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Inheritance of Emergence Time and Seedling Growth at Low Temperatures in Four Lines of Maize

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Summary. The improvement of rate of seedling emergence and early seedling growth of maize (*Zea mays* L.) under cool conditions has been an objective of breeding programs in cool regions for many years. To study inheritance of emergence time, and to determine if differences in emergence time were due to differences in seedling growth, F_1, F_2 and backcross generations of a diallel cross of two rapidly emerging lines from CIMMYT Pool 5, 5-113 and 5-154, and two elite Corn Belt Dent lines, A619 and A632, were grown in controlled environment rooms at low temperatures.

The lines from Pool 5 emerged significantly faster than A619 and A632 over a range of low temperature conditions. This difference occurred both when the lines themselves were tested and when the lines were tested as male and female parents in crosses. The Pool 5 lines converted a higher proportion of their original seed to new root and shoot tissue than did A619 and A632, indicating that they had a faster seedling growth rate. Primarily this was due to a faster loss of seed reserve, rather than a more efficient conversion process.

A significant difference occurred between A619 and A632 for emergence time, but this was not due to a difference in seedling growth rate.

Reciprocal differences occurred only in the F_1 generation in crosses involving A619, and then marked effects could be attributed to the male parent. Reciprocal differences tended to disappear in the F_2. This suggested that the genotype of the embryo and endosperm was of much greater importance than the genotype of the maternal parent in determining differences of time to emergence and seedling growth.

Mid-parent heterosis occurred for time to emergence and seed loss, a measure of mean rate of utilization of seed reserve, in all crosses. High parent heterosis occurred in several crosses for these traits. High parent heterosis occurred in all crosses for efficiency of utilization of seed reserve.

A generation means analysis indicated that both additive and dominance effects were present for rate of seedling growth in crosses between A632 and the Pool 5 lines.

Key words: Maize – Inheritance – Low temperature emergence – Low temperature growth

Introduction

The improvement of rate of seedling emergence and early seedling growth of maize (*Zea mays* L.) under cool conditions has been an objective of maize breeding programs in cool regions for many years. Furthermore, conservation tillage systems, which save fuel and control soil erosion, are of increasing importance in these regions. These tillage systems can decrease soil temperatures during the early part of the growing season and accentuate the need to develop cultivars with vigorous early growth (Mock and Erbach 1977).

Lines that have an exceptional ability to emerge rapidly under cool conditions have recently been selected from Pool 5 (Eagles and Hardacre 1979a, b; Eagles and Brooking 1981), a breeding population developed by CIMMYT for highland areas of the tropics (CIMMYT 1974). However, these lines are not of the Corn Belt Dent type and are agronomically unacceptable for the production of hybrids for temperate regions. The efficient design of a program to use Pool 5 lines to develop acceptable hybrids with improved emergence under cool conditions requires information on the inheritance of emergence time in crosses between Pool 5 and Corn Belt Dent lines. An objective of these experiments was to obtain some of this information, with particular emphasis on the separation of maternal effects from effects due to the genetic constitution of the embryo and endosperm, as maternal effects can be of great importance in determining early seedling growth in maize (Pesev 1970; Burris 1977).

Before photosynthesis commences, rate of growth of a cereal seedling depends on rate of conversion of endosperm into new root and shoot tissue, which in turn depends on rate of utilization of the endosperm and efficiency of the conversion process (Yoshida 1973; Yamaguchi 1978). Another objective was to determine if differences between Pool 5 and Cornbelt Dent lines for emergence time were due to differences in seedling growth rate, and if so, to obtain information on the inheritance of parameters measuring seed utilization rate and growth efficiency.

Materials and Methods

The 4 lines used in this study were A619, A632, 5-113 and 5-154. A619 and A632 were widely used Corn Belt Dent inbred lines that differ in emergence rate (Navratil and Burris 1980), whereas 5-113 and 5-154 were partially inbred lines derived from Pool 5 and were known to emerge rapidly at low temperatures (Eagles and Hardacre 1979a).

