Theor Appl Genet (1988) 76:459–464

Inheritance of emergence time at low temperatures in segregating generations of maize

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Received November 23, 1987; Accepted March 9, 1988
Communicated by A. Hallauer

Summary. North Carolina Design III and generation means analyses were used to study the inheritance of seedling emergence time and a related seedling growth parameter in crosses between 5–154, a line from CIMMYT Pool 5 with rapid seedling emergence under cool conditions, and two Corn Belt Dent lines of maize (*Zea mays* L.). The crosses were evaluated at low temperatures in controlled environment rooms. Additive genetic variances were larger than dominance variances in both crosses and estimates of the average levels of dominance were in the partial dominance range. Dominance was in the direction of rapid seedling emergence and rapid utilization of seed reserve. Estimates of minimum numbers of effective factors provided evidence for polygenic inheritance.

Key words: *Zea mays* L. – Inheritance – Low temperature emergence – Genetic variances – Genetic effects

Introduction

The development of hybrid cultivars of maize (*Zea mays* L.) with vigorous early seedling growth under cool conditions is an important objective of maize breeding programs in cool, temperate regions. Lines that can emerge more rapidly under cool conditions than the Corn Belt Dent lines commonly used to produce hybrids for temperate regions have been identified in CIMMYT Pool 5 (Eagles and Hardacre 1979a; Eagles and Brooking 1981). CIMMYT Pool 5 was developed for highland areas of the tropics (CIMMYT 1974).

Previous studies have shown that differences between selected Pool 5 lines and Corn Belt Dent inbred lines for rate of seedling emergence under cool conditions are primarily determined by nuclear genes, which affect the rate of conversion of seed reserve into new root and shoot tissue rather than the efficiency of the conversion process (Eagles 1982). Differences are present in comparisons between intact seeds, dissected embryos and dissected embryonic axes, indicating that they are due to growth processes in the developing seedling rather than to the mobilization of reserves in the endosperm, sucrose synthesis in the scutellum or sucrose uptake (Christeller 1984). Because growth processes are involved, differences could persist beyond the stage when growth is dependent on the mobilization of endosperm reserves (Christeller 1984; Hardacre and Eagles 1986).

Previous studies have indicated that both additive and dominance effects are involved in determining differences between Pool 5 and Corn Belt Dent lines for time to emergence under cool conditions (Eagles 1982). However, estimates of the relative magnitudes of these effects have not been published, nor have estimates of the numbers of genes or effective factors. The major objective of the experiments reported herein was to obtain estimates of additive and dominance effects and variances and the number of effective factors determining differences between 5–154, a Pool 5 line with rapid emergence under cool conditions, and two elite Corn Belt Dent lines.

Materials and methods

Genotypes

The four lines used in this study were A665, A671, H99 and 5–154. A665, A671 and H99 are Corn Belt Dent inbred lines that were important in the applied maize breeding programme of DSIR, whereas 5–154 was a line derived from Pool 5 and was known to emerge rapidly at low temperatures (Eagles and Hardacre 1979a; Eagles 1982; Eagles and Hardacre 1985).

In the 1981–82 season, a North Carolina Design III was made by backcrossing individual F_2 plants from the cross

5–154 × H99 to each of the two parents (Comstock and Robinson 1952). In addition to the two backcrosses, each F_2 plant was selfed to produce F_3 progeny and crossed to the unrelated line A665 to produce testcross progeny. A total of 69 sets, with each set containing two backcrosses, one F_3 and one testcross progeny, were available for these experiments. Selfed lines of 5–154 and H99, reciprocal hybrids of H99 and 5–154, and the hybrids A665 × 5–154 and A665 × H99 were also produced. An S_4 line of 5–154 was used to produce the original F_1 generation and was used as the female parent for the backcross generation. An S_5 line of 5–154 was used to produce the selfed lines, reciprocal hybrids and hybrid with A665 for the controlled environment experiments. By the S_3 generation little variation was present among sub-lines of 5–154 for seedling growth characters (Eagles 1982), so 5–154 was assumed to be homozygous for alleles controlling these characters.

An identical procedure was used for the cross 5–154 × A671 in the 1983–84 season, except that an S_5 version of 5–154 was used for all crosses and 68 sets of backcross, F_3 and testcross progeny were produced.

All seed for these experiments was produced at Palmerston North on ears that were hand-pollinated, hand-picked and dried at 25°–30°C with low humidity until the seed had reached approximately 12% moisture. The ears were hand-shelled and the seed was stored in a well ventilated cupboard. The moisture content just prior to the start of the controlled environment room experiments was 12.0% and this moisture content was assumed for dry matter calculations.

