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Effect of d_2 dwarfing gene on grain yield and yield components in pearl millet near-isogenic lines

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Summary

A d_2 dwarfing gene in pearl millet [*Pennisetum glaucum* (L.) R. Br.] is currently being extensively used for the development of hybrid parents. Its effect on grain yield and yield components is poorly understood. Twelve pairs of tall and dwarf near-isogenic lines developed in the diverse genetic background of three composites were evaluated for grain yield and yield components for 2 years at two locations in southern India. The d_2 gene or the genes linked to it, on an average, reduced plant height by 42%, grain yield by 14%, and head girth by 8% but increased head length and number of tillers per plant by about 5–6%. Large variations were observed among pairs (genetic background) for the difference between tall and dwarf near-isogenic lines for all of the above yield components resulting in no significant difference in five pairs and 17–35% less yield in dwarfs as compared to their tall counterparts in six pairs. Days to 50% flowering and seed weight were least affected by the d_2 gene with the average difference between tall and dwarf groups of near-isogenic lines being of the order of 1–2%. These results indicate that the advantageous effects of d_2 dwarfing gene can be effectively exploited by manipulating the genetic background. The difference between the average grain yields of tall and dwarf groups of near-isogenic lines showed considerable variation across environments with the dwarfs yielding as much as tall group in one environment and up to 30% less than the tall group in the other, thus, indicating that the d_2 gene effect may be substantially modified by the environments.

Introduction

Landrace cultivars of pearl millet [*Pennisetum glaucum* (L.) R. Br.] from a larger part of the Indian subcontinent and Africa are mostly very tall, measuring up to 3 m under good growing conditions. Progress has been made in developing high-yielding hybrids and open-pollinated varieties, but without a marked reduction in plant height. Several major genes causing substantial reduction in plant height have been reported in pearl millet (Burton & Fortson, 1966; Gupta et al., 1985; Appa Rao et al., 1986). Of these, the d_2 dwarfing gene has been more widely used than others because it was among the first ones to be discovered and has also been reported to have no adverse effect on general combining ability and several developmental traits (Thakare & Murty, 1972). Pearl

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millet improvement programs in the United States, particularly those for grain production, are all based on the utilization of this dwarfing gene. Its use on the Indian sub-continent and in Africa, in breeding dwarf pearl millets has been less extensive.

The Cereals Program at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) initiated a major effort in 1975 to introduce the d_2 dwarfing gene into diverse genetic backgrounds of seven tall composites. During the backcross program and in the years that followed, 12 pairs of tall and dwarf near-isogenic lines were developed in the diverse genetic background of three composites. The objective of this research was to study the effect of d_2 gene on grain yield and yield components using these near-isogenic lines.

Materials and Methods

Development of near-isogenic lines. The tall and dwarf near-isogenic lines were developed at ICRISAT Center in the diverse genetic background of three composites: Early Composite (EC), Medium Composite (MC), and Nigerian Composite (NC) (Table 1). EC was constituted at ICRISAT Center by random mating 194 geographically diverse lines, mostly of Indian origin, which flowered in <45 days in the 1973 rainy season. MC was also constituted at ICRISAT Center by random mating 197 geographically diverse lines of Indian and African origin, which flowered in 45–55 days in the 1973 rainy season. NC, which flowered at ICRISAT Center in >50 days, was constituted involving 200 S_4 progenies from Nigeria and other West African germplasm at Samaru, Nigeria. It was introduced to ICRISAT in 1973.

A d_2 dwarfing gene from GAM73 (a synthetic bred in Senegal) was introduced into EC, MC and NC by three backcrosses. Seven to eight tall plants in each of a range of BC_3F_3 progenies segregating for tall and dwarf plants were selfed. BC_3F_4 progenies were planted in family blocks. One BC_3F_4 progeny from each family block was selected at random, which segregated for tall and dwarf plants, and 7–8 tall plants were selfed to generate BC_3F_5 progenies, which were planted in family blocks the same way as BC_3F_4 progenies. This process was repeated till the BC_3F_8 generation, when both tall and dwarf plants from a segregating progeny of each family block were selfed to isolate, in BC_3F_9 progeny, tall and dwarf near-isogenic lines. Each of the four near-isogenic pairs of EC were derived from four different BC_3F_3 progenies (Table 1). Seven near-isogenic pairs of MC were derived from four different BC_3F_3 progenies: three of these pairs were from the same BC_3F_3 but from different BC_3F_4 progenies, and two pairs were from the same BC_3F_4 but from different BC_3F_5 progenies.