In 1979, a full diallel including parent lines and reciprocals was made with 5-113 and 5-154 each represented by an S_2 line. To best represent the partially inbred lines 5-113 and 5-154, pollen for each ear was collected from several plants when 5-113 or 5-154 were used as males in crosses. Four ears of each cross or parental line were produced, and seed from each ear was kept as a separate family. The parental lines were produced by selfing, hence seed from each ear of 5-113 or 5-154 was an S_3 line.

In 1980, the procedure used to produce the diallel was identical to that used in 1979, except that 5-113 and 5-154 were each represented by an S_3 line. The S_3 line to be used was not selected on the basis of emergence time. In fact, there was little variation among the S_3 lines of 5-113 or 5-154 for emergence time.

An F_2 diallel was produced in 1980 by selfing 6 F_1 plants grown from a bulk of seed of the 4 families of each cross of the diallel produced in 1979. Each selfed ear was kept as a separate family. In addition, a backcross generation was produced by collecting pollen from the 6 F_1 plants used to produce the F_2 generation and pollinating 4 ears of the original female parent of the cross. For example, if A619×5-113 was the F_1, the backcross female parent was A619, while if 5-113×A619 was the F_1, the backcross female parent was the S_3 line of 5-113.

All seed for these experiments was produced on ears which were hand-pollinated, hand-picked, and dried at 25 °C to 30 °C to 12% moisture with low humidity. The ears were hand-shelled. The seeds were sown in cylindrical propagating pots (5.5 cm diameter×9.5 cm depth) on the surface of a sterilized potting mixture of fine gravel, peat and vermiculite (70:15:15 v/v) with the embryo in a vertical position. Each pot contained 3 seeds of one family (entry). The combined weight of the seeds in each pot was recorded before sowing and a moisture content determined for each entry to enable seed dry weight to be calculated. The seeds were sprayed with a concentrated solution of Captan, covered with 4 cm of the potting mixture, and placed in a controlled-environment room. The seeds were kept moist throughout the experiments using water at the same temperature as the room.

In 1979 the experiment was grown in 3 controlled-environment rooms, the first at a constant 11 °C (±0.3 °C), the second at 15 °C (±0.3 °C) for 12 h of each day and 5 °C (±0.5 °C) for 4 h of each day with changeover periods of 4 h duration, and the third at 15 °C (±0.3 °C) for 12 h of each day and 10 °C (±0.3 °C) for 8 h of each day with changeover periods of 2 h duration. The experimental design in each room was a randomized complete block with 8 replications. Each replication contained 4 families of each of the 12 crosses and 4 parental lines. Time to emergence data were collected each day. To minimize both radiation-induced temperature increases within pots and photosynthetic activity, water-screened low intensity lighting was used while collecting data, with a maximum daily duration of lighting of 6 h. The experiment in each room was terminated when daily emergency had ceased or reached a very low level.

In 1980 the experiment was grown in a room with the same conditions as used in the third room in 1979 (15/10 °C), and the experimental design was a randomized complete block with 6 replications. Each of the 4 families from each parental line, backcross or F_1, and each of the 6 families from each F_2 were entered separately. In 1980 emergence had ceased after 28 days. Then the seedlings were carefully washed from the potting mixutre and a dry weight was obtained for the residual seed and root plus shoot tissue on a per pot basis. Pots with one or more diseased seedlings were discarded.

Three seedling growth parameters were calculated in 1980. These were (1) conversion ratio, which was defined as W/S, where W was the dry weight of new root and shoot and S was the dry weight of original seed, (2) seed loss, which was defined as (S–R)/S, where R was the dry weight of the remnant seed after 28 days and (3) efficiency, which was defined as W/(S–R).

Emergence was not complete for the experiments. Therefore, a two stage statistical analysis was conducted using procedures similar to those suggested by Kempthorne (1957). Least squares estimates of family means were obtained from

$$Y_{ijk} = \mu + v_i + r_j + e_{ijk}$$

where Y_{ijk} was the observation from the k-th individual in the j-th replicate of the i-th family, μ was the overall mean, v_i was the contribution of the i-th family, r_j was the contribution of the j-th replicate and e_{ijk} was the residual variation. Then diallel cross and generation means analyses were conducted ignoring any differences in the reliabilities of the family means. Any bias from using this procedure, compared to the computationally difficult procedure of estimating all effects by least squares, was expected to be small because the percentage emergence (Table 1) and percentage of pots remaining for analysis of seedling growth parameters (90% of pots) were high and therefore the data was nearly orthogonal. Furthermore, replication differences were small.

