Inheritance of Vegetative Growth Index and Related Traits in Pearl Millet

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ABSTRACT

Growth index (GI) is a measure of plant dry weight produced per unit of land area per day (grams per square meter per day). The objective of this study was to elucidate the inheritance pattern of GI for pearl millet [*Pennisetum glaucum* (L.) R. Br.]. A generation means analysis was conducted to determine the relative importance of additive, dominance, heterotic, and additive × additive epistatic genetic effects for GI. Two elite open-pollinated and three landrace varieties of pearl millet were mated, and the parents, parents selfed, F_1s, F_1s selfed, and F_1s random mated were evaluated in 1990 and 1991 at the International Crops Research Institute for the Semi-Arid Tropics, near Hyderabad, India. Traits measured were GI at 10 d after bloom date (GI1) and at maturity (GI2), bloom date, biomass, harvest index, and plant height. The fully fitted genetic model for the generation means explained from 88 to 95% of the variation among the generations sum of squares for the various traits. Additive effects accounted for the largest proportion of the variation among generation means for all traits except GI2 and biomass, where additive × additive epistatic effects were of greatest importance. Even though inheritance patterns for GI1 and GI2 were dissimilar, a breeding method that emphasizes selection for additive genetic effects should be suitable for improving them.

SELECTION for increased growth index (GI; kilograms per hectare per day) was proposed by Takeda and Frey (1977) for increasing grain yield of cereals with short growth duration. In India, pearl millet is a short-duration cereal crop grown for grain and fodder, so its productivity may benefit from selection for increased GI. Bramel-Cox et al. (1984) devised a method for estimating GI for pearl millet, and Bramel-Cox et al. (1986) used this method to select lines with significantly greater GI.

The efficiency of a breeding method for improving a trait depends largely on the trait's inheritance pattern. The GI of pearl millet is quantitatively inherited (Rattunde et al., 1989; Bramel-Cox et al., 1986), but its inheritance pattern has not been studied. Therefore, our objective was to determine the relative importance of four genetic parameters in the inheritance of GI measured 10 d after bloom date (GI1) and at maturity (GI2) and of four traits related to GI.

MATERIALS AND METHODS

Development of Genetic Materials

The five open-pollinated populations of pearl millet used to initiate this study were (i) ECC6, a variety from the sixth cycle of selection for grain yield and earliness in the Early Composite developed at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT); (ii) VC F_2, the selfed progeny from mating ICMV 87901 and ICMV 82132, both high grain yielding, early maturity varieties developed at ICRISAT; and (iii) three ICRISAT landrace accessions, IP 3226, IP 3175, and IP 6098, collected in western and central Rajasthan state in India and in Niger, respectively. The five parents were mated at ICRISAT during November to January, 1989–1990, via a diallel plan without reciprocals. Matings between each pair of the open-pollinated parents were produced by full-sib crosses between at least 100 plants of each parent of mating, except for the matings between IP 3226 × IP 6098, IP 3175 × IP 6098, and VC F_2 × IP 6098, in which 97, 68, and 50 full-sib crosses, respectively, were produced. A plant was used in a mating only once as either a female or a male. At maturity, the seed-parent panicle of each full-sib progeny within a mating was cut, sun-dried, and threshed separately. Next, 10-mL samples of seed from each full-sib progeny within a mating were composited, and those composites represented a mating between two of the open-pollinated parents.

During March to May 1990, F_1s of the matings were remade and the mating composites produced during November to January, 1989–1990, were selfed and random mated. Also, the parent populations were random mated and selfed. To random-mate a parent population or the F_1 between two parents, at least 150 full-sib progenies were formed within each F_1 or parent population. Similarily, the self-pollinated generation of the parent populations and F_1 matings were produced by self pollinating at least 150 plants in each parent or F_1 mating. At maturity, each selfed or full-sib progeny within a parent population or F_1 mating was harvested, sun-dried, and threshed separately. Next, 10-mL samples of seed from all selfed panicles or full-sib panicles for a parent population or F_1 mating were composited. These composites were the sources of seed for the evaluation experiments. Thus, seed lots of all generations evaluated were produced in the same season and field.

Field Evaluations

Evaluations of the various populations were conducted in field experiments at ICRISAT during June to October of 1990 and 1991. The experiments contained 40 experimental entries representing the five parents random mated, the five parents selfed, the F_1s of the 10 matings, the F_1s of the 10 matings random mated, the F_1s of the 10 matings selfed, and eight (1990) or nine (1991) checks. The checks were ICMV 87901, ICMV 82132, ICMV 84400 (in 1991 only), and WCC75, which are high yielding varieties developed at ICRISAT; HHB67, an early hybrid; ICMH 423 and ICMH 501, early and medium ICRISAT hybrids, respectively; and Higrop C_0 and Senpop C_1, gene pools formed by intermating improved pearl millet varieties with landrace accessions and wild and weedy pearl millet subspecies [ssp. *monodii* (Maire) Br. and *stenostachyum* Kloyzcsh ex. A.Br. and Bouche].

