Plant Breeding **111**, 306—311 (1993)

ISSN 0179-9541

A Test of the "Tall-Dwarf" Hypothesis in Pearl Millet, *Pennisetum glaucum* (L.) R. Br.

F. R. Bidinger and D. S. Raju

International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502 324, India

With 1 figure and 3 tables

Received February 17, 1993 / Accepted April 26, 1993
Communicated by F. G. H. Lupton

Abstract

Positive height-grain yield relationships exist for many cereals, but cannot be fully used in breeding because of lodging and harvestability problems in tall cultivars. Law et al. (1978) proposed a "tall-dwarf" hypothesis for wheat, in which the positive effects of minor height genes could be exploited by selecting for them in a major dwarfing gene background. The applicability of this hypothesis to pearl millet was tested by crossing a set of dwarf S_1 progenies (from a single population) which varied in height onto two male-sterile lines. Mean (by S_1 pollinator) hybrid grain yield was closely related to mean hybrid height ($r^2 = 0.60$) over a range of mean yields of 3.0—3.9 t ha^{-1} and a range of mean heights of 126—165 cm. The effect of height was expressed as an increase in grain number in one cross and as an increase in grain mass in the other, indicating the importance of background genetic effects on yield-height relationships in dwarf hybrids. The concept of "tall-dwarfs" appears to be applicable to pearl millet.

Key words: *Pennisetum glaucum* — grain yield — plant height — dwarf hybrids

The relationship between height and grain yield in cereals depends upon the action of both major and minor genes affecting plant height. The action of the minor genes results in a general, positive relationship of height and yield, which has been reported in a number of cereals: bread wheat (Dyck and Baker 1975, Flintham and Gale 1983), barley (Riggs and Hayter 1975), durum wheat (Gale et al. 1981, Joppa 1973), and pearl millet (Jindla and Gill 1984, Rattunde et al. 1989). The practical agronomic limitations to the exploitation of this relationship, however, have meant that selection has historically been for intermediate height rather than tall phenotypes (Law et al. 1978).

Most cereal species also contain major dwarfing genes which cause large reductions in plant height. In bread wheat several of these genes have a positive pleiotropic effect on grain yield (Gale and Youssefian 1985, Fischer and Quail 1990) and have been widely used in plant breeding in the past 20 years. There is less evidence for significant positive effects of major dwarfing genes on yield in barley (Ali et al. 1978, Zahour et al. 1987) or durum wheat (Joppa 1973, McClung et al. 1986). In sorghum (Campbell et al. 1975, Windscheffel et al. 1973) and pearl millet (Bidinger and Raju 1990, Rai and Rao 1991), dwarfing genes have generally negative effects on grain yield. Nevertheless they are widely used in breeding because of the improved lodging resistance and/or mechanical harvestability they offer. Law et al. (1978) proposed a "tall-dwarf" model for bread wheat to combine the benefits of the *rht* genes for reduced height with the positive relationship of yield and minor height genes found in their studies. In this model they proposed fixing dwarfing gene(s) in populations at an early stage, followed by positive selection for

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Journal article No. 1210 of the International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502 324, India.

height in subsequent generations. Several subsequent experiments (GALE et al. 1981, FLINTHAM and GALE 1983) have confirmed the basis of this hypothesis, but there have been reports of exceptions (FISCHER and QUAIL 1990).

Although there is no evidence of a general positive effect on yield by the common d_2 dwarfing gene in pearl millet, the dwarf phenotype is very attractive for more intensive management systems and is therefore of considerable interest to plant breeders. As there is evidence of a positive yield-height relationship in pearl millet, the "tall-dwarf" model may thus also be applicable to this crop. The objective of this research was to test this hypothesis using a series of dwarf hybrids made with a set of dwarf S_1 progenies (from a single composite) which differed in height, presumably due to the presence of minor genes, as pollinators.