A diallel cross analysis of variance was conducted by first separating the variation due to selfs from the variation due to crosses, as in analysis III of Gardner and Eberhart (1966), then analysing the variation due to crosses using method 3 of Griffing (1956). Single degree of freedom contrasts for the

Table 1. Mean emergence percentage for the four temperature environments

Temperature (°C)	Year	Emergence (%)
11	1979	87
15/5	1979	97
15/10	1979	96
15/10	1980	97

reciprocals were calculated using standard procedures. The method of Yates (1947) was applied to calculate individual male and female general combining ability effects for the F_1 and F_2 generations. For the backcross generation, least squares estimates of the male and female general combining ability effects were made from

$$Y_{ijk} = \mu + gf_i + 0.5\ gm_i + 0.5\ gm_j + e_{ijk}$$

where Y_{ijk} was the observation from the k-th family produced by crossing the i-th line as female with the F_1 progeny of the i-th and j-th lines, gf_i was the contribution of the female general combining ability of the i-th line, gm_i was the contribution of the male general combining ability of the i-th line, and e_{ijk} was the residual variation.

A generation means analysis was conducted on two of the crosses where reciprocal effects were negligible, using the method of Hayman (1958).

Results

Differences among parental lines for emergence time were large in all environments (Tables 2, 3). In all environments the order of emergence was 5-154, 5-113, A632 and A619 respectively. However, A619 and A632 were fully inbred, whereas 5-113 and 5-154 were not, so the difference between the Pool 5 and Corn Belt Dent lines may have been due in part to a difference in level of inbreeding, as inbreeding depression for time to emergence can occur in maize (Eagles and Hardacre 1979a, b).

Large differences for emergence time occurred among the crosses, with 5-113×5-154 almost 40% faster than A619×A632 in the 11 °C and 15/5 °C environments of 1979 and approximately 30% faster in the 15/10 °C environments of 1979 and 1980 (Tables 2 and 4). In all environments, the crosses A619×5-113 and A619×5-154 emerged significantly faster than A619 × A632, and A632 × 5-113 and A632 × 5-154 emerged significantly faster than A632×A619 (Tables 2 and 4), indicating that 5-113 and 5-154 influence emergence time when used as male parents over a range of low temperature conditions.

Emergence was much slower in the 11 °C environment than the 15/10 °C environment, with the 15/5 °C environment intermediate (Table 2). Despite these large differences, means for crosses grown in any of the environments were highly correlated with means obtained from the other two (minimum r = 0.95), indicating that genotype×environment interactions were of little importance in these experiments. Furthermore, the correlations between mean emergence times obtained in 1979 and those obtained for the F_1 generation in 1980 were also high (minimum r = 0.96), indicating that environment of seed production and the difference in level of inbreeding of 5-113 and 5-154 used to produce seed for the two years were not important in determining emergence time in these experiments.

Table 2. Mean emergence time (days) for the parental and F_1 generations grown in three temperature environments in 1979

Line or cross	Temperature (°C)		
	11	15/5	15/10
A619	47.2	31.1	25.0
A632	36.1	27.6	19.0
5 - 113	28.4	20.3	16.8
5 - 154	24.3	18.1	15.0
A619 × A632	35.9	28.9	20.7
A619 × 5 - 113	29.5	23.9	18.6
A619 × 5 - 154	30.1	22.5	18.3
A632 × A619	32.8	26.6	19.0
A632 × 5 - 113	25.5	21.1	15.8
A632 × 5 - 154	23.9	19.5	15.1
5 - 113 × A619	27.6	21.8	16.8
5 - 113 × A632	25.2	20.8	15.6
5 - 113 × 5 - 154	22.4	17.2	14.1
5 - 154 × A619	28.4	21.0	16.9
5 - 154 × A632	25.0	19.8	15.3
5 - 154 × 5 - 113	22.8	17.7	14.1
Mean	29.1	22.4	17.2
L.S.D. (P = 0.05)	1.7	1.4	0.8

