15.8	16.0	16.35	LSD =	1.33
PP#6					14.5	17.5	16.75	AVG H(%)=	-5.33
S						17.8	17.00		

Table 5.36 Mean values for kernel depth (mm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	4.60	5.29	5.25	4.93	4.85	4.13	4.89	CV (%) =	11.08
CG		5.98	7.38	6.53	6.53	6.88	6.52	AVG(P) =	5.55
JH			6.25	7.93	7.93	6.85	7.07	AVG(F1) =	6.29
PP#1				5.55	7.30	5.73	6.48	LSD =	0.95
PP#6					6.73	6.93	6.71	AVG H(%)=	13.47
S						4.18	6.10		

cm and 0.15 cm shorter, respectively, than the F1 mean. Ear length of Avati Pichinga was 6.3 cm longer at Kauai than at Waimanalo. The cross between PP#1 and PP#6 only expressed a heterotic effect of 6.0% compared to the average of other crosses over varieties.

Ear diameter Mean values for ear diameter are presented in Table 5.34. Average heterosis was 6.9%. F1 means ranged from 2.9 cm to 4.1 with an average diameter of 3.55 cm. The narrowest ears were produced by Avati Pichinga which had an array mean that was 0.31 cm below the F1 mean. But, Avati Pichinga was 0.77 cm wider at Kauai than at Waimanalo. Japanese Hulless produced hybrids with the widest ears, with an array mean that was 0.35 cm above the F1 average.

Kernel rows Mean values for the number of kernel rows and array means are given in Table 5.35. Average heterosis from parents to hybrids was -5.3%. F1 means ranged from 15.1 rows to 20.0 rows with an average of 17.0 rows. Japanese Hulless produced hybrids with the greatest number of rows with an array mean of 19.5. The other 5 varieties has array mean values that were an average of 0.48 rows below the F1 average. Avati Pichinga had 2.7 more kernel rows at Kauai than at Waimanalo.

Table 5.37 Mean values for tassel length (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	47.0	46.2	45.7	47.0	48.9	43.2	46.2	CV (%) =	11.37
CG		39.4	47.0	43.8	48.3	48.9	46.8	AVG(P) =	43.69
JH			38.7	48.3	46.4	50.1	47.5	AVG(F1) =	47.30
PP#1				47.0	48.3	47.6	47.0	LSD =	7.44
PP#6					52.0	50.1	48.4	AVG H(%)=	8.26
S						38.1	48.0		

Table 5.38 Mean values for length of central spike (cm).

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	29.9	30.1	29.9	27.9	29.9	26.0	28.7	CV (%) =	16.91
CG		16.5	26.0	22.2	21.6	21.6	24.3	AVG(P) =	23.69
JH			21.6	23.5	26.0	26.0	26.3	AVG(F1) =	25.87
PP#1				28.0	26.0	23.5	24.6	LSD =	6.04
PP#6					26.7	27.9	26.3	AVG H(%)=	9.18
S						19.7	25.0		

Table 5.39 Mean values for total stem number.

Parents	AP	CG	JH	PP#1	PP#6	S	F1 array mean	Total means and Statistic	
AP	2.0	1.2	3.3	2.8	3.0	2.5	2.5	CV (%) =	22.42
CG		2.3	2.5	2.5	2.3	2.5	2.2	AVG(P) =	2.13
JH			3.0	3.0	3.0	3.0	3.0	AVG(F1) =	2.46
PP#1				1.8	1.8	1.3	2.3	LSD =	0.75
PP#6					2.5	2.5	2.5	AVG H(%)=	15.98
S						1.3	2.4		

Kernel depth Mean values for kernel depth and array means are presented in Table 5.36. Average heterosis was 13.5%. F1 means ranged from 4.13 mm to 7.93 mm with an average of 6.29 mm. Avati Pichinga produced hybrids with the shortest kernels with an array mean that was 1.4 mm below the F1 mean. Japanese Hulless produced the longest kernels with an array mean of 7.07 mm for its hybrids.

Tassel length Mean values for tassel length are given in Table 5.37. Average heterosis between parents and F1 was 8.3%. F1 means ranged from 43.2 cm to 50.1 cm with an average of 47.3 cm. Hybrids with the shortest tassels were produced by Avati Pichinga which had an array mean of 46.2 cm. Philippine Pop #6 produced hybrids with the longest tassels with an array mean of 48.4 cm. The hybrid between PP#1 and PP#6 had a depressed heterosis of -2.4%, again suggesting their relationship. As shown in Figure 5.6, tassel length is significantly correlated to ear length at 0.01 level of probability.

Central spike length Mean values for central spike length and their array means are given in Table 5.38. Average heterosis of hybrids over midparent was 9.2%. F1 means ranged from 21.6 cm to 30.1 cm with an average of 25.87 cm. Avati Pichinga produced hybrids with the longest central spikes, having an array mean that was 2.87 cm longer than the F1 average. The cross between PP#1 and PP#6 showed a heterotic effect of -4.8% below the midparent value. Unlike the results at Waimanalo, central spike length was not significantly correlated to ear length at Kauai.

Stem number Mean values for the total number of stems are presented in Table 5.39. Heterosis over the midparent mean was 16.0%. At Waimanalo heterosis was 34.1% for stem number. F1 means ranged from 1.22 stems to 3.25 stems with an F1 average of 2.46 stems. Japanese Hulless produced hybrids with the most number of stems with an array mean of 2.95, while Curagua Grande had the lowest array mean of 2.19.

5.3.3. Analysis of Variance

Tables 5.40 to 5.41 presents the analysis of variance for 10 of the characteristics measured at the Kauai Branch Station. Between entries, significant differences were seen at P= .01 for all of the traits except tassel length, which showed significant differences at P= 0.05. The F1 were significantly different from varietal parents at P= 0.01 for all traits except ear height. Varieties were significantly different at P=0.01 for all traits except ear height which was significantly different at the 0.05 probability level. Differences between the F1 were significant at P=0.01 for all of the traits except tassel length and length of the central spike.

Table 5.40 Analysis of variance mean squares for grain yield, days to silking, plant height, ear height and ear length.

Source	df	Mean Squares				
		Grain yield	Days to silking	Plant height	Ear height	Ear length
Entries	19	9.63**	59.29**	839.32**	382.02**	25.91**
F1 vs Varieties	1	43.55**	45.34**	4180.06**	286.03	67.84**
Between Varieties	5	17.27**	69.88**	967.59**	312.58*	64.52**
Between F1	13	4.09**	56.29**	533.01**	416.11**	7.84**
Reps	3	3.43	1.55	747.04	155.54	7.59
Error	57	1.10	2.51	110.28	115.92	1.39

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5.41 Analysis of variance mean squares for ear diameter, kernel row, kernel depth, tassel length and spike length.

Source	df	Mean squares				
		Ear diameter	Kernel row	Kernel depth	Tassel length	Length of c. spike
Entries	19	0.554**	25.69**	5.54**	58.98*	53.24**
F1 vs Varieties	1	1.103**	11.34**	11.25**	214.10**	529.71**
Between Varieties	5	0.397**	59.50**	3.88**	132.88**	73.39**
Between F1	13	0.572**	13.79**	5.74**	18.62	8.83
Reps	3	0.099	0.08	0.82	13.80	15.70
Error	57	0.047	0.93	0.48	29.10	19.14

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

5.3.4. Combining Ability

Tables 5.42 and 5.43 present the combining ability mean squares based on Gardner and Eberhart's Analysis 3 (1966) and the mean square ratio of GCA to SCA. General combining ability was significant at P= 0.01 for ten of the traits. Specific combining ability was significant at P=0.01 for the total number of stems and it was significant at the 0.05 probability level for grain yield and ear length. Tassel length was omitted from this analysis because it exhibited no significant variation due to GCA or SCA. General combining ability made up most of the genetic variation, with the Mean Square GCA to SCA ratio ranging from 1.37 to 68.40 for ear diameter.

5.3.5. General and Specific Combining Ability Effects

Grain yield Estimates of general and specific combining ability effects for yield are presented in Table 5.44. The parents Philippine Pop #1 and #6 were good general combiners contributing to increased yields with significant estimates of 0.10 and 0.11, respectively. Avati Pichinga and Japanese Hulless significantly contributed to decrease yields with GCA effects of -0.11 and -0.10, respectively.

Days to Silking Estimates of general and specific combining ability effects for days to silking are presented in Table 5.45. Avati Pichinga significantly lengthened the

Table 5.42 General (GCA) and specific (SCA) combining ability mean squares for grain yield, days to silking, plant height, ear height and ear length.

Source	df	Mean squares				
		Grain yield	Days to Silking	Plant height	Ear height	Ear length
GCA	5	0.036 **	37.02 **	279.08 **	225.82 **	4.20 **
SCA	9	0.008 *	1.11	45.64	24.99	0.78 *
ERROR	60	0.003	0.60	26.64	27.62	0.33
MS GCA/SCA		4.63	33.45	6.11	9.04	5.37

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5.43 General (GCA) and specific (SCA) combining ability mean squares for ear diameter, kernel depth, kernel row, length of central spike and stem number.

Source	df	Mean squares				
		Ear diameter	Kernel depth	Kernel row	Length of c. spike	Tot.stem number
GCA	5	0.38 **	3.59 **	9.18 **	16.69 **	0.47 **
SCA	9	0.01	0.20	0.32	3.98	0.34 **
ERROR	60	0.01	0.11	0.22	4.56	0.07
MS GCA/SCA		68.40	17.65	28.28	4.20	1.37

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

number of days to silking with a GCA value of 5.93. Curagua Grande, Philippine Pop #1 and Philippine Pop #6 strongly reduced the number of days to silking with GCA values of -2.07, -2.34 and -1.09, respectively. The hybrid with the greatest number of days to silking was AP x JH, which significantly exceeded the expectation of either parent at P=0.05 by 1.38 units.

Plant height Estimates of general and specific combining ability effects for plant height are summarized in Table 5.46. Avati Pichinga, Curagua Grande and Japanese Hulless significantly contributed to increase plant height with GCA values of 7.50, 6.73 and 8.31, respectively. Philippine Pop #1 and Supergold contributed to decrease plant height at P=0.01 with GCA values of -8.04 and -9.31. Philippine Pop #6 reduced plant height at P=0.05 with a GCA value of -5.19. The greatest reduction in plant height over the expectation of either parent occurred in the cross JH x PP#6 with an SCA value of -11.95. A negative SCA effect was observed for the hybrid PP#1 x PP#6.

Ear height Estimates of general and specific combining ability effects for ear height are given in Table 5.47. Avati Pichinga and Japanese Hulless notably acted to raise ear height with GCA values of 10.24 and 8.53. Philippine Pop #1 and #6 strongly reduced ear height at P=0.05 and P= 0.01, respectively. The cross JH x PP#6 which had the

Table 5.44 Estimates of general and specific combining ability effects for grain yield.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	0.10 *	-0.09 *	0.01	0.02	-0.05	-0.11 **
CG		-0.05	0.06	-0.09 *	-0.03	0.00
JH			-0.02	0.01	0.15 **	-0.10 **
PP#1				0.04	-0.10 *	0.10 **
PP#6					0.01	0.11 **
S						0.01

Table 5.45 Estimates of general and specific combining ability effects for days to silking.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	-0.50	1.38 *	-0.81	0.94	-1.00	5.93 **
CG		-0.37	-0.56	0.69	0.75	-2.07 **
JH			0.65	-0.85	-0.79	-0.03
PP#1				-0.54	1.27 *	-2.34 **
PP#6					-0.23	-1.09 **
S						-0.40

Table 5.46 Estimates of general and specific combining ability effects for plant height.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	-5.92	3.91	-1.99	7.24	-3.24	7.50 **
CG		2.16	7.06	0.41	-3.71	6.73 **
JH			-0.85	-11.95 **	6.73	8.31 **
PP#1				-0.07	-4.15	-8.04 **
PP#6					4.38	-5.19 *
S						-9.31 **

greatest reduction in plant height over the expectation of either parent, also had the greatest negative SCA effect for plant height at P=0.01.

Ear length Estimates of general and specific combining ability effects for ear length are presented in Table 5.48. Avati Pichinga, Curagua Grande and Philippine Pop #6 strongly increased ear length with GCA values of 0.55, 0.72 and 0.62, respectively. Japanese Hulless significantly reduced ear length with a GCA value to -1.98. The hybrid JH x PP#1 exhibited the most significant SCA effect, reduced by -1.24 units below the additive contribution of the parental lines.

Ear diameter Estimates of general and specific combining ability effects for ear diameter are presented in Table 5.49. Avati Pichinga and Supergold significantly reduced ear diameter with GCA effects of -0.48 and -0.18. Japanese Hulless significantly increased ear diameter at P=0.01 with a GCA effect of 0.43.

Kernel row Estimates of general and specific combining ability for the number of kernel rows is summarized in Table 5.50. Only Japanese Hulless acted to increase the number of kernel rows with a GCA effect of 3.01. Avati Pichinga, Curagua Grande and Philippine Pop #1 significantly reduced

Table 5.47 Estimates of general and specific combining ability effects for ear height.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	-5.65	1.78	-2.03	1.45	4.46	10.24 **
CG		3.82	0.65	2.88	-1.70	-3.25
JH			4.75	-8.89 *	-1.45	8.53 **
PP#1				1.25	-4.62	-5.43 *
PP#6					3.31	-7.66 **
S						-2.43

Table 5.48 Estimates of general and specific combining ability effects for ear length.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	0.29	0.44	0.83	-0.89	-0.68	0.55 *
CG		-1.02 *	0.46	-0.03	0.3	0.72 **
JH			-1.24 **	0.84	0.98 *	-1.98 **
PP#1				0.31	-0.36	-0.20
PP#6					-0.23	0.62 *
S						0.29

Table 5.49 Estimates of general and specific combining ability effects for ear diameter.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	0.07	-0.05	0.02	-0.08	0.04	-0.48 **
CG		0.03	-0.01	-0.10	0.01	0.12 *
JH			0.03	0.05	-0.07	0.43 **
PP#1				0.04	-0.08	0.01
PP#6					0.10	0.11 *
S						-0.18 **

the number of kernel rows at P=0.01. There was a negative SCA effect for the cross between PP#1 and PP#6.

Kernel depth Estimates of general and specific combining ability effects for kernel depth are given in Table 5.51. Avati Pichinga significantly acted to reduce kernel depth with GCA effects of -1.76. Japanese Hulless and Philippine Pop #6 significantly increased kernel depth with a GCA effects of 0.97 and 0.52. The cross AP x S, which produced the smallest kernels, was reduced by -0.17 units below the expectation of either parent. The cross JH x PP#1, producing some of the largest kernels of the hybrids, exceeded the expectations of either parent by 0.43 units.

Length of central spike Estimates of general and specific combining ability effects for central spike length are presented in Table 5.52. Avati Pichinga significantly increased central spike length with a GCA effect of 3.59. Curagua Grande significantly reduced central spike length with a GCA effect of -1.98. Regression analysis of central spike length to ear length proved to be non-significant for Kauai data with r=0.31. However, the correlation of tassel length to ear length was significant at P=0.01, with r=.57.

Stem number Estimates of general and specific combining ability effects for the total number of stems is presented

Table 5.50 Estimates of general and specific combining ability effects for kernel row.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	-0.20	0.47	0.60	-0.65	-0.22	-0.78 **
CG		0.41	0.29	0.03	-0.53	-0.96 **
JH			-0.69	-0.19	0.00	3.01 **
PP#1				-0.07	-0.13	-0.86 **
PP#6					0.87 *	-0.36
S						-0.05

Table 5.51 Estimates of general and specific combining ability effects for kernel depth.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	0.47	-0.25	0.15	-0.2	-0.17	-1.76 **
CG		-0.16	-0.28	-0.56 *	0.54 *	0.28
JH			0.43	0.15	-0.17	0.97 **
PP#1				0.26	-0.56 *	0.23
PP#6					0.36	0.52 **
S						-0.24

Table 5.52 Estimates of general and specific combining ability effects for length of central spike.

			SCA Effects			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	2.57	-0.11	0.02	-0.11	-2.36	3.59 **
CG		1.6	-0.11	-2.85	-1.22	-1.98 *
JH			-1.34	-0.85	0.7	0.50
PP#1				1.18	0.26	-1.55
PP#6					2.63	0.50
S						-1.07

Table 5.53 Estimates of general and specific combining ability effects for total stem number.

			S.C.A.			G.C.A.
Parents	CG	JH	PP#1	PP#6	S	Effects
AP	-1.01 **	-0.08	0.45 *	0.39	0.08	0.10
CG		-0.23	0.64 **	0.08	0.52 *	-0.34 **
JH			0.20	-0.12	0.07	0.61 **
PP#1				-0.49 *	-0.80 **	-0.27 *
PP#6					0.13	0.04
S						-0.14

in Table 5.53. Japanese Hulless significantly increased the number of tillers among its hybrids with a GCA effect of 0.61. Both Curagua Grande and Philippine Pop #1 tended to reduce tiller number.

5.3.6. Discussion

The GCA to SCA mean square ratio was greater at Kauai than at Waimanalo for grain yield. Days to silking was very similar, with a GCA to SCA ratio of 33.45 at Kauai and 32.9 at Waimanalo. Plant height had a higher GCA to SCA ratio at Waimanalo, but ear height had a higher ratio at Kauai. Ear length and ear diameter showed a very high GCA to SCA ratio that was higher at Waimanalo. The GCA to SCA ratio for kernel row was also higher at Waimanalo. For total stem number, the GCA to SCA ratio was the same at both locations.

Higher average heterosis of hybrids over midparent was observed at Waimanalo for all characters except for kernel row number, which was more negative at Kauai. There was also a definite depression in heterosis at both locations for the hybrid PP#1 x PP#6. For grain yield, the average heterosis over both locations was 82.6%, while the average heterosis of the cross PP#1 x PP#6 was only 32.5% over both locations. Plant height was more striking, with a heterosis of -0.15% below the midparent at Kauai and -1.1% below at Waimanalo. Heterosis for ear height was -6.8% below the midparent at Kauai and -1.2% below the midparent at

Waimanalo for PP#1 x PP#6. It could be that these two varieties are related lines developed by recurrent selection.

Avati Pichinga performed very differently between the two locations. Its dramatic increase in yield, plant height, ear height and ear length at Kauai made it appear to be acting more like a hybrid than a variety. It could have been contaminated by stray pollen when seed was being increased.

5.4. VARIETY DIALLEL-NIGERIA

5.4.1 Results

The six varieties and their fifteen hybrids were mailed to the International Institute of Tropical Agriculture at Ibaden, Nigeria in March 1987. The trial was consequently planted in May at Ikenne, Nigeria. Ikenne is located at 6.5 degrees North latitude and 3.9 degrees East longitude at an altitude of 150 m. The trial was managed under irrigated conditions by Dr. T.M. Islam.

Field data for the trial received from Dr. Islam in September, 1987, indicated that there had been many barren plants for all of the lines. The variety Japanese Hulless only had data measured for all of the traits in one replication. In the other replications, only data for days to silking and curvularia were recorded. In response to inquiry about barren plants, Dr. Islam responded that, "Yes, there were barren plants in the trial, mainly due to streak virus attack. We had to apply Furadan at 2 weeks and 3 weeks after planting to keep the plants alive. In general, the lines were not adapted in the ecology (forest zone of Nigeria)." (Personal communication, Dec. 3, 1987).

Due to loss of data from the trial for the varietal parent Japanese Hulless, only the F1 generation was analyzed. In addition, it was not possible to report grain yield for the trial because of the high percentage of barren plants.

5.4.2. Mean Values

F1 array mean values for eight of the characteristics measured are presented in Tables 5.54 to 5.61. Stalk lodging and husk cover were omitted because they did not show significant variation in analysis of the F1. Characteristics such as curvularia, ear rot, plant aspect, ear aspect and root lodging were scored on a scale of 1 to 5, with 5 being the worst performance and 1 being the best. CV percentage ranged from 2.88 to 19.27 for all traits.

Days to silking Mean values for days to silking and the the array mean, F1 average, % CV and LSD are given in Table 5.54. F1 means ranged from 45.5 to 53.75 days with a mean of 49.32 days and an LSD of 1.91. The average number of days to silking for the hybrids was 14.3 days earlier than at Waimanalo and 6.4 days shorter than at Kauai. Avati Pichinga, Japanese Hulless and Supergold increased the number of days to silking among their F1 by 2.53, 0.83 and 0.43 days, respectively, above the F1 average. Avati Pichinga also had the highest array mean for days to silking at Kauai and Waimanalo.

Curvularia Mean values for curvularia leaf spot are summarized in Table 5.55. F1 means for resistance to

Table 5.54. F1 array mean values for days to silking.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	53.00	53.75	50.50	49.75	52.25	51.85	CV (%) = 2.88
CG		49.75	45.50	46.25	46.50	48.20	AVG(F1) = 49.32
JH			47.75	48.75	50.75	50.15	LSD = 1.91
PP#1				46.00	51.00	48.15	
PP#6					48.25	47.80	
S						49.75	

Table 5.55. F1 array mean values for curvularia.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	4.25	2.63	2.00	2.25	2.00	2.63	CV (%) = 19.27
CG		3.50	3.13	3.38	3.13	3.48	AVG(F1) = 2.9
JH			2.88	2.88	3.25	3.03	LSD = 0.8
PP#1				2.38	2.88	2.65	
PP#6					3.00	2.78	
S						2.85	

Table 5.56. F1 array mean values for plant height (cm).

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	165.00	188.75	193.75	175.00	182.50	181.00	CV (%) = 6.25
CG		178.75	190.00	185.00	182.50	180.25	AVG(F1) = 182.92
JH			192.50	175.00	193.75	185.75	LSD = 16.34
PP#1				183.75	177.50	187.50	
PP#6					180.00	179.75	
S						183.25	

Table 5.57. F1 array mean values for ear height (cm).

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	72.50	95.00	96.25	82.50	87.50	86.75	CV (%) = 10.09
CG		83.75	92.50	90.00	87.50	85.25	AVG(F1) = 87.33
JH			92.50	82.50	93.75	89.50	LSD = 12.6
PP#1				86.25	82.50	90.00	
PP#6					85.00	85.25	
S						87.25	

curvularia ranged from 2.0 to 4.25 with a average of 2.9 and an LSD of 0.8. The F1 of Curagua Grande and Japanese Hulless were 0.58 and 0.13 points more susceptible than the F1 average for the trial. Avati Pichinga had the lowest array mean for curvularia at 2.6.

Plant height Mean values for plant height and array means are presented in Table 5.56. F1 means ranged from 165.0 to 193.8 cm with an average of 182.9 cm and an LSD of 16.34. The F1 average was 26.7 cm shorter than the hybrids at Waimanalo and 88.8 cm shorter than the hybrids at Kauai. Philippine Pop #1, Japanese Hulless and Supergold produced F1 whose array mean exceeded the F1 average by 4.58, 2.93 and 0.33 cm, respectively.

Ear height Mean values for ear height are given in Table 5.57. F1 means ranged from 72.5 to 96.25 cm with an average of 87.33 and an LSD of 12.6 cm. At Waimanalo the average plant height of hybrids was 7.4 cm higher, while at Kauai it was 24.2 cm higher. Philippine Pop #1 and Japanese Hulless produced hybrids with the highest ears, with array mean values 2.67 and 2.17 above the F1 mean.

Ear rot Mean values for ear rot and array means are presented in Table 5.58. F1 means ranged from 2.0 to 3.38 with an average of 2.57 and an LSD of 0.57. Philippine Pop #1 produced hybrids with the most resistant ears to ear rot

Table 5.58. F1 array mean values for ear rot.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	3.00	2.63	2.13	2.13	2.25	2.43	CV (%) = 15.64
CG		3.38	2.50	2.75	2.63	2.85	AVG(F1) = 2.57
JH			2.50	3.38	2.50	2.88	LSD = 0.57
PP#1				2.00	2.63	2.35	
PP#6					2.13	2.48	
S						2.43	

Table 5.59. F1 array mean values for plant aspect.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	4.25	3.50	2.98	2.75	3.13	3.32	CV (%) = 14.74
CG		4.00	3.63	4.38	3.88	4.03	AVG(F1) = 3.59
JH			3.75	4.13	4.00	3.88	LSD = 0.76
PP#1				2.75	3.38	3.30	
PP#6					3.50	3.50	
S						3.58	

Table 5.60. F1 array mean values for ear aspect.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	3.25	2.75	2.25	2.25	2.50	2.60	CV (%) = 12.33
CG		3.13	2.63	2.88	2.75	2.93	AVG(F1) = 2.73
JH			2.75	3.50	2.63	2.95	LSD = 0.48
PP#1				2.25	3.00	2.58	
PP#6					2.38	2.65	
S						2.65	

Table 5.61. F1 array mean values for root lodging.

Parents	CG	JH	PP#1	PP#6	S	F1 Array mean	Total means and Statistics
AP	4.25	2.75	2.00	2.25	2.00	2.65	CV (%) = 19.27
CG		3.75	3.38	4.00	2.75	3.63	AVG(F1) = 2.9
JH			3.25	2.50	3.25	3.10	LSD = 0.8
PP#1				2.25	2.50	2.68	
PP#6					2.75	2.75	
S						2.65	

with an array mean value 0.22 below the F1 average. Japanese Hulless and Curagua Grande produced hybrids with the most susceptible ears to ear rot, with array mean values that were 0.31 and 0.28, respectively, above the F1 average.