Field tests. The near-isogenic lines were planted in a split-plot design with four replications in 1985 and 1986 rainy seasons at ICRISAT Center (18 oN) and Bhavanisagar (11 oN) in southern India. Pairs were randomly assigned to main plots, and tall and dwarf near-isogenic lines were assigned to subplots. Each plot consisted of 4 rows, 4-m long, spaced 60-cm apart at ICRISAT Center and 50-cm apart at Bhavanisagar. Each trial received 40 kg N and 40 kg P_2O_5 (plus 20 kg K_2O at Bhavanisagar only) ha^{-1} as the basal dose, followed by another 40 kg N ha^{-1} top dressed 15–20 days after planting. Trials were overplanted and thinned 10–12 days after planting to one plant at 10-cm spacing within rows. Whenev-

Table 1. Origin of tall (T) and dwarf (D)† pearl millet near-isogenic lines

Near-isogenic pair	Origin	
	Recurrent composite	F_9 progeny from
1	Early Composite (EC)	BC_3F_3-33
2		BC_3F_3-119
3		BC_3F_3-159
4		BC_3F_3-203
5	Medium Composite (MC)	BC_3F_4-4-3
6		BC_3F_4-4-4
7		BC_3F_4-4-7
8		BC_3F_3-31
9		BC_3F_5-121-6-2
10		BC_3F_5-121-6-3
11		BC_3F_3-191
12	Nigerian Composite (NC)	BC_3F_3-143

† GAM 73 was used as the d_2 dwarfing gene donor population.

er necessary, the trials were irrigated to overcome the confounding effects of drought and maturity on phenotypic expression. The two central rows of each plot were used for observation on days to 50% flowering, head count, plant count, and grain yield on the plot basis. The number of effective tillers plant^{-1} was estimated from plant count and head count data. Seed weight was estimated from three random samples of 100 seeds from each plot. In the 1985 trial, plant height, head length and head girth were taken on a random sample of 5 plants from each plot at ICRISAT Center and 10 plants at Bhavanisagar; in the 1986 trial, all three observations were taken on a random sample of 3 plants per plot at both locations.

Statistical analysis. Two locations and the two years provided four test environments. Height, environment, and near-isogenic pairs (genetic background) were all considered to have fixed effects. The total sum of squares due to genotype was partitioned into those between pairs (genetic background) and those between near-isogenic lines within the pair. The latter was further partitioned into those due to height and height × genetic background interaction in a combined analysis of variance over four environments. The overall difference between tall and dwarf groups of near-isogenic lines was tested by comparing the height mean square (1 df) with the pooled error mean square (144 df). The difference between tall and dwarf near-isogenic lines of individual pair for all the characters except seed weight was tested by comparing individual near-isogenic pair mean square (1 df) with its corresponding error mean squares (12 df) because the error mean squares across pairs were heterogenous for all the characters except seed weight. The difference between the tall and dwarf near-isogenic lines of individual pairs for seed weight was tested using the pooled error mean square (144 df).

Results

The average plant height of the dwarf group of near-isogenic lines was 84 cm (46% less than tall) at ICRISAT Center and 99 cm (40% less than tall) at Bhavanisagar (Table 2). The height of both tall and dwarf groups of near-isogenic lines was more at Bhavanisagar than at ICRISAT Center. The proportionate increase in height at Bhavanisagar over

Table 2. Mean performance of tall and dwarf groups of near-isogenic lines in 1985 and 1986 rainy season at ICRISAT Center and Bhavanisagar

Character	Height group	ICRISAT Center		Bhavanisagar	
		1985	1986	1985	1986
Grain yield (kg ha^{-1})	Tall	1630	990	1920	2040
	Dwarf	1120**	770**	1970	1800**
Plant height (cm)	Tall	157	153	168	163
	Dwarf	84**	84**	99**	99**
Time to 50% flowering (d)	Tall	56	60	55	51
	Dwarf	55**	59	55	51
Head length (cm)	Tall	17.8	16.4	21.3	20.9
	Dwarf	19.1**	16.9	22.0**	21.7*
Head girth (mm)	Tall	23.8	19.8	–[†]	20.2
	Dwarf	21.8**	17.9**	–	18.6**
Tillers plant^{-1} (no.)	Tall	1.3	1.1	2.3	1.7
	Dwarf	1.4	1.2	2.6	1.7
1000 seed weight (g)	Tall	6.6	5.9	7.5	7.3
	Dwarf	6.3**	5.9	7.4	7.4

*,**, significant at 5% and 1% probability levels, respectively.

