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New sources of dwarfing genes in pearl millet (*Pennisetum americanum*) *

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Summary. Thirteen naturally occurring dwarf lines of pearl millet [*Pennisetum americanum* (L.) Leeke], identified from the world collection, varied for several morphological and agronomic characters. Extreme dwarfs were characterized by a tufted growth habit which could be distinguished from the time of germination, while the other dwarf lines could be distinguished only after anthesis. The F_1 hybrids between the tall and dwarf genotypes were tall, indicating that dwarfness is a recessive trait. In 10 out of the 13 crosses, the F_2 segregation ratio was three tall to one dwarf (3:1) suggesting that the dwarfness is controlled by a single recessive gene, while the height differences in 3 of the dwarfs (IP 8056, IP 8210 and IP 8214) were controlled by more than one gene as they showed continuous variation for plant height in F_2. When the remaining 10 single gene dwarfs were crossed to either d_1 ('Tift 238') or d_2 ('Tift 23 DB') dwarfs, only 2 crosses produced tall F_1 hybrids and they segregated for height in F_2 indicating that these 2 dwarfs are non-allelic to d_1 and d_2. Reciprocal crosses of these 2 dwarfs produced tall F_1 hybrids and showed a dihybrid segregation of 9:3:4 in F_2 indicating that the dwarfing genes of these 2 parents are non-allelic to each other. These non-allelic dwarfs were assigned the gene symbols d_3 (IP 10401), and d_4 (IP 10402).

Key words: Pearl millet – Dwarfs – Inheritance – Complementary genes – Allelic relationship

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Introduction

The identification and utilization of dwarfing genes in cereals enabled breeders to develop lodging resistant, high-yielding cultivars in rice and wheat (Athwal 1971).

Burton and Fortson (1966) reported the inheritance of dwarfness in five different dwarfs of pearl millet [*Pennisetum americanum* (L.) Leeke]. They found that dwarfness in lines D1 and D2 is controlled by either one or two recessive genes (d_1 and d_2) while in lines D3, D4, and D5 by more than two recessive genes. The d_2 dwarfing source has been widely used by breeders. It reduces height by nearly 50% by shortening all the internodes except the peduncle. The dwarf derivatives developed from the crosses made between Indian local tall cultivars and d_2 dwarfing source possessed such desirable characters as erect growth habit, upright leaves, and long compact heads (Bakshi et al. 1966). The d_2 dwarfing gene had no adverse effect on general combining ability for yield attributes in pearl millet (Murty and Tiwari 1967; Thakare and Murty 1972a, b; Chantèreau and Etassé 1976). Additional dwarfs have been reported but their inheritance is not known (Venkateswarlu and Mani 1973; Sangave 1978; Minocha et al. 1980; Koduru and Krishna Rao 1983).

Thirteen naturally occurring dwarf lines were identified from the world collection of pearl millet maintained at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), P.O. Patancheru, Andhra Pradesh. This paper reports on the mode of inheritance of dwarfness, the allelic relationships of the new dwarfing genes with the d_1 and d_2 genes and among themselves.

Materials and methods

All dwarf lines except IP 8210 and IP 8214 were found as segregants from the tall landrace populations assembled from six countries (Table 1). All the dwarf lines bred true in subsequent generations and were maintained by selfing. Culm length and leaf characteristics were considered to classify the dwarfs as semi-dwarfs, dwarfs and extreme dwarfs. The observations for different characters were recorded as per the standard pearl millet descriptors (IBPGR/ICRISAT 1981). The tall parent IP 3122 was used to determine inheritance of the dwarf stature. For studying the allelic relationships, 'Tift 23 DB' and 'Tift 238' were used as the testers for the d_2 and d_1 genes, respectively. Each of the 13 dwarf lines were crossed with 'Tift 23 DB' to determine allelism with the d_2 gene. Dwarf lines which turned out to be non-allelic to d_2 were crossed with 'Tift 238' (d_1) and dwarfs which turned out to be non-allelic to d_2 and d_1 were intercrossed among themselves. F_2 segregation for culm length was used to study the mode of inheritance of the dwarf lines and Chi-square analyses were used to determine goodness-of-fit to theoretical ratios. Complementation for plant height was used to determine the allelic nature of the dwarfing genes. Only single gene dwarf lines were assigned gene symbols, while 2 other dwarfs which showed complementation for height were not assigned gene symbols as the differences in height were controlled by more than one gene.