Plant aspect Mean values for plant aspect are presented in Table 5.59. F1 means ranged from 2.75 to 4.25 with an average of 3.59 and an LSD of 0.76. Philippine Pop#1 produced the most vigorous hybrids with an array mean that was 0.29 points better than the F1 average. Japanese Hulless and Curagua Grande produced the weakest hybrids with array mean values 0.29 and 0.44 points above the F1 average.

Ear aspect Mean values for ear aspect and array means are presented in Table 5.60. F1 means ranged from 2.25 to 3.5 with an average of 2.73 and an LSD of 0.48. The hybrids with the cleanest ears were produced by Philippine Pop #1, with an array mean 0.15 points below the F1 average. The worst looking ears were produced by Japanese Hulless and Curagua Grande, which had array means 0.22 and 0.2, respectively, above the F1 average.

Root lodging Mean values for root lodging are presented in Table 5.61. F1 means ranged from 2.0 to 4.25 with an average of 2.9 and an LSD of 0.8. Supergold and Avati Pichinga produced hybrids most resistant to root lodging with array mean values 0.25 points below the F1

Table 5.62 Analysis of variance mean squares for days to silking, curvular, plant height, ear height and ear rot.

Source	df	Days to silking	Curvular	Plant height	Ear height	Ear rot
Between Hybrids	14	27.23**	1.44**	262.20*	157.02*	0.73**
Reps	3	2.33	0.38	318.19*	103.33	0.08
Error	42	2.02	0.31	130.69	77.74	0.16

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 5.63 Analysis of variance mean squares for plant aspect, ear aspect, root lodging, stalk lodging and husk cover.

Source	df	Plant aspect	Ear aspect	Root lodging	Stalk lodging	Husk cover
Between Hybrids	14	1.14**	0.57**	2.02**	0.79	0.80
Reps	3	0.85**	0.65**	0.35	0.05	0.55
Error	42	0.28	0.11	0.51	0.54	0.50

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

average. Japanese Hulless and Curagua Grande produced hybrids most susceptible to root lodging, with array mean values that were 0.2 and 0.73, respectively, above the F1 average.

5.4.3. Analysis of Variance

Tables 5.62 and 5.63 present the analysis of variance for the 15 variety crosses grown ar Ikenne, Nigeria. Of the ten traits measured, days to silking, curvularia, ear rot, plant aspect, ear aspect and root lodging showed significant differences at the 0.01 probability level. Plant height and ear height were significant at the 0.05 probability level for the 15 hybrids. As mentioned previously, stalk lodging and husk cover showed no significant differences between the F1.

Replications differed significantly at the 0.01 probability level for plant aspect and ear aspect and at the 0.05 probability level for plant height. This great variation between replications may have been due to the difference in intensity of streak virus attack across the trial.

5.4.4. Discussion

Despite the fact that the variety diallel was adversely affected by maize streak virus at Ikenne, Nigeria, information about the relative performance of the F1 could be gathered from some of the traits measured. F1 array mean results for curvularia, plant height, ear rot, plant aspect, ear aspect and root lodging clearly indicated that Philippine Pop #1's hybrids were superior, with Avati Pichinga a close second. The hybrid which performed the best throughout the trial was AP x PP#1. This hybrid was superior to all of the others for curvularia resistance, resistance to root lodging and superior ear aspect, and it scored well above the F1 mean for ear rot and plant aspect.

Judging from the decrease in the number of days to silking, plant height and ear height, Ikenne, Nigeria must have a very hot climate. Avati Pichinga and Philippine Pop #1 impart definite resistance to the adverse environmental conditions to their hybrids.

5.5. ANALYSIS OF VARIANCE FOR WAIMANALO AND KAUAI

5.5.1. Mean Values

Mean values for 10 traits that were recorded at both the Kauai Branch Station and the Waimanalo Research Station are presented in Tables 5.64 to 5.66. With the exception of plant height and the total number of stems, the data from Kauai had much higher coefficients of variation than the data recorded at Waimanalo. R-Square values were higher for all of the traits recorded at Waimanalo except total number of stems. Heterosis among the F1 generation was observed for all of the traits at both locations, however, the percentage of heterosis observed between the parental varieties and their hybrids was higher at the Waimanalo site for nine of the traits. Of the parental varieties, the performance of Avati Pichinga varied the most between the two locations. The percentage of heterosis of Avati Pichinga's hybrids was much higher at the Waimanalo site. For example, Avati Pichinga's hybrids exhibited 287.1% heterosis (over Avati Pichinga) for grain yield at Waimanalo and only 83.0% at Kauai. For ear length and length of central spike, Avati Pichinga's hybrids exhibited 35.4% and 11.4% heterosis (above Avati Pichinga), respectively, at Waimanalo and -5.5% and -3.7%, respectively, at Kauai.

Table 5.64. Mean values for grain yield, days to silking, plant height and ear height recorded at Waimanalo and Kapaa, Kauai.

Line	Waimanalo Grain yield	Kauai Grain yield	Waimanalo Days to Silking	Kauai Days to Silking	Waimanalo Plant height	Kauai Plant height	Waimanalo Ear height	Kauai Ear height
AP	157.20	246.02	77.0	61.5	144.5	266.7	68.3	106.0
CG	210.80	221.23	63.8	53.3	183.5	252.1	85.9	104.1
JH	71.70	27.85	70.5	62.8	176.4	247.6	77.1	123.2
PP#1	516.14	481.57	64.8	54.3	208.7	259.1	92.1	109.2
PP#6	410.59	651.31	62.0	53.5	179.8	275.6	70.6	104.8
S	380.55	150.67	66.5	57.5	186.6	231.1	83.5	96.5
Variety Mean	291.16	296.44	67.4	57.1	179.9	255.4	79.6	107.3
APxCG	527.13	517.56	67.0	59.0	214.3	280.0	94.7	112.9
APxJH	535.38	252.69	69.8	63.0	233.0	291.5	111.1	132.1
APxPP#1	723.72	522.11	66.0	58.5	216.8	269.2	98.8	114.3
APxPP#6	513.83	546.43	66.3	61.5	202.0	281.3	90.7	115.6
APxS	683.80	403.07	67.0	60.3	215.9	266.7	99.3	123.8
CGxJH	371.90	391.10	63.5	53.3	212.4	288.9	98.5	120.6
CGxPP#1	568.24	674.71	60.0	50.8	208.8	277.5	94.1	103.5
CGxPP#6	432.37	542.42	61.0	53.3	195.1	273.7	83.8	103.5
CGxS	580.22	519.85	61.3	54.0	210.3	265.4	98.4	104.2
JHxPP#1	491.04	508.60	63.0	54.0	209.0	271.2	94.9	119.4
JHxPP#6	414.07	545.56	62.3	53.8	204.1	262.9	86.8	103.5
JHxS	551.40	589.57	63.3	54.5	229.3	277.5	111.4	116.2
PP#1xPP#6	616.77	752.00	59.5	51.8	192.1	258.4	91.4	99.7
PP#1xS	486.45	542.80	63.0	54.3	202.9	250.2	80.4	99.1
PP#6xS	631.65	655.23	62.0	54.0	199.1	261.6	86.6	104.8
Hybrid Mean	541.86	530.91	63.7	55.7	209.7	271.7	94.7	111.5
% Heterosis	86.1	79.1	-5.6	-2.5	16.5	6.4	19.0	3.9
LSD	109.22	140.48	1.91	2.24	15.34	14.88	10.93	15.26
CV (%)	16.42	20.24	2.08	2.85	5.39	3.89	8.55	9.90
R-Square	0.86	0.83	0.89	0.89	0.83	0.74	0.74	0.54

Table 5.65. Mean values for ear length, ear diameter and kernel depth recorded at Waimanalo and Kapaa, Kauai.

Line	Waimanalo Ear length	Kauai Ear length	Waimanalo Ear diameter	Kauai Ear diameter	Waimanalo Kernel depth	Kauai Kernel depth
AP	12.1	18.4	2.2	3.0	3.44	4.60
CG	14.0	16.6	3.8	3.8	5.06	5.98
JH	7.8	7.4	3.3	3.3	5.69	6.25
PP#1	16.6	17.0	3.3	3.3	5.50	5.55
PP#6	14.9	16.2	3.5	3.5	6.13	6.73
S	12.6	13.2	3.0	3.0	5.50	4.18
Variety Mean	13.0	14.8	3.2	3.3	5.22	5.55
APxCG	16.9	18.5	3.2	3.3	5.06	5.29
APxJH	15.1	15.9	3.5	3.5	6.00	5.25
APxPP#1	17.2	18.1	3.1	3.1	5.13	4.93
APxPP#6	16.4	17.2	3.2	3.1	5.75	4.85
APxS	16.6	17.1	3.0	2.9	5.06	4.13
CGxJH	13.6	14.6	4.1	4.1	6.94	7.38
CGxPP#1	15.5	17.9	3.6	3.7	4.90	6.53
CGxPP#6	16.6	18.2	3.7	3.7	5.94	6.53
CGxS	16.1	18.2	3.4	3.5	6.06	6.88
JHxPP#1	13.9	13.5	4.0	4.0	7.38	7.93
JHxPP#6	13.7	16.4	4.0	4.1	7.25	7.93
JHxS	13.9	16.2	3.6	3.7	6.68	6.85
PP#1xPP#6	14.8	17.6	3.5	3.7	6.25	7.30
PP#1xS	15.5	16.6	3.3	3.3	5.88	5.73
PP#6xS	15.8	17.6	3.4	3.6	5.88	6.93
Hybrid Mean	15.4	16.9	3.5	3.6	6.01	6.29
% Heterosis	18.8	14.4	10.2	7.2	15.1	13.5
LSD	0.98	1.67	0.14	0.31	0.07	0.98
CV (%)	4.7	7.03	2.92	6.19	8.65	11.37
R-Square	0.93	0.87	0.96	0.80	0.80	0.80

Table 5.66. Mean values for kernel row, length of central spike and total number of stems recorded at Waimanalo and Kapaa, Kauai.

Line	Waimanalo Kernel row	Kauai Kernel row	Waimanalo Length of c. spike	Kauai Length of c. spike	Waimanalo Total no. stems	Kauai Total no. stems
AP	12.8	15.5	28.7	29.9	1.3	2.0
CG	15.6	20.0	20.4	16.5	1.3	2.3
JH	23.8	24.8	22.2	21.6	1.6	3.0
PP#1	14.1	15.5	29.7	28.0	1.3	1.8
PP#6	14.2	14.5	29.4	26.7	1.2	2.5
S	19.5	17.8	19.2	19.7	1.1	1.3
Variety Mean	16.7	18.0	24.9	23.7	1.3	2.1
APxCG	14.3	15.1	34.1	30.1	1.1	1.2
APxJH	19.0	19.8	32.3	29.9	2.1	3.3
APxPP#1	13.8	16.0	31.4	27.9	1.7	2.8
APxPP#6	15.0	15.3	31.8	29.9	2.0	3.0
APxS	15.7	16.0	30.4	26.0	1.6	2.5
CGxJH	19.6	19.5	23.9	26.0	1.9	2.5
CGxPP#1	13.6	15.5	24.9	22.2	1.4	2.5
CGxPP#6	15.0	15.8	22.2	21.6	1.3	2.3
CGxS	14.7	15.5	23.8	21.6	2.1	2.5
JHxPP#1	17.4	18.5	26.1	23.5	1.7	3.0
JHxPP#6	20.0	19.5	30.4	26.0	2.0	3.0
JHxS	20.3	20.0	24.0	26.0	2.0	3.0
PP#1xPP#6	15.0	15.8	26.7	26.0	1.8	1.8
PP#1xS	15.8	16.0	23.4	23.5	1.3	1.3
PP#6xS	16.0	17.5	26.6	27.9	1.7	2.5
Hybrid Mean	16.3	17.0	27.5	25.9	1.7	2.5
% Heterosis	-1.9	-5.3	10.2	9.2	34.3	16.0
LSD	0.97	1.37	2.43	6.19	0.54	0.75
CV (%)	4.19	5.52	6.44	17.50	24.23	22.42
R-Square	0.97	0.90	0.89	0.49	0.58	0.63

5.5.2. ANOV and Combining Ability Mean Square

The combined analysis of variance and general and specific combining ability mean squares and their percentage mean squares for the six varieties and their 15 variety crosses grown at the Waimanalo Research Station and the Kauai Branch Station are presented in Tables 5.67 to 5.70. There was a significant location effect at P= .01 for days to silking, plant height, ear height, ear length, kernel row, length of central spike and total stem number. This made up over 70% of the total variation for days to silking, plant height, ear height and total number of stems. There was also a significant difference due to replications for days to silking, plant height, ear height and the total number of stems, but this made up less than 4% of the total variation for these traits. Entries were significant for all of the traits and under entries, varieties made up the greatest part of the variation for kernel row and length of the central spike. Under entry variance, varieties vs hybrids made up most of the variation for grain yield, plant height, ear height, ear length, ear diameter, kernel depth and total number of stems. This reflected the high average heterosis observed for these traits. Hybrids were significant at P=0.01 for all of the traits but did not contribute highly to the entry variance. Combining ability due to general effects occupied the greatest percentage for all of the traits at both locations. General combining

Table 5.67. Analysis of variance and general (GCA) and specific (SCA) combining ability mean squares for grain yield, days to silking, plant height, ear height, and ear length for variety diallel at two locations.

		Mean squares				
Source	df	Grain yield	Days to silking	Plant height	Ear height	Ear length
Location	1	0.0002	388.94 **	22805.68 **	2090.21 **	12.62 **
Rep/Location	6	0.0014	15.14 **	91.95 **	15.92 **	0.49
Entries	20	0.0320 **	14.53 **	215.97 **	82.23 **	4.97 **
Varieties	5	0.0422 **	22.02 **	123.77 **	36.85 **	11.13 **
Varieties vs Hybrids	1	0.3056 **	28.46 **	2278.53 **	398.86 **	22.30 **
Hybrids	14	0.0088 **	10.86 **	101.57 **	75.82 **	1.53 **
GCA	5	0.0156 **	29.08 **	237.12 **	170.55 **	3.77 **
SCA	9	0.0051 **	0.74 **	26.27	23.19 *	0.29 *
Entries x Locations	20	0.0119 **	2.15 **	164.35 **	51.64 **	1.02 **
Pooled Error	120	0.0012	0.26	14.01	10.64	0.11

Table 5.68. Percentage mean squares of the analysis of variance and general (GCA) and specific (SCA) combining ability mean squares for grain yield, days to silking, plant height, ear height and ear length.

		Percentage mean squares				
Source	df	Grain yield	Days to silking	Plant height	Ear height	Ear length
Location	1	0.1 %	75.9 %	87.5 %	70.7 %	21.7 %
Rep/Location	6	0.3 %	3.0 %	0.4 %	0.5 %	0.8 %
Entries	20	7.6 %	2.8 %	0.8 %	2.8 %	8.5 %
Varieties	5	10.0 %	4.3 %	0.5 %	1.2 %	19.1 %
Varieties vs Hybrids	1	72.1 %	5.6 %	8.7 %	13.5 %	38.3 %
Hybrids	14	2.1 %	2.1 %	0.4 %	2.6 %	2.6 %
GCA	5	3.7 %	5.7 %	0.9 %	5.8 %	6.5 %
SCA	9	1.2 %	0.1 %	0.1 %	0.8 %	0.5 %
Entries x Locations	20	2.8 %	0.4 %	0.6 %	1.7 %	1.8 %
Pooled Error	120	0.3 %	0.1 %	0.1 %	0.4 %	0.2 %

Table 5.69. Analysis of variance and general (GCA) and specific (SCA) combining ability mean squares for ear diameter, kernel depth, kernel row, length of central spike and stem number for the variety diallel at two locations.

Source	df	Mean squares				
		Ear diameter	Kernel depth	Kernel row	Length of c. spike	Total no. stems
Location	1	0.021	0.320	4.23 **	11.32 **	26.94 **
Rep/Location	6	0.009	0.086	0.07	2.12	1.00 **
Entries	20	0.136 **	0.856 **	6.86 **	14.69 **	0.20 **
Varieties	5	0.150 **	0.725 **	12.60 **	24.61 **	0.16 **
Varieties vs Hybrids	1	0.283 **	1.277 **	1.77 **	23.08 **	1.44 **
Hybrids	14	0.121 **	0.873 **	4.27 **	10.54 **	0.13 **
GCA	5	0.334 **	2.226 **	11.57 **	25.17 **	0.14 **
SCA	9	0.003	0.121 *	0.22 *	2.42	0.12 **
Entries x Locations	20	0.024 **	0.287 **	0.79 **	2.25 *	0.10 **
Pooled Error	120	0.003	0.053	0.09	1.32	0.03

Table 5.70. Percentage mean squares for the analysis of variance and general (GCA) and specific (SCA) combining mean squares for ear diameter, kernel depth, kernel row, length of central spike and stem number.

Source	df	Mean squares				
		Ear diameter	Kernel depth	Kernel row	Length of c. spike	Total no. stems
Location	1	2.0 %	4.7 %	10.0 %	9.6 %	89.0 %
Rep/Location	6	0.9 %	1.3 %	0.2 %	1.8 %	3.3 %
Entries	20	12.6 %	12.5 %	16.2 %	12.5 %	0.7 %
Varieties	5	13.8 %	10.6 %	29.7 %	20.9 %	0.5 %
Varieties vs Hybrids	1	26.1 %	18.7 %	4.2 %	19.6 %	4.8 %
Hybrids	14	11.1 %	12.8 %	10.1 %	9.0 %	0.4 %
GCA	5	30.7 %	32.6 %	27.2 %	21.4 %	0.5 %
SCA	9	0.3 %	1.8 %	0.5 %	2.1 %	0.4 %
Entries x Locations	20	2.2 %	4.2 %	1.9 %	1.9 %	0.3 %
Pooled Error	120	0.3 %	0.8 %	0.2 %	1.1 %	0.1 %

ability effects made up the greatest percentage of the entry variance for ear diameter, kernel depth and length of the central spike. Specific combining ability was significant at P=0.01 for grain yield, days to silking and total number of stems. It was significant at P=0.05 for ear height, ear length, kernel depth and kernel row.

The variation due to the interaction between entries and locations was significant at P=0.01 for all of the traits except length of the central spike, which was significant at P=0.05. The percentage of the total variation due to the interaction between entries and locations was below 4.3% for all of the traits, however.

5.5.3. General and Specific Combining Ability Effects

Estimates of general, specific and parental effects for the six varieties and their 15 hybrids over two locations are presented in Tables 5.71 to 5.73. Estimates for grain yield, days to silking and plant height are presented in Table 5.71. As parents, Avati Pichinga, Curagua Grande and Japanese Hulless were low yielders at both locations, while Philippine Pop #1 and Philippine Pop #6 were high yielders. Imparting this trait upon its hybrids, Philippine Pop #1 performed as expected over both locations, contributing to high yields but Avati Pichinga unexpectedly contributed to high yields among its F1 at Waimanalo while conforming to expectations as a low yielder at Kauai. As a parent, Avati

Table 5.71. Estimates of general, specific and parental effects for grain yield, days to silking and plant height for the variety diallel at two locations.

	Kauai Grain yield	Waimanalo Grain yield	Kauai Days to silking	Waimanalo Days to silking	Kauai Plant height	Waimanalo Plant height
Mean	0.33	0.32	57.12	67.42	255.36	179.92
Average heterosis	0.26	0.28	-1.40	-3.77	16.37	29.76
			Parental Effects			
Avati Pichinga	-0.06 *	-0.15 **	4.38 **	9.58 **	11.32 **	-35.42 **
Curagua Grande	-0.09 **	-0.09 **	-3.88 **	-3.67 **	-3.26	3.58
Japanese Hulless	-0.30 **	-0.24 **	5.63 **	3.08 **	-7.76 **	-3.52
Philippine Pop #1	0.20 **	0.25 **	-2.88 **	-2.67 **	3.69	28.78 **
Philippine Pop #6	0.39 **	0.13 **	-3.63 **	-5.42 **	20.24 **	-0.12
Supergold	-0.16 **	0.10 **	0.38	-0.92 **	-24.23 **	6.68 **
			GCA Effects			
Avati Pichinga	-0.11 **	0.07 **	5.93 **	4.44 **	7.50 **	8.41 **
Curagua Grande	0.00	-0.06 **	-2.07 **	-1.38 **	6.73 **	-1.87
Japanese Hulless	-0.10 **	-0.10 **	-0.03	0.88 **	8.31 **	9.86 **
Philippine Pop #1	0.10 **	0.05 *	-2.34 **	-1.69 **	-8.04 **	-4.69
Philippine Pop #6	0.11 **	-0.03	-1.09 **	-1.81 **	-5.19 *	-13.99 **
Supergold	0.01	0.06 **	-0.40	-0.44	-9.31 **	2.28
			SCA Effects			
APxCG	0.10 *	-0.03	-0.50	0.29	-5.92	-1.91
APxJH	-0.09 *	0.01	1.38 *	0.79	3.91	5.06
APxPP#1	0.01	0.08 *	-0.81	-0.40	-1.99	3.41
APxPP#6	0.02	-0.08 *	0.94	-0.03	7.24	-2.09
APxS	-0.05	0.02	-1.00	-0.65	-3.24	-4.47
CGxJH	-0.05	-0.03	-0.37	0.35	2.16	-5.26
CGxPP#1	0.06	0.05	-0.56	-0.59	7.06	5.69
CGxPP#6	-0.09 *	-0.03	0.69	0.54	0.41	1.28
CGxS	-0.03	0.04	0.75	-0.59	-3.71	0.21
JHxPP#1	-0.02	-0.01	0.65	0.16	-0.85	-5.84
JHxPP#6	0.01	-0.02	-0.85	-0.46	-11.95 **	-1.44
JHxS	0.15 **	0.05	-0.79	-0.84	6.73	7.49
PP#1xPP#6	0.04	0.06	-0.54	-0.65	-0.07	1.11
PP#1xS	-0.10 *	-0.17 **	1.27 *	1.47 **	-4.15	-4.37
PP#6xS	0.01	0.07	-0.23	0.60	4.38	1.13

Pichinga took a long time to silk at both locations. This characteristic was inherited by additive gene action and exhibited by the F1 at both locations. Japanese Hulless was short as a parent at both locations but in hybrid combination it tended to increase plant height. Curiously, Avati Pichinga was short as a parent at Waimanalo but tall at Kauai. In hybrid combination, however, Avati Pichinga raised plant height at both locations.

Estimates of general, specific and parental effects are presented in Table 5.72 for ear height, ear length and ear diameter. As seen previously in Table 5.70, 30.7% of the total variation for ear diameter was due to general combining ability. This is confirmed by the negative parental effects of Avati Pichinga and Supergold producing hybrids that are narrow eared, while the positive parental effects of Curagua Grande, Japanese Hulless and Philippine Pop #6 all produce hybrids tending to have wide ears. Over both locations, Philippine Pop #6 tended to be low eared as a variety and produced hybrids that were also low eared. Avati Pichinga was low eared as a parent, but produced high eared hybrids. As a parent, Japanese Hulless produced short ears and was consistent over both locations in imparting this characteristic to its hybrids.

Estimates of general, specific and parental effects for kernel depth, kernel row number, length of the central spike

Table 5.72. Estimates of general, specific and parental effects for ear height, ear length and ear diameter of the variety diallel at two locations.

	Kauai Ear height	Waimanalo Ear height	Kauai Ear length	Waimanalo Ear length	Kauai Ear diameter	Waimanalo Ear diameter
Mean	107.30	79.54	14.77	12.99	3.32	3.22
Average heterosis	4.22	15.15	2.12	2.44	0.24	0.28
			Parental Effects			
Avati Pichinga	-1.28	-11.29 **	3.58 **	-0.87 **	-0.32 **	-1.00 **
Curagua Grande	-3.18	6.31 **	1.78 **	0.96 **	0.50 **	0.33 **
Japanese Hulless	15.90 **	-2.49	-7.42 **	-5.19 **	0.01	0.51 **
Philippine Pop #1	1.90	12.56 **	2.25 **	3.56 **	-0.05	-0.04
Philippine Pop #6	-2.55	-8.99 **	1.40 **	1.91 **	0.20 **	0.23 **
Supergold	-10.78 **	3.91 *	-1.60 **	-0.37 *	-0.33 **	-0.04
			GCA Effects			
Avati Pichinga	10.24 **	5.22 **	0.55 *	1.24 **	-0.48 **	-0.38 **
Curagua Grande	-3.25	-1.03	0.72 **	0.37 *	0.12 *	0.10 **
Japanese Hulless	8.53 **	7.25 **	-1.98 **	-1.73 **	0.43 **	0.42 **
Philippine Pop #1	-5.43 *	-3.48	-0.20	-0.05	0.01	-0.02
Philippine Pop #6	-7.66 **	-8.57 **	0.62 *	0.03	0.11 *	0.06 *
Supergold	-2.43	0.62	0.29	0.15	-0.18 **	-0.18 **
			SCA Effects			
APxCG	-5.65	-4.23	0.29	-0.16	0.07	-0.02
APxJH	1.78	3.88	0.44	0.14	-0.05	-0.03
APxPP#1	-2.03	2.32	0.83	0.58 *	0.02	0.00
APxPP#6	1.45	-0.69	-0.89	-0.31	-0.08	0.00
APxS	4.46	-1.28	-0.68	-0.24	0.04	0.06
CGxJH	3.82	-2.47	-1.02 *	-0.43	0.03	0.03
CGxPP#1	0.65	3.92	0.46	-0.25	-0.01	-0.03
CGxPP#6	2.88	-1.29	-0.03	0.75 **	-0.10	0.00
CGxS	-1.70	4.07	0.30	0.10	0.01	0.02
JHxPP#1	4.75	-3.57	-1.24 **	0.27	0.03	0.05
JHxPP#6	-8.89 *	-6.63 *	0.84	0.01	0.05	0.06
JHxS	-1.45	8.78 **	0.98 *	0.00	-0.07	-0.10 *
PP#1xPP#6	1.25	8.76 **	0.31	-0.59 *	0.04	-0.05
PP#1xS	-4.62	-11.43 **	-0.36	-0.01	-0.08	0.03
PP#6xS	3.31	-0.14	-0.23	0.14	0.10	0.00

Table 5.73. Estimates of general, specific and parental effects for kernel depth, kernel row, length of central spike and stem number of the variety diallel at two locations.

