THE INFLUENCE OF EXTENDED VEGETATIVE DEVELOPMENT AND d_2 DWARFING GENE IN INCREASING GRAIN NUMBER PER PANICLE AND GRAIN YIELD IN PEARL MILLET

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ABSTRACT

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As in other cereals, grain yield in pearl millet is directly related to grain number m^{-2} . Hence, an attempt was made to increase grain numbers by (1) increasing the length of vegetative period (to increase potential grain number per panicle and increase leaf area and light interception before flowering) by using a non-inductive long photoperiod during the early stages of crop growth, and (2) using a dwarfing gene to vary assimilate partitioning between panicle and stem prior to flowering.

Extended day length delayed panicle initiation (PI) and flowering and increased leaf area index and assimilate production. Time to flowering was directly related to assimilate allocation to individual panicles, and to grain number per panicle. Delayed PI, however, reduced panicle numbers. Dwarf hybrids partitioned more assimilates to panicles and less to stems, which was also associated with more grains per panicle.

The increase in grain number per panicle was offset by decrease in panicles per plant so that neither longer vegetative stage nor dwarfing gene caused in increase in grain yield. With increase in grain numbers per panicle in the dwarfs, grain density (grains cm⁻² surface area of panicle) also increased resulting in the dwarf hybrids producing smaller grains and failing to benefit from the increased grain numbers per ear.

INTRODUCTION

Cereals have a relatively clear separation between the different growth stages of their life cycle. Besides genetic control, the actual duration for each growth stage depends largely on environmental conditions, of which photoperiod and temperature are the most important. Changing the relative duration of successive phases in the growth of cereals offers scope for yield improvement. Varying the duration of the pre-heading phase in wheat (*Triticum aestivum* (L.) em Thell) directly increased grain number per ear (Raw-

son, 1970; Wall and Cartwright, 1974). This suggests that for maximum grain yield in a particular environment the pre-heading phase needs to be sufficiently long to maximise grain number per ear.

Radiation interception during the immediate pre-flowering period has been shown to be related to grain number per unit area and grain yield in a number of cereals (Biscoe and Gallagher, 1977). Supplementary radiation prior to anthesis not only increased assimilate production but also increased the assimilate allocated to the wheat spike, which in turn increased grain number per ear (Stockman et al., 1983).

The competition for assimilates between rapidly growing stem and panicles during the pre-anthesis period and lack of sufficient assimilates to match the demand leads to the death of the last-formed spikelet primordia in barley (Kirby and Riggs, 1978). Greater availability of assimilates and less competition from growing stems can alleviate this limitation to yield by increasing the survival of the last-formed yield components. The effects of a dwarfing gene in reducing such competition for assimilates between stem and the ear is well known in wheat (Brooking and Kirby, 1981). Reductions in height contribute to the increase in yield potential by increasing grain numbers in wheat (Fischer, 1983) and in maize (Fischer and Palmer, 1983).

Pearl millet (*Pennisetum americanum* (L.) Leeke) is a short-season crop with high growth rates. Our analysis of the growth of this crop (ICRISAT, 1978) indicates that early panicle initiation (PI) results in a smaller leaf area index (LAI) and consequently a lower biomass. A small increase in time to PI leads to substantially higher LAI, greater light interception and higher dry matter production. Such an increase in preflowering assimilate production increased grain number m^{-2} substantially in several crops of a hybrid BJ 104. As in other cereals (Biscoe and Gallagher, 1977), grain yield in pearl millet is directly related to grain number m^{-2} (ICRISAT, 1980). This indicates that an opportunity exists for yield improvement through increase in storage capacity.

The objective of the work reported here was to test this hypothesis by increasing the storage capacity of the crop in the following two ways: (1) Increasing both the length of vegetative period and LAI, using a non-inductive long photoperiod, leading to an increase in assimilate production and grain number per panicle; and (2) using the d_2 dwarfing gene to improve partitioning of assimilates to the panicle by reducing the competition by the stem.