Results and discussion

Thirteen dwarf lines were characterized by reduced plant height at maturity as well as reduction in leaf blade length. They showed considerable variation for flowering, length of culm, peduncle and spike, tiller number, length and width of leaf blade, grain number and 1,000 grain weight (Table 1). The reduced plant height was mainly due to reduced length of the basal internodes and not to the reduction in the number of internodes as reported in other crops (Govil et al. 1981).

Classification of the dwarfs

Semi-dwarfs. The length of culm and peduncle of these lines is about one metre. These resemble tall lines till flowering. The height differences became clear only after anthesis. The lines included in this category are IP 8056 (Fig. 1), IP 8210 and IP 8214 (Fig. 2).

Dwarfs. The culm and peduncle length measures about 50 cm. These are indistinguishable from the tall lines till flowering. The lines grouped in this category are IP 8008, IP 8058, IP 8112, IP 8157, IP 8208, IP 8227, IP 8228, IP 10399, 'Tift 23 DB' and 'Tift 238'.

Extreme dwarfs. They can be distinguished from others by their tufted growth habit due to shortening of the internodes and leaf sheaths near the base of the plant. They produce very short, dark green leaves and tiller profusely. They are distinguishable from the time of germination by their reduced coleoptile length and broad, short, thick and dark green leaves. They are both male and female fertile but seed set is very poor as in IP 10401 (Fig. 3) and IP 10402 (Fig. 4).

Inheritance

All the dwarf lines when crossed with tall IP 3122 as either male or female parent produced tall F_1 plants indicating that dwarfness is a recessive character. In the F_2 generation, 3 types of segregation for plant height were observed (Table 2). In type 1 segregation, plant height was continuous from tall to dwarf. Classification of F_2 segregants either as tall or dwarf was not possible. The dwarfs IP 8056, IP 8210 and IP 8214 showed this type of segregation and the dwarfness in these lines is not controlled by a single gene. Similar results were earlier reported by Burton and Fortson (1966).

In type 2 segregation, dwarf plants were indistinguishable from the tall plants until flowering or anthe-

Table 1. Morphological and agronomic characteristics of newly identified dwarf lines of pearl millet

Identity	Origin	DFL	LBL (cm)	LBW (mm)	TT (no.)	CL (cm)	PDL (cm)	SPL (cm)	GNS (no.)	GWT (g/1,000)
T 23 DB	USA	52	31.8	17.2	4.0	22.5	19.0	14.7	1,440	6.3
T 238	USA	54	53.0	28.0	5.0	43.0	24.0	24.0	2,254	4.1
IP 8008	India	55	32.6	33.0	3.0	16.2	29.0	19.4	1,527	5.5
IP 8056	Niger	59	58.0	36.0	1.0	45.0	21.0	79.4	3,174	10.9
IP 8058	Niger	70	41.8	27.0	2.2	41.0	20.4	19.0	1,603	5.2
IP 8112	Senegal	73	42.8	25.0	2.3	42.4	21.8	21.4	1,670	5.8
IP 8157	Cameroun	80	46.0	30.4	3.0	32.4	26.1	38.4	2,460	5.5
IP 8208	Uganda	59	45.6	29.0	4.5	30.7	16.3	13.6	750	7.5
IP 8210	India	61	47.0	24.0	2.0	66.3	19.9	20.1	1,688	5.4
IP 8214	Mauritania	54	55.6	27.0	2.0	93.3	20.0	6.4	985	4.1
IP 8227	ICRISAT	73	52.4	30.2	2.0	10.8	11.0	20.9	679	4.6
IP 8228	ICRISAT	51	35.0	32.0	5.0	15.6	19.9	14.2	934	5.5
IP 10399	ICRISAT	63	44.8	30.0	2.5	38.9	21.2	21.5	2,585	5.5
IP 10401	India	70	22.6	20.0	5.0	8.6	5.0	9.2	235	4.5
IP 10402	ICRISAT	71	24.2	14.0	4.0	2.0	16.5	10.1	108	3.9