	Kauai Kernel depth	Waimanalo Kernel depth	Kauai Kernel row	Waimanalo Kernel row	Kauai Length of c.spike	Waimanalo Length of c.spike	Kauai Tot.stem number	Waimanalo Tot.stem number
Mean	5.55	5.22	18.00	16.65	23.69	24.92	2.13	1.30
Average heterosis	0.75	0.79	-0.96	-0.33	2.18	2.52	0.34	0.41
					Parental Effects			
Avati Pichinga	-0.95 **	-1.78 **	-2.50 **	-3.85 **	6.16 **	3.78 **	-0.13	0.00 **
Curagua Grande	0.43 **	-0.16 **	2.00 **	-1.05 **	-7.22 **	-4.57 **	0.13	0.00
Japanese Hulless	0.70 **	0.47 **	6.75 **	7.15 **	-2.14 *	-2.72 **	0.88 **	0.30 **
Philippine Pop #1	0.00	0.28 **	-2.50 **	-2.55 **	4.26 **	4.73 **	-0.38 **	0.00 **
Philippine Pop #6	1.18 **	0.91 **	-3.50 **	-2.50 **	2.96 **	4.48 **	0.38 **	-0.10
Supergold	-1.37 **	0.28 **	-0.25	2.80 **	-4.02 **	-5.72 **	-0.88	-0.20 *
					GCA Effects			
Avati Pichinga	-1.76 **	-0.76 **	-0.78 **	-0.98 **	3.59 **	5.66 **	0.10	-0.02
Curagua Grande	0.28	-0.29 **	-0.96 **	-1.14 **	-1.98 *	-2.55 **	-0.34 **	-0.19 *
Japanese Hulless	0.97 **	1.05 **	3.01 **	3.65 **	0.50	0.28	0.61 **	0.28 **
Philippine Pop #1	0.23	-0.13 **	-0.86 **	-1.53 **	-1.55	-1.19 **	-0.27 *	-0.17
Philippine Pop #6	0.52 **	0.25 **	-0.36	-0.17	0.50	0.08	0.04	0.06
Supergold	-0.24	-0.12 **	-0.05	0.17	-1.07	-2.28 **	-0.14	0.03
					SCA Effects			
APxCG	0.47	0.10 *	-0.20	0.10	2.57	1.71 *	-1.01 **	-0.40 **
APxJH	-0.25	-0.30 **	0.47	0.01	-0.11	0.67	0.08	0.12
APxPP#1	0.15	0.01	0.60	-0.07	0.02	-0.55	0.45 *	0.17
APxPP#6	-0.20	0.25 **	-0.65	-0.18	-0.11	-1.37 *	0.39	0.24
APxS	-0.17	-0.06	-0.21	0.14	-2.36	-0.46	0.08	-0.13
CGxJH	-0.16	0.17 **	0.41	0.72 **	1.60	-1.31	-0.23	0.09
CGxPP#1	-0.28	-0.69 **	0.29	-0.10	-0.11	1.21	0.64 **	0.04
CGxPP#6	-0.56 *	-0.04	0.03	-0.02	-2.85	-2.81 **	0.08	-0.28
CGxS	0.54 *	0.46 **	-0.53	-0.70 *	-1.22	1.20	0.52 *	0.55 **
JHxPP#1	0.43	0.45 **	-0.69	-1.04 **	-1.34	-0.42	0.20	-0.13
JHxPP#6	0.15	-0.06	-0.19	0.20	-0.85	2.55 **	-0.12	-0.05
JHxS	-0.17	-0.26 **	0.00	0.11	0.70	-1.49 *	0.07	-0.03
PP#1xPP#6	0.26	0.12 **	-0.06	0.37	1.18	0.32	-0.49 *	0.19
PP#1xS	-0.56 *	0.12 **	-0.13	0.83 **	0.26	-0.56	-0.80 **	-0.28
PP#6xS	0.36	-0.26 **	0.87 *	-0.38	2.63	1.31	0.13	-0.10

and total number of stems over two locations is presented in Table 5.73. As was seen in Table 5.70, 32.6% of the total variation for kernel depth was due to general combining ability, the reason for this can be clearly seen in Table 5.73. As parents, Avati Pichinga had a short kernel, while Japanese Hulless and Philippine Pop #6 had long kernels. In hybrid combination, Avati Pichinga had a negative effect, producing short kerneled hybrids, while Japanese Hulless and Philippine Pop #6 had a positive effect, producing long kerneled hybrids. For the number of kernel rows, 27.2% of the total variation was due to general combining ability. The evidence of this is seen in the fact that Avati Pichinga and Philippine Pop #1, as parents, had few kernel rows and their hybrids also tended to have few kernel rows. Japanese Hulless, as a parent, had many kernel rows and its hybrids also reflected this trait. Over both locations, Avati Pichinga had a long central spike and its hybrids also tended to have long central spikes. Curagua Grande had a short spike at both locations and its hybrids tended to have the same characteristic. For total number of stems, the only variety that was consistent over locations was Japanese Hulless. As a parent it tended to have more stems than the other varieties and its hybrids were also significant in having a high number of stems.

5.5.4. Discussion

With regard to the combined analysis of Waimanalo and Kauai it seems that in general, much more heterosis was expressed from the varietal parents to the F1 generation at Waimanalo than Kauai. It is my suspicion that part of the reason for this was the very different performance of Avati Pichinga between the two locations. As pointed out previously, Avati Pichinga exhibited much greater heterosis among its F1 at Waimanalo than Kauai. At Kauai, Avati Pichinga behaved as a hybrid rather than as a variety. If Avati Pichinga were contaminated with hybrids at Kauai, this would help explain these differing results.

Between the two locations, there was not one particular hybrid that performed better than the others. All of these traits were dominated by general combining ability rather than specific combining ability, therefore selection should be based upon the variety with superior GCA. Over both locations, Philippine Pop #1 made a significant contribution to increased yield. It tended to shorten the number of days to silking, and reduce plant and ear height.

6. GENERATION MEAN ANALYSIS

6.1. STATISTICAL METHODS

Two popcorn inbreds and one Hawaiian dent inbred were used as parents for generation mean analysis (GMA) involving three F1, three F2 and three backcross populations. This resulted in a total of 15 populations that were planted in four randomized complete block trials at two locations; the Waimanalo Research Station and the Kauai Branch Station. At the Kauai Station, 90-100 plants were measured for each generation and trait measured and 70-80 plants were similarly measured at Waimanalo.

For characters showing significant variation between generations, the scaling test was performed according to Hayman and Mather (1955) to test the goodness of fit of the additive-dominance model. The four tests of scale are as follows, where P1 is parent number 1, P2 is parent number 2, B1 is the backcross to parent 1, B2 is the backcross to parent 2, F1 is the hybrid between P1 and P2, and F2 is derived from sibs of the F1:

SCALE	MEAN	VARIANCE	INTERACTION
A	= 2B1-P1-F1	A = 4V(B1)+V(P1)+V(F1)	axd
B	= 2B2-P2-F1	B = 4V(B2)+V(P2)+V(F1)	axd
C	= 4F2-2F1-P1-P2	C = 16V(F2)+4V(F1)+V(P1)+V(P2)	axa,dxd
D	= 2F2-B1-B2	D = V(F2)+V(B1)+V(B2)	axa,dxd

P1 is parent number 1, P2 is parent number 2, B1 is the backcross to parent 1, B2 is the backcross to parent 2, F1 is the hybrid between P1 and P2 and F2 is derived from sibs of the F1. When interaction of additive and/or dominance components is present, the 't' values comparing the variances are expected to be significant at 0.05 if greater than 1.96 and significant at 0.01 if greater than 2.58 (assuming the total population size of the individual parts of the equation exceeds 120). According to Hayman and Mather (1955), C and D of the scaling test assesses dominance x dominance and additive x additive interactions, while A and B assess the additive x dominance interaction. If there is no interaction (the 't' values are non-significant) a model using genetic variances proposed by Mather and Jinks (1977) is used for estimation of additivity and dominance. The genetic variance model is as follows:

NOTATION **MEAN**

$E = 1/4x[V(P1)+V(P2)+2V(F1)]$

$A = D = 4V(F2)-2x[V(B1)+V(B2)]$

$D = H = 4x[V(B1)+V(B2)-V(F2)-E]$

E is the variance due to environment, expressed as an average of variances of the genetically homogeneous parents and F1. D is the additive variance and H is the dominance variance. In this paper D is replaced by the symbol A for additive variance and H is replaced by D for dominance variance. There are certain biological assumptions which must be met before this simplified model can be used and these are (1) normal diploid behavior at meiosis, (2) no maternal or cytoplasmic effects, (3) no multiple alleles, (4) linkage equilibrium, (5) no selection (6) no epistasis and (7) parents homozygous for the traits being measured (Sprague 1966). Despite these restrictions, this is the best and most valid model available at this time.

When 't' of one of the scales is significant at the 0.05 level of significance, the six parameter model of

Hayman (1958) is preferred to estimate non-allelic interaction with Gamble's (1962) notation. These are estimated as follows:

NOTATION **MEAN**

$$m = F2$$

$$a = B1-B2$$

$$d = [(F1-4\times F2)-((1/2)\times P1)] - [((1/2)\times P2)+(2B1+2B2)]$$

$$aa = [(2\times B1)+(2\times B2)] - (4\times F2)$$

$$ad = [B1-((1/2)\times P1)] - [B2+((1/2)\times P2)]$$

$$dd = [P1+P2+2F1] + [(4\times F2)-(4\times B1)-(4\times B2)]$$

In these formulae, 'a' is presumed to measure the pooled additive genetic effect, 'd' measures the pooled dominance or non-additive effect, 'aa' measures the pooled interactions between additive effects, 'ad' measures the additive by dominance effect and 'dd' measures the pooled interaction between dominance effects. The six parameter model is based on the mean of the F2. In the absence of epistasis, the F2 mean should be midway between the midparent and the F1 mean. In a complementary cross, involving complimentary genes, the F2 mean should be nearer to the midparent mean value, and in the duplicate cross it should be nearer to the F1 mean (Hayman 1958). The additive effect (a) is correlated to the ad interaction and the dominance effect (d) is correlated to the aa and dd interactions (Jinks and Stevens 1959). Also, if epistatic effects are not present, estimates of 'a' and 'd' effects are meaningful and unbiased by linkage disequilibrium; if epistatic effects are present, estimates of 'a' and 'd' effects are biased by that epistasis and linkage disequilibrium (Hallauer and Miranda 1981).

Heritability estimates were made from the environmental (E), additive (A) and dominance (D) variance components in two ways. Narrow sense heritability was estimated as the proportion of the additive variance to the total variance, A/(A+D+E). It was also estimated according to Warner's (1952) formula, on the basis of the F2 and backcrosses in this manner; (1/2 A)/VF2. Broad sense heritability was estimated by the proportion of genotypic variance to the total variance; (A+D)/(A+D+E). Where a negative number appears for additive or dominance variance it is treated as 0 to estimate heritability, as variance cannot in reality be negative. Since heritability estimates cannot be made from the 6 parameter model, the liberty has been taken to analyze heritability using the model of genetic variances in the presence of non-allelic interactions. Even though the estimate of broad sense heritability is inaccurate in the presence of non-allelic interactions, it does reflect heterotic effects to a degree. Narrow sense heritability is a more accurate estimate of heritability in the presence of epistatic interactions because it is only affected by additive types of epistasis. According to Hallauer and Miranda (1981), only additive types of epistasis are fixable or usable by the plant breeder.

6.2. RESULTS

Crosses between the two popcorn inbreds, I28 and Sg18 and the dent inbred Hi26 and their F1, F2 and backcross progenies were evaluated for yield, plant height, ear height, tassel length, central spike length, ear length, ear diameter, number of kernel rows, kernel depth, kernel width, weight of 1000 kernels, root lodging and stalk lodging. No significant variation occurred, however, for ear diameter, root lodging and days to silking. Only the results for yield and stalk lodging at one location, and ear length, length of central spike, tassel length, kernel row number, kernel depth, kernel width, 1000 kernel weight, ear height, plant height at two locations are included in this discussion.

Analysis of each character is presented by a page of tables that cover averages of the parents, F1, F2 and backcross progenies and heterosis estimates. These are followed by the scaling test of allelic interaction and the six parameter analysis of significant epistasis. Lastly is the table of additive, dominance and environmental variance together with the estimates of narrow and broad sense heritabilities derived from those variances. On a separate page are the frequency distributions of the F1 and segregating generations and parental means for each cross by location.

6.2.1. Yield

Genetic analysis and heritability estimates for yield in kilograms per hectare for the three crosses at Waimanalo are presented in Tables 6.1 to 6.3. The average yields of the parents, F1, F2 and backcross generations, parental midpoint and heterosis are presented in Table 6.1. The highest yield of 3624.78 kg/ha was obtained by the F1 generation of Hi26 x Sg18. Heterosis for the crosses was high, ranging from 74.2% to 104.6% for I28 x Sg18. Segregating generations exceeded the midparent value for all crosses and the F1 exceeded the high parent mean. For I28 x Sg18, both backcrosses exceeded the high parent mean. For both crosses to Hi26, the backcross to the high parent was equal to or greater than the high parent and the backcross to the low yielding parent was greater than the midparent value. Yields for Hi26 and the two popcorn inbreds were lower than usual due to the shortening day length between mid-September and November, root and stalk lodging caused by heavy rainfall and high winds and grain lost from ears to hungry birds.

In the frequency distribution of the F1 and segregating generations in Figure 6.1, it can be seen that in all of the crosses, the F1 and segregating generations tend towards or

Table 6.1. Average yield (kg/ha) of parents, F1, F2 and backcross progenies at Waimanalo.

Cross	Parent			Hybrid	Segregating Generations			Heterosis(2)
1 x 2	P1	P2	MP(1)	F1	F2	B1	B2	
Hi26 x I28	3049.52	602.59	1826.06	3251.10	2400.74	3043.85	1999.43	78.0 %
Hi26 x Sg18	3049.52	1111.97	2080.75	3624.78	2248.38	3254.38	2100.25	74.2 %
I28 x Sg18	602.59	1111.97	857.28	1753.58	1319.08	1179.04	1290.26	104.6 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.2. Scaling test and six parameter generation mean analysis for grain yield at Waimanalo.

	Scaling Test				Six Parameter Analysis				
	A	B	C	D	a	d	aa	ad	dd
Hi26 x I28	-212.9	145.2	-551.4	-241.8	1044.4 **	1908.7 **	483.6	-179.0	-415.8
Hi26 x Sg18	-165.5	-536.3 **	-2417.5 **	-857.9 **	1154.1 **	3259.8 **	1715.7 **	185.3	-1014.0
I28 x Sg18	1.9	-285.0 *	54.6	168.9 *	-111.2	558.6 *	-337.7	143.5	620.9

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.3. Genetic variances and heritability estimates for grain yield at Waimanalo.

	Variances			Heritability		
	A	D	E	nh(1)	nh(2)	bh(3)
Hi26 x I28	317387.7	49115.5	555355.0	0.22	0.34	0.40
Hi26 x Sg18	778766.1	-818670.0	498199.2	0.57	0.61	0.61
I28 x Sg18	-118020.0	271637.8	139925.0	0.00	0.00	0.66

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

exceed the high parent mean. Additivity is expressed in the crosses between Hi26 and the popcorn parents, while between the two popcorn parents overdominance and additivity is evident.

Table 6.2 gives the scaling test for non-allelic interaction according to Mather and Jinks (1977). I28 x Sg18 tested significant at 0.05 for two of the scales but did not show any epistatic genetic interaction in the six parameter model. Dominance effect was significant at 0.05 and in Table 6.3, I28 x Sg18 showed significant dominance variance which gave it a bh (broad sense heritability) of 0.67. Hi26 x I28 tested non-significant in the scaling test which leads us to look directly at its variance components in Table 6.3. The cross showed high additive variance with an even higher variance due to environmental effects. For this reason, Hi26 x I28 exhibited a low bh and narrow sense heritabilities of 0.38 and 0.22, respectively. Hi26 x Sg18 tested significant at 0.01 for three scales and showed a significant aa (additive x additive) genetic interaction in the six parameter analysis for non-allelic interaction (Hayman 1958). Due to the 'a' value and axa interaction, this cross exhibits high nh (narrow sense heritabilities) of 0.57 and 0.60 and a bh of 0.60.

For grain yield, the average broad sense heritability (bh) over three crosses was 0.55, while the average of both

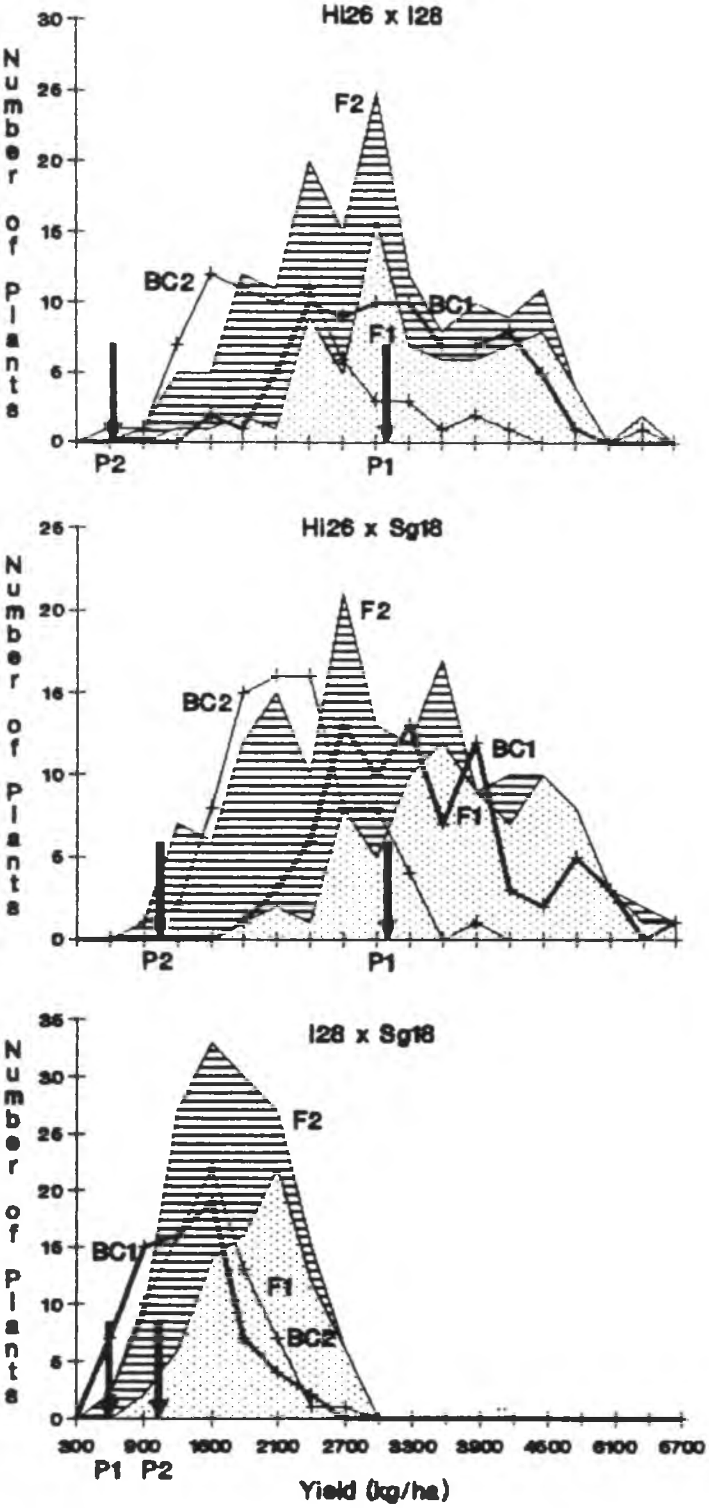


Figure 6.1. Frequency distribution of F1, F2 and backcross progenies for grian yield at Waimanalo.

narrow sense heritability (nh) estimates was 0.45. Error variance made up 40% or more of the total phenotypic variance of all of the crosses, which tended to reduce heritability. Hi26 x Sg18 exhibited the greatest average nh of 0.57 due to a high additive variance and aa epistatic interaction. The greatest bh at 0.67 was exhibited by I28 x Sg18, as a result of its high heterosis, indicating the importance of dominance effects in this cross. This agrees with Moreno-Gonzalez and Dudley (1981) who indicate that for grain yield, dominance is the major component of heterosis.

6.2.2. Ear Length

Generation mean analysis for ear length at two locations is presented in Tables 6.4 through 6.6 and Figures 6.2 and 6.3. Table 6.4 gives the average ear length in centimeters for the six generations at Waimanalo and Kauai. For the two crosses involving Hi26, average heterosis was 2.5% higher at Waimanalo than at Kauai. For the crosses between the two popcorns, I28 and Sg18, heterosis was 11.6% higher at Waimanalo than at Kauai. For all three crosses at both locations the F1 exceeded the high parent. At both locations for all three crosses, the F2 population mean is greater than the parental midpoint, tending toward the high parent. Also, over both locations, the hybrid Hi26 x Sg18 showed greater heterosis than the cross with I28; 10.7% higher at Waimanalo and 12.3% higher at Kauai. At Kauai the

Table 6.4. Average ear length (cm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Waimanalo	Hi26 x I28	14.0	7.1	10.5	14.8	12.5	13.6	11.9	39.9 %
	Hi26 x Sg18	14.0	9.7	11.8	15.3	12.4	14.0	13.0	29.2 %
	I28 x Sg18	7.1	9.7	8.4	12.4	10.8	9.9	10.6	48.0 %
Kauai	Hi26 x I28	16.6	9.3	13.0	16.7	14.6	16.8	14.6	28.8 %
	Hi26 x Sg18	16.6	9.9	13.3	17.9	15.0	17.1	14.2	35.0 %
	I28 x Sg18	9.3	9.9	9.6	13.1	11.0	10.4	11.7	36.0 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.5. Scaling test and six parameter generation mean analysis for ear length at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	-1.5 *	2.0 **	-0.8	-0.6	1.7 **	5.4 **	1.2	-1.8 *	-1.7
	Hi26 x Sg18	-1.4 *	1.0	-4.5 **	-2.1 **	1.0 **	7.6 **	4.1 **	-1.2	-3.8 *
	I28 x Sg18	0.4	-0.9	1.7	1.1 **	-0.7	1.7	-2.3 *	0.6	2.8
Kauai	Hi26 x I28	0.2	3.3 **	-0.7	-2.1 **	2.2 **	7.9 **	4.2 **	-1.5 *	-7.7 **
	Hi26 x Sg18	0.2	1.6	-2.2 *	-1.3 **	3.0 **	7.2 **	2.5 *	-0.4	-2.9
	I28 x Sg18	-1.5 **	0.5	-1.4	-0.2	-1.3 **	3.9 **	0.4	-1.0	0.6

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.6. Genetic variances and heritability estimates for ear length at two locacations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	3.7	-0.3	4.1	0.31	0.47	0.47
	Hi26 x Sg18	11.9	-15.4	4.9	0.85	0.71	0.71
	I28 x Sg18	-3.2	10.9	2.2	0.00	0.00	0.83
Kauai	Hi26 x I28	0.7	7.7	3.5	0.06	0.06	0.71
	Hi26 x Sg18	3.5	-6.4	4.6	0.36	0.43	0.43
	I28 x Sg18	0.6	7.0	2.1	0.08	0.06	0.78

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

backcross to the high parent exceeds the value of the high parent for all three crosses and for I28 x Sg18, both backcrosses exceed the high parent.

Frequency distributions of ear length are presented in Figures 6.2 and 6.3 using the same axis scale for ear length, ranging from 2 to 24 centimeters at both locations. In general, the F1, F2 and backcrosses are all skewed towards the long-eared parent, with the backcrosses to the long parent exceeding or equaling that parent and the backcross to the short-eared parent exceeding the midparent mean. It was apparent that the difference between the parental means in the cross Hi26 x Sg18 is much greater at Kauai than at Waimanalo (Table 6.4). From Figures 6.2 and 6.3, it can be seen that at Waimanalo the backcross mean to the long eared parent is equal to the parental mean for Hi26 x Sg18 but at Kauai the backcross mean exceeds the high parent. This also holds true for Hi26 x I28, where the backcross to the high parent exceeds the high parent mean at Kauai, but is below the high parent mean at Waimanalo. At both locations, the frequency distribution shows the means of Sg18 and I28 to be very close, so that the segregating generations all exceed the mean of the long-eared parent.