MATERIALS AND METHODS

Site and season

The study was conducted at ICRISAT Center, Hyderabad, India, at 17.5°N in 1981 on Alfisol (clayey, skeletal, mixed, hyperthermic, deep, Udic Rhodustalf). The rainfall for the June-October growing season was

 $1072\,$ mm, which was 36% above the average annual precipitation for this season.

Crops and management practice

The study included two commercial F1 hybrids, BJ 104 and MBH 110, and an unreleased ICRISAT hybrid ICH 412, as tall hybrids (talls), and three experimental d_2 dwarf hybrids (dwarfs) from the ICRISAT breeding program. The two commercial hybrids were early flowering and of similar height to the dwarfs, although they did not contain the dwarfing gene (Table 1).

TABLE 1

Effect of normal (ND) and extended (ED) day length on days to panicle initiation (PI), days from PI to flowering (GSII), days to flowering, total leaf number and height in pearl millet hybrids

	Tall			Dwarf		
ан сайтаан ал	BJ 104	MBH 110	ICH 412	81A×349	81A×350	81A×T4
Days to PI						
ND	17	14	23	23	23	23
ED	29	28	36	35	34	35
Days in GSII						
ND	27	27	37	29	27	27
ED	36	37	44	33	30	29
Days to flowering			•			
ND	44	41	60	52	50	50
ED	65	62	80	68	64	64
Leaf number						
ND	15.8	13.0	19.3	-17.2	17.3	17.5
ED	21.0	18.5	24.3	21.3	20.3	19.3
Height (cm)	•.					Z^{2}
ŇD	145	142	228	155	143	138
ED	257	282	316	199	182	151

The three dwarf experimental hybrids, which were all made on the same female parent, were of intermediate maturity. ICH 412 was bred from an African pollinator and was taller and later than the other entries in the trial. The six hybrids were machine-sown in July 1981 in rows 75 cm apart and running approximately east—west. The crop was thinned to 10 cm between plants within rows, equivalent to 13.3 plants m⁻². Diammonium phosphate at the rate of 40 kg ha⁻¹ N and P₂O₅ was applied as a basal fertilizer and urea at 45 kg N ha⁻¹ was banded on the sides of the ridges 30 days after seedling emergence. Plots were inter-cultivated for weed control.

Day-length treatment

Two day-length treatments, normal day (ND) and extended day (ED), were used to vary the time of PI. The day length in ND varied from 13 to 13.5 h. In ED the day length was extended to 16.5 h, using flood lights (500 watt tungsten filament bulbs) mounted at 3.5 m height. The minimum intensity of the light received at the end of the plot (9 m from the light source) was 15-20 lux, well above the minimum light intensity required to cause developmental delay (G. Alagarswamy, unpublished results).

Experimental design

Day-length treatments formed the main plots and the six hybrids the subplots in a split-plot design; the treatments were replicated four times. Each sub-plot of six rows of 9 m long was divided into three portions: one for light interception measurements and destructive harvesting of plants for growth analysis; one for leaf counts and phenology observations; and one (15 m^2) for yield determination where the plants were left undisturbed until maturity.

Phenology

Two weeks after seedling emergence, five plants per plot were harvested daily and the shoot apices dissected to determine time of PI as suggested by Maiti and Bidinger (1981). When 50% of the plants sampled had initiated, it was assumed that the crop had reached PI stage. Days to flowering were recorded when stigmas emerged in the main shoot panicles on half of the plants in the plot. The number of expanded leaves per plot were counted at PI on the main shoots of 15-20 plants and again at the time of flowering. Plant height was measured from the base of the stem to the tip of the panicle at the flowering and harvest stages.

Growth sampling

For the estimation of total dry matter and green leaf lamina area, plants were cut at ground level in 1.2-m² sampling quadrats from the central two rows of each plot at PI, flowering and physiological maturity. Leaf area was measured and plant parts were then dried in a forced-draught oven at 70°C for 48 h and weighed.