Materials and Methods

Genetic materials: The relationship of height and grain yield was evaluated in two sets of 28 d_2 dwarf (BURTON and FORTSON 1966) F_1 hybrids. These were made by crossing a set of 28 S_1 d_2 lines selected for a range in height on two d_2 male-sterile lines. The dwarf S_1 lines were selected from the dwarf version of the Nigerian Composite created by backcrossing the d_2 gene into the standard height version of the composite (RAI 1990). Approximately 1000 S_0 plants were grown in a spaced (0.75 × 0.50 m) planting in the rainy season of 1985. The main panicle of all plants was selfed, height to the base of the main panicle was measured on the main culm, and flowering date and panicle number per plant were recorded.

The height distribution of the S_0 plants was divided into 10 equal classes and seven progeny selected from each class, based on a criterion of having time to flowering and fertile tiller number similar to the overall population mean. These were grown in replicated (3) two-row plots in the rainy season of 1986; mean progeny height, uniformity, flowering time, and panicle length and number were recorded. Three S_1 progenies were then selected from each height class on the basis of similarity to the overall population mean for panicle length and number and flowering time. Remnant seed of these progenies was sown in the 1986/87 dry season and 28 of the lines crossed onto dwarf male-steriles 833A and 81A. This produced a set of 56 F_1 dwarf hybrids with a range from 118 to 170 cm height (stem length).

Hybrid evaluation: The hybrids were grown during the rainy seasons of 1987 and 1988 at ICRISAT Center, Patancheru, India in four row plots 4 m long in three (1988) or four (1987) replications, with normal (0.75 × 0.10 m) plant spacing. The trials were adequately fertilized (80 kg N and 25 kg P per ha) and one supplemental irrigation was given in 1987 to avoid drought stress. Observations on time to flowering, height, panicle number and grain yield were recorded on the center 3 m of the two central rows of each plot, to assure that there were no competition effects from neighboring plots of different height (FISCHER 1979). Height was measured by holding a 3 m long rod at the (visually) estimated mean height to the base of the panicle and measuring the vertical distance from the soil surface to the rod. Grain yield was measured by harvesting and threshing the entire sample area (4.5 m^2). Triplicate 100 grain samples from the bulk threshed grain of each plot were used to calculate mean mass per grain and grain number per panicle.

Data were analyzed over the two years, considering replicates as nested within year. The sums of squares for hybrid were partitioned into effects of male-sterile (A line), S_1 pollinator (R line) and their interaction. The R line effect was partitioned into an effect of height (1 df) and the residual (26 df) by regression of R line mean (across hybrids and years) value for each variable on R line mean (across hybrids and years) height. The magnitude of the relationship of height with yield and yield component variables was also assessed by correlation analysis for each set of hybrids (i.e. for each A line mean) and for the mean R line effect.

Results

Growing conditions were near-optimum in 1987, resulting in a trial mean yield of 399 g m^{-2}; yield in 1988 was lower at 277 g m^{-2} (Table 1). Year differences were significant for all yield components (Table 2). There were also small, but significant differences on grain yield between the hybrids produced in the two A lines, primarily associated with the higher grain numbers per panicle on the later-flowering and taller 81A hybrids (Tables 1 and 2).

The range among R line means (means across years and hybrids) was significant for all variables (Tables 1 and 2). Selection for height among the original S_1 lines was effective in producing a significant range in stem length among the R line means (126 to 165 cm, SE = 0.8). The range in R line mean grain yield (301 to 390 g m^{-2}) and in most yield components was as broad as that in height. The range in time to flowering was considerably more restricted (4 days), and differences in height and

Table 1. Mean effects of year, A line (averaged over years and R lines) and R line (averaged over years and A line) on yield components, height and time to flowering

	Year means		A line means		R line means
Variable	1987	1988	81A	833A	range
Grain yield (g m^{-2})	399	277	355	337	301— 390
Panicle number m^{-2}	19.4	15.8	17.9	17.7	15.9— 21.4
Grain number panicle^{-1}	2640	2400	2740	2330	2150—3020
Grain mass (mg)	8.02	7.47	7.33	7.23	6.81— 9.02
Height (cm)	147	148	155	140	126— 165
Flowering (d)	45.3	46.6	47.0	44.8	44.2— 48.6

Table 2. Mean squares for grain yield and yield components. R line effects are partitioned into a linear effect of height and the residual by regression