The scaling test in Table 6.5 indicates significant non-allelic interaction at 0.05 and 0.01 levels of significance for all of the crosses at both locations. In

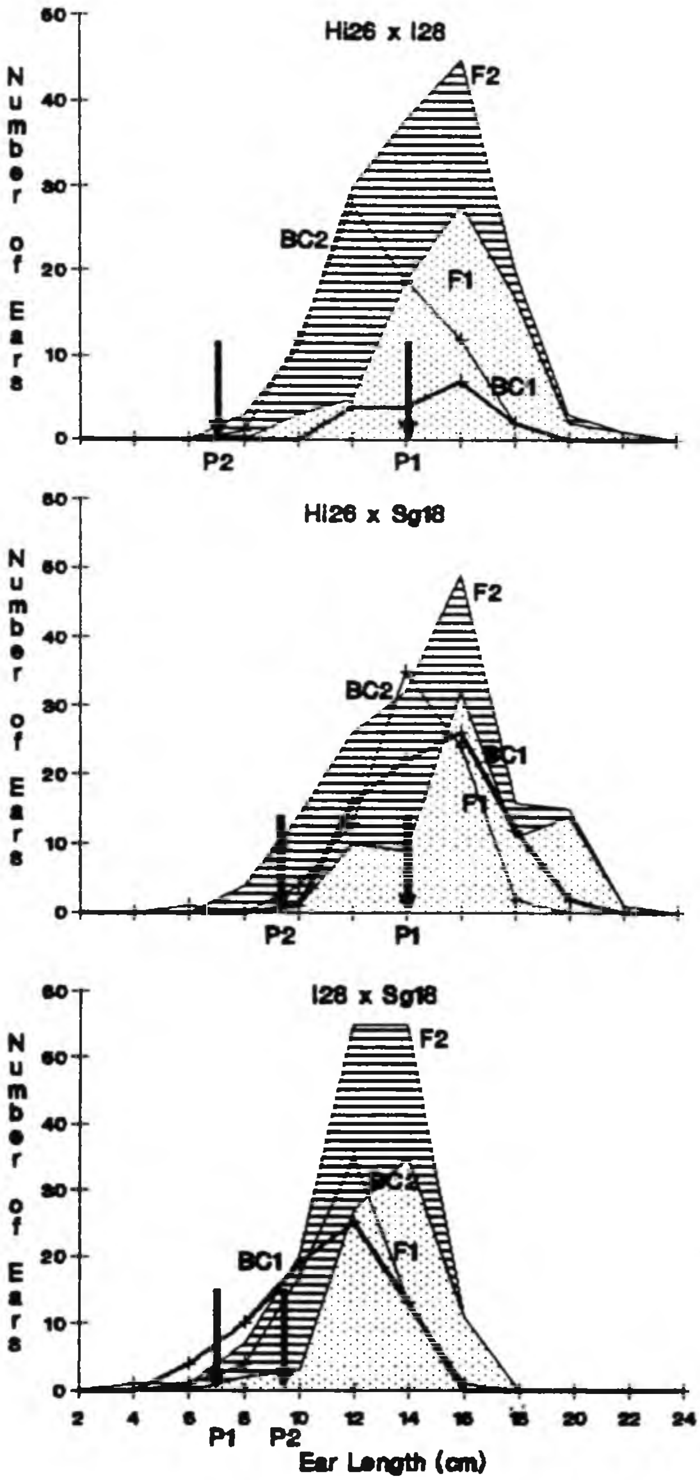


Figure 6.2. Frequency distribution of F1, F2 and backcross progenies for ear length at Waimanalo.

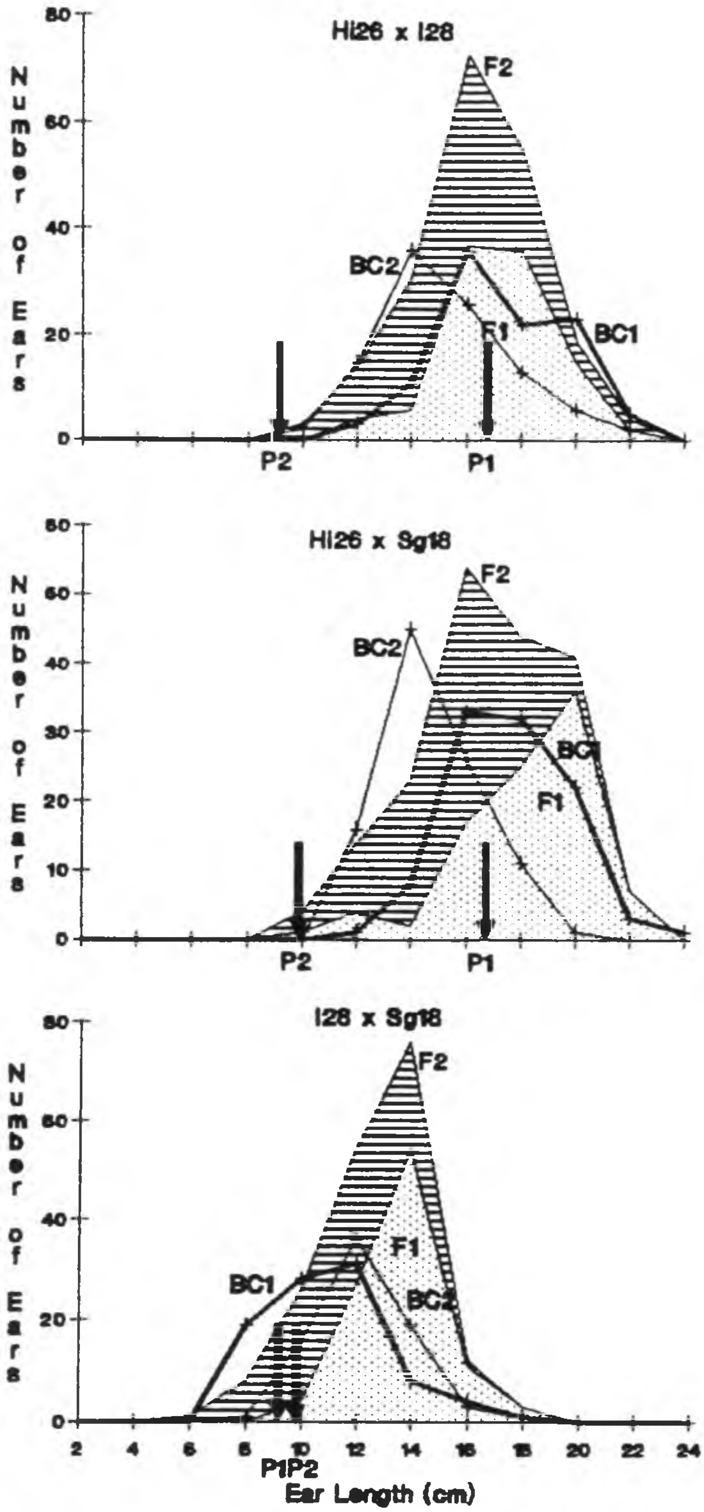


Figure 6.3. Frequency distribution of F1, F2 and backcross progenies for ear length at Kauai.

the six parameter analysis, I28 x Sg18 shows significant negative aa interaction at Waimanalo and a significant negative additive effect at Kauai, with a high degree of dominance. Additivity is negative because it is in the direction of Sg18 (P2). The whole effect is due to heterosis, resulting in a bh of 0.83 at Waimanalo and 0.78 at Kauai. Hi26 x I28 shows significant duplicate ad (additive x dominance) interaction at Waimanalo, coupled with dominance effects that are 3 times greater than additive effects. The same cross at Kauai shows significant duplicate gene action between dominance effects and dd (dominance x dominance) interaction and additive effects and ad interaction. Dominance effects are 3.6 times higher than additive effects for this cross at Kauai. Broad sense heritability was higher for this cross at Kauai but nh was higher at Waimanalo. Hi26 x Sg18 gives significant complementary aa interaction at both locations, but aa interaction along with the ratio of dominance to additivity is higher at Waiamnalo than at Kauai.

The average bh over two locations for ear length was 0.66, while the average nh was 0.39. I28 x Sg18 exhibited the highest bh for this trait of 0.81, which was largely due to high dominance effects and a negative aa interaction in the direction of the long-eared popcorn parent. The degree of dominance ((VD/VA)1/2) for I28 x Sg18 is 3.32 at Kauai.

Hi26 x Sg18 showed the highest average nh over two locations of 0.59, which was due to aa epistasis. Narrow sense heritability was insignificant for Hi26 x I28 at Kauai due to aa and dd interactions which canceled their effects leaving dominance expressed.

6.2.3. Length of the Central Spike

Generation mean analysis and heritability estimates for central spike length are presented in Tables 6.7 to 6.9. Average length of the central tassel spike for the six generations of three crosses at two locations is presented in Table 6.7. Average heterosis of the F1 was 2.7% higher at Kauai than at Waimanalo, largely because of the high heterosis of I28 x Sg18 at Kauai. The segregating generation means were higher than the parental midpoint value at both locations tending towards a longer spike length. The backcrosses to the long spiked parent exceeded that parent for all crosses at both locations. For I28 x Sg18 at Kauai, the backcross to the short spiked parent exceeded the mean value of the long spiked parent. The F2 generation mean of I28 x Sg18 also exceeded the long spiked parental mean at both locations.

The frequency distribution of the F1, segregating generations and mean value of the parents for central spike length are given in Figures 6.4 and 6.5. Increments of the axis are by 2 cm at Waimanalo and by 2.4 cm at Kauai due to

Table 6.7. Average length of central spike (cm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	P2	MP(1)	Hybrid F1	Segregating Generations F2	B1	B2	Heterosis(2)
Waimanalo	Hi26 x I28	22.2	12.3	17.3	22.2	19.9	22.6	17.8	28.7 %
	Hi26 x Sg18	22.2	17.0	19.6	24.4	20.7	24.5	20.8	24.3 %
	I28x Sg18	12.3	17.0	14.7	18.8	17.9	16.8	18.2	28.2 %
Kauai	Hi26 x I28	22.9	13.1	18.0	22.8	20.3	24.3	19.7	26.5 %
	Hi26 x Sg18	22.9	16.4	19.7	25.0	22.3	25.6	22.2	27.2 %
	I28 x Sg18	13.1	16.4	14.8	20.0	18.2	17.0	19.1	35.3 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.8. Scaling test and six parameter generation mean analysis for length of central spike at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	0.8	1.1	0.7	-0.6	4.8 **	6.2 **	1.2	0.1	-3.2
	Hi26 x Sg18	2.3 *	0.2	-5.1 **	-3.8 **	3.7 **	12.3 **	7.6 **	0.5	-10.1 **
	I28 x Sg18	2.4 **	0.6	4.6 **	0.8	-1.4 **	2.5 *	-1.6	0.5	-1.4
Kauai	Hi26 x I28	2.8 **	3.6 **	-0.2	-3.3 **	4.5 **	11.4 **	6.6 **	-0.4	-13.0 **
	Hi26 x Sg18	3.3 **	3.0 **	-0.1	-3.2 **	3.4 **	11.8 **	6.5 **	0.2	-12.9 **
	I28 x Sg18	1.0	1.8	3.5 *	0.3	-2.0 **	4.5 **	-0.7	-0.4	-2.1

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.9. Genetic variances and heritability estimates for length of central spike at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	-8.9	47.8	9.5	0.00	0.00	0.83
	Hi26 x Sg18	7.9	0.9	9.5	0.29	0.43	0.48
	I28 x Sg18	-3.1	8.5	3.8	0.00	0.00	0.69
Kauai	Hi26 x I28	-5.5	32.5	11.1	0.00	0.00	0.75
	Hi26 x Sg18	1.5	-10.0	12.7	0.07	0.11	0.11
	I28 x Sg18	10.3	-1.0	8.4	0.39	0.55	0.55

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

the conversion of measurements taken in inches to centimeters. It is apparent that the parental means are furthest apart at both locations for Hi26 x I28 and closest for I28 x Sg18. The variance of the F2 of I28 x Sg18 is much greater at Kauai than at Waimanalo. From all of the graphs it is visually apparent that the backcross to the long spiked parent exceeds the length of that parent for all of the crosses at both locations.

In Table 6.8, the scaling test shows significance at 0.05 and 0.01 for all of the crosses except Hi26 x I28 at Waimanalo. Even though the test of scale was significant, I28 x Sg18 showed no interaction using the six parameter analysis. At both locations, additive effects were negative, indicating a shift towards Sg18 (P2) and a high degree of dominance. Heritability estimates in Table 6.9, indicated that the cross exhibited only bh at Waimanalo but narrow sense heritability was also significant at Kauai. Broad sense heritability was higher at Waimanalo because the error variance was lower than at Kauai. Hi26 x Sg18 showed significant and high dominance effects at both locations with duplicate dd effects and complementary aa interaction. The dd interaction depressed heritability estimates at both locations. Hi26 x I28 showed no significant non-allelic interaction at Waimanalo. Dominance variance for Hi26 x I28 was very high at that location, giving the cross a bh of

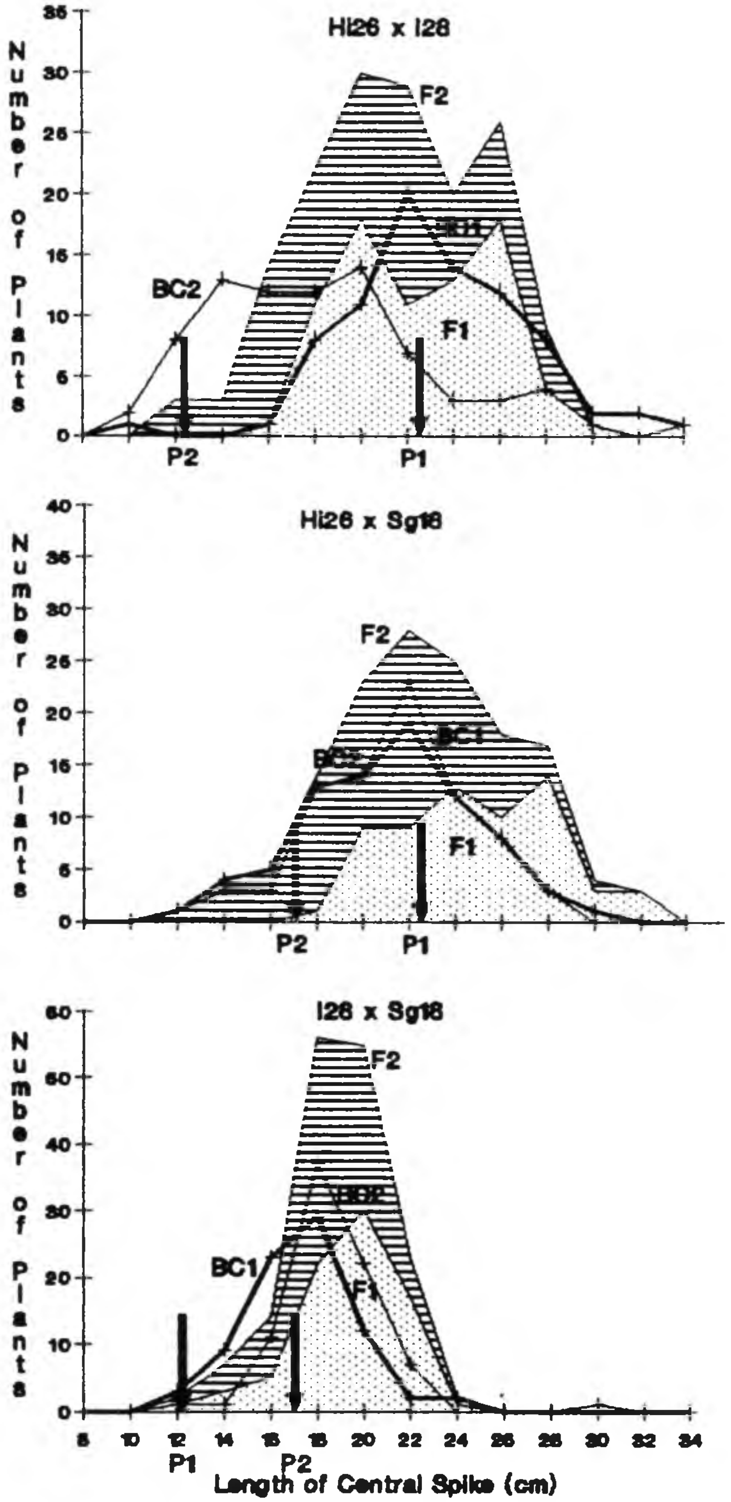


Figure 6.4. Frequency distribution of F1, F2 and backcross progenies for length of central spike at Waimanalo.

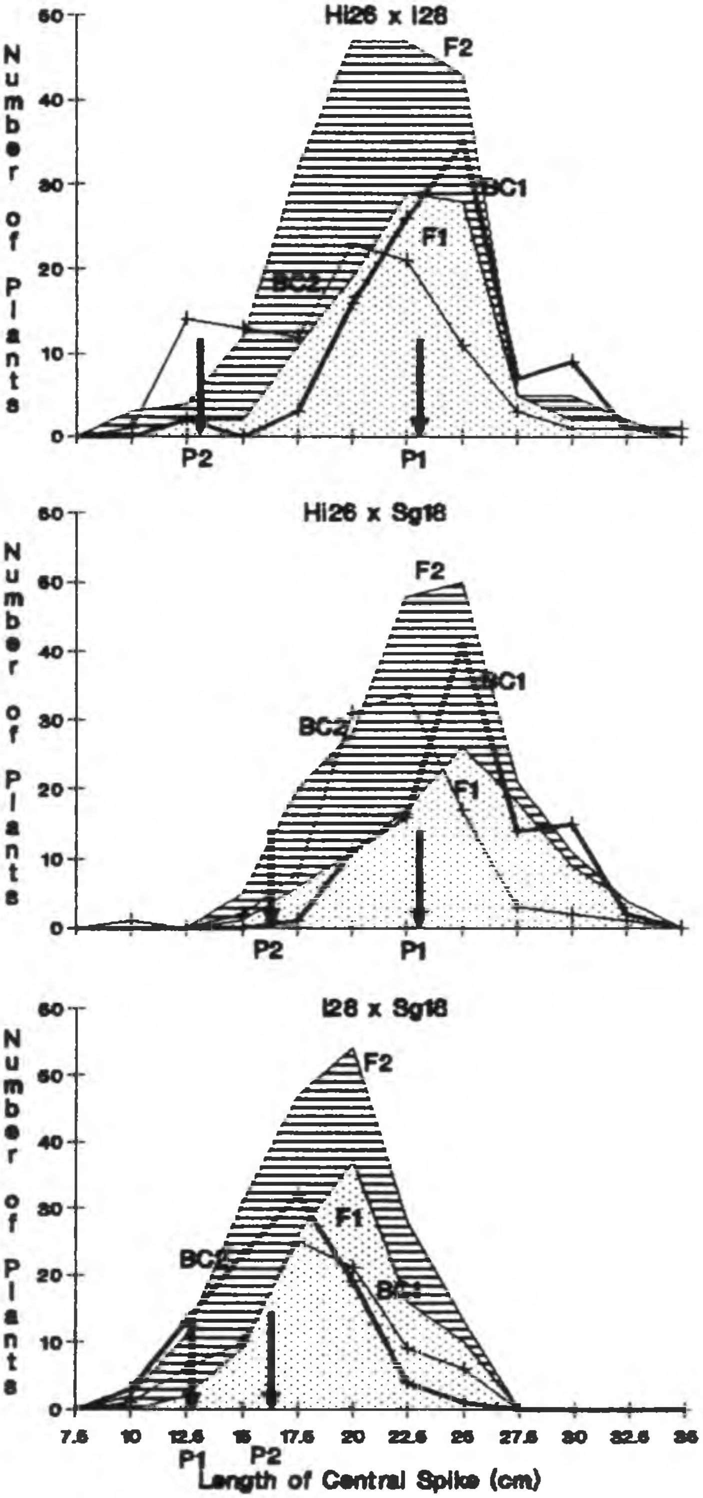


Figure 6.5. Frequency distribution of F1, F2 and backcross progenies for length of central spike at Kauai.

0.83. At Kauai, duplicate dd and complementary aa interaction was apparent for Hi26 x I28 and bh was lower than at Waimanalo partly because of the higher error variance

6.2.4. Tassel Length

Generation mean analysis and heritability estimates for tassel length at two locations are presented in Tables 6.10 to 6.12. Table 6.10 presents the average tassel length of the parents, F1 and segregating generations and the midparental mean and heterosis of the F1. Average heterosis is 5.7% higher at Kauai than at Waimanalo. The mean values of the segregating generations are higher than the midparental means for all crosses at both locations. Backcrosses to the high parent exceeded the high parent mean value for all crosses at both locations. For Hi26 x Sg18, the backcross to the short tasseled parent also exceeded the long parent mean value at both locations. The F2 mean exceeded the long tasseled parent for Hi26 x Sg18 at Waimanalo and for I28 x Sg18 at Kauai.

Frequency distribution graphs for tassel length are presented for the three crosses in Figures 6.6 and 6.7. X axis increments are by 2 cm at Waimanalo and by 2.5 cm at Kauai due to the conversion of inches to centimeters. Parental means of Hi26 and I28 are furthest apart at both locations. Hi26 and Sg18 are only separated by 3.4 cm. at

Table 6.10. Average tassel length (cm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross	Parent			Hybrid	Segregating Generations			Heterosis(2)
	1 x 2	P1	P2	MP(1)	F1	F2	B1	B2	
Waimanalo	Hi26 x I28	31.7	19.5	25.6	32.9	29.4	32.4	26.5	28.4 %
	Hi26 x Sg18	31.7	28.3	30.0	36.2	31.9	35.5	32.1	20.7 %
	I28 x Sg18	19.5	28.3	23.9	29.6	27.8	25.5	29.0	24.2 %
Kauai	Hi26 x I28	38.7	23.8	31.3	40.3	34.6	41.2	34.1	29.0 %
	Hi26 x Sg18	38.7	31.4	35.1	44.8	37.8	43.9	39.5	27.7 %
	I28 x Sg18	23.8	31.4	27.6	36.9	31.5	28.7	33.3	33.7 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.11. Scaling test and six parameter generation mean analysis for tassel length at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	0.15	0.6	0.84	0.04	5.89 **	7.18 **	-0.08	-0.22	-0.68
	Hi26 x Sg18	3.03 *	-0.24	-4.59	-3.69 **	3.36 **	13.59 **	7.38 **	1.64	-10.16 **
	I28 x Sg18	1.8 *	0.07	4.06 **	1.1	-3.5 **	3.6 *	-2.2	0.87	0.3
Kauai	Hi26 x I28	3.4 **	4.1 **	-4.9 *	-6.20 **	7.09 **	21.4 **	12.3 **	-0.34	-19.8 **
	Hi26 x Sg18	4.3 **	2.8 **	-8.6 **	-7.8 **	4.4 **	25.4 **	15.7 **	0.8	-22.8 **
	I28 x Sg18	-3.4 **	-1.8	-3.1	1.02	-4.6 **	7.3 **	-2.05	0.8	7.2 *

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.12. Genetic variances and heritability estimates for tassel length at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	13.8	28.7	16.0	0.23	0.24	0.73
	Hi26 x Sg18	36.3	-30.4	16.3	0.67	0.69	0.69
	I28 x Sg18	0.1	8.0	6.4	0.00	0.01	0.56
Kauai	Hi26 x I28	4.4	20.2	14.2	0.10	0.11	0.63
	Hi26 x Sg18	-2.0	-11.0	21.5	0.00	0.00	0.00
	I28 x Sg18	24.4	-9.8	7.6	0.70	0.76	0.76

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2

(2) Narrow sense heritability estimated by: A/(A + D + E)

(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

Waimanalo, while at Kauai they are 7.6 cm. apart. It is apparent that in all of the crosses at both locations the backcross to the long tasseled parent exceeds that parent. The F2 is centered around or exceeds the high parent as well.

