

Effects of the d_2 dwarfing gene in pearl millet*

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Summary. Dwarf varieties have had virtually no impact on the production of pearl millet, in contrast to the case of wheat, rice, and sorghum. This research compared tall and dwarf near-isogenic F_1 hybrids to attempt to determine if there were deleterious effects of the d_2 dwarfing gene that might account for the lack of release/cultivation of dwarf pearl millet cultivars. Dwarf isohybrids on average yielded less than the talls, because of a smaller average seed size combined with a similar grain number per unit area. There was, however, a larger contribution of background genetic variation (pollinator, male-sterile, and interaction effects) to hybrid variation for nearly all characters measured, including seed size, than there was of the dwarfing gene. Selection of dwarf parents capable of producing hybrids with equal seed size and yield to that of tall parents should not be difficult.

Key words: Pearl millet – Dwarfing gene – Parental effects – Near-isogenic hybrids

Introduction

During the last 20 years, dwarfing genes have had a large impact on the breeding of wheat and rice worldwide, and of sorghum in temperate zones. In all three cereals, dwarfing genes have provided protection from lodging, and have allowed the productive use of high levels of inputs. In the case of sorghum, dwarf hybrids have made mechanical harvesting possible. In wheat, in addition to these benefits, the *Rht* series of dwarfing genes has beneficial pleiotropic effects on yield potential through increases in grain numbers per spike or in tiller number (Gale and Youssefian 1985).

Dwarfing genes have been known in pearl millet [*Pennisetum glaucum* (L.) R. Br.] for more than 20 years (Burton and Fortson 1966) and have been used, at least experimentally, by plant breeders for almost as long (Bakshi et al. 1966; Chanterreau and Etasse 1976; Lambert 1983; Thakare and Murty 1972). To the authors' knowledge, however, dwarf varieties or hybrids have had virtually no impact on the production of the crop, in contrast to the history of dwarf varieties of wheat, rice, or sorghum.

Reports from West Africa of comparisons of dwarf and standard height varieties indicated yield advantages of 5%–15% in the dwarfs (Lambert 1983). However, these varieties had problems of greater disease susceptibility and poor grain filling (Niangedo and Ouendeba 1987), and have never been grown by farmers. Comparisons of dwarf and tall versions of a set of seven composites of both Indian and African origin indicated no overall yield advantage to the dwarfs (K.N. Rai, personal communication). In India, where more than 40 varieties and hybrids have been released since the 1960s, only a single dwarf cultivar has been released, which was never widely grown.

This research was undertaken to more critically examine the effects of the d_2 dwarfing gene (Burton and Fortson 1966) on growth and yield in a set of near-isogenic tall/dwarf F_1 hybrids of pearl millet. The specific purpose was to determine if there is any evidence of adverse effects associated with the d_2 gene, which might be responsible for the lack of impact of dwarf cultivars on pearl millet production.

Materials and methods

Hybrids

The near-isogenic tall/dwarf hybrids were made by crossing four pairs of near-isogenic tall (D_2D_2)/dwarf (d_2d_2) inbred lines on

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Table 1. Mean, ranges, and standard error for the 32 hybrids, and the mean effects of the various components of the hybrids for growth, yield, and yield components

	Stem ht. (cm)	Biomass (g m ⁻²)	HI (%)	Grain yield (g m ⁻²)	Grain no. (10 ⁻² m ⁻²)	Grain mass (mg grain ⁻¹)	Flowering (days)
Hybrid							
Mean	150	785	37.7	289	37.6	7.95	44.7
Range	104–196	613–985	32.1–42.1	236–337	27.2–49.6	5.00–10.68	39.9–50.8
SE ^a	0.79	2.7	0.53	1.8	0.65	0.245	0.26
F-ratio	***	***	***	***	***	***	***
Height class							
Tall	177	846	36.8	303	37.1	8.40	44.9
Dwarf	122	724	38.7	276	38.0	7.51	44.5
F-ratio	***	***	***	***	NS	***	***
A lines							
843 A	141	741	38.4	278	32.9	8.74	41.3
81 A	159	852	35.6	297	46.1	6.50	49.0
833 A	148	789	37.3	289	37.2	7.81	45.1
842 A	152	760	39.7	293	34.4	8.73	43.5
F-ratio	***	***	***	**	***	***	***
R lines (pairs)							
ECIL-33-6-2-3/2	160	826	39.3	317	36.0	9.01	44.7
ECIL-159-4-4-7/8	137	732	37.5	271	38.6	7.11	44.4
MCIL-31-5-2-2/12	145	743	38.3	279	42.4	6.71	44.1
NCIL-143-4-5-3/6	158	838	35.9	291	33.4	8.97	45.7
F-ratio	***	***	***	***	***	***	***
CV%	5	11	9	13	14	9	2

