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PHOTOPERIODIC RESPONSE OF PARENTAL LINES AND F_1 HYBRIDS IN PEARL MILLET

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ABSTRACT

A low degree of photoperiodic sensitivity is a requirement for broad adaptation in a short-day species such as pearl millet [*Pennisetum glaucum* (L.) R. Br.]. The photoperiodic sensitivity of parental (male sterile and pollinator) lines of pearl millet and their F_1 hybrids was assessed in two experiments. Photoperiodic sensitivity was defined as delay in flowering in artificially extended daylengths of 14.5 or 15.5 h, over flowering under natural daylength of 13.9 h. Flowering time of hybrids was correlated to that of parental lines under normal and extended daylengths. The delay in midparent flowering time was a very effective predictor of hybrid delay in flowering. Line × tester analysis indicated effects of both general and specific combining ability, depending on the materials studied.

Key words: *Pennisetum glaucum*, pearl millet, photoperiodic response, adaptation.

There is considerable variation in the growing-season length across the major pearl millet growing areas both in the Indian subcontinent and in West Africa. In both cases, shorter growing seasons (8–12 weeks) are at higher latitudes, although the actual latitude of millet cultivation differs considerably between Northwest India (21–28° N) and the West African Sahel (13–15° N) [1, 2].

Pearl millet is primarily a quantitative short-day plant [3, 4]. Consequently, its flowering will be earlier in shorter than in longer daylengths (i.e., in lower than higher latitudes). This flowering habit is, thus, in direct contrast to the requirement for earlier flowering in the short-season, higher-latitude zones of both the major millet growing areas, than in the longer-season, lower-latitude zones. This presents a particular problem for materials originating from breeding programmes in the central/southern zone in India which, unless they have a low degree of photoperiodic sensitivity, are likely to flower too late to fit in the shorter seasons of the northwestern zone.

The majority of genetic studies on the photoperiodic response in pearl millet [5–9] have been conducted on crosses between materials with a quantitative photoperiodic response (Gero, Souna, "day-neutral" types) and materials with the qualitative or obligate photoperiodic response [5] found in the long-duration, West African millet growing zones (Maiwa, Sanio, "short day" types). These studies suggest that

photoperiodic response is either under additive genetic control [5–7], or there is partial dominance for the quantitative response [6, 8, 9]. The only study of a cross among solely quantitative photoperiod-response types, in which the progenies were evaluated under varying daylengths, also suggests that photoperiodic response is largely under additive genetic control [3].

This paper reports studies on photoperiodic response in a broad range of parents (cytoplasmic male sterile lines and pollinators) and their F_1 hybrids. It also presents additional data on the nature of genetic control of the quantitative photoperiodic response, and demonstrates that the photoperiodic response of F_1 hybrids can be effectively predicted from the response of the parental lines used in making the hybrids.

MATERIALS AND METHODS

ASSESSMENT OF PHOTOPERIODIC RESPONSE

Photoperiodic response was assessed by measuring the delay in time to flowering under extended daylengths of approximately 15.5 h (Experiment I) or 14.5 h (Experiment II), compared to flowering under 13.9 h, which is the normal daylength at the ICRISAT Center (17° N) in mid-July when the pearl millet crop sown in late June reaches floral initiation. The 14.5 h treatment is the daylength in mid-July at 26° N, the center of the major millet growing zone in Northern India, and the 15.5 h treatment is the daylength at 36° N, representing the potential pearl millet growing area in the temperate semi-arid zone.

The extended daylength of 15.5 h (Experiment I) was arranged by providing an additional 1.4 h (1984) or 1.6 h (1985) of light to field-grown crops, using 100 W incandescent bulbs fixed on a grid of 3×5 m at a height of 1.5 m above the soil surface. (The difference between years resulted from a miscalculation of daylength in 1984; but it does not seem to have affected the results.) This arrangement of bulbs provided a minimum light intensity (visible spectrum) of 15–20 lux at crop height, which is above the response threshold of 10–12 lux for pearl millet. In 1984, the daylength was extended in the evening only whereas in 1985 it was extended by approximately equal periods in the morning as well as in the evening. The extended daylength of 14.5 h in both years in Experiment II was given by extending the day by an additional 0.6 h in the evening only. Other procedures were similar to Experiment I.

Flowering was recorded when stigmas on 50% of the main panicles per plot had emerged, and expressed as days from crop emergence (approximately 3 days after sowing). Daily mean temperatures during the experimental period (June 15–August 30) were 26.4, 26.4, and 26.2°C in 1984, 1985, and 1986, respectively.