The scaling test in Table 6.11 gives similar results as the scaling test for central spike length in Table 6.8. Hi26 x I28 at Waimanalo shows no significance of scale, but rather a dominance variance in Table 6.12 of 28.7 which gives a 1.44 degree of dominance for long tassel. Because of the high degree of dominance, bh is 0.73, while the average nh is 0.24. At Kauai, the same cross shows complimentary aa interaction and duplicate dd interaction along with a high degree of dominance. The dd interaction reduces heritability, so that bh is 0.63 while nh is below 0.11. Hi26 x Sg18 shows duplicate dd interaction and complimentary aa interaction along with a high degree of dominance at both locations. Broad sense heritability is 0.69 at Waimanalo with a average nh of 0.68. There is no heritability at Kauai because of the high error variance for the cross and the high dd interaction. Additive effects are significant and negative towards Sg18 (P2) in the cross I28 x Sg18 at both locations. There is a more significant and greater degree of dominance effects at Kauai with complimentary dd interaction. Broad sense heritability is

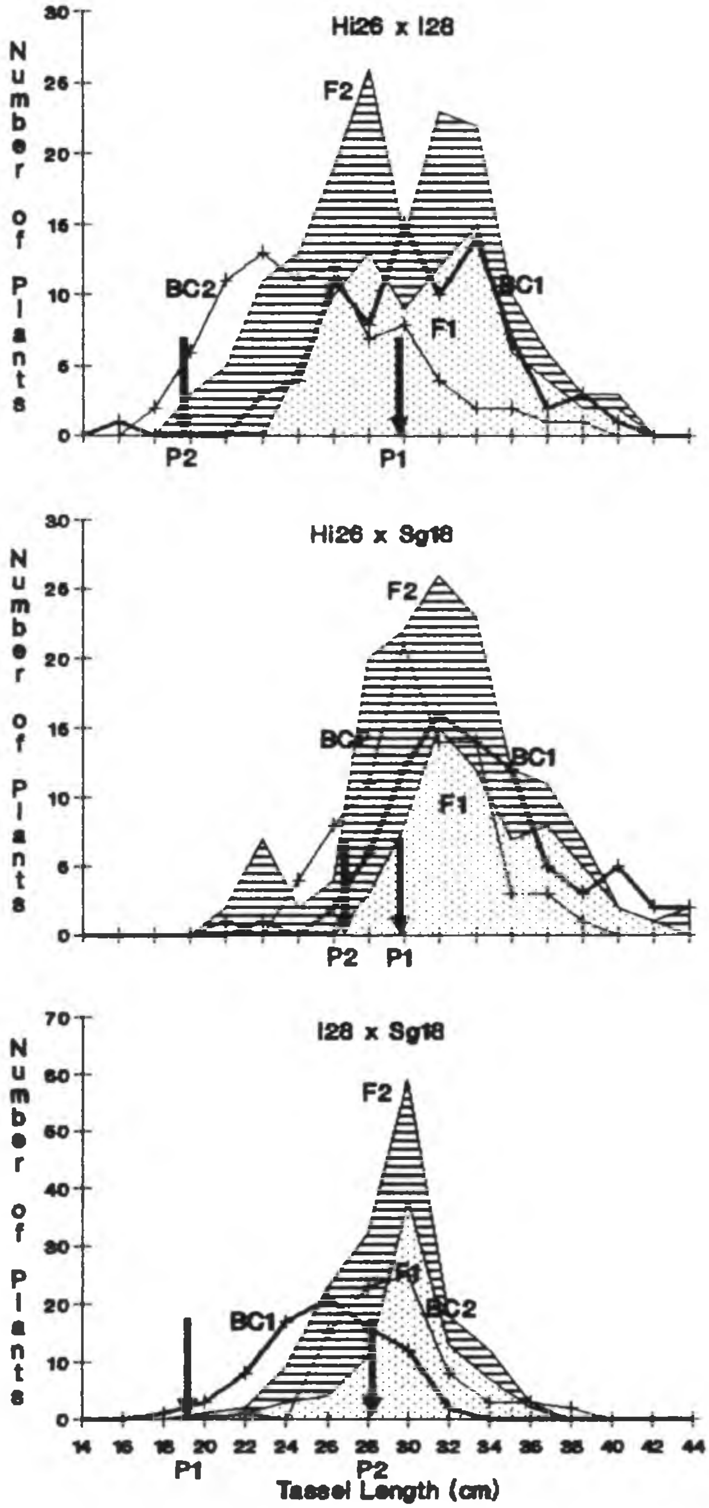


Figure 6.6. Frequency distribution of F1, F2 and backcross progenies for tassel length at Waimanalo.

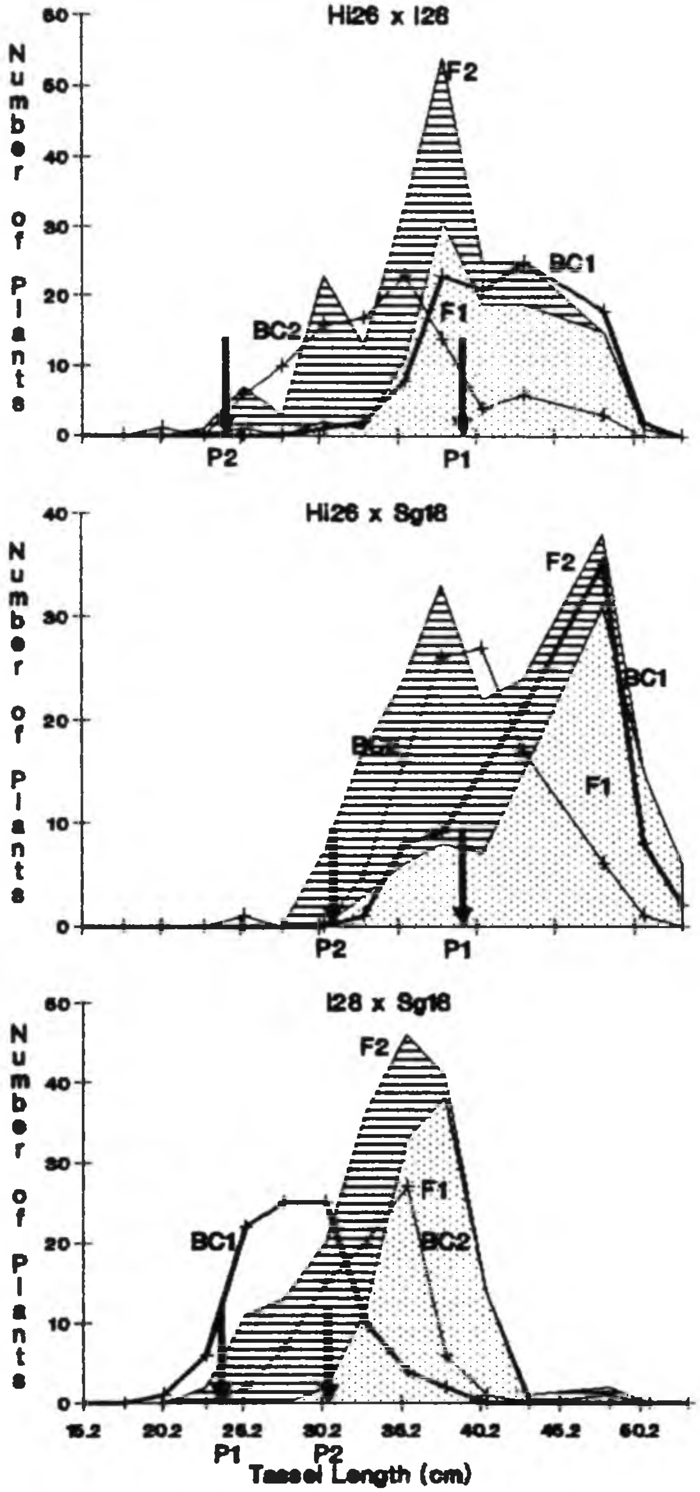


Figure 6.7. Frequency distribution of F1, F2 and backcross progenies for tallel length at Kauai.

0.76 and the average nh is 0.73 at Kauai, while at Waimanalo bh is only 0.56 and nh is 0.01.

For tassel length and length of the central spike, the average broad sense heritability was higher than the average narrow sense heritability for all crosses over two locations. The average bh for length of central spike was 0.57 and 0.68 for tassel length. The average nh was 0.30 for length of central spike and 0.41 for tassel length. For both characteristics over two locations, Hi26 x I28 gave the highest average bh due to high dominance effects, usually coupled with dd and aa interactions that canceled out. Crosses with Sg18 showed the highest nh for both characteristics when there was aa interaction not too badly confounded by -dd interaction.

6.2.5. Relationship of Tassel and Spike to Ear Length

Analysis of the correlation between ear length and the length of the central spike (lcs) and entire tassel length (tl) are highly significant, as can be seen in Figures 6.8 to 6.11. The following table summarizes the correlations:

Location: Waimanalo		
Correlatives		r
ear length	tl	0.92
ear length	lcs	0.95
Location: Kauai		
ear length	tl	0.90
ear length	lcs	0.93

The correlation between ear length and spike measurements are high and significant at both locations. To see if the generation mean analysis is similar for the three characters, narrow sense heritability was compared for the three characteristics using the cross Hi26 x Sg18 at both locations:

Hi26 x Sg18			Waimanalo				
	a	d	aa	ad	dd	nh	VE
tl	3.4**	13.6**	7.4**	1.6	-10.2**	0.68	16.3
lcs	3.7**	12.3**	7.6**	0.5	-10.1**	0.36	9.5
el	1.0**	7.6**	4.1**	-1.2	-3.8**	0.78	4.9
Hi26 x Sg18			Kauai				
tl	4.4**	25.4**	15.7**	0.8	-22.8**	0.0	21.5
lcs	3.4**	11.4**	6.5**	0.2	-12.9**	0.09	12.7
el	3.0**	7.2**	2.5**	-0.4	-2.9	0.40	4.6

At Waimanalo, nh is closest between tassel length and ear length, epistatic interaction is similar between the three traits. There is duplicate dd interaction that nullifies the opposite aa interaction except for ear length were aa is 0.3 higher than dd, making nh higher for that trait. The ratio of d/a is 4.04 for tassel length, 3.32 for

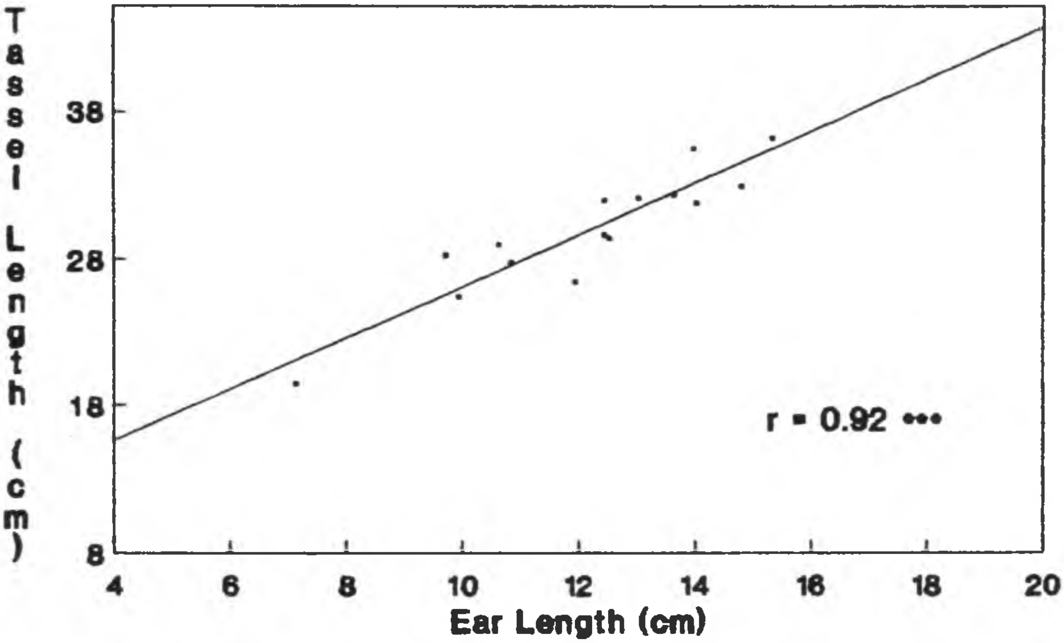


Figure 6.8. Correlation of tassel length to ear length at Waimanalo.

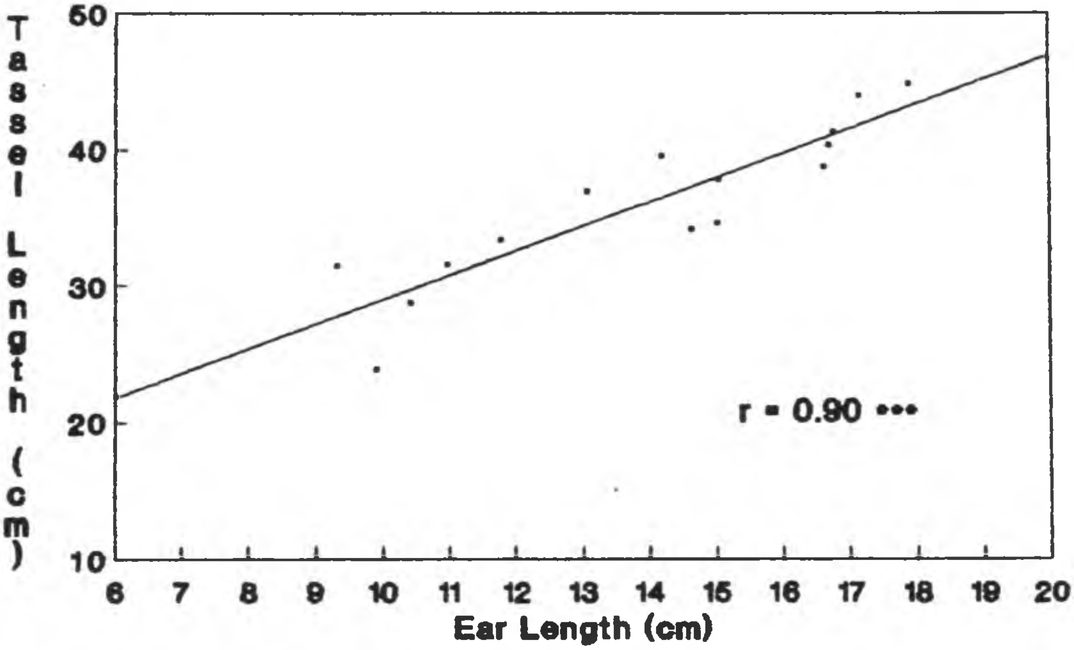


Figure 6.9. Correlation of tassel length to ear length at Kauai.

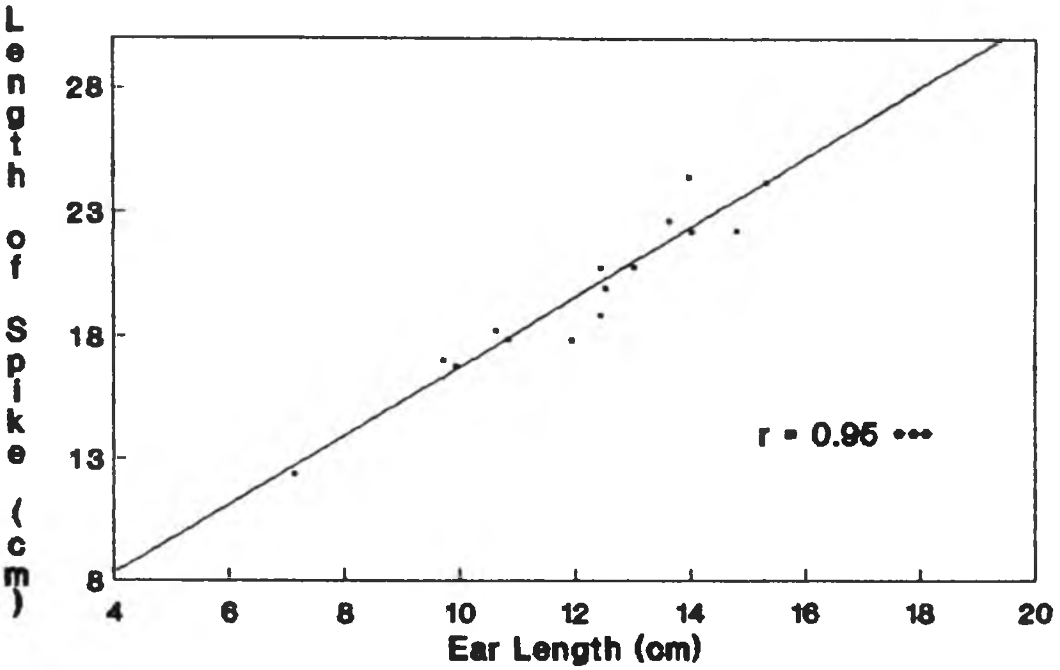


Figure 6.10. Correlation of central spike length to ear length at Waimanalo.

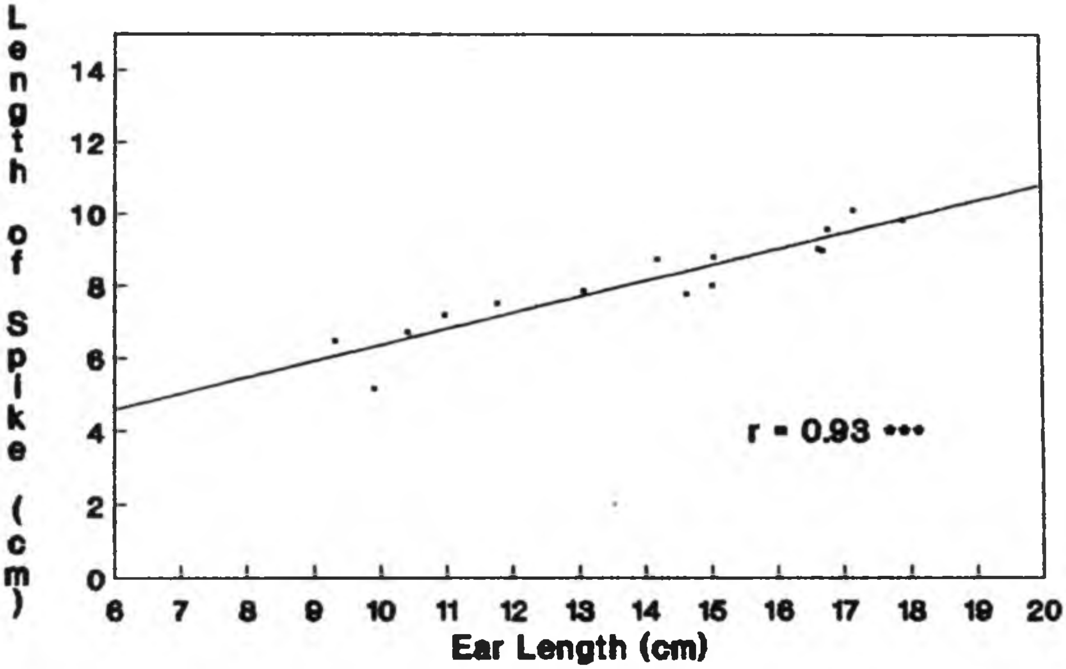


Figure 6.11. Correlation of central spike length to ear length at Kauai.

length of central spike and 7.6 for ear length. At Kauai, the high error variance completely nullified the heritability estimate for tassel length and length of central spike. The ratio of d/a is 2.4, with aa interaction significant at 0.05 level of probability. The aa interaction and d/a ratio appears to be higher for ear length than the other characteristics. This data indicates a similar epistatic interaction and d/a ratio for tassel length, length of central spike and ear length for the cross Hi26 x Sg18.

6.2.6. Kernel Row Number

Tables 6.13 to 6.15 present the generation mean analysis and heritability estimates for the number of kernel rows at two locations. Generation mean values for the number of kernel rows of parents, F1, F2 and backcross progenies at two locations and the midparental value and heterosis of the F1 are given in Table 13. At both locations, the F1 mean values of Hi26 x I28 and Hi26 x Sg18 only averaged 1.8% higher than the midparental mean, while the F1 mean of I28 x Sg18 averaged 11.9% higher than the midparental mean. The F2 generation mean was below the midparental mean at both locations for Hi26 x Sg18. The F2 mean was greater than the midparent for the other two crosses and exceeded the high parent for I28 x Sg18 at Kauai. Means of backcrosses to the high parent exceeded or

Table 6.13. Average kernel rows of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Waimanalo	Hi26 x I28	14.2	13.4	13.8	14.1	14.4	13.9	14.7	2.2 %
	Hi26 x Sg18	14.2	16.1	15.2	15.6	14.5	15.0	15.3	2.7 %
	I28 x Sg18	13.4	16.1	14.7	16.8	15.1	14.4	16.0	13.7 %
Kauai	Hi26 x I28	13.5	14.4	13.9	14.0	14.2	13.7	14.5	0.6 %
	Hi26 x Sg18	13.5	14.9	14.2	14.5	13.8	14.2	14.9	2.0 %
	I28 x Sg18	14.4	14.9	14.7	16.2	15.5	15.5	15.7	10.2 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.14. Scaling test and six parameter generation mean analysis for kernel row at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	-0.55	2.00 **	1.90	0.23	-0.80 **	-0.16	-0.46	-1.28	-1.00
	Hi26 x Sg18	0.25	-1.12 *	-3.40 **	-1.27 **	-0.25	2.90 *	2.50 *	0.69	-1.70
	I28 x Sg18	-1.30 *	-0.88	-2.74 *	-0.28	-1.67 **	2.60 *	0.57	-0.20	1.61
Kauai	Hi26 x I28	-0.02	0.56	0.64	0.05	-0.77 **	-0.05	-0.10	-0.30	-0.43
	Hi26 x Sg18	0.36	0.40	-2.10 *	-1.43 **	-0.73 **	3.14 **	2.85 **	-0.02	-3.61 **
	I28 x Sg18	0.44	0.34	0.33	-0.23	-0.18	1.90 **	0.45	0.05	-1.23

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.15. Genetic variances and heritability estimates for kernel row at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	2.5	1.4	2.8	0.28	0.37	0.58
	Hi26 x Sg18	5.8	-0.9	3.0	0.55	0.66	0.66
	I28 x Sg18	0.4	8.1	3.1	0.04	0.03	0.73
Kauai	Hi26 x I28	0.8	3.9	2.2	0.12	0.12	0.69
	Hi26 x Sg18	-2.0	7.0	2.5	0.00	0.00	0.74
	I28 x Sg18	-0.4	3.7	2.0	0.00	0.00	0.65

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

were equal to the high parent mean for all crosses except Hi26 x Sgl8 and Hi26 x I28 at Waimanalo. All means of backcrosses to the low parent were below or equal to the midparent value except for the low parent backcrosses of I28 x Sgl8 at Kauai and Hi26 x I28 at Waimanalo, which exceeded the high parent mean.

Figures 6.12 and 6.13 present the frequency distribution of segregating generations and F1 and the parental means for the number of kernel rows. At both locations, the parental means of all of the crosses are very close together. The parental mean values of I28 and Sgl8 are 2.7 cm apart at Waimanalo but only 0.5 cm apart at Kauai. In graphs of Hi26 x I28 and Hi26 x Sgl8 at both locations, the parents are so close together that the segregating generations appear to be over the midparental mean. Only in I28 x Sgl8, do the segregating generations shift so that they are above the high parent at Waimanalo and exceeding the high parent at Kauai.

In the scaling test in Table 6.14, the crosses Hi26 x I28 and I28 x Sgl8 at Kauai show no significant epistatic interaction. But going on to the six parameter analysis for non-allelic interaction, only Hi26 x Sgl8 shows significant epistasis at both locations. At Kauai, Hi26 x Sgl8 shows additive effects in the negative direction (towards the parent with more kernel rows), significant dominance, and aa

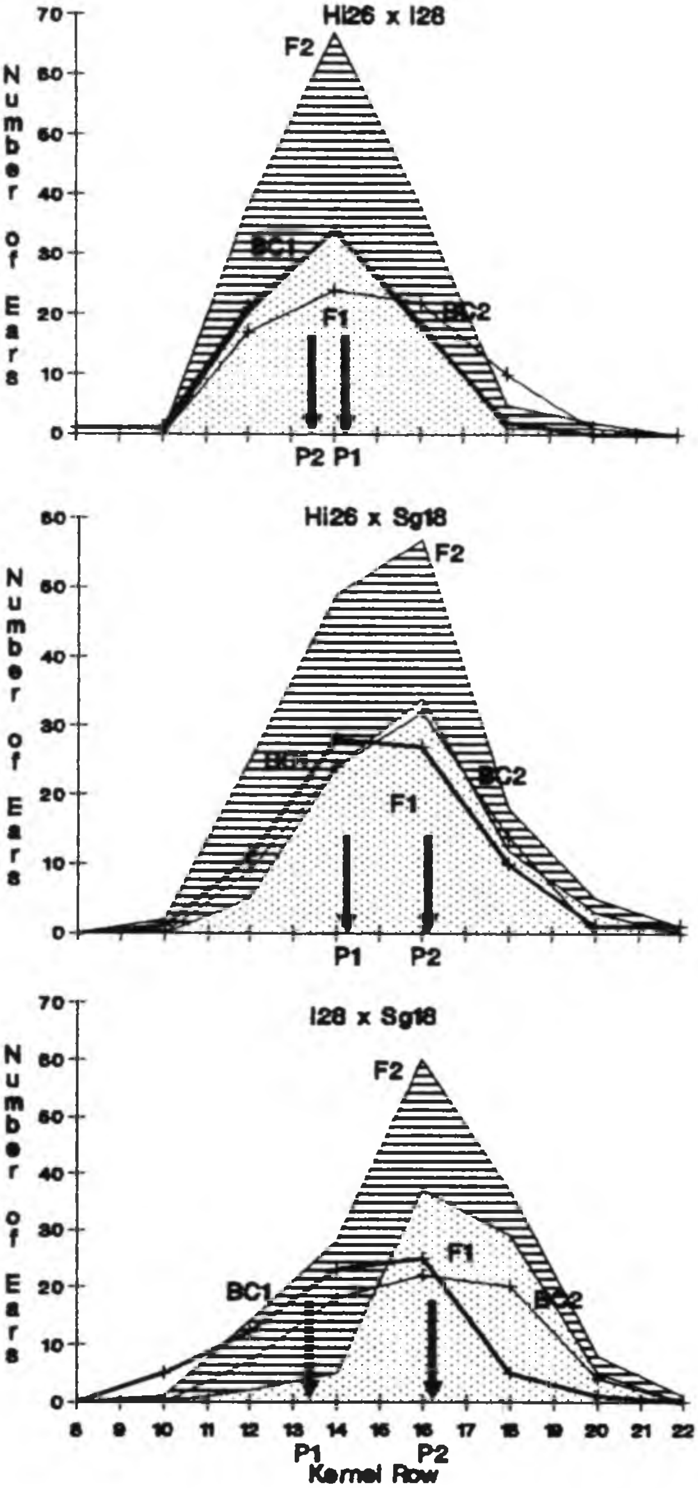


Figure 6.12. Frequency distribution for F1, F2 and backcross progenies for kernel row number at Waimanalo.