Controlled-environment experiments

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 four seeds of one entry. The weight of each seed was recorded before sowing. 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.

The 5–154 × H99 cross was grown in two controlled-environment rooms in 1982. The first was 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 second was 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. 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 emergence data.

The 5–154 × A671 cross was grown in one controlled-environment room in 1984. The conditions were the same as those used in the first room in 1982 (15/10°C).

The design used in each controlled-environment room was a randomized complete block with four replications. Each genotype in the backcross to 5–154, backcross to H99 or A671, and testcross to A665 was entered once (a total of 16 seeds) and each hybrid was entered twice (Table 1). The parental lines were entered twice for 5–154 × H99 and four times for 5–154 × A671 (Table 1).

After 28 days in the 15/10°C rooms and 35 days in the 15/5°C room emergence had virtually ceased. Then the seedlings were washed from the potting mixture, diseased seedlings noted and discarded, and a dry weight was obtained for the residual seed and root plus shoot tissue on a per pot basis.

A seedling growth parameter, seed weight loss, was defined as (S − R)/S, where S was the dry weight of the original seed and R was the dry weight of the remnant seed. This parameter estimates the mean rate of utilization of seed reserve and, in the absence of variation in efficiency, estimates the mean rate of conversion of original seed to new root and shoot tissue (Eagles 1982).

Emergence was not complete for these experiments. For time to emergence data with a two-way classification (for example, replications and F_3 lines), means and variance components were calculated using the method of Harvey (1975) for two-way classifications without interaction. For time to emergence data with a three-way classification (for example, replications, parents and males in the North Carolina III analysis) and for seed weight loss data, means and mean squares were calculated by a weighted analysis procedure using the REG computer pro-

Table 1. Number of seeds sown and mean emergence percentage for 10 generations of the cross 5-154 × H99 grown in 2 temperature environments and for 10 generations of the cross 5-154 × A671 grown in 1 temperature environment

Generation	5-154 × H99			5-154 × A671	
	No. sown	Temperature		No. sown	Temperature
		15/10°C Emergence (%)	15/5°C Emergence (%)		15/10°C Emergence (%)
P_1 [a]	32	84.4	84.4	64	100.0
P_2	32	71.9	0.0	64	98.4
F_1	32	100.0	90.6	32	100.0
F_1 reciprocal	32	96.9	100.0	32	100.0
BC_1 [b]	1104	98.6	90.8	1088	98.8
BC_2	1104	91.5	60.3	1088	94.9
F_3	1104	92.1	66.8	1088	96.1
Testcross	1104	99.1	91.8	1088	99.7
A665 × P_1	32	100.0	96.9	32	100.0
A665 × P_2	32	100.0	87.5	32	100.0

[a] P_1 = 5-154, P_2 = H99 or A671

[b] BC_1 = backcross to P_1, BC_2 = backcross to P_2

gram (Gilmour 1981). Variance components were calculated using Henderson's Method 3 (Henderson 1953).

Estimates of additive (σ^2_A) and dominance (σ^2_D) genetic variances and average degree of dominance ($\bar{d}$) were calculated from analyses of variance of North Carolina Design III progenies (Comstock and Robinson 1952; Hallauer and Miranda 1981). Approximate standard errors of variance components were calculated using methods described by Hallauer and Miranda (1981), but recognising that these standard errors could be biased because of unbalanced data (Kempthorne 1957). For the 15/10 °C environments where data was almost complete (Table 1), this bias is probably negligible. Estimates of additive (a) and dominance (d) effects from a generation means analysis were calculated by weighted regression (Hayman 1958; Hallauer and Miranda 1981). Estimates of minimum numbers of effective factors (n) were obtained from the Castle-Wright formula (Wright 1968) using estimates of additive genetic variance from Design III progenies.

Results and discussion

Controlled-environment experiments

The mean percentage emergence was greater than 90% for all lines, hybrids and segregating generations grown in the 15/10 °C environment, except for the parental lines of 5–154 × H99 (Table 1). The number of seedlings that emerged for 5–154 and H99 were 27 and 23, respectively, which should provide reliable estimates of emergence time. The high percentage emergence in the 15/10 °C environment indicates that bias due to unequal subclass numbers should be small for estimates of parameters from this environment.

Almost all seedlings that failed to emerge were infected by fungi, indicating that emergence percentages would not have increased if the experiments had continued beyond 28 days. The occurrence of fungal infection, despite fungicidal treatment, agrees with previous observations (Eagles and Brooking 1981; Menkir and Larter 1987).