[†] Data not recorded.

that observed at ICRISAT Center, however, varied from 7% for the tall group to 18% for the dwarf group. Large differences among tall lines (126–190 cm) as well as among dwarf lines (73–111 cm) were observed (Table 3) with the difference between tall and dwarf near-isogenic lines ranging from 46 to 100 cm (36–53%).

Mean grain yields of both tall and dwarf groups were higher at Bhavanisagar (1800–2040 kg ha^{-1}) than at ICRISAT Center (770–1630 kg ha^{-1}) (Table 2). Also, the yield superiority of the tall group over the dwarf group was much less evident at Bhavanisagar (−2% in 1985 and 13% in 1986) than at ICRISAT Center (45% in 1985 and 28% in 1986). The yield levels of both height groups varied from one year to the other, much more at ICRISAT Center than at Bhavanisagar, and there was no indication of any relationship between the extent of yield superiority of the tall group over the dwarf group, and the yield level of the environment at a given location. Mean grain yields over locations varied from 950 to 2250 kg ha^{-1} for tall lines and from 880 to 1870 kg ha^{-1} for dwarf lines (Table 3). In 5 of the 12 pairs, there was no significant difference between the tall and dwarf near-isogenic lines; in 6 pairs, tall near-isogenic lines significantly outyielded their dwarf counterparts by 20–53%, and in one pair the dwarf near-isogenic line outyielded its tall counterpart by 8% (Table 3). There was no significant relationship between the yielding ability of the genetic background and the magnitude of yield differences between the tall and dwarf near-isogenic lines.

The head length of the dwarf group was significantly more than the tall group in three trials and similar to the tall group in one trial (Table 2). The head girth of the dwarf height group was significantly less than the head girth of tall height group in all three trials where it was recorded. Large differences among lines were observed for head length (15–24 cm for tall; 14.4–26.2 cm for dwarf) and for head girth (15.4–24.2 mm for tall; 15.9–22.2 mm for dwarf) (Table 4). In six pairs dwarf near-isogenic lines had significantly (12–19%) longer heads than their tall counterparts whereas in four pairs tall near-isogenic lines had significantly (7–16%) longer heads than their dwarf counterparts. In eight pairs, dwarfs had significantly less head girth (6–9% less in five pairs and 15–22% less in three pairs) than their tall counterparts whereas there was no significant difference between the tall and dwarf near-isogenic lines in four pairs.

Table 3. Mean performance of tall and dwarf near-isogenic lines for plant height, time to 50% flowering, and grain yield over four environments

Near-isogenic pair	Plant height (cm)		Time to 50% flowering (d)		Grain yield (kg ha^{-1})	
	Tall	Dwarf	Tall	Dwarf	Tall	Dwarf
1	173	110**	53	55**	1520	1470
2	126	80**	53	51	1610	1300**
3	138	73**	51	53**	1390	1150*
4	180	111**	56	53**	1560	1560
5	176	109**	56	54**	1810	1700
6	174	95**	55	52**	1850	1840
7	167	91**	53	53	1850	1700
8	160	85**	58	56**	950	1020**
9	151	87**	59	61*	2250	1870**
10	150	83**	64	63	1910	1390**
11	134	85**	49	48	1350	880**
12	190	90**	59	63**	1670	1090**
Mean	160	92**	56	55**	1640	1420**
Dwarf (% Tall)	–	58	–	98	–	86

*, **, significant at 5% and 1% probability levels, respectively.

Dwarf near-isogenic lines produced as many tillers per plant as their tall counterparts in most of the pairs except in four pairs in which dwarf near-isogenic lines had significantly more tillers per plant than their tall counterparts, and in one pair, the tall near-isogenic line had more number of tillers than its dwarf counterpart. Days to 50% flowering and seed weight were least affected by height modification due to d_2 dwarfing gene. Substantial differences were found among the lines both for days to flowering (49–64 d for tall; 48–63 d for dwarf), and for 1000 seed weight (5.3–8.5 g for tall and 5.1–8.4 g for dwarf) (Tables 3, 4). However, the difference between tall and dwarf near-isogenic lines for seed weight exceeded 10% in only one out of seven pairs for which the differences were significant, and were within 5% for days to flowering in eight pairs for which the differences were significant. Excluding plant height (the primary character affected by the d_2 dwarfing gene), the difference between tall and dwarf near-isogenic lines was significant for at least one character in all the pairs and in only one pair for all the six characters. The difference between tall and dwarf near-isogenic lines was significant for four characters in four pairs, for three characters in five pairs, and for two characters in one pair.