^a SE of individual hybrid values

, * Significant at the 0.01 and 0.001 levels of probability, respectively, by *F*-test

four dwarf (d_2d_2) male-sterile lines (Table 1). The near isogenic inbred lines were derived from progenies segregating for the d_2 gene, from a backcrossing program to produce dwarf versions of standard height composites. Tall plants in progenies segregating for dwarfness were selfed each generation from the $BC_3 F_3$ to $BC_3 F_7$. Phenotypically similar tall and dwarf plants were selected in segregating progenies in the F_6 generation, and were advanced by an additional generation of selfing. Crossing four tall/dwarf pairs onto four dwarf phenotypically diverse male-sterile lines produced 16 pairs of tall (D_2d_2) and dwarf (d_2d_2) hybrids. Hybrids were used in preference to the original inbred lines (which have significant inbreeding depression) as the dwarfing gene, if used commercially, would most likely be in F_1 hybrid form. The consequences of the tall being heterozygous rather than homozygous at the D_2d_2 locus are not known, but comparisons of homozygous and heterozygous tall hybrids in sorghum indicated no overdominance effects (Campbell et al. 1975).

Evaluation

The 16 pairs of hybrids were grown in replicated field trials at the ICRISAT Center during the rainy seasons of 1985, 1986, and 1987 in a randomized block design, without blocking by height. Individual plots were four (1986–1987) or six (1985) rows of 0.75 × 4.0 m. All observations were taken on a 3.0-m length of the center two rows (1986–1987) or the center four rows (1985). Plots were well fertilized (85–100 kg N ha⁻¹ plus 20–25 kg P ha⁻¹), and were overplanted and thinned to a uniform plant stand of 12 plants m⁻². Weed control was by cultivation and a

single-hand weeding; no significant disease or pest incidence occurred in any year.

Data were recorded on flowering, plant height, biomass, grain yield, and yield components in all 3 years. Analysis of all data was done according to the field design, considering replicate as contained within year, and partitioning the sums of squares for hybrid (31 *df*) into effects of height (1 *df*), male-sterile, and pollinator pair (3 *df* each), and the various interactions among these effects. The effects of the d_2 gene on the measured variables were assessed by comparing the proportion of the sums of squares for hybrids that was attributable to height, as opposed to that attributable to parental effects and interactions of height and parental effects.

Results and discussion

Differences in tall and dwarf isohybrids

Individual trial mean yields were 2.63 tons ha⁻¹ in 1985, 3.42 tons ha⁻¹ in 1986, and 2.62 tons ha⁻¹ in 1987, which are normal values for non-irrigated experiment station yields. Individual hybrids differed significantly for all characters measured (Table 1).

The effects of the alleles at the D_2/d_2 locus (henceforth called height class) were significant for all variables measured except grain number m⁻² (Table 1). Some of the differences between the tall and dwarfs were expected (lesser straw length and total biomass, and a

higher harvest index (HI) in the dwarfs (Table 1) from results of similar comparisons in wheat (review by Gale and Yousefian 1985), barley (Ali et al. 1978), and sorghum (Windscheffel et al. 1973). Similarly, the smaller individual grain mass found in the dwarf millet hybrids has been widely reported in dwarf lines of other crops (e.g., Gale and Yousefian 1985; Ali et al. 1978; Campbell et al. 1975).

Grain numbers per unit area were not different in the tall and dwarf hybrids (Table 1) and, as a consequence, grain yields were significantly less in the dwarfs than in the tall, following differences in grain mass. Millet appears to differ from wheat (Gale and Yousefian 1985) and possibly barley (Ali et al. 1978), in which increases in grain number in dwarf lines, achieved either by increases in grain number per spike (mainly in winter wheat) or in spike number (spring wheat and barley), offset the decrease in individual grain mass. Sorghum, on the other hand, appears to be more similar to millet, as most reports indicate a smaller grain size without a compensating increase in grain number in dwarf isolines/hybrids (Campbell et al. 1975; Cassady 1965; Schertz 1973).

Why there is a much more consistent increase in grain numbers associated with the *Rht*₁ or *Rht*₂ alleles in wheat (versus the tall *rht* allele) than there is in dwarf sorghum or millet is not clear from the literature. Increases in grain number per spike in winter wheat may be due to its having an indeterminate number of floret primordia per spikelet, which may make wheat much more responsive, at least under some environmental conditions, to a reduction in competition between spike and stem during the later part of stem elongation, when the florets are developing and final floret number is being determined (Brooking and Kirby 1981; Bush and Evans 1988). Crops with a predetermined floret number per spikelet, such as barley, sorghum, and millet, may be less likely to respond in this fashion to a change in partitioning between stem and spike/panicle.

The differences in individual grain mass between the tall and dwarf isohybrids were examined in more detail by plotting individual grain mass for both tall and dwarf hybrids against grain number per unit area, as the latter is generally the major determinant of individual grain mass in most cereals. This was clearly the case in these hybrids, as grain number accounted for 71% of the variation in individual grain mass (Fig. 1). It is clear from this plot, however, that the relationship of the two variables differed in the tall and dwarf hybrids for grain numbers greater than about 34,000 m⁻². Most (but not all) of the dwarfs had a grain mass of the order of 1 mg per grain (12%–20%) less than that of the tall over the range of 34,000–50,000 grains m⁻². Thus, the yield disadvantages of the dwarfs were specifically associated with a poorer ability to fill grains in genetic backgrounds that produce higher grain numbers.