EXPERIMENTAL MATERIALS

Experiment I consisted of 11 pollinators from diverse genetic backgrounds with varying degree of photoperiodic sensitivity, 2 widely used male sterile lines (81A and 5141A), and 22 hybrids produced by crossing each pollinator with both male

sterile lines (Table 1). They were sown under both normal and extended daylengths (adjacent blocks in the same field) in randomized complete block designs with two replications in the rainy seasons of 1984 (13 June) and 1985 (20 June) at ICRISAT Center. Each plot was a single 4 m row in 1984 (40 plants) and a single 2 m row (20 plants) in 1985.

Table 1. Time to flowering in normal daylength (13.9 h) and delay in flowering in extended daylength (Expt. I: 15.5 h, Expt. II: 14.5 h) in parental lines. (Data are means of the two years)

Experiment	Time to flowering in normal daylength (days)	Delay in flowering in extended daylength (days)
Experiment I:		
Male sterile lines:		
81A	55	10
5141A	55	15
Pollinators:		
(B 282 × 3/4 EB-100-11-4)-2	53	8
(B 282 × 3/4 EB-100-6-8)-2-1-8	49	9
(B 282 × S10LB-89)-1-1-1	49	10
(LCSN 72-1-2-5 × J 104)-2-1	51	10
(J 1399 × B 282-6-1)-2-1-1	54	11
(E 298 × LCSN 72-1-2-3)-6-2-1	54	11
IPC 50-3-1-2	53	12
EB-273-3-1 × F4FC 1498-1-1-48-2-3	52	13
(5054B × F4FC 1498-1-1-4)-7-1-1-1	50	14
(5054B × F4FC 1498-1-1-2)-4-3-1	49	15
(F4FC 1498 × J 104-2)-1-1-1	49	18
SE[1]	±0.7	
CV%	3.2	
Experiment II:		
Male sterile lines:		
834A	49	4
843A	41	6
111A	54	10
81A	54	11
5141A	54	18
Pollinators:		
IP 2696-30	38	3
Souna B	56	9
J 104	46	9
SS 16	62	22
SS 14	74	(29)[2]
SE[1]	±0.9	
CV%	2.5	

[1]SE and CV% for combined set, i.e., parents and hybrids.
[2]1985 data only, line did not flower in 105 days in extended days in 1986.

Experiment II consisted of 5 diverse male sterile lines, 5 very diverse pollinators, and 25 hybrids from them (Table 1). The pollinators (primarily of West African origin) had a broad range of photoperiodic sensitivity: 3–30 days delay in flowering under extended daylength. All 35 entries were planted in 4 m single-row plots (40 plants) in randomized complete block design with four replications in the rainy seasons of 1985 (19 June) and 1986 (23 June), in adjacent normal and extended daylength blocks as in Experiment I.

STATISTICAL ANALYSIS

The predictability of photoperiodic response was tested by regression analysis of the photoperiodic response of the hybrids on that of parents. Two regression models were used; model I used the midparent value as independent variable, whereas model II included the photoperiodic response of both parents plus an interaction term:

Model I: $H = a + b\,(M)$, where H and M are the delay in flowering in the hybrid and midparent, respectively; and a and b are the intercept and regression coefficient, respectively.

Model II: $H = a + b(A) + c(P) + d(A \times P)$; where H, A, and P are the delay in flowering in the hybrid, male sterile line and pollinator, respectively; a is the intercept; and b, c, and d are the regression coefficients.

The genetic architecture of photoperiodic response was evaluated by a line × tester analysis, following the method of Kempthorne [10]. Male sterile lines in both experiments were used as testers, which resulted in a 11 lines × 2 testers set for Experiment I and 5 lines × 5 testers set for Experiment II.

RESULTS AND DISCUSSION

PHOTOPERIODIC RESPONSE OF PARENTAL LINES

The two male sterile lines used in Experiment I, 81A and 5141A, were significantly different in their response to photoperiod. Both flowered in 55 days under normal daylength but 5141A was delayed by 5 days more than 81A (15 v. 10 days) under extended daylength (Table 1). Two of the male sterile lines used in Experiment II, 843A and 834A, had significantly lower photoperiodic responses (4 and 6 days delay in flowering) than either 81A or 5141A which were delayed by 11 and 18 days, respectively. The fifth male sterile line used in Experiment II, 111A, had flowering time and photoperiodic response similar to 81A.

All the pollinators in Experiment I flowered within a span of 5 days (49–54 days) under normal (13.9 h) daylength but were delayed by 8–18 days under extended daylength (Table 1). In contrast, the pollinators tested in Experiment II were more diverse, flowering in 38–74 days under normal daylength, and ranging from least sensitive (IP 2696–30) to highly sensitive (SS 14) (Table 1).