Grain yield and yield components

At maturity, panicles were harvested from an area of 15 m^2 , counted, oven-dried and machine-threshed. The grains were oven-dried and weighed. Three 100 grain samples were counted and dry weights recorded. Grain numbers per panicle and grain number m^{-2} were derived using panicle number and grain dry weight. Due to the asynchrony of flowering among tillers, panicles from plant samples taken at harvest, rather than from those taken at flowering stage, were used to calculate panicle non-grain dry weight (PNGDW). PNGDW was derived as the difference between panicle and grain dry weights at maturity. Reproductive efficiency (defined as number of grains produced per unit of PNGDW) was derived using PNGDW and grain number per panicle. Grain packing (grain numbers cm⁻² panicle surface) was determined at three positions in the central region of 10—15 panicles per plot, and panicle length was measured. These panicles were then hand threshed and 100 grain dry weights were determined.

Light interception

Percent light interception was measured between 12.00 and 14.00 h in all the replicates using 90-cm-long tube solarimeters placed at ground level. Measurements were made every week during the season. Daily percent interception values were obtained from polynomial regressions between percent interception measured in all the replicates and days after seedling emergence (the percentage variance accounted for by the regressions ranged from 86 to 97%). Absolute daily incident solar radiation was obtained from the ICRISAT meteorological observatory situated 1 km from the experimental site. The daily radiation interception was estimated using the incident solar radiation data and the calculated daily percentage light interception. Cumulative intercepted radiation for each of the growth sampling intervals was then calculated. The efficiencies of conversion of light energy (e) were determined as the slopes of the linear regression of dry weight on accumulated intercepted radiation for the period from seedling emergence up to flowering and for the grain-filling period.

RESULTS

Effects of delayed panicle initiation

Being quantitative short-day plants, all varieites reached PI, flowering and maturity earlier under normal daylengths (ND) compared to extended daylengths (ED) (Table 1). Days to flowering were closely related to days to PI (r=0.92, P<0.001), but there were genotypic differences (2–9 days; Table 1) in changes in the length of growth stage II (from PI to flowering). Delayed PI markedly increased the leaf numbers and plant height. Mean leaf numbers on the main stem were directly related to days to PI (r=0.97, P<0.001).

Delay in PI increased LAI at PI (Fig. 1). As with leaf area, there were positive correlations between time to PI and the total dry matter produced at PI (r=0.97) and at flowering (r=0.92, P<0.001). In addition to this, the delay in



Fig.1. Leaf area index as a function of days to panicle initiation for tall (\circ) and dwarf (\triangle) hybrids; solid symbols represent values for extended day. Each point is the mean of four values.



Fig. 2. Relation between panicle non-grain dry weight (PNGDW) at maturity and days to 50% flowering for tall (\circ) and dwarf (\triangle) hybrids; solid symbols represent values for extended day. Data are means of four values for each hybrid.

flowering increased the amount of assimilates allocated to the reproductive structures (panicles, Fig. 2). Averaged over all the hybrids, a 10-day delay in flowering increased the PNGDW by 1 g per panicle.

Grain number per panicle increased with the length of time to PI; grain number was related to final leaf number (r=0.78, P<0.01). Both early and late hybrids responded similarly. The delay in PI caused by ED reduced the panicle number per plant at maturity, and increased the grain number per panicle (Table 2). The influence of delayed PI on crop grain yield varied among hybrids. There was a 10% increase in grain yield in BJ 104 and MBH 110, whereas there was a significant yield reduction in all dwarf hybrids.

TABLE 2

	Tall			Dwarf			
		MBH 110	ICH 412	81A×349	81Ax350	81A×T4	
Panicle	· · · ·						
No. per plant							
ND	3.4 ± 0.25	1.8 ± 0.20	1.6 ± 0.16	1.7 ± 0.20	2.0 ± 0.28	2.4 ± 0.14	
\mathbf{ED}	2.1 ± 0.38	1.3 ± 0.06	1.6 ± 0.11	1.2 ± 0.07	1.4 ± 0.08	1.6 ± 0.11	
Grain							
No. per panicle	9						
ND	1126 ± 277	1572 ± 74	2476 ± 49	2752 ± 263	1811 ± 125	1794 ± 251	
\mathbf{ED}	2428 ± 99	2409 ± 64	*	3254 ± 522	2869 ± 182	2731 ± 183	
Grain dry							
weight				1			
ND	291 ± 19.5	5349 ± 9.8	8 267 ± 10.3	307 ± 13.4	324 ± 24.2	264 ± 21.1	
ED	321 ± 19.1	$7 385 \pm 12.4$	4 *	238 ± 17.7	291 ± 30.4	236 ± 14.2	