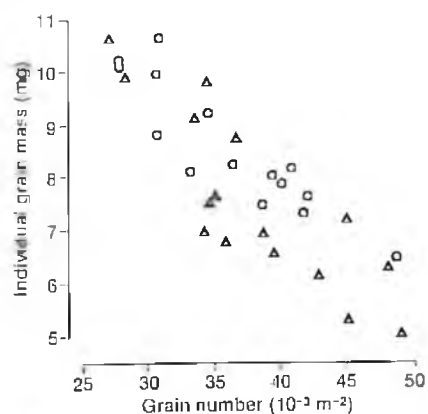


Fig. 1. Relationship of individual grain mass and grain number per unit area for the tall (○) and dwarf (▲) isogenic hybrids. Data are means of 3 years.

Relative contribution of the dwarfing gene

In addition to the effects of the dwarf habit, there were also significant effects of both male-sterile and pollinator for all variables measured, as assessed by the mean effects of parents over the hybrids made with them (Table 1). Hybrids made with 843A, e.g., flowered earlier, produced less biomass, and were lower yielding than hybrids on the other three male steriles. Similarly, hybrids made with ECIL-33-6-2-3/2 and NCIL-143-4-5-3/6 were taller, produced more biomass, had larger grains, and outyielded those made with the other two pollinator pairs.

Since the dwarf habit represents an alternative that a plant breeder may or may not employ, it seemed most logical to compare its effects directly to those of his other alternative – the choice of parents. This was done by partitioning the sums of squares (SS) for hybrid in the ANOVA among the component effects (Table 2). Height class, as expected, accounted for the majority of variation in stem length (83%) and biomass (43%). The effect of height class on harvest index, however, was half or less than the effects of both parental groups. In addition, the interaction of height class and pollinator accounted for a greater proportion of the variation in HI than did height class alone. Thus, attempts to manipulate HI (for example) would be likely to be more successful through choice of parental lines than by the use of the *d*₂ dwarfing gene.

Variation in hybrid grain yield and yield components was more strongly influenced by variation among parental lines than it was by differences in height class (Table 2). Grain number differences in the hybrids were primarily a result of male-sterile line differences (64% of the SS). Pollinator differences were primarily responsible for differences in grain mass (47% of SS) and grain yield (35% of SS). Interactions between height class and parental line were generally smaller than the individual effects of each, with the exception of a relatively large effect of pollinator × height class on grain yield (17% of

Table 2. Percentages of the sums of squares for hybrids accounted for by the various component sources of variance within hybrid

	df	Stem ht.	Biomass	HI	Grain yield	Grain no.	Grain mass	Flowering
Hybrid	31	100	100	100	100	100	100	100
Height class	1	83***	43***	12***	20***	1	9***	1***
A line	3	5***	20***	33***	6***	64***	36***	88***
R line	3	10***	26***	23***	35***	27***	47***	41***
A × R lines	9	<1***	4	8*	11***	2	5***	3***
HI × A line	3	1***	1	6**	6**	<1	1**	<1*
HI × R line	3	<1**	3	15***	17**	3***	1***	4***
HI × A × R lines	9	<1*	2	3	4	2	1**	1***

*, **, *** Significant at the 0.05, 0.01, and 0.001 levels of probability, respectively, by *F*-test

the SS for hybrid). Therefore, despite lower mean grain mass and grain yield in the dwarf isohybrids, the partition of variance makes it clear that, by selection of parental lines, it is possible to produce d_2 dwarf hybrids with yields equal to those of the tall hybrids. In fact the highest yielding hybrid in the trial was a dwarf – 842A × ECIL-33-6-2-2 – with a grain mass of more than 9 mg grain⁻¹. While the relative effects of male-sterile or pollinator may be specific to the lines used, the general effects of genetic background on expression of the d_2 gene are clearly large.

Large effects of genetic background on the performance of dwarf isolines have been widely reported in other crops (e.g., Ali et al. 1978; Cassady 1965; McClung et al. 1986), and specifically studied in wheat by Bush and Evans (1988). These authors found large interactions of *Rht* genes and not only specific genetic background, but also *Rht* genes and environmental conditions, which were expressed as differences in crop growth, stem length, ear number, grain number per ear, and grain yield. The results of this study clearly support Bush and Evans' (1988) findings: in spite of a mean depressive effect of the dwarfing gene on individual grain mass and grain yield, the effects of the specific parental combination, particularly the interaction of dwarfing gene and pollinator in the case of grain yield, clearly outweigh the effects of the dwarfing gene on the hybrid phenotype. This is clearly illustrated in Fig. 1, in which two of the dwarf hybrids produced both a high grain number per unit area and a grain size equal to that of the best tall hybrids (for their grain number). Thus, breeding programs on dwarf pearl millet should be successful if they are designed to take advantage of positive interactions between the dwarf habit and specific genetic background which, these data indicate, are large and useful.

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