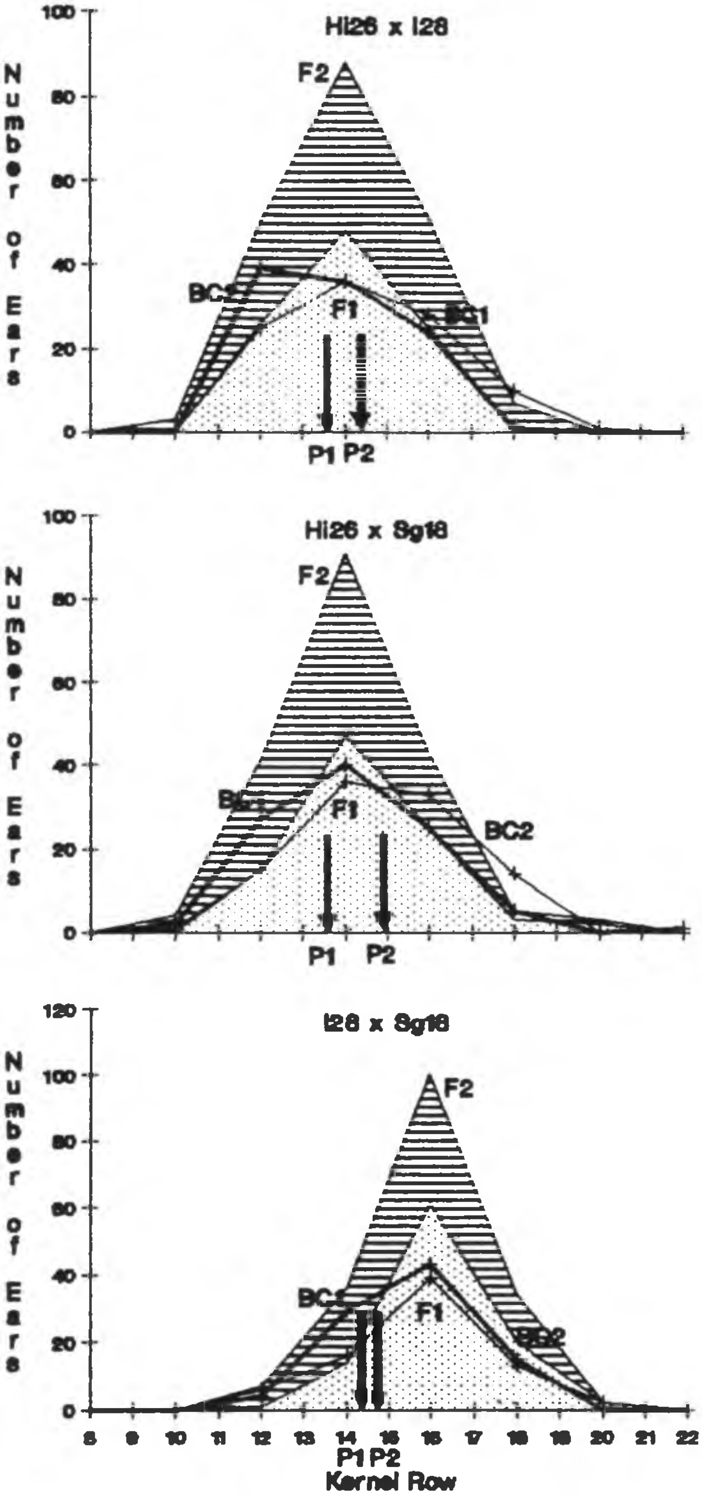


Figure 6.13. Frequency distribution of F1, F2 and backcross progenies for kernel row number at Kauai.

and dd interactions that cancel effects, leaving dominance as the major effect. At Waimanalo, the cross shows significant dominance effects at 0.05 along with complimentary aa interaction that is significant at 0.05. Heritability for Hi26 x Sg18 is higher for the broad sense at Kauai, but the average nh is 0.61 at Waimanalo because of the additive epistatic effect. Hi26 x I28 at Waimanalo shows significance for scale B, but no interaction according to the six parameter model. Looking at the variance components in the three parameter model for Hi26 x I28, most of the genetic variance is additive at Waimanalo but it is dominant at Kauai. This is reflected in the estimate of heritability, which is high in the broad sense at Kauai with 2.2 degrees of dominance. I28 x Sg18 shows no significant non-allelic interaction at either location, but does show significant negative additive effects towards the parent with the higher row number at Waimanalo. At both locations, the dominance variance is much greater than the additive variance. At Waimanalo, the degree of dominance is 4.5 and broad sense heritability is higher than at Kauai.

The average bh for the number of kernel rows over two locations was 0.67, while the average nh was only 0.27. Narrow sense heritability was brought down by low or absent additive variance because there was not enough separation between parents. The dominance seen in I28 x Sg18 clearly represents the heterotic effect of the F1 and segregating generations. Hi26 x I28 also reflected dominance effects at both locations. Only Hi26 x Sg18 revealed epistasis with additive effects at Waimanalo, but at Kauai the epistatic effects canceled out, leaving only dominance.

6.2.7. Kernel Depth

Table 6.16 to 6.18 present the generation mean analysis and heritability estimates for kernel depth at two locations. The average kernel depth (mm) of parents, F1, F2 and backcross progenies at two locations and their midparental values and heterosis is presented in Table 6.16. Segregating generation mean values at Kauai are all greater than the midparental mean but at Waimanalo backcrosses to the low parent of the crosses Hi26 x Sg18 and Hi26 x I28 are below the midparent value. The average heterosis for the two crosses with Hi26 is higher at Waimanalo than at Kauai, but the heterosis of I28 x Sg18 is 11.7 % higher at Kauai. The F2 population mean is greater than the midparental value for all crosses at both locations. The backcross to the high parent exceeds that parent in all crosses at Kauai, but only in the crosses with Hi26 at Waimanalo. The F1 exceeds the high parent mean in the cross Hi26 x Sg18 at Waimanalo and in Hi26 x Sg18 and I28 x Sg18 at Kauai.

Frequency distributions of the three crosses at each location for kernel depth is presented in Figures 6.14 and

Table 6.16. Average kernel depth (mm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross	Parent			Hybrid	Segregating Generations			Heterosis(2)
	1 x 2	P1	P2	MP(1)	F1	F2	B1	B2	
Waimanalo	Hi26 x I28	9.52	6.49	8.01	9.20	8.57	9.77	7.82	14.9 %
	Hi26 x Sg18	9.52	7.30	8.41	9.83	8.55	10.00	8.10	16.9 %
	I28 x Sg18	6.49	7.30	6.90	7.20	7.16	6.99	7.18	4.4 %
Kauai	Hi26 x I28	9.40	6.88	8.14	9.19	8.24	9.60	8.46	12.9 %
	Hi26 x Sg18	9.40	7.13	8.27	9.75	8.50	9.85	8.56	18.0 %
	I28 x Sg18	6.88	7.13	7.01	8.13	7.40	7.42	7.42	16.1 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.17. Scaling test and generation mean analysis for kernel depth at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	0.8 **	-0.1	-0.1	-0.4 *	1.9 **	2.1 **	0.9	0.4	-1.6 *
	Hi26 x Sg18	0.4	-0.9 **	-2.3 **	-0.9 **	1.8 **	3.2 **	1.7 **	0.7	-1.2
	I28 x Sg18	0.3 *	-0.1	0.5	0.1	-0.2 *	0.0	-0.3	0.2	0.1
Kauai	Hi26 x I28	0.6 **	0.8 **	-1.7 **	-1.6 **	1.1 **	4.2 **	3.2 **	-0.12	-4.7 **
	Hi26 x Sg18	0.5 **	0.2	-2.1 **	-1.4 **	1.3 **	4.3 **	2.8 **	0.15	-3.6 **
	I28 x Sg18	-0.16	-0.4 **	-0.7 *	-0.03	0.0	1.2 **	0.06	0.13	0.5

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.18. Genetic variances and heritability estimates for kernel depth at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	-0.10	1.04	0.52	0.00	0.00	0.67
	Hi26 x Sg18	-2.34	5.23	0.54	0.00	0.00	0.91
	I28 x Sg18	0.36	-0.39	0.22	0.55	0.62	0.62
Kauai	Hi26 x I28	-0.41	1.14	0.45	0.00	0.00	0.72
	Hi26 x Sg18	0.43	-0.40	0.46	0.38	0.48	0.48
	I28 x Sg18	0.54	-0.39	0.15	0.83	0.78	0.78

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

6.15. The x axis ranges from 5 millimeters to 12.5 millimeters with increments of 0.5 millimeters in all graphs. Parental means in crosses with Hi26 are far apart, with an average of 2.2 mm between Hi26 and Sg18 and an average of 2.7 mm between Hi26 and I28 at both locations. In contrast, I28 and Sg18 are only an average of 0.5 mm apart at both locations, with I28 being the smaller kerneled popcorn. Despite their closeness, the graphs of I28 x Sg18 show a skewdness towards the longer kerneled parent of the F1 and segregating generations. Crosses with Hi26 also show a skewdness towards the high parent of segregating generations but at both locations the backcross to the low parent is centered about the midparental mean.

Table 6.17 gives the scaling test of adequacy of the additive-dominance model and six parameter analysis of allelic interaction for kernel depth. All crosses at both locations tested significant at 0.01 degree of probability for at least one of the scales except for I28 x Sg18 at Waimanalo. For Hi26 x I28 at Kauai, dd effects cancel aa effects resulting in a bh of 0.72. At Waimanalo the -dd effect lowers bh to 0.67. Hi26 x Sg18 shows a high degree of dominance effect at Waimanalo due to the complimentary aa interaction. At Kauai there is duplicate dd interaction that cancels aa effect and reduces dominance, allowing additivity to be expressed. Broad sense heritability is

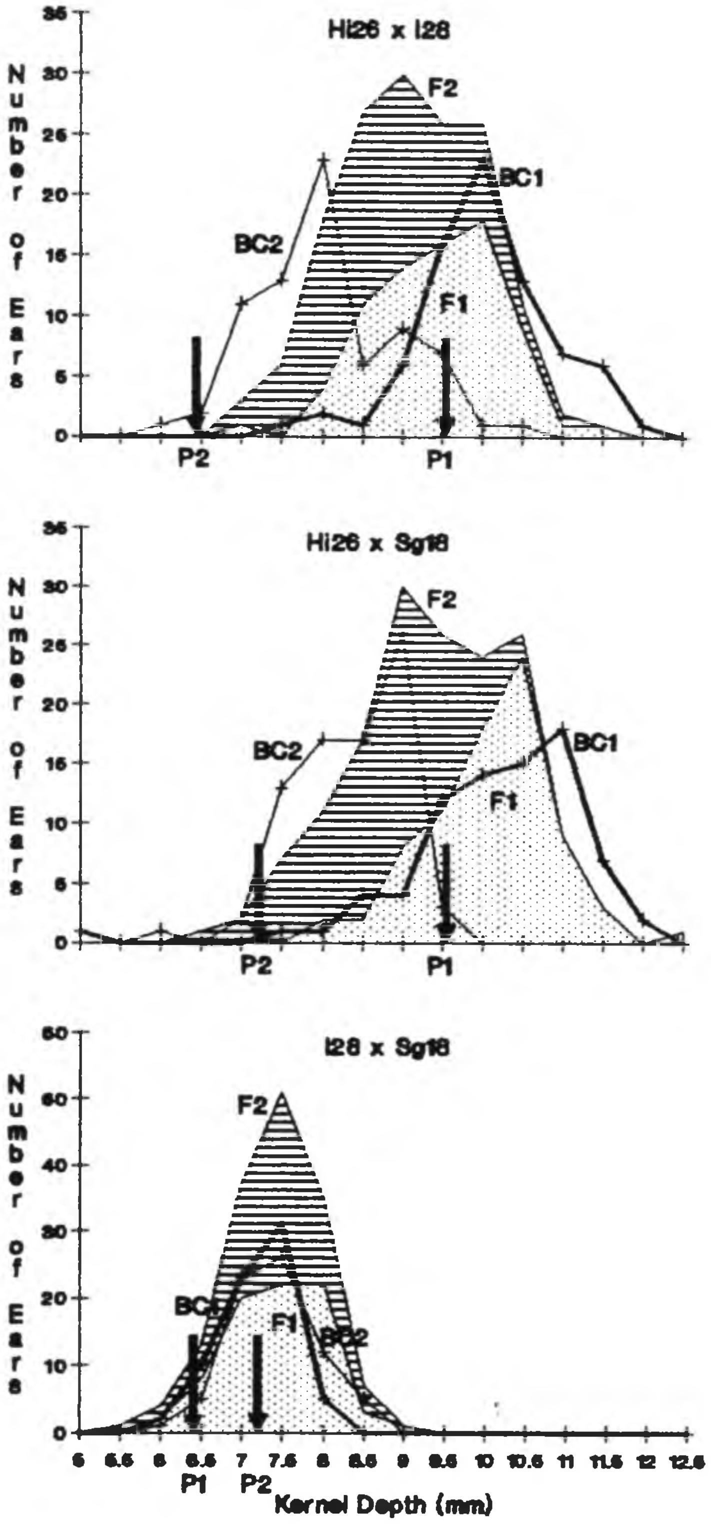


Figure 6.14. Frequency distribution of F1, F2 and backcross progenies for kernel depth at Waimanalo.

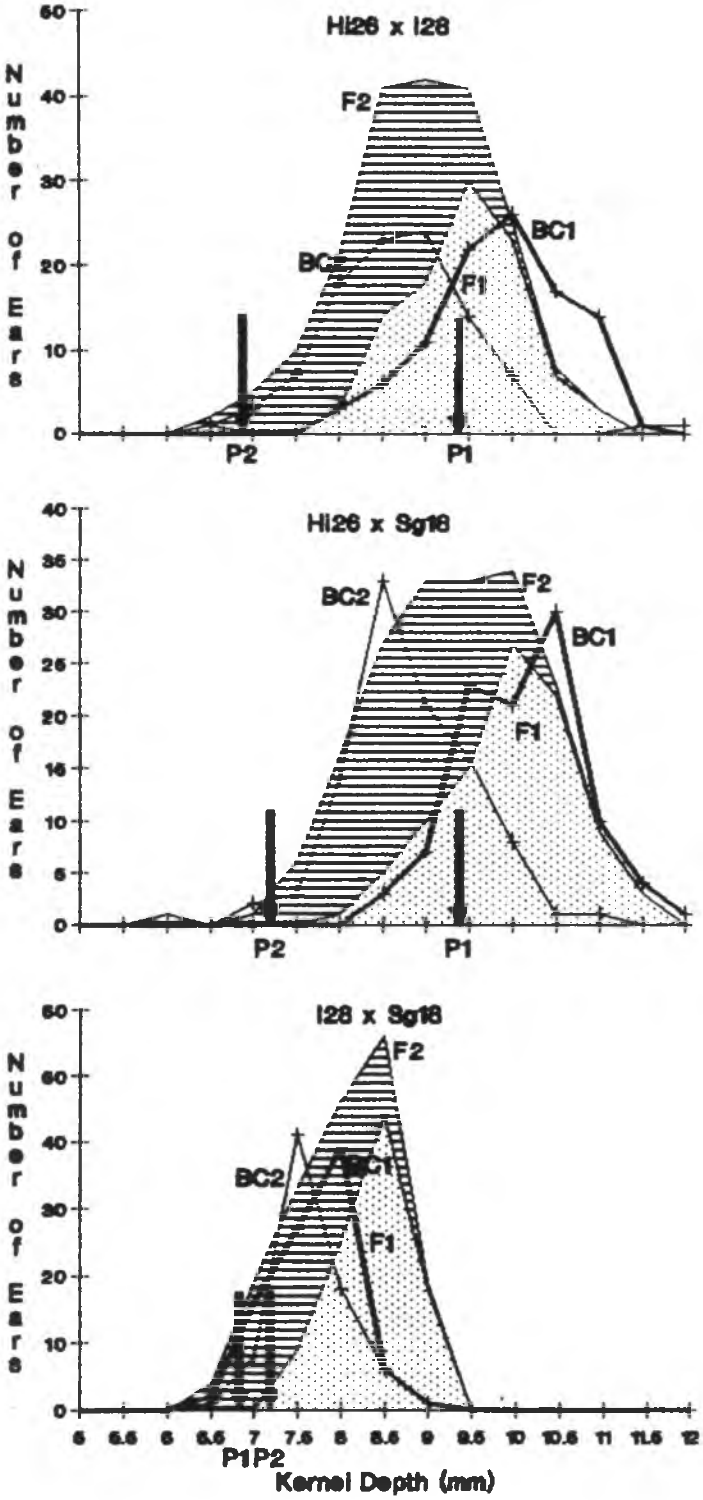


Figure 6.15. Frequency distribution of F1, F2 and backcross progenies for kernel depth at Kauai.

0.91 at Waimanalo and reduced to 0.48 at Kauai, but the average narrow sense heritability is increased to 0.43 at Kauai due to the expression of additivity. I28 x Sg18 shows a negative additive effect towards Sg18 (P2) at Waimanalo and a dominance effect at Kauai but no non-allelic interactions. At both locations, only additive variance is significant, being higher at Kauai. Broad and narrow sense heritabilities are also higher at Kauai, being 0.78 for bh and an average of 0.81 for nh. At Waimanalo, bh is 0.62 and the average nh is 0.59.

For kernel depth, heritability was in the direction of increased kernel depth with the average bh over three crosses at two locations of 0.71. The average nh over two crosses at two locations was 0.60. All of the crosses exhibited the same average bh over both locations, while the highest average nh of 0.70 was shown by I28 x Sg18. I28 x Sg18 exhibited a high nh due to the high additive variance at both locations since there was no significant epistatic action. In crosses with Hi26, epistatic interaction between aa and -dd reduced additive effects leaving dominance to express itself. In the measurements of kernel characteristics and popping expansion taken for the parents and F1 of the variety diallel, it was found that the correlation between kernel depth and popping expansion was 0.57, significant at the 0.05 level of probability.

Correlation is negative, indicating that shorter kernels probably give a higher popping expansion than longer ones. This data indicates that kernel depth is a heritable trait that can be used as one indication of probable popping performance.

6.2.8. Kernel Width

Generation mean analysis and heritability estimates for kernel width are presented in Tables 6.19 to 6.21. Average kernel width (mm) of parents, F1, F2 and backcross progenies and the midparental mean and heterosis for two locations is found in Table 6.19. The F1 mean is below the midparental mean for all of the crosses except for Hi26 x Sg18 at Kauai. Because of this, the average heterosis at Waimanalo is -8.0%, while at Kauai it is -1.6%. For all crosses at both locations, the F2 population mean is less than or equal to the midparental value. For I28 x Sg18 at both locations and Hi26 x Sg18 at Waimanalo, the backcross means are below the midparental mean. The segregating generations of I28 x Sg18 at Kauai are all below the mean of the low parent. At Waimanalo, all but the backcross to the high parent are below the low parent mean for I28 x Sg18.

Frequency distribution of the segregating generations, the F1 and parental means for kernel width is presented in Figure 6.16 for the three crosses at Waimanalo and in Figure 6.17 for the three crosses at Kauai. X axis intervals for

Table 6.19. Average kernel width (mm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	P2	MP(1)	Hybrid F1	Segregating Generations F2	B1	B2	Heterosis(2)
Waimanalo	Hi26 x I28	4.39	3.54	3.97	3.56	3.64	3.74	3.53	-10.2 %
	Hi26 x Sg18	4.39	4.02	4.21	4.06	4.22	4.08	4.07	-3.4 %
	I28 x Sg18	3.54	4.02	3.78	3.38	3.47	3.31	3.62	-10.6 %
Kauai	Hi26 x I28	4.39	4.01	4.20	3.95	4.04	4.28	4.07	-6.0 %
	Hi26 x Sg18	4.39	4.11	4.25	4.33	4.36	4.12	4.30	1.9 %
	I28 x Sg18	4.01	4.11	4.06	4.03	3.96	3.94	3.89	-0.7 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.20. Scaling test and generation mean analysis for kernel width at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	-0.5 **	0.0	-0.5	0.0	0.2 **	-0.4	0.0	-0.2	0.6
	Hi26 x Sg18	-0.3 **	0.1	0.3	0.3 **	0.0	-0.7 **	-0.6 *	-0.2	0.8 *
	I28 x Sg18	-0.3 **	-0.2 *	-0.5 **	0.0	-0.3 **	-0.4 **	0.0	-0.07	0.5 *
Kauai	Hi26 x I28	0.22	0.18	-0.13	-0.27	0.21	0.28	0.54	0.02	-0.95
	Hi26 x Sg18	-0.4 **	0.17	0.29	0.3 *	-0.18 *	-0.52	-0.6 *	-0.32	0.91 *
	I28 x Sg18	-0.17	-0.35 **	-0.34	0.1	0.04	-0.21	-0.18	0.1	0.7 *

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.21. Genetic variances and heritability estimates for kernel width at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	0.37	-0.40	0.17	0.73	0.69	0.69
	Hi26 x Sg18	0.54	-0.50	0.12	1.03	0.82	0.82
	I28 x Sg18	-0.002	-0.001	0.07	0.00	-0.03	-0.03
Kauai	Hi26 x I28	-0.20	0.92	0.41	0.00	0.00	0.69
	Hi26 x Sg18	0.19	-1.24	0.59	0.25	0.24	0.24
	I28 x Sg18	0.01	-0.45	0.25	0.05	0.04	0.04

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

kernel width are 0.2 mm at both locations, ranging from 2.6 mm to 6.2 mm. The mean kernel width of Hi26 is the same at Waimanalo and at Kauai, but the kernel width of the two popcorns very greatly between the two locations. The average kernel width of I28 is 0.47 mm wider at Kauai than at Waimanalo, and Sg18 is 0.09 mm wider. Because of this difference between the two locations, the separation of parental means is much greater at Waimanalo than at Kauai. At Waimanalo, the graphs of Hi26 x I28 and of I28 x Sg18 show a shift of all of the segregating generations towards the low parent. At Kauai, there appears to be no shift of generations in the cross of I28 x Sg18, and in the other crosses the wide frequency distribution of the F2 and backcrosses makes it difficult to determine in what direction any shift is occurring.

The scaling test for the additive-dominance model is presented in Table 6.20. Only Hi26 x I28 at Kauai test non-significant for allelic interaction. At Waimanalo, this cross shows a significant additive effect in the six parameter analysis, increasing the average nh to 0.71. Only dominance variance is expressed for Hi26 x I28 at Kauai, giving it a bh of 0.69 and no narrow sense heritability. At Waiamnalo, Hi26 x Sg18 is affected by dominance in the negative direction (towards the popcorn parent), and an aa interaction that was significant enough to increase the

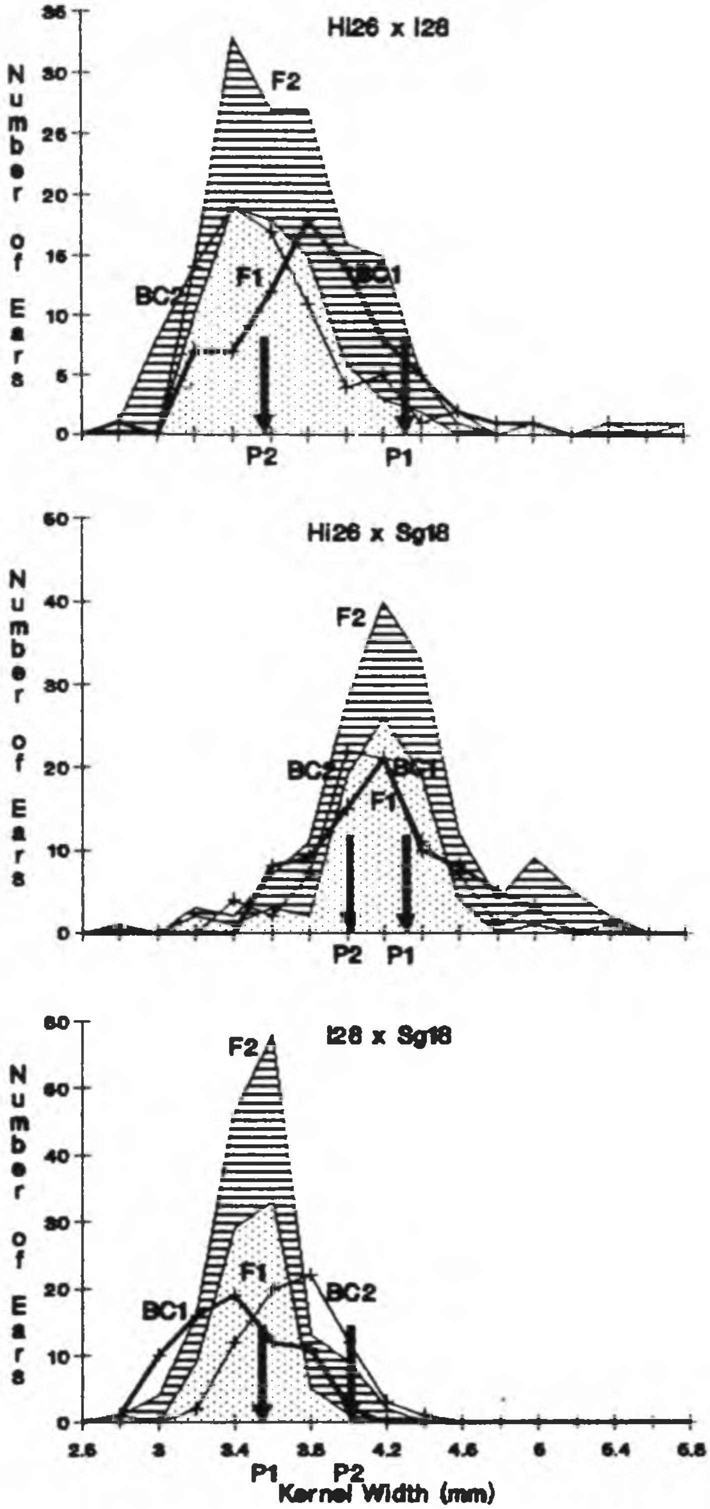


Figure 6.16. Frequency distribution of F1, F2 and backcross progenies for kernel width at Waimanalo.