Effect of normal (ND) and extended (ED) day length on panicle number per plant and grain number per panicle and grain dry weight (g m^{-2}) in pearl millet hybrids (mean ± S.E.)

*Data not presented due to severe ergot (Claviceps fusiformis Lov.) infection.

Effect of the d_2 dwarfing gene

Delayed PI increased plant height by about 70% in talls, but in the dwarfs there was only a 20% increase. Node numbers increased in both the talls and dwarfs, but the mean internode length increased only in talls (Table 3).

Changes in height and leaf number due to a delay in PI affected light interception. In the talls the percent light interception was higher throughout their life cycle in the ED compared to ND treatments. In contrast there

TABLE 3

Plant height, node number, inter-node length, maximum percent light interception and maximum LAI in tall and dwarf pearl millet hybrids at flowering stage in normal and extended day length (mean \pm S.E.)

	Plant height (cm)	Node No.	Internode length (cm)	Maximum light interception (%)	Maximum LAI
Normal day					
Tall	172 ± 28.2	16 ± 1.8	10.6 ± 0.8	66 ± 3.5	3.1 ± 0.6
Dwarf	145 ± 5.0	17 ± 0.1	8.4 ± 0.3	71 ± 2.1	3.4 ± 0.1
Extended day		a 1			
Tall	285 ± 17.1	21 ± 1.7	13.5 ± 0.9	78 ± 1.7	4.5 ± 0.1
Dwarf	177 ± 14.0	20 ± 0.6	8.7 ± 0.5	76 ± 0.7	4.8 ± 0.2

were only small, non-significant differences between ED and ND in the dwarfs (Fig. 3). In the talls the maximum percent light interception increased by 18% due to delayed PI, while in dwarfs there was only a 7% increase, despite a similar increase in LAI in both the groups (Table 3).



Fig. 3. Temporal changes in percent light interception of (A) tall hybrid BJ 104 and (B) dwarf hybrid $81A \times 350$ in normal (open symbols) and extended (closed symbols) day length. Arrow marks date of 50% flowering.

TABLE 4

Panicle non-grain dry weight (PNGDW), stem dry weight and total dry weight at maturity, and PNGDW as percent of PNGDW + stem for tall and dwarf pearl millet hybrids in normal and extended day (mean \pm S.E.)

	PNGDW (g/m ²)	Stem dry weight (g m ⁻²)	Total dry weight (g m ⁻²)	PNGDW/ PNGDW+Stem (%)
Normal day				
Tall	102 ± 20.5	371 ± 90.6	961 ± 117.7	22 ± 2.4
Dwarf	113 ± 7.3	296 ± 13.2	886 ± 10.1	28 ± 2.1
Extended day		× .		
Tall	115 ± 25.6	854 ± 39.4	1561 ± 50.2	12 ± 1.8
Dwarf	113 ± 6.4	448 ± 9.9	1051 ± 17.4	20 ± 1.1

The effects of the dwarf character on assimilate distribution were estimated by PNGDW. PNGDW per panicle was 3.88 and 5.41 g in ND and ED respectively (averaged over all hybrids), due to a linear increase in PNGDW per panicle with time to PI (r=0.85, P<0.01). However, the PNGDW on g m⁻² basis did not vary in absolute terms between talls and dwarfs both in ND and in ED, because of the reduction in panicle number m⁻² (Table 4). Delayed PI increased stem weights by 130% in the talls and 50% in the dwarfs. Therefore, only when PNGDW was expressed as percent of PNGDW plus stem weight was a greater proportion of assimilate apportioned to the panicles in dwarfs compared to talls in both ND and ED (Table 4).

