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Diallel Analysis of Plant and Ear Heights in Tropical Maize (*Zea mays* L.)

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Plant breeders and geneticists often use diallel mating designs to obtain genetic information about a trait of interest from a fixed or randomly chosen set of parental lines. Diallel designs and analyses have been developed for parents that range from inbred lines to genetically broad-based varieties. The object of this study was to determine the combining ability for the plant and ear height by both Griffing Method and Gardner & Eberhart Method, and compare the results obtained by two methods. Hybrids and parents averaged over hybrids differed significantly for plant and ear height. Relative ear position over plant height (REPH) was also calculated from plant and ear heights. By Griffing Method, general combining ability (GCA) was significant in plant height. Specific combining method (SCA) was highly significant in all three measurements. Average heterosis for the plant and ear heights were 33.3% and 61.9%, respectively. However, REPH showed 21.6% heterosis effect. The traits with low heterosis showed higher ratios of GCA/SCA, while these ratios were smaller in traits with high heterosis. REPH could be used as one of valuable selection criteria over plant and ear heights in the breeding program for low ear height. Above mentioned two statistical methods produced some different results.

INTRODUCTION

The height of the stalk is determined by the number and length of the internode in maize. In this way, plant height can vary from 0.3 m to 7.0 m, depending on the variety and growing conditions. Usually, early maturing varieties are shorter, and late maturing ones are taller. In a tropical climate, where the growing season may be as long as 11 months, some late maturing varieties reach a plant height of 7 m. As a result of inbreeding, plant and ear height decrease, and the population become more homogeneous until it reaches the “inbred minimum”. Plant and ear height not only depend on the genetic background of the varieties, but are also influenced by many environmental effects and the cultivated method. Owing to increased plant density, plant and ear height may increase as the plants compete for light (Park *et al.*, 1989; Mason *et al.*, 1974). Taller plants attached with more leaves need a larger growing area and lower plant density compared with shorter one (Begna *et al.*, 2000). Manson *et al.* (1974) reported that dry matter yield showed a significant positive correlation to plant height and to ear height. Plant height is principally determined by the variety and sowing date (Baktash and Mazaal, 1985), and is also very important characters not only for breeding of new varieties of maize, but for green and dry matter production, and even for grain yield and harvest. This trait is controlled by the expression of many genes and by the interactions between these genes.

Ear height is one of the most important selection criteria in most maize breeding program. Especially, ear height is of importance when it comes to root and stalk lodging. High ear position is like to become more susceptible to root and stalk lodging. Thus, plant breeders prefer to select for lower ear position. Looking at a relative ear position over plant height (REPH) may supplement selection for low ear position by ear height only. Plant height has been considered less important for selection. However, it may not be true in some areas where tall plant has disadvantage in maize seed production due to wind effect. For instance, maize breeders have attempted to incorporate a semi-dwarf gene such as *brachytic-2* (*br₂*) dwarfing gene which shortens the internodes below the ear to reduce plant height.

In spite of this gene, they produced the same or almost the same yield as their normal counterparts. This is why using these dwarf lines in breeding facilitates selection for lower ear height without significant yield losses. Another type of dwarfism, supposedly caused by the simultaneous effect of many genes, shortens the internodes only above the ear, so that plant height decreases without changing the ear height or other parts of the plant (Legg and Fleming, 1973). Selection for cold tolerance also decreases the plant height and cause early flowering (Mock and Bakri, 1976). During selection, other characteristics may change, together with the improved trait. Selection for earliness, for example, decreases plant and ear height, according to many authors (Nyhus *et al.*, 1989; Troyer and Larkins, 1985). In contrast, selection for higher yield increase plant and ear height (Thompson, 1983). There are some cases when plant height increase while ear height decrease (Yap and Tan, 1974).