		Mean squares			
Source	df	Grain yield[a]	Panicle no. m^{-2}	Grain no. panicle^{-1}[a]	Grain mass
Year[b]	1	1141**	1194*	5464***	0.286**
Rep (year)	5	3.72	117	106	0.015
Hybrid	55	5.48***	14.72***	787***	0.036***
A line	1	32.52***	4.74	15747***	0.784***
R line	27	6.62***	23.15***	836**	0.036***
Height	1	108***	0.07	2919***	0.062***
Residual	26	2.72**	24.04***	756***	0.035***
A × R lines	27	3.34***	6.66	184*	0.0090***
Hybrid × year	55	1.68	5.68	131	0.0057**
Error	270	1.29	5.73	115	0.0034
CV (%)		10.4	13.4	13.4	7.8

a) Data are MS × 10^{-3}.
b) Year effect tested against replication (year) m.s.

yield and yield components among R line means were not related to differences in time to flowering.

The effect of height differences among the R lines means (tested by partitioning the sums of squares for the different variables into a linear effect of height and a residual) was significant for grain yield, grain number per panicle and grain mass (Table 2). Variation in stem height among R line means accounted for 60 % of the variation in grain yield (Fig. 1).

The effect of R line mean height was not strongly expressed through any individual yield component. The proportion of the sums of squares for mean grain number and mean grain mass which were accounted for by the regression of these variables on mean stem height was small (13 % for grain number and 6 % for grain mass). The effect of variation in height on yield components differed in the two sets of hybrids. Increased height was associated with an increase in grain mass in the 81A hybrids and with an increase in grain number per panicle in the 833A hybrids (Table 3). In neither set were there any effects of height on panicle number per unit area.

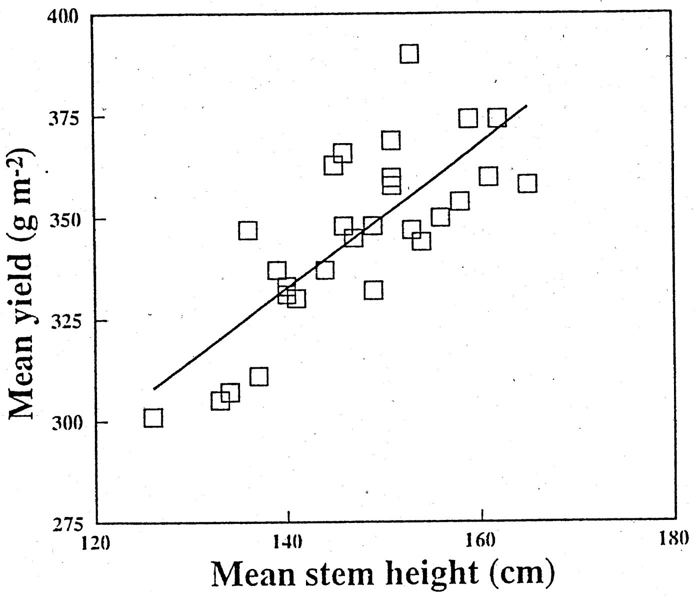

Fig. 1. Relationship of stem height and grain yield. Data are pollinator means over the two A lines and 2 years trials ($Y = 88.7 + 1.74X$; $r^2 = 0.60$; $P < 0.001$)

Table 3. Correlations of plant height with yield and yield components for 81A and 833A hybrids and for the R line means (across hybrids). Data are means of 1987 and 1988 results (n = 28)

Plant height vs.	81A hybrids	833A hybrids	R line means
Grain yield	0.48^{**}	0.84^{***}	0.78^{***}
Panicle number	0.14	−0.26	−0.01
Grain number panicle^{-1}	−0.01	0.64^{***}	0.36^{+a}
Grain mass	0.37^{*}	0.23	0.25
Days to flowering	−0.31	−0.20	−0.31

a) + = $P < 0.10$.