PHOTOPERIODIC RESPONSE OF HYBRIDS

The daylength response of individual hybrids was closely related to that of their parents in both experiments. For example, there was a mean difference of 4 days in photoperiodic response between the hybrids on 81A and on 5141A in Experiment I (Fig. 1); reflecting the difference of 5 days in response between the two male sterile lines. Similarly, the photoperiodic response of each of the two sets of hybrids in this experiment was related to that of the pollinators ($r = 0.74$, $P < 0.01$ for the hybrids of 5141A and $r = 0.80$, $P < 0.01$ for those of 81A) (Fig. 1).

The two regression models of photoperiodic response in the hybrids predicted an average of approximately 70% of the observed variation in photoperiodic response of the hybirds for individual year data and, as expected, somewhat better for the mean data (Table 2). There was little difference in the performance of the two models; the midparent model was equally effective as the more complex model involving individual-parent and interaction effects (Table 2). Even in Experiment II, where the parents varied widely in their daylength response, the midparent value was a good general predictor of daylength response of the hybrids (Fig. 2). There was no evidence of deviation from the general pattern for any of the male sterile lines (not shown in Fig. 2). The least sensitive (IP 2696–30) and most sensitive (SS 14) pollinators did tend to produce less and more sensitive hybrids than the midparent levels of sensitivity, respectively (Fig. 2).

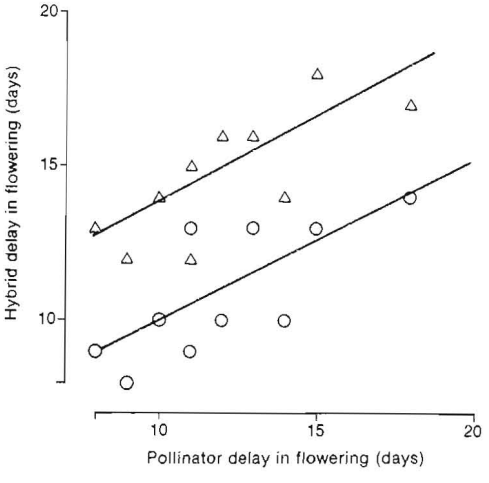

Fig. 1. Delay in flowering under extended daylength in hybrids of 81A (○) and 5141A (△) in relation to the delay in flowering in the pollinators. Data are means of 2 years, Experiment I.

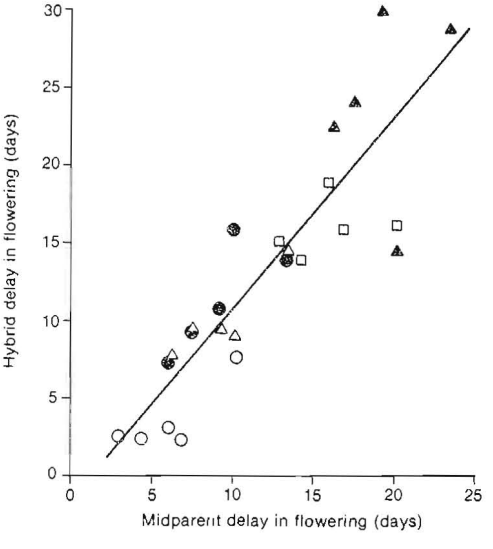

Fig. 2. Delay in flowering under extended daylength in 25 hybrids, in relation to the midparent delay in flowering. Data are for 1986, Experiment II. Symbols identify the pollinators: IP 2696–30 (○), J 104 (●), Souna B (△), SS 14 (▲), and SS 16 (□).

Table 2. Regression intercept (a) and coefficient (b), and coefficients of determination (r^2, R^2) of regression prediction of photoperiodic response in pearl millet hybrids (see text for explanation of models)

	Model I			Model II
	a ± SE	b ± SE	r^2	R^2
Experiment I:				
1984	− 2.16 ± 2.935	1.27 ± 0.257	0.52***	0.64***
1985	+ 0.27 ± 1.833	1.04 ± 0.143	0.71***	0.68***
Mean	− 2.64 ± 1.956	1.26 ± 0.158	0.75***	0.75***
Experiment II:				
1985	− 0.58 ± 2.114	1.13 ± 0.159	0.69***	0.74***
1986	− 1.34 ± 1.601	1.18 ± 0.119	0.81***	0.84***
Mean	− 1.16 ± 1.736	1.17 ± 0.130	0.78***	0.82***

***Significant at 0.001 level.

The results of line × tester analysis differed in the two experiments but were quite consistent across the years. The effects of both the lines and testers were highly significant and that of line × tester interaction was nonsignificant in both years in Experiment I (Table 3). All three effects were, however, highly significant in both years of Experiment II. While the contribution of testers was more than that of lines in Experiment I, the reverse was true in Experiment II. Estimates of variances due to general combining ability (σ^2 gca) and specific combining ability (σ^2 sca) indicated that the genetic variance in the set of lines in Experiment I, which consisted of less diverse material was entirely accounted for by σ^2 gca, whereas the genetic variance in Experiment II, which contained widely diverse lines, was accounted for by both σ^2 gca and σ^2 sca, although the latter was higher in magnitude. Thus, the relative importance of additive and nonadditive genetic variances was greatly influenced by the genetic diversity of the materials.