Many breeders have studied selection for lower ear height. The most outstanding of them might be Harville (1977), who produced many early and late maturing,

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low-eared varieties by recurrent selection. Plant height is strongly associated with the flowering date, because internode formation stops at floral initiation, which means that earlier flowering maize is usually shorter (Troyer and Larkins, 1985). A modern variety produces high yields despite early flowering. There is also a correlation between earliness and ear height. The higher the ear is, the later the plant matures (Surányi and Mándy, 1955), but earliness and lower ear height have no absolute reciprocity. There are correlations between many other traits and plant height. The number of leaves (Allen *et al.*, 1973) and the grain yield are significantly correlated with plant and ear height (McKee *et al.*, 1974). Obilana and Hallauer (1974) found a significant correlation between plant and ear height in unselected inbred. Plant height is usually considered to be a simple inherited trait, determined by only a few genes. Edward *et al.* (1987) identified QTLs for plant height in maize. Hui *et al.* (1997) found 30 QTLs for plant and ear height. According to Veldboom *et al.* (1994), QTLs for plant height are in close proximity to loci of qualitative traits affecting plant height. Lee and Veldboom (1993) found a marker on the long arm of chromosome 1 which is closely linked to a QTL for plant height.

According to Sheridan (1988), there are at least 27 loci influencing the quantitative expression of this trait. Beavis *et al.* (1991) identified 14 QTLs, most of them linked to the loci of qualitative traits. Either dominance (Guo *et al.*, 1986) or additive effects (Russell, 1976) are considered more important in the expression of plant and ear height, though some authors assign the differences in plant and ear height to extrachromosomal effects (Baynes and Brawn, 1973). Plant and ear heights showed a great deal of heterosis. In order to elucidate heterosis in the quantitative analyses, those traits may play an important role.

Plant breeders and geneticists often use diallel mating designs to obtain genetic information about a interest trait from a fixed or randomly chosen set of parental lines. The diallel genetic design and its various modifications have been used by breeders to evaluate the potential of populations for intrapopulation improvement and the usefulness of parents in inter-population breeding programs, and to select inbred lines in hybrid development programs. Although several strategies for diallel analysis have been proposed, few of them are commonly applied. Diallel analyses have been developed for parents that range from inbred lines to genetically broad-based varieties (Griffing, 1956; Gardner and Eberhart, 1966). Computer programs have been developed for Griffing's diallel analyses (Burow and Coors, 1994; Magari and Kang, 1994; Zhang *et al.*, 2005). Diallel analyses of broad-based populations (Gerrish, 1983; Mungoma and Pollak, 1988; Crossa *et al.*, 1990; Quendeba *et al.*, 1996; Widstrom and Snock, 1998) have generally been conducted according to Gardner and Eberhart (1966) analysis. The Griffing (1956) method and Gardner and Eberhart (1966) method have been widely used in various crops

(Dorrance *et al.*, 1998; Bourland *et al.*, 1999; Soriano Viana, 2000; Nigussie and Zelleke, 2001; Pratta *et al.*, 2003; Doerksen *et al.*, 2003; Subhan *et al.*, 2003; Bodzon, 2004; Hakizimana *et al.*, 2004; Zhang *et al.*, 2005). The main reasons that justify the widespread use of the Griffing (1956) method are its generality, since the parents can be pure lines, inbred lines, or populations of a self-pollinated, cross-pollinated or intermediate species, and the ease of analysis and interpretation; the latter also characterizes the method developed by Gardner and Eberhart (1966). The genetic interpretation of parameters in the Gardner & Eberhart and the Griffing models and the relationship between them are have been discussed by Vencovsky (1970) and Cruz and Vencovsky (1989), thereby making the methods more accessible to breeder.

Diallel analysis of self- and cross-pollinating populations is used to study the genetic control of quantitative traits (Jinks and Hayman, 1953), to assess general and specific combining abilities (Griffing, 1956) and to perform heterosis analysis (Gardner and Eberhart, 1966) and to provide plant breeders the valuable and practical genetic information involved in materials they are dealing with. Griffing (Griffing, 1956) and Gardner & Eberhart (Gardner and Eberhart, 1966) methods are currently used in data analysis. The object of this study was to determine the general and specific combining abilities (GCA and SCA) for the plant and ear height by using both Griffing Method and Gardner & Eberhart Method and to compare the results obtained by two methods in a set of diallel crosses.