Discussion

The "tall-dwarf" hypothesis thus appears to be applicable to dwarf pearl millet hybrids as well as to dwarf wheat varieties. Variation in mean R line height was strongly related to grain yield in the hybrids made with them, accounting for 60 % of the mean (by R line) hybrid yield. Similar (if not always as marked) relationships of height and grain yield in dwarf genotypes have been reported in bread wheat (Law et al. 1978, Flintham and Gale 1983) and durum wheat (Gale et al. 1981, Joppa 1973).

The expression of the yield advantage in the hybrids made with the taller R lines differed depending on the specific A line used to make the hybrids. There was a much larger effect of R line height on grain yield in the 833A hybrids, than in the 81A hybrids, which was expressed as an increase in grain number per panicle (Table 3). The smaller effect of R line height in the 81A hybrids was associated only with a small change in grain mass. These differences were large enough to result in significant A × R line interactions for both yield components, as well as for grain yield (Table 2). As differences in grain yield in cereals are more often associated with differences in grain number than in grain mass, the larger effect of R line height on grain yield in the 833A hybrids is not unexpected.

The simplest explanation of differences in the associations of height and yield components in the two different A lines is that they are the expression of background genetic effects on these associations (Gale et al. 1981, Joppa 1973, Pinthus 1987). Alternatively, it is tempting to suggest that the greater effect of stem height in the 833A hybrids may have been related to the fact that they were shorter than the 81A hybrids (118—140 cm vs. 133—170 cm). In two wheat studies in which height effects have been compared in tall and semidwarf isolines (JOPPA 1973, GALE et al. 1981), the effect of increased height on yield was found to be greater in the semidwarfs than in the talls, and to be associated with an effect on grain numbers in the semidwarfs. Although this is similar to the case of the 833A vs. 81A hybrids, there is no way to distinguish between the effects of the height differences and other differences between the two A lines in this experiment.

The experiment did confirm that significant gains in grain yield should be possible through selection for increased height in dwarf hybrid parents. This procedure may in fact be more important for pearl millet than for wheat as the opportunity for significant gains in yield from the use of major dwarfing gene(s) does not appear to exist in pearl millet (BIDINGER and RAJU 1990). With the present set of R lines derived from the Dwarf Nigerian Composite, an increase in height of 10 cm in the mean R line height was equivalent to a yield gain of 175 kg ha^{-1}, over a range of 125—165 cm height, or a potential total gain of 700 kg ha^{-1}.

Zusammenfassung

Überprüfung der „Tall-Dwarf"-Hypothese für Perlhirse, *Pennisetum glaucum* (L.) R. Br.

Bei vielen Getreidearten gibt es einen positiven Zusammenhang zwischen Pflanzenhöhe und Kornertrag, der jedoch wegen Neigung zum Lager und Schwierigkeiten bei der Ernte langhalmiger Sorten in der Züchtung nicht voll genutzt werden kann. LAW et al. (1978) stellten eine „Tall-Dwarf"-Hypothese für Weizen auf, wonach die vorteilhaften Wirkungen von Minorgenen für die Pflanzenhöhe genutzt werden können, wenn auf sie bei einem Hintergrund von Majorgenen für Kurzstrohigkeit ausgelesen wird. Die Anwendbarkeit dieser Hypothese auf Perlhirse wurde aufgrund von Kreuzungsserie kurzstrohiger S_1-Nachkommenschaften (aus einer einzelnen Population) überprüft, die in der Pflanzenhöhe dem männlich sterilen Partner entsprachen. Der mittlere Kornertrag der Hybriden (bei S_1 als Bestäuber) war mit der Pflanzenhöhe eng korreliert ($r^2 = 0,60$), wobei die Durchschnittswerte für die Erträge von 3,0 bis 3,9 t/ha und für die Pflanzenhöhen von 126 bis 165 cm reichten. Bei einer Kreuzung war die Pflanzenhöhe mit einer Zunahme der Kornzahl, bei einer anderen Kreuzung mit einer Erhöhung des Korngewichts verbunden. Damit wird die Bedeutung der genetischen Hintergrundeffekte für die Beziehungen zwischen Ertrag und Pflanzenhöhe bei Kurzstroh-Hybriden deutlich. Das Konzept der „Tall-Dwarf"-Hypothese scheint auch auf Perlhirse anwendbar zu sein.

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