Discussion

Quantitative characters are usually controlled by a balance among polygenes. Allelic changes at major gene loci may change this balance, resulting in the modification of several quantitative traits (Atkins & Norris, 1955; Jagathesan et al., 1961; Tsunewaki & Koba, 1979). The d_2 dwarfing gene in the present study reduced the plant height of the tall near-isogenic lines by 35–53%, depending on the genetic background. Although there was no relationship between the extent of reduction in plant height and the extent of changes in other morphological characters ($P > 0.05$), grain yield and head girth of the dwarf lines were generally less and head length and tillers plant^{-1} were generally more than their tall counterparts. Days to 50% flowering, followed by seed weight, were least affected due to height modification. Whether the changes in plant characters other than height were due to the pleiotropic effects of d_2 gene, or due to linkage drag cannot be ascertained from this study. Comparisons of near-isogenic lines in maize, sorghum, wheat, barley, and oats suggest pleiotropism (Qualset et al., 1965; Casady, 1965; Lee & Brewbaker, 1984) as well as linkage drag (Brinkman & Frey, 1977; Tsunewaki & Koba, 1979) causing changes in numerous quan-

Table 4. Mean performance of tall and dwarf near-isogenic lines for grain yield components over four environments

Near-isogenic pair	Head length (cm)		Head girth (mm)		Tillers plant^{-1} (no.)		1000 seed weight (g)	
	Tall	Dwarf	Tall	Dwarf	Tall	Dwarf	Tall	Dwarf
1	24.0	22.5**	22.4	18.8**	1.5	1.3**	7.9	7.6*
2	15.0	17.0**	19.4	18.0**	1.9	2.3*	5.8	6.2*
3	18.3	18.4	17.1	17.3	1.7	1.6	6.8	6.3**
4	19.2	22.3**	15.4	15.9	2.2	2.3	6.5	6.7
5	17.2	19.3**	23.1	21.3*	1.4	1.6	6.5	6.3
6	17.9	21.2**	22.6	22.2	1.4	1.5	6.8	8.4**
7	16.7	14.4**	21.2	19.9*	1.5	1.8*	7.1	6.5*
8	21.2	21.8	22.0	19.2**	1.5	1.7**	5.3	5.1
9	17.9	16.6**	24.2	22.0**	1.7	1.7	7.1	6.8
10	16.3	19.0**	22.2	21.4	1.7	1.6	7.1	7.5*
11	22.7	26.2**	24.2	20.5**	1.5	1.6	6.5	6.4
12	22.9	20.7*	21.5	16.8**	1.3	1.6*	8.5	7.2**
Mean	19.1	20.0**	21.3	19.5**	1.6	1.7**	6.8	6.7
Dwarf (% Tall)	–	105	–	92	–	106	–	99

*, **, significant at 5% and 1% probability levels, respectively.

titative characters. Zeven et al. (1983) studied 176 near-isogenic lines in the background of 11 wheat cultivars and observed a large number of possible cases of linkage drag. The near-isogenic lines used in the present study were developed by selecting and selfing plants heterozygous at D_2/d_2 locus for seven generations. The comparison of near-isogenic lines derived from such a prolonged selfing should overcome the linkage drag effects but studies in lima bean (Harding & Allard, 1965) and wheat (Tsunewaki & Koba, 1979) have shown some linkages to persist much longer than expected during the course of the development of near-isogenic lines. Since the lines used in this study were not completely isogenic, the difference between them for characters other than plant height could also be due partly to minor genetic differences at other loci.

Genotype-dependent differences between tall and dwarf near-isogenic lines for several characters indicate that changes in these characters associated with height changes due to d_2 gene can be greatly modified by manipulating the genetic background. For instance, the average grain yield of dwarf near-isogenic lines varied between 63–113% of their tall counterparts. In 4 of the 12 pairs, dwarf near-isogenic lines yielded not less than 96% of their tall counterparts.