Lines 5-113 and 5-154 had significantly higher conversion ratio and seed loss values than A619 and A632 (Table 3). However, A632 had a lower conversion ratio than A619 even though A632 emerged before A619. Efficiencies of A619, 5–113 and 5-154 were similar but significantly higher than for A632. Seed weights of A619, A632 and 5-154 were similar, with the seed weight of 5-113 lower (Table 3). Seed weight was not related to emergence time or the seedling growth parameters in this or the other generations so will not be considered further.

The diallel analysis of emergence time for the F_1 generation in 1980 revealed that most of the variation

Table 3. Mean emergence time (days), conversion ratio (%), seed loss (%); efficiency (%) and seed weight (g) for the parental lines in 1980

Line	Emergence time	Conversion ratio	Seed loss	Efficiency	Seed weight
A619	23.7	21.1	33.4	63.4	0.27
A632	18.8	18.0	31.4	58.2	0.27
5 - 113	16.5	32.1	49.8	64.7	0.24
5 - 154	14.7	34.3	52.2	65.8	0.28
Mean	18.4	26.3	41.7	63.0	0.27
L.S.D. (P = 0.05)	0.7	2.1	3.4	4.3	0.05

Table 4. Mean emergence time (days), conversion ratio (%), seed loss (%) and efficiency for the midparental (P), F_1 and F_2 generation grown in 1980

Cross	Emergence time			Conversion ratio			Seed loss			Efficiency		
	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2
A619 × A632	21.3	19.8	20.9	19.6	26.0	18.5	32.4	39.4	30.3	60.8	66.1	61.3
A632 × A619	–	18.7	20.5	–	28.8	21.5	–	42.7	33.6	–	67.8	64.4
A619 × 5 – 113	20.1	17.5	18.4	26.6	35.1	32.6	41.6	49.2	47.3	64.1	71.1	69.0
5 – 113 × A619	–	16.6	18.2	–	42.2	31.0	–	59.2	46.0	–	71.4	66.9
A619 × 5 – 154	19.2	17.3	19.6	27.7	35.6	29.6	42.8	51.9	43.9	64.6	68.8	67.2
5 – 154 × A619	–	15.8	18.6	–	39.5	29.6	–	55.9	45.8	–	71.1	64.8
A632 × 5 – 113	17.7	16.0	16.3	25.1	32.5	29.0	40.6	46.4	43.6	61.5	69.9	66.8
5 – 113 × A632	–	16.2	16.5	–	32.8	26.2	–	48.1	42.1	–	68.0	63.3
A632 × 5 – 154	16.8	14.7	16.1	26.2	37.2	28.2	41.8	54.2	44.8	62.0	68.7	63.0
5 – 154 × A632	–	14.7	16.2	–	38.1	27.5	–	55.5	43.9	–	68.6	62.5
5 – 113 × 5 – 154	15.6	14.0	15.6	33.2	41.1	37.8	51.0	59.1	55.9	65.3	69.7	67.6
5 – 154 × 5 – 113	–	14.0	15.3	–	41.6	37.6	–	58.0	56.5	–	71.7	67.5
Mean	18.4	16.3	17.7	26.3	35.9	29.1	41.7	51.6	44.4	63.0	69.4	65.3
L.S.D. (P = 0.05)	0.5	0.6	1.2	1.5	3.5	3.1	3.5	4.7	3.9	3.1	2.0	2.4

Table 5. Mean squares from the F_1 and F_2 diallel cross analyses of emergence time, conversion ratio, seed loss and efficiency for 1980