Mean emergence percentage in the 15/5 °C environment ranged from 0.0%–100.0% (Table 1), indicating that bias due to unequal subclass numbers could be important for parameters estimated from this environment. Again, almost all seedlings that failed to emerge were infected by fungi, except for inbred H99. No seedlings of H99 had emerged after 35 days (Table 1); however, 6 seedlings that were apparently free from fungal attack were found when the seedlings were washed from the potting mixture. This indicates that the emergence time for H99 exceeded 35 days in this environment.

Differences between parental lines for emergence time were large and statistically significant for both crosses (Table 2). This agrees with the conclusion of Eagles (1982) that 5–154 emerges faster than Corn Belt Dent inbred lines under cool conditions. Reciprocal differences for the F_1 generation were small and statistically not significant for both crosses. This agrees with previous results for 5–154 × A632 but disagrees with previous results for 5–154 × A619 (Eagles 1982). Further studies are required to draw general conclusions about the occurrence of reciprocal differences in maize crosses for emergence time under cool conditions.

Differences between parental lines for seed weight loss were large and statistically significant for both crosses (Table 3). This also agrees with the previous conclusion that 5–154 utilizes seed reserve more rapidly than

Table 2. Mean emergence time (days) for 10 generations of the cross 5-154 × H99 grown in 2 temperature environments and for 10 generations of the cross 5-154 × A671 grown in 1 temperature environment

Generation	5-154 × H99		5-154 × A671
	Temperature (°C)		Temperature (°C)
	15/10	15/5	15/10
P_1 [a]	13.6 ± 0.2 [c]	19.0 ± 0.4	14.8 ± 0.2
P_2	22.6 ± 0.2	> 35.0	20.2 ± 0.2
F_1	14.4 ± 0.2	21.1 ± 0.4	15.6 ± 0.3
F_1 reciprocal	14.3 ± 0.2	21.7 ± 0.4	15.4 ± 0.3
BC_1 [b]	13.9 [d]	20.4 ± 0.1	15.5 [d]
BC_2	17.4 [d]	27.5 ± 0.1	18.5 ± 0.1
F_3	16.3 [d]	24.9 ± 0.1	17.4 ± 0.1
Testcross	15.4 [d]	25.0 ± 0.1	17.0 [d]
A665 × P_1	13.6 ± 0.2	21.2 ± 0.4	16.0 ± 0.3
A665 × P_2	17.2 ± 0.2	28.7 ± 0.4	18.2 ± 0.3

[a] P_1 = 5-154, P_2 = H99 or A671
[b] BC_1 = backcross to P_1, BC_2 = backcross to P_2
[c] Standard error associated with each mean
[d] Standard error less than 0.05

Table 3. Mean seed weight loss (%) for 10 generations of the cross 5-154 × H99 grown in 2 temperature environments and for 10 generations of the cross 5-154 × A671 grown in 1 temperature environment

Generation	5-154 × H99		5-154 × A671
	Temperature (°C)		Temperature (°C)
	15/10	15/5	15/10
P_1 [a]	50.9 ± 1.3 [c]	38.2 ± 2.2	49.8 ± 1.0
P_2	28.6 ± 1.4	16.4 ± 2.7	35.7 ± 1.0
F_1	57.0 ± 1.2	49.1 ± 1.7	51.8 ± 1.4
F_1 reciprocal	59.1 ± 1.2	41.1 ± 1.5	57.8 ± 1.4
BC_1 [b]	58.4 ± 0.2	44.1 ± 0.3	48.4 ± 0.3
BC_2	43.5 ± 0.3	26.6 ± 0.3	42.4 ± 0.2
F_3	45.9 ± 0.2	31.1 ± 0.3	39.3 ± 0.3
Testcross	54.1 ± 0.3	36.8 ± 0.2	43.5 ± 0.3
A665 × P_1	53.1 ± 1.2	42.3 ± 1.2	47.2 ± 1.4
A665 × P_2	41.4 ± 1.2	24.4 ± 1.4	35.1 ± 1.4

[a] P_1 = 5-154, P_2 = H99 or A671
[b] BC_1 = backcross to P_1, BC_2 = backcross to P_2
[c] Standard error associated with each mean

Corn Belt Dent lines (Eagles 1982). Seed weight loss means for the F_1 generation exceeded the high parent means (Table 3). Reciprocal differences were erratic across environments and crosses (Table 3).