Most mutants are initially deleterious, having adverse effects on characters of economic importance and survival values. A pertinent question then is whether these mutants are deleterious because of their inherent physiological deficiencies, or because they appear less efficient than normal types in an already well-integrated normal genetic background which can be altered to make them more efficient and productive. Results of this study indicate that with the d_2 gene, perhaps, the latter is true. Barley breeding work at Minnesota (Ali et al., 1978) shows that in the early part of the program, dwarfs were dramatically inferior to their tall counterparts for grain yield. It was, however, possible through the manipulation of the genetic background to increase the yielding ability of dwarf lines. A comparison of tall and dwarf versions of seven pearl millet composites of diverse origin developed at ICRISAT showed no difference in the grain yields of tall and dwarf bulks in five composites (K.N. Rai, unpublished). In the background of two tall composites, both of Nigerian origin, dwarf versions yielded significantly more than their tall counterparts.

The association of dwarfism with lower seed weight (e.g., Ali et al., 1978; Joppa, 1973; Casady, 1965) is stated to be a common phenomenon causing low-yielding ability of dwarf genotypes in cereals. The present study shows that seed weight was one of the traits least affected by dwarfism. The relative seed size and yielding ability of tall and dwarf near-isogenic lines, however, need further investigation under varying agronomic situations. The availability of near-isogenic lines now in diverse genetic background provides appropriate materials to conduct agronomic and physiological studies with these genotypes or on near-isogenic hybrids which could be developed by crossing these near-isogenic lines on d_2 dwarf male-sterile lines.

References

Ali, M.A.M., S.O. Okiror & D.C. Rasmusson, 1978. Performance of semi dwarf barley. Crop Sci. 18: 418–422.

Appa Rao, S., M.H. Mengesha & C. Rajagopal Reddy, 1986. New sources of dwarfing genes in pearl millet (*Pennisetum americanum*) Theor. Appl. Genet. 73: 170–174.

Atkins, I.M. & M.J. Norris, 1955. The influence of awns on yield and certain morphological characters of wheat. Agron. J. 47: 218–220.

Brinkman, M.A. & K.J. Frey, 1977. Growth analysis of isoline-recurrent parent grain yield differences in oats. Crop Sci. 17: 426–430.

Burton, G.W. & J.C. Fortson, 1966. Inheritance and utilization of five dwarfs in pearl millet (*Pennisetum typhoides*) breeding. Crop Sci. 6: 69–72.

Casady, A.J., 1965. Effect of a single height (Dw) gene of sorghum on grain yield, grain yield components, and test weight. Crop Sci. 5: 385–388.

Gupta, S.K., M.N. Premachandran & R.N. Choubey, 1985. Inheritance of a new dwarfing source in pearl millet. Z. für Pflanzenzchtg. 94: 255–258.

Harding, James & R.W. Allard, 1965. Genetic variability in highly inbred isogenic lines of the lima bean. Crop Sci. 5: 203–206.

Jagathesan, D., C. Bhatia & M.S. Swaminathan, 1961. Effect of induced awn mutation on yield in wheat. Nature 190: 468.

Joppa, L.R., 1973. Agronomic characteristics of near-isogenic tall and semidwarf lines of durum wheat. Crop Sci. 13: 743–746.

Lee, M.H. & J.L. Brewbaker, 1984. Effects of brown midrib-3 on yields and yield components of maize. Crop Sci. 24: 105–108.

Qualset, C.O., C.W. Schaller & J.C. Williams, 1965. Performance of isogenic lines of barley as influenced by awn length, linkage blocks and environment. Crop Sci. 5: 489–494.

Thakare, R.B. & B.R. Murty, 1972. Effect of dwarfing genes on combining ability in pearl millet (*Pennisetum typhoides* (Burm f.) Stapf and CE Hubb). Indian J. Agric. Sci. 42: 392–397.

Tsunewaki, K. & T. Koba, 1979. Production and genetic characterization of the co-isogenic lines of a common wheat *Triticum aestivum* cv. S-615 for ten major genes. Euphytica 28: 579–592.

Zeven, A.C., D.R. Knott & R. Johnson, 1983. Investigation of linkage drag in near isogenic lines of wheat by testing for seedling reaction to races of stem rust, leaf rust and yellow rust. Euphytica 32: 319–327.