Source of variation	d. f.	Emergence time		Conversion ratio		Seed loss		Efficiency	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Parents and crosses	15	25.65**	29.28**	201.9**	195.6**	297.4**	347.1**	50.8**	38.9**
Parents v crosses	1	55.22**	6.76**	1,095.5**	102.8**	1,171.3**	94.4**	507.6**	75.1**
Among parents	3	60.83**	60.83**	256.9**	256.9**	474.5**	474.5**	41.1**	41.1**
Among crosses	11	13.36**	22.72**	105.6**	187.3**	169.6**	335.3**	11.9**	35.0**
G. C. A.	3	44.80**	79.16**	294.0**	661.2**	466.3**	1,191.8**	29.1**	94.4**
S. C. A.	2	2.13**	4.31**	62.3**	8.5	101.3**	20.9	4.9	1.8
Reciprocals	6	1.39**	0.63*	25.9**	10.0	44.0**	11.8	5.6	16.3**
(A619 × A632) v (A632 × A619)	1	2.29**	0.43	16.4	28.2*	23.0	36.1	5.4	25.0*
(A619 × 5 – 113) v (5 – 113 × A619)	1	1.58**	0.11	99.7**	8.8	193.4**	6.3	0.1	16.7
(A619 × 5 – 154) v (5 – 154 × A619)	1	4.33**	2.76**	37.4**	0.2	36.0	17.1	12.4	19.6*
(A632 × 5 – 113) v (5 – 113 × A632)	1	0.11	0.20	0.2	17.7	5.2	8.6	6.9	34.3*
(A632 × 5 – 154) v (5 – 154 × A632)	1	0.00	0.00	1.3	2.2	3.4	2.8	0.2	1.0
(5 – 113 × 5 – 154) v (5 – 154 × 5 – 113)	1	0.00	0.29	0.3	2.7	3.2	0.2	8.6	1.2
Among families	48[a]	0.19	0.23	4.8	6.4	9.2	10.4	3.4	4.9

[a] Degrees of freedom for among families for the F_2 analyses = 72

*, ** Significant at 5% and at 1% probability level

could be attributed to general combining ability, with smaller but statistically significant specific combining ability and reciprocal effects (Table 5). Results of the 1979 analyses are not presented because of their similarity to the 1980 analysis. A closer analysis of the reciprocal effects revealed that they only occurred in crosses involving A619, with the cross with A619 as the female always slower to emerge than the reciprocal cross with A619 as the male (Tables 2 and 4). The reciprocal differences for A619 × A632 and A619 × 5-113 disappeared in the F_2 generation, but persisted for A619 × 5-154 (Table 5).

Table 6. Estimate of male (M) and female (F) general combining ability effects for emergence time (days), conversion ratio (%), seed loss (%) and efficiency (%) for the F_1, F_2 and backcross generations grown in 1980

Character	Generation	Line							
		A619		A632		5 – 113		5 – 154	
		M	F	M	F	M	F	M	F
Emergence time	F_1	1.6	2.4	0.8	0.5	-0.7	-0.9	-1.6	-2.0
	F_2	2.4	2.7	0.2	0.0	-1.5	-1.4	-1.0	-1.4
	Backcross	1.6	3.1	0.8	-0.2	-0.6	-1.0	-1.8	-1.9
Conversion ratio	F_1	-0.3	-3.8	-5.2	-4.7	1.7	3.5	3.7	5.1
	F_2	-2.8	-3.2	-6.6	-5.0	5.3	4.5	4.1	3.8
	Backcross	-1.7	-5.4	-5.9	-3.7	2.5	4.7	5.1	4.4
Seed loss	F_1	-0.8	-5.2	-5.9	-5.8	1.1	4.3	5.6	6.6
	F_2	-4.4	-5.6	-7.9	-6.4	6.4	5.7	5.9	6.2
	Backcross	-2.0	-8.0	-6.3	-5.1	1.0	7.7	7.3	5.4
Efficiency	F_1	0.5	-0.5	-2.3	-1.4	1.8	0.9	0.0	1.0
	F_2	0.1	0.6	-3.5	-1.8	2.8	1.6	0.6	-0.4
	Backcross	-0.8	-0.2	-3.5	-0.8	3.7	-0.6	0.6	1.6

The diallel analysis of the F_1 generation for conversion ratio also revealed large and highly significant differences among lines for general combining ability, with smaller but highly significant specific combining ability and reciprocal differences (Table 5). Again, reciprocal differences were significant only for crosses involving A619, and the cross with A619 as the female parent always had a lower conversion ratio than the reciprocal cross (Table 4). In the F_2 generation, large and highly significant differences occurred for general combining ability, but not for specific combining ability or reciprocal effects (Table 5). The analysis of seed loss was similar to the analysis of conversion ratio; but for efficiency, differences for specific combining ability and reciprocal effects were not significant in the F_1 generation, and only reciprocal differences were significant in the F_2 generation.