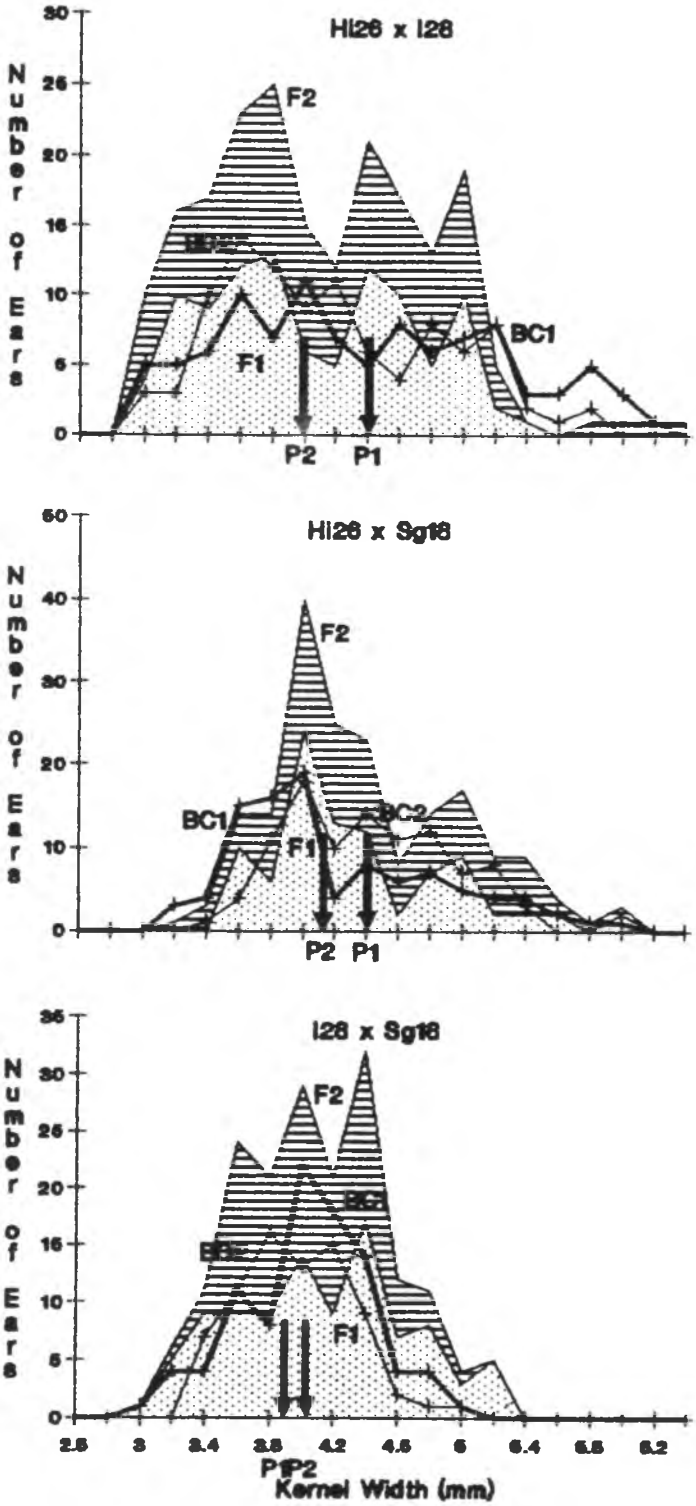


Figure 6.17. Frequency distribution of F1, F2 and backcross progenies for kernel width at Kauai.

average nh to 0.93. At Kauai, the same cross shows an additive effect in the negative direction (towards the popcorn parent) along with negative aa interaction and a duplicate positive dd interaction. Because of the magnitude of the dd interaction and the high error variance, the average nh is reduced to 0.24. I28 x Sgl8 gives negative additive and dominance effects along with duplicate dd interaction at Waimanalo because of the shift in progeny towards the narrow kerneled parent. Because of the high error variance and negative additive and dominance variance, there is no heritability for this cross at Waimanalo. At Kauai, only a dd interaction is apparent at 0.05 level of probability which acts to reduce heritability to non-significance.

Kernel width exhibited the lowest average bh of all the characteristics measured at two locations of 0.50, while the average nh for three crosses over two locations was 0.48. Heritability reflected a tendency toward decreased kernel width except for Hi26 x I28, where it was towards the wider kerneled parent. The cross which showed the highest nh over two locations was Hi26 x Sgl8, with an average nh of 0.59. In general, there was not enough separation between the parents for this trait and epistatic effects tended to be canceling. The relationship between kernel width and popping expansion (called kernel thickness), measured for the parents and F1 of the variety diallel was non-significant, with a r value of 0.20.

6.2.9. Kernel Weight

Generation mean analysis and heritability estimates for kernel weight are presented in Tables 6.22 to 6.24. Average kernel weight of the parents, F1 and segregating generations and heterosis at two locations is presented in Table 6.23. The average heterosis of the crosses with Hi26 was 11.6% higher at Kauai than at Waimanalo. This was due to the high heterosis of Hi26 x Sg18 at Kauai. The average heterosis of I28 x Sg18 was 30.3% higher at Kauai than at Waimanalo. In all of the crosses at both locations the F1, F2 and backcross to the high parent generation means were higher than the midparent value. For I28 x Sg18 at Kauai, the means of the F1, F2 and backcross to the high parent were higher than the high parent mean. For I28 x Sg18 at Waimanalo, the F1 was equal to the high parent mean while the F2 exceeded it.

Frequency distribution of the F1 and segregating generations and the parental means for 1000 kernel weight is presented in Figures 6.18 and 6.19. At both locations, the x axis ranges from 40 up to 340 grams with increments of 20 grams. The crosses Hi26 x I28 and Hi26 x Sg18 show a wide difference between parental means, with Hi26 being the heavy parent and the popcorns being the lighter parent. In all of

Table 6.22. Average weight of 1000 kernels (g) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Waimanalo	Hi26 x I28	224.0	77.4	150.7	179.9	156.5	206.0	129.2	19.4 %
	Hi26 x Sg18	224.0	93.8	158.9	198.8	165.4	214.3	141.1	25.1 %
	I28 x Sg18	77.4	93.8	85.6	93.7	95.0	87.7	90.9	9.5 %
Kauai	Hi26 x I28	188.3	62.6	125.5	158.9	112.0	179.1	130.9	26.7 %
	Hi26 x Sg18	188.3	76.3	132.3	184.9	134.2	183.6	129.6	39.7 %
	I28 x Sg18	62.6	76.3	69.5	97.1	77.0	80.3	74.6	39.8 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.23. Scaling test and generation mean analysis for kernel weight at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	8.1	1.0	-35.1	-22.1 **	76.8 **	73.4 **	44.1 *	3.5	-53.2
	Hi26 x Sg18	5.9	-10.3	-53.7 **	-24.6 **	73.2 **	89.2 **	49.3 *	8.1	-44.9
	I28 x Sg18	4.3	-5.7	21.2 *	11.3 **	-3.2	-14.5	-22.6 *	5	24.0
Kauai	Hi26 x I28	10.8	40.3 **	-120.8 **	-86.0 **	48.2 **	205.5 **	172.0 **	-14.7	-223.1 **
	Hi26 x Sg18	-6.0	-2.1	-97.6 **	-44.7 **	54.1 **	142.0 **	89.4 **	-1.96	-81.3 **
	I28 x Sg18	0.91	-24.3 **	-25.0 **	-0.85	5.7 **	29.3 **	1.7	12.58 **	21.6 **

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

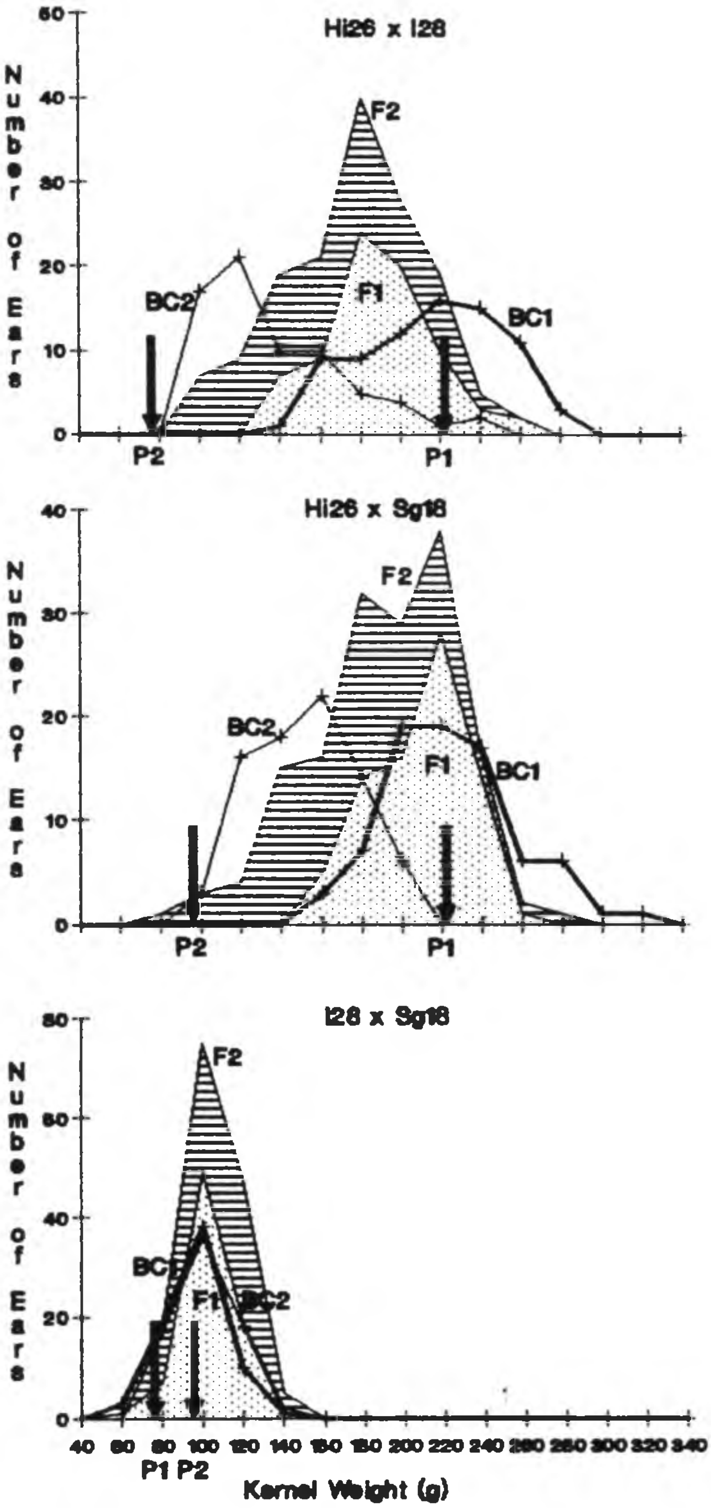
Table 6.24. Genetic variances and heritability estimates for kernel weight at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	512.8	1131.9	815.0	0.19	0.21	0.67
	Hi26 x Sg18	2288.5	-1640.5	692.5	0.80	0.77	0.77
	I28 x Sg18	363.0	-61.8	127.4	0.62	0.74	0.74
Kauai	Hi26 x I28	-2321.5	4745.7	646.0	0.00	0.00	0.88
	Hi26 x Sg18	259.2	-193.1	579.1	0.20	0.31	0.31
	I28 x Sg18	286.9	-77.8	82.6	0.69	0.78	0.78

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

the crosses the backcross to the heavy kerneled parent is distributed around the mean of that parent and may even exceed its value. The backcross to the small kerneled parent is distributed around the midparent except in I28 x Sg18 where the parental means are too close together. In all of the crosses, the F2 population shadows the F1, having a wider distribution in the negative direction (toward the small kerneled parent).

The scaling test in Table 6.23 shows all of the crosses at both locations exhibit significant non-allelic interaction. At Waimanalo, both crosses with Hi26 express nearly equal additive and dominance effects in the six parameter model with complimentary axa interaction at 0.05 level of significance. The complimentary aa interaction increases the average nh for these two crosses at Waimanalo. At Kauai, Hi26 x I28 exhibits a dominance effect that is 4.2 times greater than the additive effect, while for Hi26 x Sg18 it is 2.6 times greater. For these two crosses at Kauai, the epistatic aa and -dd interact to cancel their effects. For Hi26 x Sg18, dominance effects are higher than for Hi26 x I28 resulting in a bh of 0.88 for the former and only 0.31 for the later at Kauai. At Waimanalo, bh is 0.67 for Hi26 x I28, while the average nh is 0.20 due to complimentary axa interaction. For Hi26 x Sg18, bh is 0.77, while the average nh is 0.79 because the complementary aa


Hi26 x I28

Hi26 x Sg18

I28 x Sg18

Figure 6.18. Frequency distribution of F1, F2 and backcross progenies for 1000 kernel weight at Waimanalo.

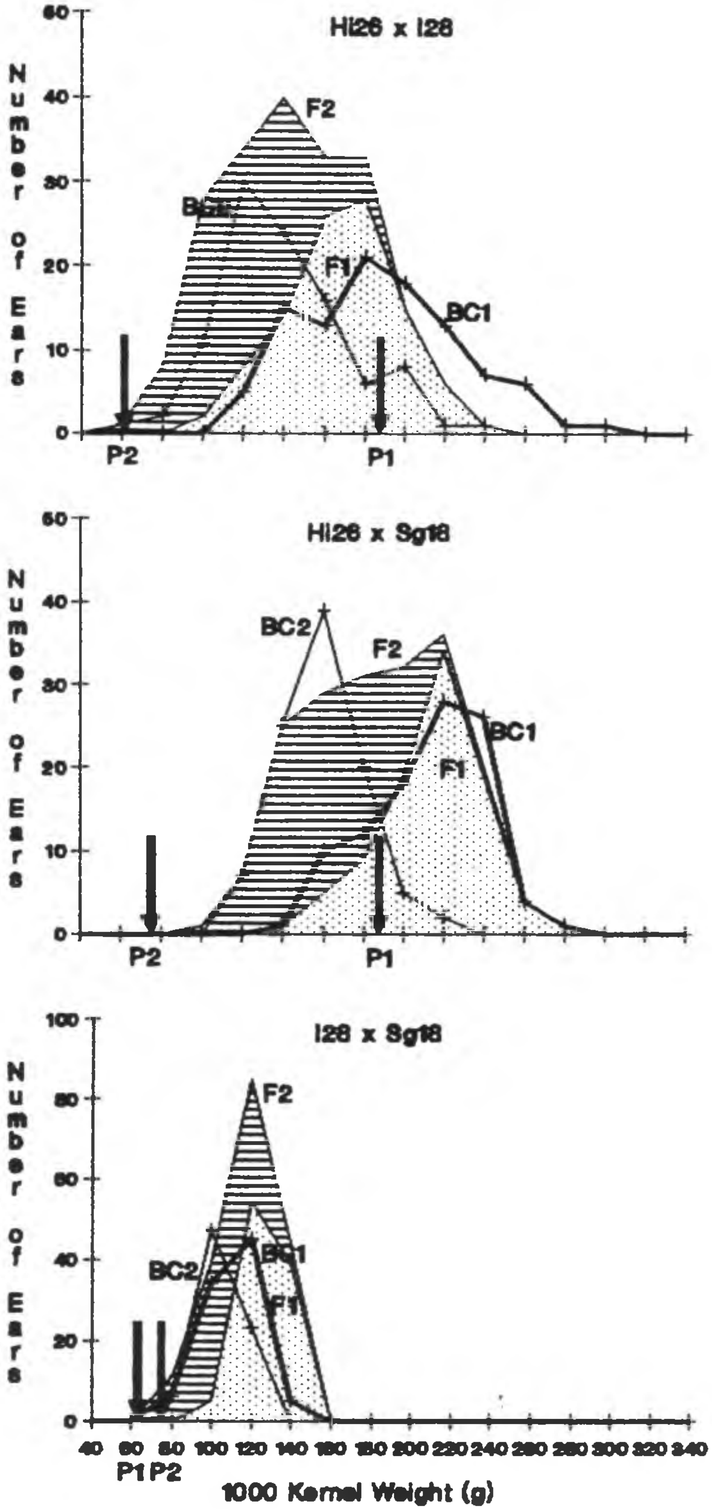


Figure 6.19. Frequency distribution of F1, F2 and backcross progenies for 1000 kernel weight at Kauai.

interaction and dominance effects are higher than for Hi26 x I28. At Waimanalo, I28 x Sg18 only shows significant negative axa interaction at the 0.05 level of significance indicating a shift in segregating generations towards Sg18, the heavier popcorn parent. At Kauai, the cross exhibits dominance effect that is 5 times greater than the additive effect, and duplicate dd interaction that does not completely diminish the aa effect. Significant additive variance at both locations give I28 x Sg18 an average nh of 0.68 at Waimanalo and 0.74 at Kauai. Broad sense heritability is 0.74 at Waimanalo and 0.78 at Kauai.

For kernel weight, the average bh over three crosses at two locations was 0.70, while the average nh was 0.66 in the direction of the heavier kerneled parent. Hi26 x I28 showed the highest bh over two locations of 0.78, while I28 x Sg18 showed the highest nh of 0.71. A very strong dominance effect and canceling epistatic effects at the Kauai location largely accounted for the high average bh for Hi26 x I28. Additive x additive effects at Waimanalo and complimentary axa interaction that increased the additive effect at Kauai accounted for the high average nh of I28 x Sg18. Additive x additive effects also accounted for the high average nh of 0.79 for Hi26 x Sg18 at Waimanalo.

6.2.10. Stalk Lodging

Generation mean analysis and heritability estimates for stalk lodging are presented in Tables 6.25 to 6.27. The degree of stalk lodging was rated on a scale of 1 to 5, were 1 is no lodging and 5 is completely lodged. Average rating for stalk lodging of the parents, F1 and segregating generations and heterosis estimates are presented in Table 6.25. The average heterosis for crosses with Hi26 was 14%, in the direction of P1, the most lodge resistant parent. Among the crosses with Hi26, the mean values of segregating generations were all lower than the midparent value, except for B2 in Hi26 x I28. For Hi26 x I28, the F2 and B1 were lower than the F1 mean towards the lodge resistant parent. The F2 was lower than the F1, in the direction of the lodge resistant parent in Hi26 x Sg18. Between the popcorn parents, Sg18 proved to be more lodge resistant than I28. Heterosis is only -2.1%, but the F2 is centered around the F1 and the backcross to Sg18 is lower than the midparent value.

In Table 6.26, the scaling test indicates that there are epistatic effects for all of the crosses. In the six parameter analysis, I28 x Sg18 shows positive additive effects, in the direction of I28. There is complimentary aa interaction and duplicate dd interaction, with the dd interaction reducing the additive effect. Heritability for

Table 6.25. Average stalk lodging rating of parents, F1, F2 and backcross progenies at Waimanalo.

Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Hi26 x I28	1.88	3.63	2.76	2.43	2.28	2.33	3.53	-11.8 %
Hi26 x Sg18	1.88	2.56	2.22	1.86	1.63	2.19	2.16	-16.2 %
I28 x Sg18	3.63	2.56	3.10	3.03	3.00	4.31	3.21	-2.1 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table 6.26. Scaling test and six parameter generation mean analysis for stalk lodging at Waimanalo.

	Scaling Test A	 B	 C	 D	Six Parameter Analysis a	 d	 aa	 ad	 dd
Hi26 x I28	0.34	0.99 *	-1.27	-1.30 **	-1.20 **	2.28 **	2.60 **	-0.33	-3.93 **
Hi26 x Sg18	0.63	-0.09 **	-1.66 **	-1.10 **	0.03	1.83 **	2.20 **	0.36	-2.74 **
I28 x Sg18	1.97 **	0.84	-0.24	-1.52 **	1.10 **	2.98 **	3.05 **	0.57	-5.86 **

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6.27. Genetic variances and heritability estimates for stalk lodging at Waimanalo.

	Variances A	 D	 E	Heritability nh(1)	 nh(2)	 bh(3)
Hi26 x I28	-1.76	3.63	2.20	0.00	0.00	0.62
Hi26 x Sg18	-4.34	4.83	1.81	0.00	0.00	0.73
I28 x Sg18	0.49	-0.93	1.91	0.13	0.20	0.20

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2·
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

this cross is low and insignificant. In Hi26 x I28, there is a strong negative additive effect in the direction of Hi26, aa interaction is complementary to dominance effects but dd interaction nullifies its effect and reduces dominance effects. Bh for this cross is 0.62. Hi26 x Sg18 only shows dominance effect with complimentary aa interaction that is reduced by duplicate dd interaction. Heritability again is only significant in the broad sense, being higher than for Hi26 x I28.

Because of the high dominance effect for stalk lodging resistance, it would be hard to recover resistance in backcrosses. Also, another method of testing for resistance such as stalk thickness is necessary as the present method can only be tested under severe weather conditions, such as happened to occur at Waimanalo when this trail was rated. The fact that the same conditions did not occur at Kauai is the reason why the data from that location for stalk lodging was non-significant. It is apparent that under normal weather conditions, the F1 and segregating generations of popcorn are not susceptible to stalk or root lodging, which would put into question the necessity of crossing to a tropical dent inbred to increase stalk strength. However, in spite of these drawbacks, it is apparent that stalk lodging resistance is a heritable trait which is important to improvement of popcorn.

Plant Height Generation mean analysis for plant height and related tables and graphs are to be found in Appendix B. In summary, the average heterosis for the three crosses over two locations was 25%. Hi26 x I28 tested non-significant for non-allelic interaction at Waimanalo. The cross showed a high additive variance that resulted in a bh of 0.76 and a average nh of 0.74. The same cross at Kauai, showed significant complimentary aa interaction that was reduced by the -dd so that nh was reduced to 0.47. At both locations, Hi26 x Sg18 showed canceling aa and -dd interaction. Additive effects were high at Waimanalo resulting in an average nh of 0.71, at Kauai additive effects were lower resulting in an average nh of 0.69. I28 x Sg18 tested non-significant in the scaling test at Waimanalo. The cross had a bh of 0.81 because the degree of dominance was 3.0. The overall average nh for all of the crosses was 0.55, which indicates high additive effects and high heritability for plant height.

Ear Height Generation mean analysis and related tables and graphs for ear height can be seen in Appendix B. The average heterosis for ear height over two locations for three crosses was 30.6%. Hi26 x Sg18 shows a duplicate dd interaction and complimentary aa interaction at both locations. Heritability in the narrow sense averaged 0.63 for the cross over two locations. As a parent, I28 had the lowest ear height at Waimanalo, but at Kauai it was reported to be nearly as high as Hi26. This resulted in a much lower nh at Kauai, because the parents were closer together in ear height. The average nh at Waimanalo was 0.49 for this cross. Results for I28 x Sg18 were also different between locations, because at Waimanalo Sg18 had the higher ear height, while at Kauai I28 had the higher ear height. At Waimanalo, nh was a very high 0.96 and there was a high additive variance. At Kauai, there was only dd interaction because the backcross to the better parent (I28) was lower than the backcross to Sg18. Additive variance was lower than at Waimanalo, so that the average nh was 0.61. Over all crosses at both locations, the average nh was 0.59, which indicated a high additive genetic effect for this trait.