Line means for emergence time and seed weight loss were significantly correlated in all segregating generations except for the testcross generation of 5–154 × A671 (Table 4). This suggests a causal, or pleiotropic, relationship between seed weight loss and emergence time in these crosses, but the possibility of genetic linkage between separate gene loci controlling emergence time and seed weight loss cannot be excluded. The correlations were of intermediate magnitude, which suggests that other factors, such as efficiency of utilization of seed reserve or root to shoot ratio, contributed to variation in emergence time. Undetected fungal infection could have affected seed weight loss and consequently influenced the correlations.

Table 4. Phenotypic correlations between emergence time and seed weight loss for segregating generations of the crosses 5-154 × H99 and 5-154 × A671

Cross	Generation[a]	Temperature °C	Correlation coefficient
5-154 × H99	F_3	15/10	−0.51**
	BC_1	15/10	−0.46**
	BC_2	15/10	−0.72**
	Testcross	15/10	−0.38**
	F_3	15/5	−0.63**
	BC_1	15/5	−0.30*
	BC_2	15/5	−0.70**
	Testcross	15/5	−0.48**
5-154 × A671	F_3	15/10	−0.34**
	BC_1	15/10	−0.46**
	BC_2	15/10	−0.61**
	Testcross	15/10	−0.21

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

[a] BC_1 = backcross to 5-154, BC_2 = backcross to H99 or A671

Estimates of additive genetic variance (σ_A^2) were larger than estimates of dominance variance (σ_D^2) for emergence time and seed weight loss for both crosses (Table 5). Estimates of the total genetic variance (σ_g^2) obtained from the F_3 generation were of similar magnitude to estimates of additive genetic variance obtained from the backcross generations. Because frequencies of segregating alleles were expected to be 0.5 in the F_3 generation, the total genetic variance among F_3 lines was expected to be $\sigma_A^2 + \frac{1}{4}\sigma_D^2$ (Hallauer and Miranda 1981). Estimates of $\sigma_A^2 + \frac{1}{4}\sigma_D^2$ calculated from the backcross generations were within two standard errors of $\hat{\sigma}_g^2$ (data not presented), indicating that the backcross and F_3 generations were providing similar estimates of variance components.

The ratio of dominance to additive genetic variance ranged from 0.16–0.52 for emergence time and from 0.09–0.57 for seed weight loss (Table 5). These ratios are similar to estimates obtained for other traits in maize, including ear height, ear length and grain moisture but excluding grain yield (Hallauer and Miranda 1981).

For both emergence time and seed weight loss, estimates of the average level of dominance ($\bar{d}$) were between 0 and 1 for 5–154 × H99 and slightly greater than 1 for 5–154 × A671 (Table 5). These results indicate that, on average, genes controlling emergence time and seed weight loss in the cross 5–154 × H99 were partially dominant, while in the cross 5–154 × A671 they were fully dominant. From generation means, dominance was in the direction of rapid emergence and high seed weight loss (Table 2). However, estimates of $\bar{d}$ can be substantially influenced by linkage (Comstock and Robinson

Table 5. Genetic variances, genetic affects and numbers of effective factors estimated for emergence time and seed weight loss for two crosses

Parameter[a]	Emergence time			Seed weight loss		
	5-154 × H99		5-154 × A671	5-154 × H99		5-154 × A671
	15/10 °C	15/5 °C	15/10 °C	15/10 °C	15/5 °C	15/10 °C
σ_A^2	0.97 ± 0.25[b]	3.19 ± 0.69	0.98 ± 0.23	31.5 ± 6.7	27.9 ± 6.5	15.0 ± 3.9
σ_D^2	0.27 ± 0.06	0.52 ± 0.17	0.51 ± 0.12	10.5 ± 3.4	2.6 ± 1.4	8.5 ± 2.1
σ_g^2	0.96 ± 0.17	4.34 ± 0.86	1.16 ± 0.23	28.3 ± 5.5	23.7 ± 5.3	11.7 ± 2.8
σ_D^2/σ_A^2	0.28	0.16	0.52	0.33	0.09	0.57
$\bar{d}$	0.75	0.61	1.02	0.81	0.42	1.07
a	−3.6 ±0.3	−7.0 ±0.1	−2.9 ±0.2	14.5 ± 1.0	17.6 ± 0.9	5.9 ± 1.1
d	−3.1 ±0.8	−4.3 ±0.4	−1.7 ±0.5	19.1 ± 2.5	16.8 ± 3.0	21.8 ± 3.7
d/a	0.86	0.61	0.59	1.32	0.95	3.69
n	10.4	10.0	3.7	1.9	2.1	1.7

[a] σ_A^2 = additive genetic variance, σ_D^2 = dominance genetic variance, σ_g^2 = total genetic variance, $\bar{d}$ = average degree of dominance, a = additive effect, d = dominance effect, n = minimum number of effective factors

[b] Standard error associated with each variance component or effect

1952; Moll and Robinson 1967). The extent of bias depends on whether coupling or repulsion phase linkage predominates and on the degree of linkage disequilibrium. These crosses involved highly selected, diverse parents, so linkage disequilibrium should have been extreme and coupling phase linkage should have predominated. With complete coupling phase linkage no bias exists (Comstock and Robinson 1952), but as this was unlikely, average levels of dominance were probably overestimated. This suggests a preponderance of partially dominant genes controlling both traits in both crosses.