The experiments were conducted in randomized block de-

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Abbreviations: GI, vegetative growth index; GI1, vegetative growth index measured 10 d after 50% bloom; GI2 vegetative growth index measured at maturity; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics.

Table 1. Traits measured on population generations of pearl millet, their abbreviations, methods of measurement or computation, and units.

Trait	Abbreviation	Method†	Units
Bloom date	BD	Days after planting when 50% of plants had primary panicles with emerged stigmas	d
Growth index at BD + 10 d	GI1	PDW/(BD + 10)	g m^{-2} d^{-1}
Growth index at maturity	GI2	SY/(BD + 10)	g m^{-2} d^{-1}
Biomass	BM	PY + SY	g m^{-2}
Harvest index	HI	(GY/BM)100	%
Plant height	PH	Distance from soil to tip of 50% of panicles in the plot	cm

† Traits measured for computations: PY = mass of panicles from 3-m length of four rows; GY = mass of grain from 3-m length of four rows; PDW = aboveground plant dry weight at 10 d after 50% bloom date from 1-m length of four rows; SY = mass of stover from 3-m length of four rows.

signs with three replications on Udic Rhodustalf soils. A plot consisted of four 4-m rows with rows spaced 75 cm apart. The experiments received preplant broadcast applications of 40 and 17 kg ha^{-1} of N and P, respectively, and a side-dressing of 40 kg ha^{-1} of N at 20 d postemergence. Planting dates were 25 June in 1990 and 14 July in 1991. At ca. 14 d after emergence, seedlings were thinned to one plant per 15 cm of row (118 500 plants ha^{-1}). Plots were hand weeded. In 1991, the experiment was irrigated at 14 and 50 d after sowing. Bloom date and plant height were assessed on a whole-plot basis (Table 1). Ten days after bloom date, all plants from the terminal 1 m of the four rows of a plot were cut at ground level and weighed. A sample of the plants was chopped, weighed, and dried at 65°C, and dry matter per plot at 10 d after bloom date was determined for use in computation of GI1. At maturity, panicles of the plants in the remaining 3 m in each row of a plot were cut, dried at 65°C, weighed, and threshed. Next, stover from the plot was cut and weighed. A sample of the stover was chopped, weighed, and dried at 65°C, and dry matter per plot at maturity was determined for use in computation of GI2.

Statistical Analysis

All statistical analyses were performed using PROC GLM of PC-SAS (SAS, 1988). Analyses of variance were performed on the data from individual years and then combined across years. Another analysis was conducted upon the means of the population generations in each year and across years by using a model of Eberhart and Gardner (1966). In their model, each generation mean for a trait is written as a function of *m*, the mean of the generation, and the cumulative additive (*a*), dominance (*d*), heterotic (*h*), and additive × additive epistatic (*aa*) genetic effects. The genetic parameters, beginning with *m*, were fitted sequentially to the data via least squares regression, and the sums of squares associated with each genetic parameter were determined. Mean squares due to fitting each genetic parameter were (i) tested for significance and (ii) compared with the generations sum of squares for a trait. The generations sum of squares not accounted for by the fully fitted genetic model was termed residual, and it represented effects involving dominance epistasis and linkage.

Significance of mean squares due to main effects, interactions, and genetic parameters was tested by using the entry × year mean square. When the entry × year effect was nonsignificant, it was pooled with the error mean square and the pooled error was used for performing the *F* tests.

RESULTS AND DISCUSSION

Significant differences occurred among generations for all six traits (Table 2). Additive genetic effects were significant for all traits except GI2, dominance effects were significant for all traits except GI1, heterotic effects were significant for all traits except GI1 and GI2, and additive × additive epistasis effects were significant for all traits except GI1. Residual effects were significant for bloom date, harvest index, and plant height.

Inheritance patterns for GI1 and GI2 were different. For GI1, only additive genetic effects were significant, whereas for GI2, only dominance and additive × additive epistatic genetic effects were significant. Different inheritance patterns for GI1 and GI2 were not expected because in the materials studied by Bramel-Cox et al. (1984) accumulation of vegetative dry weight in pearl millet diminished markedly 10 d after bloom date. Therefore, GI estimated either at 10 d after bloom date (i.e., GI1) or at maturity (i.e., GI2) should be determined by similar genetic effects.

In an attempt to understand why GI1 and GI2 had different inheritance patterns, means for the F_1, F_1 selfed, and the F_1 random-mated generations for GI1 and GI2 were computed (Table 3). Means for GI1 and GI2 were similar for the F_1 and for the F_1 selfed generations,

Table 2. Mean squares for generations, four genetic parameters, and residual effects of generation means for six traits of pearl millet evaluated in 1990 and 1991 at International Crops Research Institute for the Semi-Arid Tropics Center and analyzed by using Eberhart-Gardner (1966) model.