MATERIALS AND METHODS

Plant material and growth conditions

Five elite public inbreds of tropical Maize (*Zea mays* L.) that were widely utilized in University of Hawaii were used in this study. Two tropically adapted inbreds (Hi26 and Hi34) have been bred at University of Hawaii, and Pi17, Pi23 and Pi31 originating from Philippines and converted in Hawaii, and they all using for silage and grain. The resulting ten hybrids and five inbreds were planted on September, 2004 at Waimanalo Research Station, University of Hawaii on Oahu at 21° N latitude and 30 m elevations. The experimental design was a randomized complete block (RCB) design with three replications. Each plot was a single row (5 m length) with 0.20 m between hills. Two untreated seeds were planted and resulting plants were thinned to one per hill at around three weeks after planting.

Evaluation method of traits and statistical analysis

Data samples of five plants per plot were used for statistical analysis. Ear heights were measured on five plants in each plot from the soil surface to the base of the top ear. Heterosis effects (percentage) for plant and ear height were calculated from the mid-parental value of the two parents as $(F_1 - MP) / MP \times 100$, where F_1 is cross and MP is average of two parents included in F_1 .

The diallel crosses were analyzed following Griffing (1956) method 2 (including parents without reciprocals), model 1 (fixed) and model 2 (random):

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + e_{ijk}$$

where Y_{ij} is the mean phenotypic value, μ is the general mean, g_i and g_j are the general combining ability (GCA) effect, s_{ij} is the specific combining ability (SCA) effect and e_{ijk} (between i th and j th lines) is the error. Analysis III of Gardner & Eberhart Method was also used with Ordinary Least Squares (OLS) estimation (Huber *et al.*, 1992). The model for estimating the combining ability effects for each cross was

$$C_{ij} = \mu_c + g_i + g_j + s_{ij}$$

where μ_c was the mean of the population crosses, g_i (or g_j) was the GCA effect, and s_{ij} was the SCA effect for the cross between the i th and j th parents such that $s_{ij} = s_{ji}$ (no reciprocal effect).

RESULTS AND DISCUSSION

Overall performance of the experiment followed a

typical pattern at this time of season. With regard to plant height, ear height and relative ear position over plant height (REPH), variance analysis indicated plant height among replications was significantly different, while ear height and REPH showed no significant difference among replication (Table 1). The trial results are in agreement with those of Viana and Matta (2003). Especially, the difference in plant height among replications may be considered due to Hawaii's trade wind while ear height seemed less influenced by the trade wind. Differences in plant height, ear height and REPH for five parents and ten F_1 hybrids were highly significant ($p < 0.01$) except REPH for ten hybrids with significance at 5% level of probability.

Plant height for five parents and ten hybrids (Table 2) ranged from 142.2 cm (Pi31) to 177.53 cm (Hi26) and from 189.87 cm (Pi23 \times Pi31) to 229.8 cm (Hi26 \times Pi17). The highest inbred line Hi26 produced highest hybrids in average while the lowest inbred line Pi31 made lowest hybrids. In general, the hybrids made by the inbred lines Pi23, Pi31 produced lower plant height. Average heterosis effect for plant height was 33.3% and the hybrid by the inbred line Pi31 showed highest and

Table 1. Analysis of variance for plant height, ear height and REPH of five parents and their ten diallel crosses

Source	Df	Mean squares		
		Plant height	Ear height	REPH ^a
Total	224			
Reps	2	2,757.35 **	498.57 ^{ns}	46.31 ^{ns}
Entries	14	12,303.56 **	7,434.48 **	461.12 **
Parents	4	2,971.91 **	1,319.53 **	319.75 **
P vs H	1	136,904.00 **	94,873.68 **	4,596.89 **
Hybrids	9	2,606.47 **	436.77 **	64.42 *
Exp. Error	28	367.47	195.13	24.54
Sample Error	180	33.32	29.38	11.2

*, **, 5% and 1% levels of significant, ^{ns}, not significant. ^aREPH; Relative ear position over plant height.