DFL = Days to 50% flowering; LBL = Leaf blade length; LBW = Leaf blade width; TT = Total tillers; CL = Culm length; PDL = Peduncle length; SPL = Spike length; GNS = Grain number/spike; GWT = Grain weight
SE was very minimum within a line

Figs. 1 and 2. Semi-dwarfs: **1** IP 8056 with very long spikes; **2** IP 8214 with very short globose spikes

Table 2. Segregation for plant height in the F_2 populations of the crosses of dwarfs with IP 3122, a tall parent

Cross Dwarf × IP 3122	F_2 plants (no.)		χ^2 3:1	P-value
	Tall	Dwarf		
'Tift 23 DB'	392	123	0.342	0.5–0.7
IP 8008	351	114	0.058	0.8–0.9
IP 8056	Continuous			
IP 8058	538	173	0.169	0.5–0.7
IP 8112	358	123	0.084	0.7–0.8
IP 8157	531	169	0.274	0.5–0.7
IP 8208	403	124	0.608	0.3–0.5
IP 8210	Continuous			
IP 8214	Continuous			
IP 8227	364	117	0.117	0.7–0.8
IP 8228	398	139	0.224	0.5–0.7
IP 10399	327	105	0.111	0.7–0.8
IP 10401	278	87	0.264	0.5–0.7
IP 10402	215	65	0.476	0.3–0.5

sis and then internode elongation took place in the tall plants and the height differences became conspicuous. The F_2 populations of dwarfs IP 8008, IP 8058, IP 8112, IP 8157, IP 8208, IP 8227, IP 8228, IP 10399 and 'Tift 23 DB' showed this type of segregation. The tall and dwarf plants segregated in a 3 : 1 ratio.

In type 3 segregation, plant height in the F_2 generation was discontinuous and two distinct height classes were observed. Intermediate plant height segregants were not observed in these F_2 populations. The tall and dwarf plants segregated in a 3 : 1 ratio indicating that plant height is conditioned by a single recessive gene. Reduced culm length, tufted growth habit and dark green leaf characters were associated with reduced plant height indicating the pleiotropic effect of the height gene. Internode length was greatly reduced and therefore these lines are considered as extreme dwarfs (IP 10401 and IP 10402). All the F_2 dwarf segregants bred tue in the F_3 generation.

Figs. 3 and 4. Extreme dwarfs: **3** IP 10402 with condensed internodes and poor spike exsertion; **4** IP 10402 with tufted growth habit and good spike exsertion

Allelic relationships with d_2 and d_1

Of the 13 F_1 hybrids between the newly identified dwarf lines and d_2, only 4 were tall while the remaining 9 were dwarf (Table 3). In all 13 crosses, the F_1's were somewhat taller than the dwarf parents which could be due to heterosis.

The F_2 populations of the crosses which produced tall F_1 plants segregated for tall : dwarf in a 9 : 7 ratio or for tall : dwarf1 : dwarf2 in a 9 : 3 : 4 ratio suggesting complementary action for plant height. As the 2 parental dwarfs (IP 10401 and IP 10402) have distinct morphological characters, it was possible to differentiate the parental dwarfs even in the segregating populations, and when the F_2 populations were classified as tall and the 2 parental dwarf types, the segregation ratio of 9 : 3 : 4 was observed (Table 3). The 2 dwarfs (IP 8056 and IP 8214) which showed continuous variation for plant height when crossed to tall parent (Table 2) were not assigned any gene symbol as the height differences in them were due to more than one gene. The remaining single gene dwarfs (IP 10401 and IP 10402) were considered to be non-allelic to d_2.