For emergence time, both male and female general combining ability estimates from the F_1 and backcross generations ranked the lines in the order 5-154, 5-113, A632 and A619 (Table 6). This order is the same as for the parental lines themselves (Table 3). In the F_2 generation, 5-113 and 5-154 did not differ in emergence time; however, the large differences between the Pool 5 and Corn Belt Dent lines remained. Likewise for conversion ratio, seed loss and efficiency, general combining ability estimates separated the Pool 5 and Corn Belt Dent lines in the same way as data from the lines themselves (Tables 3, 6). The similarity between combining ability effects estimated from different generations strongly suggests that differences among A619, A632, 5-113 and 5-154 for these seedling growth parameters were highly heritable.

Emergence time for the F_1 generation was always less than the mid-parent mean, indicating mid parent heterosis for rapid emergence in all crosses (Table 4). In all crosses, the F_1 emerged before the F_2, but did not always emerge before the faster of the two parents (Tables 3 and 4). For example, in the cross 5-154×A619, 5-154 emerged in 14.7 days, the F_1 in 15.8 days, the F_2 in 18.6 days and A619 in 23.7 days. The S_4 line, 5-154, was not fully inbred and may become slower with further inbreeding. However, a similar situation occurred with A632×A619, where the F_1 had an emergence time similar to A632 and A619×A632 was slower than A632. The 15/10 °C environment produced similar results in 1979, but in the more extreme 11 °C environment A632×A619 emerged significantly faster than A632 (Table 2).

Conversion ratio for the F_1 generation was always significantly greater than the mid-parental mean (Table 4). Furthermore, the F_1 estimate exceeded the high parent and F_2 estimates in all crosses (Tables 3 and 4), and for many crosses the difference was statistically significant, indicating high parent heterosis. The F_1 was always higher than the mid-parent for seed loss, but not always higher than the high parent. The F_1 exceeded the high parent for efficiency in all crosses, and all F_1's exceeded 65.8%, the efficiency of the most efficient parental line, 5-154.

Generation means analyses were conducted on two of the crosses, A632×5-113 and A632×5-154, where reciprocal differences were negligible in a cross between a Corn Belt Dent and Pool 5 line. The analyses showed that for both crosses significant additive and dominance effects were present for conversion ratio, significant additive effects were present for seed loss and significant dominance effects occurred for efficiency. For emergence time, significant additive and dominance effects were present only in the cross A632×5-154.

Discussion

The conversion ratio parameter used in my experiment was similar to "growth attributable to seed reserve" as used by Yoshida (1973), and measured the mean rate of conversion of original seed to new root and shoot tissue over the period of the experiment. Conversion ratio was a product of seed loss, which measured mean rate of utilization of seed reserve, and efficiency, which as identical to the growth efficiency parameter of Tanaka and Yamaguchi (1968).

The lines derived from Pool 5, 5-113 and 5-154, emerged significantly faster than the Corn Belt Dent lines A619 and A632 over a wide range of low temperature conditions. This difference occurred regardless of whether the lines themselves were tested, or whether they were tested as male or female parents in crosses. Furthermore, 5-113 and 5-154 had much greater conversion ratios, indicating that their more rapid emergence was primarily due to a more rapid seedling growth rate. This suggests, but does not prove, that 5-113 and 5-154 have a faster metabolic rate at low temperatures than A619 and A632.

Line A632 emerged more rapidly than A619, which agreed with the observations of Navratil and Burris (1980); however, A632 had lower conversion ratio values than A619, indicating that factors other than rate of conversion of seed reserves into new root and shoot tissue can be important in determining differences of emergence time in maize. A difference of root to shoot ratio or shoot weight per unit length could explain the observed differences between A619 and A632, but were not evaluated in my experiments.