6.3. DISCUSSION

Epistasis was present in all of the characteristics measured. The magnitude of epistasis may have been increased by environmental effects as it was more prevalent at the Kauai location where environmental variance was generally higher. Where there was significant and positive aa interaction and equally significant and negative dd interaction, their collective effect was nullified. According to Mather (1949), narrow sense heritability is a more accurate estimate of heritability than broad sense heritability in the presence of epistasis. Both estimates of narrow and broad sense heritabilities in the presence of epistasis do not seem too reliable because they depend upon the mathematical difference in variances between the F2 and backcross generations, whereas the epistatic model is based upon the mathematical differences in population means. From the data, it was readily apparent that as the error variance increased, heritability estimates decreased. Over the three crosses at both locations, broad sense heritability was higher than both estimates of narrow sense heritability for all of the traits measured. The average broad sense heritability was higher at Waimanalo than at Kauai for all traits except for the number of kernel rows. The average of both narrow sense heritability estimates was also higher at Waimanalo than at Kauai for all traits except for kernel depth and length of central spike. The lower heritability estimates at Kauai were due to a higher error variance or a lower additive variance.

For the traits of grain yield, number of kernel rows, ear length, kernel weight, kernel width, kernel depth, ear height, plant height, length of central spike and spike length the crosses involving Sg18 as one of the parents showed the highest narrow sense heritability or general combining ability. For all of the same traits except for kernel weight, length of central spike and tassel length the crosses involving Sg18 as one of the parents also exhibited the highest level of broad sense heritability or specific combining ability. Because of the additive inheritance of kernel depth and kernel weight, which are significantly correlated to popping expansion, seed selections could be made from the B1 ears to the recurrent pop parent on the basis of size. These could then be grown and backcrossed again to the recurrent pop parent, selected again on the basis of seed size. The B2 would then be grown, and ears harvested, test popping part of each harvested ear and selecting those ears with superior popping expansion to plant as the reconstituted Sg18.

According to Crumbaker et al. (1949), it is necessary to backcross twice to the recurrent popcorn parent to recover popping volume equal to the popcorn parent. The problem with selecting on the basis of seed size is that any gains in yield by outcrossing to a dent will be lost, unless the ear size has substantially increased. The most desirable characteristic to be inherited from a dent would be stalk strength and root lodging resistance. Data from this trial indicates that stalk lodging resistance is dependent upon specific combining ability, and would be a very difficult characteristic to recover through successive backcrosses to the recurrent pop parent. The inbred lines of popcorn tested at Waimanalo did not seem to be exceptionally susceptible to stalk or root lodging. Data from the inbred diallel, showed that some inbred lines of popcorn, such as KP58K, have a definite resistance to stalk lodging. Others such as I28 were more susceptible. I28 in hybrid combination with KP58K was more susceptible to stalk lodging than either parent. SCA was more significant than GCA controlling inheritance of the trait, but except for that exceptionally poor performance with I28, KP58K did seem to impart a degree of resistance to stalk lodging to all of its hybrids.

7. SUMMARY

Three popcorn breeding populations were used for this thesis which involved two diallel analyses and one analysis of segregating generations. Popcorn inbreds were used to examine the inheritance of popping expansion, yield and its components and the relationship between tassel characteristics and ear length. Open pollinated varieties were used to assess the inheritance of popping expansion and relationship of popping expansion to kernel characteristics. An analysis was made of advanced segregating generations using two popcorn inbreds and one tropical dent. The inheritance of kernel characteristics, yield, stalk lodging and the relationship between tassel characteristics and ear length were investigated.

In the diallel of popcorn inbreds, grain yield exhibited a high degree of variance due to specific combining ability (92.9%), while popping expansion exhibited a high variance (62.5%) due to general combining ability. Superior crosses for both grain yield and popping expansion were R18-1-9 x KP58K, R18-1-9 x I28, Sg18 x KP58K and Sg18 x I28. Three-way crosses among these lines were recommended as a means of maintaining high popping expansion and increasing grain yield.

Both grain yield and popping expansion were controlled by general combining ability in the diallel of varieties. Over two locations, Philippine Pop #1 showed superior yields in hybrid combination. At Waimanalo, the race Avati Pichinga and the variety Supergold gave the highest hybrid array means for popping expansion. Kernel width and kernel volume were most highly correlated to popping expansion, with r values of -0.74 and -0.68, respectively.

Tassel length was highly correlated to ear length with r=0.57 in the variety population and r=0.68 in the inbred population. In the analysis of generation means, length of the tassel spike was correlated to ear length with r equal to 0.95 and 0.93, while tassel length was correlated with r values of 0.92 and 0.90. Tassel and ear length showed similar epistatic interaction and degree of dominance effects.

Analysis of advanced generations for all of the traits measured revealed that epistasis was present and significantly increased by environmental "noise" and the high s.e. of Hi26. The expression of heterosis influenced non-additive effects. Kernel weight and depth showed additive inheritance, indicating that it should be possible to select among backcross progeny by kernel size, to recover initial popping expansion of the popcorn parent after outcrossing to a dent.

APPENDIX A

A1. Analysis of variance mean squares for ear number, ear aspect, tiller number, plant aspect, stalk lodging and root lodging for the inbred diallel.

		Mean squares					
Source	df	Ear Number	Ear Aspect	Tiller Number	Plant Aspect	Stalk Lodging	Root Lodging
Entries	14	0.053	5.95**	0.783**	2.06**	674.14**	33.31
F1 vs Inbreds	1	0.114	49.41**	2.955**	5.63**	946.41*	13.00
Between Inbreds	4	0.099	1.20*	0.265*	3.45**	888.08**	45.68
Between F1	9	0.026	3.23**	0.773**	1.04	548.80*	30.07
Reps	3	0.392	0.46	0.363	0.71	448.19	103.64
Error	42	0.059	0.45	0.107	0.68	205.33	27.65

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

A.2. General (GCA) and specific (SCA) combining ability mean squares and their mean square ratios.

		Mean squares			
Source	df	Tiller number	Plant aspect	Stalk lodging	Ear aspect
GCA	4	0.16**	0.37	160.81*	1.24**
SCA	10	0.21**	0.57**	171.62**	1.59**
ERROR	42	0.03	0.17	51.33	0.11
GCA/SCA		0.30	0.25	0.37	0.31

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

A.3. Estimated variance components and their percent value.

Source	Tiller number	Plant aspect	Stalk lodging	Ear aspect
GCA	0.04	0.066	36.49	0.37
%	26.69	15.03	24.66	30.58
SCA	0.09	0.202	60.14	0.74
%	56.85	46.36	40.65	60.19
ERROR	0.027	0.169	51.33	0.113
%	16.46	38.6	34.69	9.23

APPENDIX B

Table B.1. Average plant height (cm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Waimanalo	Hi26 x I28	237.8	155.5	196.7	232.5	214.9	231.7	197.6	18.2 %
	Hi26 x Sg18	237.8	191.8	214.8	249.6	228.4	251.5	224.9	16.2 %
	I28 x Sg18	155.5	191.8	173.6	211.9	191.6	181.1	200.0	22.0 %
Kauai	Hi26 x I28	156.9	109.8	133.4	168.1	139.6	156.1	145.8	26.0 %
	Hi26 x Sg18	156.9	106.0	131.5	175.6	136.4	168.9	147.8	33.6 %
	I28 x Sg18	109.8	106.0	107.9	143.8	124.7	116.8	123.8	33.2 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table B.2. Scaling test and six parameter generation mean analysis for plant height at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	-7.1	7.2	1.3	0.6	34.0 **	34.7 **	-1.2	3.6	0.9
	Hi26 x Sg18	15.5 **	8.4 *	-15.4	-19.6 **	26.6 **	74.0 **	39.3 **	1.8	-63.1 **
	I28 x Sg18	-5.2	-3.6	-4.6	2.1	-19.0 **	34.0 **	-4.3	-0.4	13.1
Kauai	Hi26 x I28	-12.7 **	13.7 **	-44.5 **	-22.7 **	10.3 **	80.1 **	45.5 **	-13.2	-46.5 **
	Hi26 x Sg18	5.3	13.9 **	-68.6 **	-43.9 **	21.2 **	132.0 **	87.8 **	-4.3	-107.0 **
	I28 x Sg18	-19.9 **	-2.1	-4.7	8.6 **	-7.0 **	18.6 *	-17.2 *	-8.9	39.2 **

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table B.3. Genetic variances and heritability estimates for plant height at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	763.4	-358.5	236.3	0.72	0.76	0.76
	Hi26 x Sg18	568.5	-364.0	217.3	0.69	0.72	0.72
	I28 x Sg18	46.0	409.0	104.0	0.10	0.08	0.81
Kauai	Hi26 x I28	229.5	-129.0	203.8	0.40	0.53	0.53
	Hi26 x Sg18	520.4	-452.1	232.5	0.69	0.69	0.69
	I28 x Sg18	242.4	-44.2	124.2	0.52	0.66	0.66

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

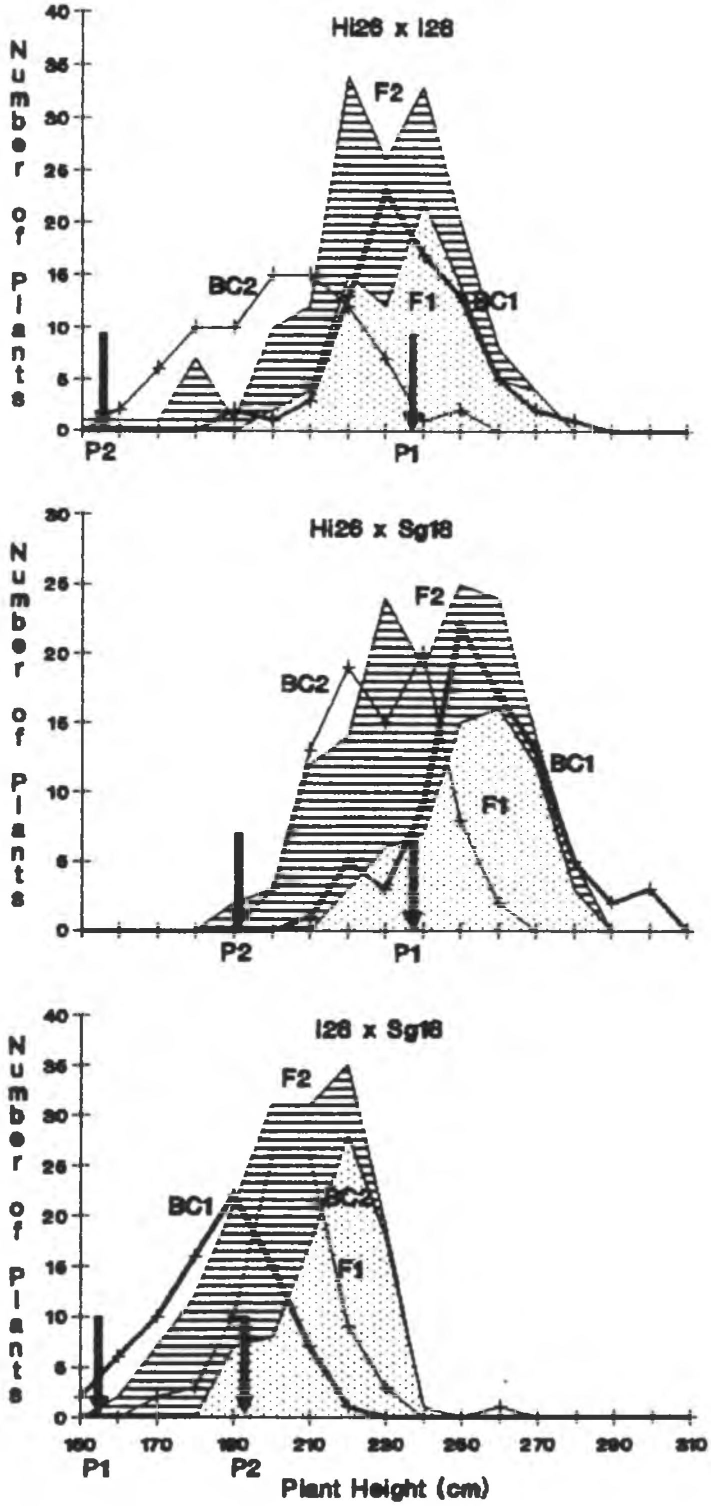


Figure B.1. Frequency distribution of F1, F2 and backcross progenies for plant height at Waimanalo.

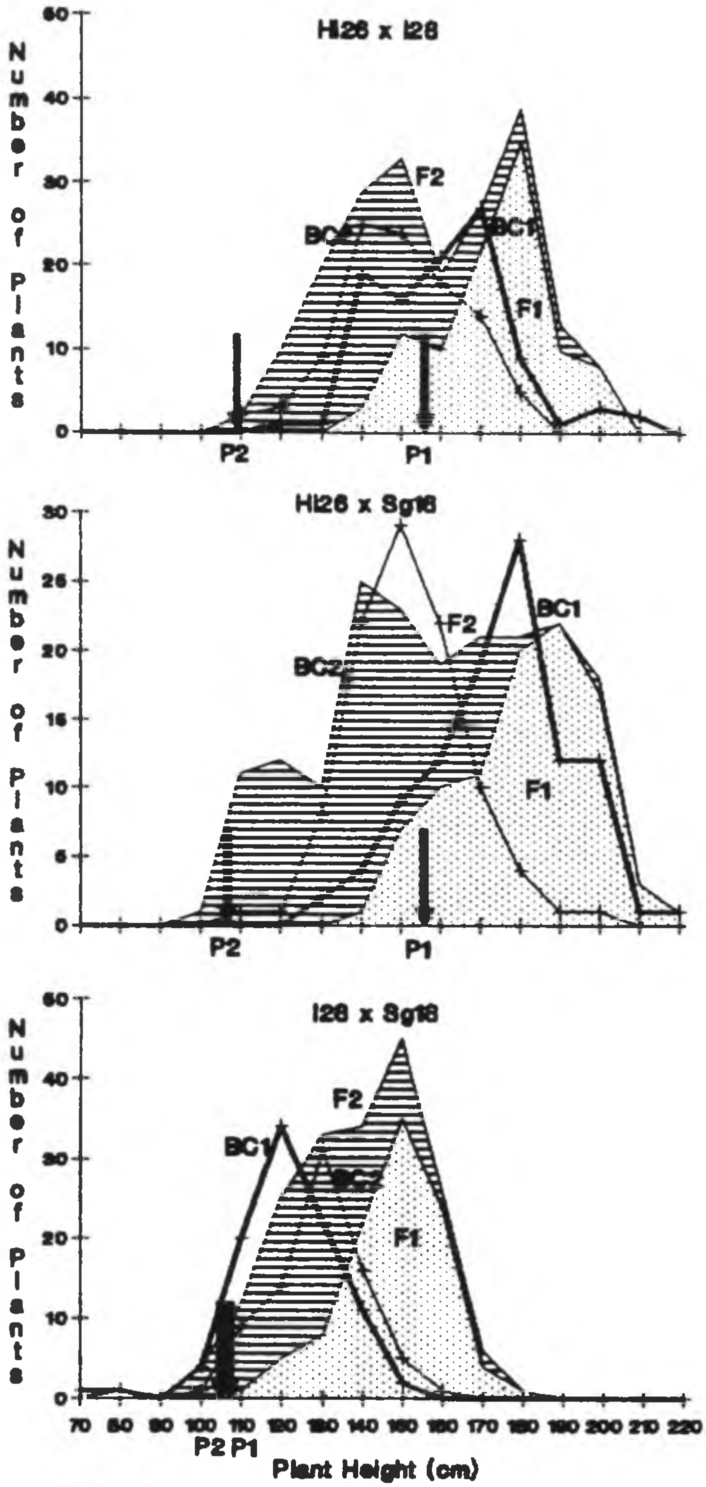


Figure B.2. Frequency distribution of F1, F2 and backcross progenies for plant height at Kauai.

Table B.4. Average ear height (cm) of parents, F1, F2 and backcross progenies at two locations.

Location	Cross 1 x 2	Parent P1	 P2	 MP(1)	Hybrid F1	Segregating Generations F2	 B1	 B2	Heterosis(2)
Waimanalo	Hi26 x I28	98.5	69.0	83.8	102.0	95.2	102.0	88.4	21.8 %
	Hi26 x Sg18	98.5	87.1	92.8	112.4	101.5	108.5	103.2	21.1 %
	I28 x Sg18	69.0	87.1	78.1	101.4	85.0	81.2	90.0	29.8 %
Kauai	Hi26 x I28	54.1	49.5	51.8	65.8	51.9	55.3	59.8	27.2 %
	Hi26 x Sg18	54.1	42.1	48.1	73.5	50.3	67.1	58.2	52.8 %
	I28 x Sg18	49.5	42.1	45.8	59.9	48.5	46.8	47.5	30.8 %

(1) MP = (P1 + P2)/2 (2) Heterosis (%) = ((F1 - MP)/MP) x 100

Table B.5. Scaling test and six parameter generation mean analysis for ear height at two locations.

		Scaling Test				Six Parameter Analysis				
Location	Cross	A	B	C	D	a	d	aa	ad	dd
Waimanalo	Hi26 x I28	3.5	5.7	9.3	0.0	13.7 **	18.2 *	-0.1	-1.1	-9.2
	Hi26 x Sg18	6.2	6.8 *	-4.3	-8.7 **	5.4 **	36.8 **	17.3 *	0.3	-30.3 **
	I28 x Sg18	-8.0 **	-8.6 **	-18.7 **	-1.1	-8.8 **	25.5 **	2.2	0.3	14.3
Kauai	Hi26 x I28	-9.3 **	4.3	-27.5 **	-11.3 **	-4.5 **	36.6 **	22.6 **	-6.8	-17.6
	Hi26 x Sg18	6.7 *	0.9	-42.0 **	-24.8 **	8.9 **	75.0 **	49.6 **	2.9	-57.1 **
	I28 x Sg18	-15.7 **	-6.9 **	-17.4 **	2.6	-0.7	8.9	-5.2	-4.4	27.8 **

*,** Significant at the 0.05 and 0.01 probability levels, respectively.

Table B.6. Genetic variances and heritability estimates for ear height at two locations.

		Variances			Heritability		
Location	Cross	A	D	E	nh(1)	nh(2)	bh(3)
Waimanalo	Hi26 x I28	198.30	48.70	118.90	0.43	0.54	0.68
	Hi26 x Sg18	354.40	0.00	127.40	0.71	0.74	0.74
	I28 x Sg18	387.90	0.00	46.60	1.02	0.89	0.89
Kauai	Hi26 x I28	66.60	0.00	156.80	0.22	0.30	0.30
	Hi26 x Sg18	170.40	0.00	124.30	0.46	0.58	0.58
	I28 x Sg18	105.90	0.00	53.50	0.55	0.66	0.66

(1) Narrow sense heritability (Warner 1952): (0.5 x A)/VF2
(2) Narrow sense heritability estimated by: A/(A + D + E)
(3) Broad sense heritability estimated by: (A + D)/(A + D + E)

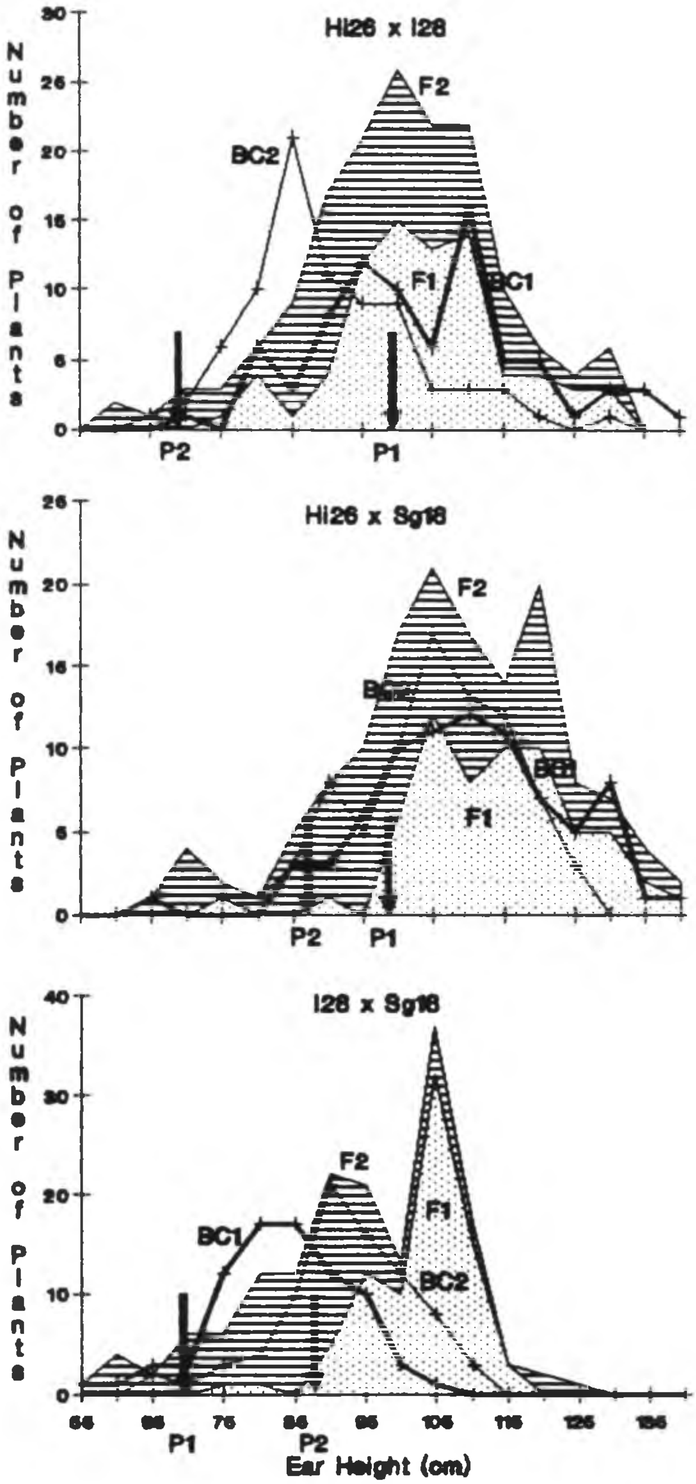


Figure B.3. Frequency distribution of F1, F2 and backcross progenies for ear height at Waimanalo.

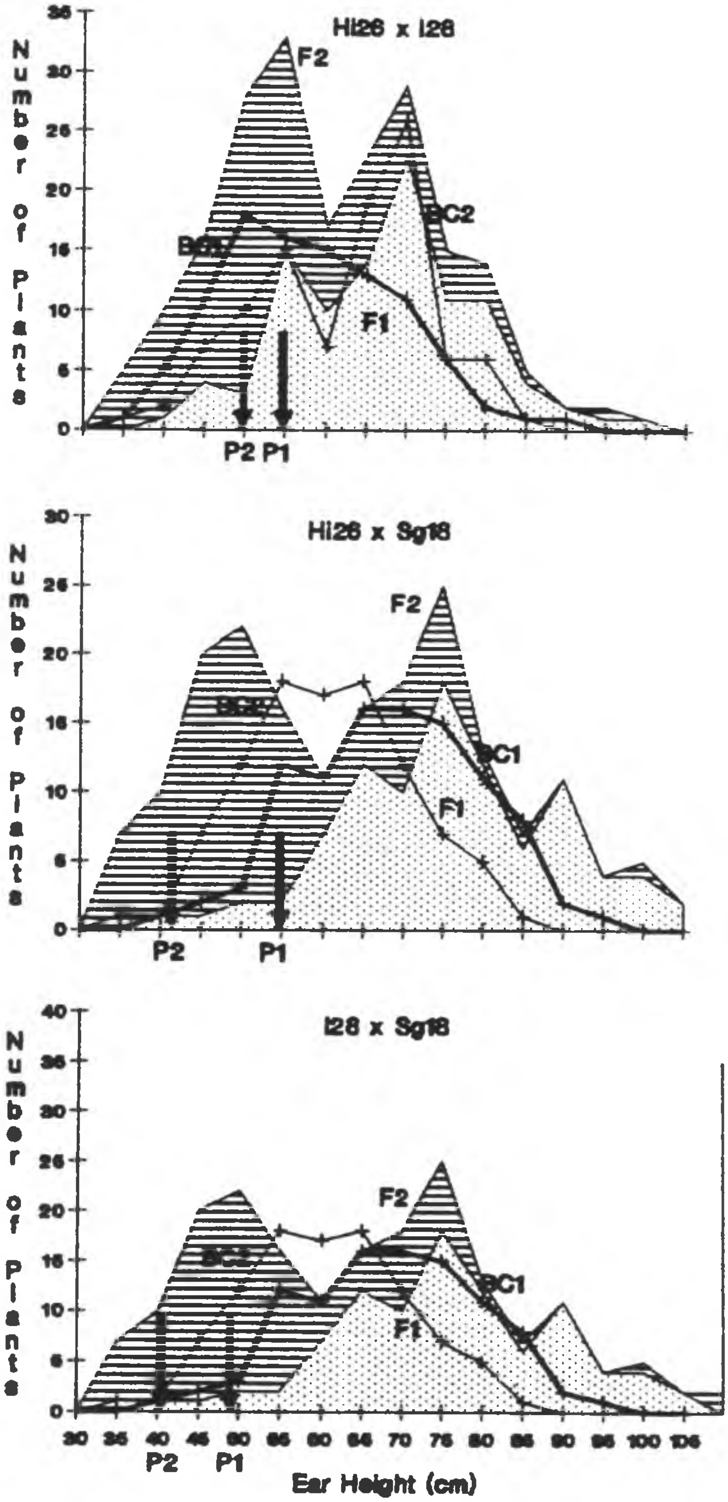


Figure B.4. Frequency distribution of F1, F2 and backcross progenies for ear height at Kauai.

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