When these 2 dwarfs were crossed to d_1 dwarf, both the crosses produced tall F_1 hybrids. The F_2 populations segregated for tall : dwarf1 : dwarf2 in a 9 : 3 : 4 ratio (Table 4) suggesting complementary gene action for plant height. The F_1 behaviour and the F_2 segregation clearly suggest that the dwarfing genes in these 2 lines are non-allelic to d_2 and d_1.

Intercrosses of these 2 dwarfs (which are non-allelic to d_2 and d_1) produced tall F_1 hybrids. The F_2 populations segregated distinctly for plant height and the plants were easily classified as tall (352), dwarf1 (126) or dwarf2 (152) which showed a good fit for 9 : 3 : 4 ratio (P-Value 0.5–0.7). The F_2 segregation ratio of 9 : 3 : 4 and the occurrence of tall F_1 hybrids when the dwarfs were intercrossed indicate that these dwarfing genes are non-allelic to each other.

Though several dwarfs were reported in pearl millet (Koduru and Krishna Rao 1983), only two dwarfs were assigned gene symbols d_1 and d_2 (Burton and Fortson 1966). In continuation of these gene symbols, the newly identified dwarfing genes may be designated as d_3 (IP 10401) and d_4 (IP 10402).

Table 3. Mean F_1 height and F_2 segregation for height in crosses of 'Tift 23 DB' (d_2 dwarf) with 13 newly identified dwarf lines

Cross Dwarf×d_2	Mean F_1 height (cm)	F_2 plants (no.) Tall	Dwarf 1	Dwarf 2	Ratio	χ^2	P-value	Allelic relation to d_2
IP 8008	95	0	368	0	–	–	–	d_2
IP 8056	205	278	203	0	9:7	0.467	0.3–0.5	?
IP 8058	102	0	412	0	–	–	–	d_2
IP 8112	98	0	348	0	–	–	–	d_2
IP 8157	90	0	515	0	–	–	–	d_2
IP 8208	87	0	426	0	–	–	–	d_2
IP 8210	115	0	458	0	–	–	–	?
IP 8214	205	235	187	0	9:7	0.054	0.8–0.9	?
IP 8227	80	0	371	0	–	–	–	d_2
IP 8228	92	0	402	0	–	–	–	d_2
IP 10399	115	0	362	0	–	–	–	d_2
IP 10401	195	272	095	131	9:3:4	0.603	0.7–0.8	?
IP 10402	200	256	083	109	9:3:4	0.156	0.9–0.95	?

Table 4. Mean F_1 height and F_2 segregation for height in crosses of 'Tift 238' (d_1 dwarf) with 4 dwarfs which showed complementation for height to d_2 dwarf

Cross	F_1 height (cm)	F_2 plants (no.) Tall	Dwarf 1	Dwarf 2	Ratio	χ^2	P-value
d_1 × IP 8056	226	141	110	0	9:7	0.001	0.95–0.98
IP 8056 × d_1	225	96	85	0	9:7	0.758	0.3 –0.5
d_1 × IP 8214	120	0	172	0	–	–	–
IP 8214 × d_1	115	0	155	0	–	–	–
d_1 × IP 10401	185	58	18	23	9:3:4	0.237	0.8 –0.9
IP 10401 × d_1	173	98	36	43	9:3:4	0.298	0.8 –0.9
d_1 × IP 10402	184	30	11	14	9:3:4	0.079	0.95–0.98
IP 10402 × d_1	175	121	43	52	9:3:4	0.230	0.8 –0.9

Possible utilization

These dwarfs possess several agronomically desirable characters. The long spikes of IP 8056, early maturity of IP 8214, long dense bristles of IP 8227, profuse synchronous tillering of IP 8157, IP 8228 and IP 10401 are the additional merits of these dwarf lines. In pearl millet improvement, only d_2 gene has been extensively used to reduce culm length. The availability of new dwarfing genes possessing one or more desirable agronomic traits offers scope for diversifying dwarfing sources in pearl millet improvement.

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