Table 2. Average values (cm), heterosis effect (%), and SCA and GCA effects for plant height of five parents and their ten diallel crosses

Parent	Parent					Array mean
	Hi26	Hi34	Pi17	Pi23	Pi31	
Hi26	177.53 ^a	223.60	229.80	213.13	223.40	222.48*
		38.11 ^b	34.99	27.21	39.77	35.00**
		20.81 ^c	22.99	11.15	26.79	13.09***
Hi34		146.27	210.47	207.60	201.47	210.78
			36.21	36.66	39.47	37.16
			19.28	21.23	20.48	-2.53
Pi17			163.07	204.13	193.27	209.42
				27.33	26.46	31.22
				13.75	8.26	1.49
Pi23				157.67	189.87	203.68
					26.16	29.44
					9.68	-3.33
Pi31					142.20	202.00
						33.22
						-8.71

*Grand mean = 192.23 cm, parental mean = 157.35 cm, F_1 mean = 209.67. **Grand mean = 33.3%. ***GCA effect, SE of SCA = 3.74, SE of GCA = 7.64. ^aAverage plant height (cm). ^bHeterosis effect (%). ^cSCA effect (s_{ij}).

lowest heterosis. Zanoni and Dudely (1980) observed quite similar mid-parent heterosis (39.4%) from inbred crosses. All crosses showed positive heterosis effects. Heterosis effects was ranged from 39.7% for the cross Hi26 × Pi31 and the cross Hi34 × Pi31 to 26.6% for the cross Pi23 × Pi31.

Mean squares for GCA and SCA effects for plant height were significant at 5% and 1% levels, respectively (Table 5). The SCA effect was greater than GCA effect, indicating greater importance of dominance gene effects for plant height. Among five parent lines, the highest inbred line Hi26 had highest GCA effect and the inbred line Pi31 showed lowest GCA effect (Table 2). The SCA effects of the ten hybrids ranged from 8.26 for the cross Pi17 × Pi31 to 26.79 for the cross Hi26 × Pi31. Hybrids by three Philippine inbred lines exhibited lowest SCA effects as expected. In general, the hybrid with inbred line Hi26 showed highest SCA effects except for the cross Hi26 × Pi23 (11.15) that gave low SCA effect that was even less than GCA effect.

Average values of ear height for two parents, Hi26 and Pi36 were 59.40 cm, 80.80 cm, respectively (Table 3). Among hybrids, the cross Hi26 × Hi34 was highest while the cross Pi23 × Pi31 showed lowest plant height. Ear height seemed to follow same pattern with plant height. Average heterosis effect for ear height was 61.9%, which was about twice as much that of plant height. Average heterosis effect for five inbreds ranged from 58.2% for Hi26 to 67.3% for the inbred line Pi31. The lowest inbred line Pi31 had the highest heterosis and vice versa. The cross Hi26 × Pi23 showed the lowest heterosis of 42.3%.

Unlike plant height, only mean square for SCA effect of ear height was highly significant (Table 5). The SCA effect was about six times greater than that of GCA effect and the ratio of GCA to SCA was 0.15. The GCA effects of ear height for five inbreds ranged from -5.28

for Pi31 to 4.59 for Hi26 (Table 3). The cross Pi23 × Pi31 had the lowest SCA for not only plant height but also ear height. However, the SCA effects for the cross Pi17 × Pi23 and the cross Pi17 × Pi31 were similar to SCA effect of the cross Hi26 × Hi34. Inbred lines Pi23 and Pi31 might be the closest among the Philippine inbred lines. Overall average of relative ear position was 51.7% with inbred lines being 45.3% and hybrids being 54.9% (Table 4). When crossed, ear position came up over 50%. Among inbred lines, the parent Pi17 had lowest REPH. It has its uppermost ear at 39.77% in plants. The Philippine inbred line Pi31 had its ear in middle line in plants ranked highest in REPH. REPH becomes valuable when compared to ear height. Although the inbred line Pi31 had lowest ear height, it had higher ear position in plant. Thus, it is very important to consider REPH as one of selection criterion for low ear position. Array mean for inbred lines was quite similar from 53.11% for the inbred line Hi26 to 55.99% for the inbred line Hi34 when considering differences among inbreds per se. Two lowest inbred lines, Pi17 and Pi31 produced a second highest hybrid in REPH. However, lower inbred lines usually produced ears at relatively lower position.