From a generation means analysis estimates of additive effects (a) exceeded estimates of dominance effects (d) for emergence time in both crosses (Table 5). For seed weight loss, the additive effect was larger than the dominance effect only for 5–154 × H99 in the 15/5 °C environment. This suggests a preponderance of partially dominant genes for emergence time but fully dominant to overdominant genes for seed weight loss. However, the use of the ratio of dominance to additive effects as a measure of average level of dominance assumes that genes of like effect are completely associated in the parental lines and that dominance is unidirectional at all loci (Mather and Jinks 1971). The close agreement of $\bar{d}$ and d/a for emergence time in 5–154 × H99 (Table 5) suggests that genes for rapid emergence were associated in 5–154 while genes for slow emergence were associated in H99. For emergence time in 5–154 × A671 and seed weight loss in both crosses, genes for rapid emergence or rapid seed weight loss probably occurred in both parents.

Using estimates of σ_A^2 from the backcross generations and the parental lines as extremes (35 days for H99 in the 15/5 °C environment), minimum numbers of effective factors (n) were calculated. For emergence time in 5–154 × H99, n was approximately 10 in both environments (Table 5). This provides strong evidence for polygenic inheritance in this cross. For emergence time in 5–154 × A671, the estimate was 3.7, which is also indicative of polygenic inheritance. This was reinforced by examination of the distribution of F_3 lines, which showed that not one F_3 line in either cross had a mean emergence time as low as the mean of 5–154 (data not presented).

The three estimates of the minimum number of effective factors for seed weight loss were approximately two (Table 5). However, due to the likely dispersion of genes for rapid seed weight loss between 5–154 and the Corn Belt Dent parental lines, these estimates were probably spuriously low.

Comparisons with previous experiments

Previous studies of the inheritance of early seedling growth under cool conditions have evaluated traits including germination time, germination percentage, emergence time, emergence percentage and seedling weight. Many different temperatures and evaluation techniques have been used. Nevertheless, results from experiments using generation means analysis agree with my results by showing both additive and dominance effects with dominance deviations in the direction of increased germination or emergence percentage, decreased germination or emergence time and increased seedling vigour (Grogan 1970; McConnell and Gardner 1979; Eagles 1982; Maryam and Jones 1983).

Fewer studies have estimated variance components of traits associated with early seedling growth under cool conditions. Mock and Eberhart (1972) found significant genetic variation among S_1 lines in two Corn Belt Dent populations, BSSS2 and BSSS13, for emergence time, emergence percentage and seedling weight in the field and Eagles and Hardacre (1979a, 1979b) found significant additive and non-additive genetic variation in CIMMYT Pool 5 for emergence time and shoot weight. Additive, dominance and maternal variances were confounded in the study of Mock and Eberhart (1972), while maternal and dominance variances were confounded in the studies of Eagles and Hardacre (1979a, 1979b). Recurrent selection procedures improved emergence percentage and seedling dry weight in BSSS2 and BSSS13, but not emergence time (Mock and Bakri 1979; Hoard and Crosbie 1985). The lack of improvement for emergence time in BSSS2 and BSSS13 may reflect a lack of additive genetic variability or unfavourable conditions for selection (warm seasons, variable planting depth, etc.). Estimates of additive and dominance variances in my current experiments should be largely unconfounded with each other and with maternal variances. Some bias could have occurred because of unequal subclass numbers and data censoring due to a negative correlation between emergence time and emergence percentage (Hartley and Searle 1969; Eagles and Brooking 1981; Scott et al. 1984). However, this bias should have been small in the 15/10 °C environment where the data was nearly orthogonal. Therefore, my current study agrees with previous studies in showing significant genetic variability for emergence time in maize and extends these studies to show that most of the genetic variability is additive.

Acknowledgements. Mr. K. I. Sinclair for technical assistance. The technical staff of the DSIR Climate Laboratory, Palmerston North, for maintaining the controlled-environment rooms used in this study. Dr. A. R. Gilmour, formerly Massey University, Palmerston North, currently New South Wales Department of Agriculture, Australia, for assistance with the REG computer program.

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