		Traits					
Source of variation	df†	BD‡	GI1‡	GI2‡	Biomass	Harvest index	Plant height
Generations	39	132.6**	5.8**	8.7**	93 994.2**	179.0**	2 502.2*
Additive	4	394.2**	21.0**	4.0	161 063.2**	798.6**	10 779.8**
Dominance	5	69.3**	5.9	19.9**	214 132.0**	98.9**	771.2**
Heterotic	10	137.7**	3.1	3.7	45 471.8*	207.5**	1 817.0**
Additive × additive epistatic	10	142.3**	5.7	14.7**	133 532.4**	80.5**	2 464.4**
Residual	10	44.7**	2.6	3.9	16 081.8	41.4**	779.8**

*, ** Significant at 0.05 and 0.01 levels, respectively.
† df = degrees of freedom.
‡ BD = bloom date; GI1 = growth index at bloom date + 10 d; GI2 = growth index at maturity.

Table 3. Means for growth index estimated at 10 d after flowering (GI1) and at maturity (GI2) for the F_1, F_1 selfed, and F_1 random-mated generations of pearl millet.

Generation	GI1	GI2
	g m^{-2} d^{-1}	
F_1	6.36	6.39
F_1 selfed	5.54	5.64
F_1 random mated	5.20	4.50
LSD(0.05)	0.53	0.60

showing that, in these generations, GI did not change from 10 d after bloom date to maturity. This corroborates the results of Bramel-Cox et al. (1984) indicating that GI can be measured at either 10 d after bloom date or at maturity. However, for the F_1 random-mated generation, GI1 was 0.7 g m^{-2} d^{-1} greater than GI2. The means for the F_1 selfed and the F_1 random-mated generations differed by 0.34 g m^{-2} d^{-1} for GI1, whereas they differed by 1.14 g m^{-2} d^{-1} for GI2. This discrepancy likely explains why GI2 had a different inheritance pattern than did GI1. The expectations for the means of F_1 selfed and F_1 random-mated generations, respectively, are

$$Y_{12}^{s} = \mu + 0.5(a_1 + aa_1 + a_2 + aa_2) + 0.25(d_1 + d_2) + 0.5(h_{12}) + aa_{12}$$

$$Y_{12}^{r} = \mu + 0.5(a_1 + aa_1 + a_2 + aa_2) + 0.5(d_1 + d_2) + 0.5(h_{12}) + aa_{12}$$

It can be seen that the significant dominance genetic effects for GI2 could arise from the coefficient for the d effect in the F_1 random mated (0.5) being greater than that for the F_1 selfed (0.25). Furthermore, significant additive × additive epistatic effects arise because the difference between the means for F_1 selfed and F_1 random-mated generations for GI2 were much greater than the difference that occurred for GI1. Perhaps, random mating disrupted favorable epistatic genetic effects or linkages more for GI2 than for GI1.

The proportion of the generations sums of squares accounted for by the genetic model ranged from 88% for GI2 to 95% for biomass (Table 4). Thus, the model explained variation among the generation means adequately. Additive effects accounted for the largest proportion of the variation among generation means for all the traits except GI2 and biomass, and for these three traits, additive × additive epistatic effects explained the greatest proportion of variation among means. For all traits, the sum of additive effects and additive × additive epistatic effects (48 to 69% of the generations sums of squares) accounted for more of the generations sums of squares than did the sum of dominance and heterotic genetic effects (23 to 42% of the generations sums of squares). For GI1 and GI2, additive plus additive × additive epistatic effects accounted for 67 and 48% of the variation among generation means, respectively, whereas dominance plus heterotic effects accounted for 23 and 40% of the generations sums of squares, respectively.

Table 4. Percentages of generation-effect sums of squares due to the variance of the genetic parameters.

	Traits					
Genetic effect	BD†	GI1†	GI2†	Biomass	Harvest index	Plant height
Additive	30	39	5	18	46	44
Dominance	7	7	29	29	7	4
Heterotic	27	16	11	12	30	19
Additive × additive epistatic	28	28	43	36	12	25
Residual	9	10	12	5	5	8

† BD = bloom date; GI1 = growth index at bloom date + 10 d; GI2 = growth index at maturity.

Studies of inheritance of GI have been confined to oat (*Avena sativa* L.). Helsel and Frey (1983) studied 12 *A. sterilis* × *A. sativa* matings and found that the inheritance of GI was additive in seven matings and nonadditive in five. Our results tend to agree with those of Helsel and Frey (1983). Takeda et al. (1979) reported that the minimum number of effective factor pairs segregating for GI ranged from 6 to 9 for 23 intraspecific oat matings and from 3 to 9 for matings of *A. sativa* × *A. sterilis* (Takeda and Frey, 1977). Burton (1959) reported that among 818 single cross hybrids of pearl millet, 55.9% of the genetic variation for forage yield was nonadditive. Later, Burton (1968a) demonstrated that this was largely due to dominance genetic variance, although epistasis was important in some crosses (Burton, 1968b). We found that biomass, the trait most closely related to forage yield, had 40% of the variation among means accounted for by dominance and heterotic effects.

Despite having different inheritance patterns, additive and additive × additive epistatic genetic effects were of major importance in determining both GI1 or GI2. Therefore, a breeding method that will select for additive effects should be suitable for improving GI in pearl millet.

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