An average heterosis effect for REPH was 21.6%, which is less than those of plant and ear height (Table 4). Average heterosis effect for five inbred lines ranged from 16.33% for the inbred line Pi 23 to 26.37% for the inbred line Pi31. The cross Pi23 × Pi31 had the highest heterosis effect of 39.99%. Mean square for SCA effect of REPH was highly significant but not in GCA effect. The ratio of GCA to SCA for REPH was 0.42 (Table 5). The GCA effects for five parents ranged from -0.97 to 1.64 (Table 4). The three inbred lines Hi26, Pi17 and Pi31 had negative GCA effects but inbred lines Hi34 and Pi23 showed positive values. The cross Hi34 × Pi23 had the lowest SCA effect while the cross Pi17 × Pi31 was

Table 3. Average values (cm), heterosis effect (%), and SCA and GCA effects for ear height of five parents and their ten diallel crosses

Parent	Parent					Array mean
	Hi26	Hi34	Pi17	Pi23	Pi31	
Hi26	<u>80.80^a</u>	122.13	119.33	114.47	116.07	118.00*
		60.99 ^b	64.00	42.33	65.64	58.20**
		15.67 ^c	16.32	8.75	16.51	4.59***
Hi34		<u>71.00</u>	115.53	115.73	117.47	117.72
			70.21	53.20	80.22	66.11
			15.49	12.98	20.88	1.63
Pi17			<u>64.73</u>	114.73	109.60	114.80
				58.50	76.66	67.30
				15.44	16.47	-1.82
Pi23				<u>80.07</u>	102.53	111.87
					47.00	50.33
					6.70	0.88
Pi31					<u>59.40</u>	111.42
						67.13
						-5.28

*Grand mean = 100.24 cm, parental mean = 71.20 cm, F_1 = 114.76 cm. **Grand mean = 61.9%. ***GCA effect, SE of SCA = 5.57, SE of GCA = 2.73. ^aAverage ear height (cm). ^bHeterosis effect (%), ^cSCA effect (s_{ij}).

Table 4. Average percentage (%), heterosis effect (%), and SCA and GCA effects for REPH of five parents and their ten diallel crosses

Parent	Parent					Array mean
	Hi26	Hi34	Pi17	Pi23	Pi31	
Hi26	<u>45.55^a</u>	54.60	51.99	53.81	52.01	53.11*
		16.10 ^b	21.71	11.77	19.22	17.22**
		2.38 ^c	2.65	1.43	2.02	-0.97***
Hi34	<u>48.66</u>		54.89	55.88	58.45	55.99
			24.33	12.22	29.21	20.42
			3.19	0.89	5.87	1.56
Pi17			<u>39.77</u>	56.13	57.00	55.00
				24.31	39.99	27.56
				4.46	7.55	-1.50
Pi23				<u>50.81</u>	54.11	55.00
					17.00	16.33
					1.53	1.64
Pi31					<u>41.72</u>	55.45
						26.37
						-0.74

*Grand mean = 51.7%, Parental mean = 45.3%, F_1 mean = 54.9%. **Grand mean = 21.6%. ***GCA effect, SE of SCA = 1.97, SE of GCA = 0.97. ^aAverage REPH (%). ^bHeterosis effect (%), ^cSCA effect (s_p).

Table 5. Mean squares for GCA and SCA and ratios of GCA to SCA (GCA/SCA) for plant height, ear height and REPH

	Plant height	Ear height	REPH ^c
GCA ^a	467.09*	97.61ns	15.54ns
SCA ^b	961.49**	654.84**	36.82**
Ratio	0.49	0.15	0.42

*, **, 5% and 1% levels of significant

^aGCA: General Combining Ability. ^bSCA: Specific Combining Ability. ^cREPH: Relative ear position over plant height.

the highest.

There were significant differences for plant height, ear height and REPH between the parents and the hybrids. We observed great heterosis in all three traits studied. Heterosis in those traits is probably one of greatest among important agronomic traits in maize because heterosis for those traits is great. It is possible to reduce them quickly by inbreeding. Since lower REPH hybrids were generated by lower REPH parents. Inbred development for low ear position may be better achieved by starting with low REPH hybrids or population. It is worth calculating REPH based on plant and ear height in inbred lines development for new hybrids since REPH provides valuable insight in selection for low ear position. REPH also could be used as one of valuable selection criteria over plant and ear heights in the breeding program for low ear height. Care must be taken to select inbreds by plant types like those characters since even inbred lines with low ear position produced a higher ear position hybrid.

As new varieties are developed, plant and ear height are considered not only morphological traits, but also other traits, since it is closely connected with such as flowering date and yield. Especially, research on plant and ear height need to more continue in the future, and

statistical access method should be considered due to two statistical methods produced some different results.

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