IMPLICATIONS FOR BREEDING

The high degree of predictability of photoperiodic response indicates that it should be relatively easy to produce hybrids with a low degree of photoperiodic sensitivity, once parental lines with low sensitivity are identified. Even the use of less sensitive male sterile lines alone will provide some advantage (Fig. 1) but to produce hybrids with minimum sensitivity, both parents should have low photoperiodic response (Fig. 2).

Photoperiodic response can be easily evaluated under field conditions with an appropriate daylength extension treatment, as was done in this experiment, in a relatively low-latitude or short-day environment. The ICRISAT Cereals Program has begun such evaluation of all potential pollinators and B-lines of pearl millet in order to discard those with undesirable daylength sensitivity.

Table 3. Mean squares (MS) for photoperiodic response in individual experiments and years

Source of variation	Experiment I			Experiment II		
	d.f.	MS (1984)	MS (1985)	d.f.	MS (1985)	MS (1986)
Replications	1	9.09	11.00	3	9.96	36.33
Lines	10	15.97**	19.77*	4	888.85**	1364.62**
Testers	1	236.45**	138.27**	4	76.13**	122.42**
Lines × testers	10	3.11	0.87	16	50.92**	38.87**
Error	21	2.42	6.10	72	8.85	9.34
σ^2 gca		0.53	0.48		2.70	4.40
σ^2 sca	NS	NS			10.52	7.38

NS—Not significant.
*, **Significant at 0.05 and 0.01 levels, respectively.

It should be pointed out, however, that the actual flowering time in pearl millet is also affected by ambient temperature during the period between floral initiation and flowering [11]. The effectiveness of low photoperiodic response in reducing location effects on flowering time will, therefore, vary in different conditions. For example, with stable temperatures but different photoperiods across environments, photoperiodic response will be the major factor determining flowering time. If, however, locations with longer photoperiods also have higher mean temperatures (as is common in the semiarid tropics [2]), flowering would occur earlier in such locations than would be predicted from daylength response determined in a cooler environment. There is, however, sufficient genetic variation in pearl millet to effectively stabilize flowering time (and thus broaden the adaptive range of breeding materials) where photoperiodic response is an important factor.

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VARIATION AMONG PLANTS FOR SEED-OIL AND LINT CHARACTERISTICS OF COTTON (*GOSSYPIUM HIRSUTUM* L.)

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ABSTRACT

Variation between plants was analysed in 3 cultivars for 7 attributes relating to oil and lint productivity. Variation among plants for fibre length, number of seeds per boll, lint per seed, seed index, and seed-oil index was highly significant. Variation for lint per seed, seed index, and seed-oil index tended to be relatively higher in the oil cultivars.

Key words: Oil content, interplant variation, *Gossypium hirsutum*.

In the absence of any conscious selection for seed quality components in the past, the levels of oil and protein in seeds of present cultivars of cotton have remained largely unchanged over decades [1]. Differences existing among cotton cultivars for seed-oil and protein content are considered natural consequences of unselected characters, which can be improved through selection [2]. Variation between plants has been shown to exert sizeable influence on oil quality and quantity in some oilseed crops [3]. Adequate information on this aspect is not available in cotton. An attempt was made to assess the patterns of interplant variation in 3 cultivated varieties of *Gossypium hirsutum*, considering 7 attributes related to oil and lint productivity. The results are presented in this paper.

MATERIALS AND METHODS

L-147, B-1007, and SRT-1 are contemporary cultivars of Central Zone of cotton, with comparable levels of yield and maturity duration (200–210 days). They were grown at Nagpur (21° 26′ N and 79° 49′ E) in Central India. Boll samples were drawn from twenty plants within each cultivar. A sample of 3 mature bolls was picked from upper, middle, and lower fruiting branches in each plant. Data were recorded from each boll individually and average values of 3 bolls from each position were used for analysis. Three seeds from each selected boll were used for estimation of halo length. Each seed was combed gently into a halo with the help of a seed comb and measured by a halo disc by the method suggested by Iyyengar [4]. Bolls were ginned with a hand-operated gin. Seeds were counted after delinting

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