Seed loss values of 5-113 and 5-154 were much greater than seed loss values of A619 and A632, but A619 was equal in efficiency to 5-113 and 5-154. This indicates that the difference in conversion ratio between the Pool 5 and Corn Belt Dent lines was primarily due to a more rapid, rather than more efficient, utilization of seed reserve.

Efficiency for A632 was lower than for the remaining lines, and crosses in the F_1 generation were markedly more efficient than the parental lines. These differences could have been due to differences in physiological age of the seedlings at the time of harvest, chemical composition of the seed, metabolic efficiency, or a combination of these factors (Yamaguchi 1978). Yamaguchi (1978) found that efficiency increased slightly during the early stages of seedling growth then declined abruptly with the approach of endosperm exhaustion. In my experiment, efficiency was measured when between 30% and 60% of the seed weight had been lost. Hence, the genotypes were evaluated at different stages of seedling development, but before the abrupt decrease in efficiency due to endosperm exhaustion. Photosynthetic activity would also bias efficiency measurements, but light intensities were deliberately kept low while emergence was recorded, and chlorophyll synthesis was not apparent in the seedlings, so bias from this factor was probably negligible. Most likely, F_1 hybrids are metabolically more efficient than the parental inbred lines.

Despite large differences among the parental lines for emergence time and seedling growth parameters, reciprocal differences only occurred in the F_1 generation for crosses involving A619, and then, marked effects could be attributed to the male parent. This suggests that for the lines used under the conditions of this study, the genotype of the embryo and endosperm are of much greater importance than the genotype of the maternal parent in determining time to emergence and related seedling growth parameters at low temperatures. For two of the three crosses where reciprocal effects occurred in the F_1 generation the effects disappeared in the F_2, suggesting that they were not due to persistent cytoplasmic effects. For the third cross, the reciprocal effect for emergence time persisted in the F_2, but for conversion ratio in the same cross the reciprocal effect disappeared in the F_2, suggesting that sampling error was the most likely explanation for this apparently persistent cytoplasmic effect.

Lack of marked reciprocal differences and the significant effect of the male on growth of the root and shoot in this study contrasted with the results of Pesev (1970) and Burris (1977), but agreed with the results of McConnell and Gardner (1979). However, Pesev (1970) measured root and shoot lengths at a much earlier stage of seedling development than that at which root and shoot growth was measured in this experiment and Burris (1977) used a higher temperature. Possibly, maternal effects are greatest at the earliest stage of seedling development, or at favourable temperatures, or alternatively, occur with certain lines of maize only.

Rate of seedling growth in the progeny of crosses between 5-113 or 5-154 and A619 or A632 primarily should be determined by the genotype of the embryo or endosperm. Therefore, selection based on either selfed or testcross progeny should be effective. Selection for hybrid performance on the basis of selfed progeny is simpler than selection based on testcross performance, but requires the existence of additive genetic variation. The genetic interpretation of general and specific combining ability in terms of additive and non-additive variability requires the acceptance of several assumptions, including a random distribution of alleles in the parents and a common level of inbreeding in the parents (Cockerham 1963; Baker 1978) which cannot be met in these experiments. However, a large difference occurred between the estimates of general combining ability obtained from the Pool 5 and Corn Belt Dent lines, the estimates were consistent across generations, and there was a significant reduction due to fitting an additive model in the generation means analysis for conversion ratio. Therefore, there is a high probability that sufficient additive variability will be generated in the segregating generations of crosses between these Corn Belt Dent and Pool 5 lines to allow effective selection for hybrid performance to be made on selfed lines.

Only two Corn Belt Dent lines were used in this study. A619 is among the slowest emerging Corn Belt Dent lines at low temperatures, while A632 is among the fastest (Navratil and Burris 1980). A619 and A632 are closely related to some other elite Corn Belt Dent lines but not to each other (Bauman 1977). For conversion ratio and seed loss, the parameters most closely associated with seedling growth, the two lines produced similar results but were markedly different from 5-113 and 5-154. This suggests that 5-113 and 5-154 may possess alleles at loci affecting seedling growth at low temperatures which are distinct from those possessed by many elite Corn Belt Dent lines.

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