TABLE 5

Effect of plant height on yield attributes of pearl millet hybrids in normal (ND) and extended (ED) day length (mean \pm S.E.)

	Panicle number per m ⁻²	Panicle length (cm)	Grains per panicle	Grain weight (g m ⁻²)	100 grain weight (g)	Grain packing (No. cm ⁻²)
Normal day						
Tall	35 ± 4.8	20 ± 0.4	1350 ± 111	320 ± 14.8	0.81 ± 0.09	17.4 ± 1.10
Dwarf	23 ± 2.8	25 ± 0.2	2420 ± 55	299 ± 13.0	0.60 ± 0.02	19.4 ± 0.92
Extended day						
Tall	28 ± 1.7	27 ± 0.2	2120 ± 175	354 ± 16.1	0.81 ± 0.09	19.2 ± 0.45
\mathbf{Dwarf}	20 ± 0.7	32 ± 0.4	2950 ± 188	255 ± 13.8	0.51 ± 0.02	21.5 ± 0.53



Fig. 4. Effect of grain packing (grains cm^{-2} of panicle surface area) on 100 grain dry weight in dwarf hybrids, in normal (open symbols) and extended (closed symbols) day lengths.

The grain weight of individual panicles of the talls increased by 70% due to an increase in grain number per panicle, which was associated with an increase in the panicle length in the delayed PI treatment (Table 5). However, the grain yield per unit area increased only marginally, because of a significant reduction in panicle numbers. In the dwarfs the 100 grain weight was reduced substantially, in addition to the reduction in panicle number: despite a 39% increase in grains per panicle, the grain weight per panicle increased only by 19%. Delayed PI increased grain packing, which was inversely related to 100 grain weight in the dwarfs (r=0.76, P<0.01; Fig. 4). The net result was that the delayed PI treatment reduced grain yield m⁻² in dwarfs.

The total above-ground dry weight of both talls and dwarfs increased linearly with accumulated intercepted radiation (Fig. 5). The conversion efficiency was slightly greater before flowering in the talls than in the dwarfs (2.43 g MJ⁻¹ and 2.10 g MJ⁻¹ respectively, P < 0.05). The difference in values of e between the two groups during grain filling period was even more pronounced (1.50 g MJ⁻¹ and 0.66 g MJ⁻¹, P < 0.001).





DISCUSSION

Development

The non-inductive long day photoperiod treatment was effective as a tool to increase the time to PI and flowering in all hybrids. Similar effects of ED have been reported in sorghum (Caddel and Weibel, 1971) and in pearl millet (Ong and Everard, 1979). Delay in PI due to ED and genotypic differences in developmental pattern was associated with the formation of extra leaves, as found by Quinby et al. (1973) and Midmore et al. (1982). The linear relationship between final leaf number and days to flowering in pearl millet was due to a constant interval between successive leaves. However, in sorghum (Quinby et al., 1973) and rice (Evans et al., 1984), this relationship was found to be curvilinear, due to slower leaf production in varieties with a longer vegetative phase.

Assimilate production and allocation

Initial leaf area development in millet is slow and dependent upon environmental conditions early in the growing season (ICRISAT, 1978). A small increase in the number of days to PI resulted in a substantial increase in LAI. The mean LAI 25 days after seedling emergence was 1.36, three times the LAI at 15 days.

The LAI at PI was closely related to number of leaves at PI, because delayed PI was always associated with the formation of extra leaves.

Despite an increase in LAI in response to ED in both talls and dwarfs, time to PI influenced the percent light interception in talls only. The stem height modified the relationship of LAI and light interception, probably because leaf distribution as a function of height from ground level differed among talls and dwarfs (the leaves in the talls seemed to be distributed more evenly). This difference in leaf distribution was accentuated in ED, where the internode length increased only in talls. Plant height influences light distribution in maize (Yamaguchi, 1974) and in field beans (Tanaka and Fujita, 1979), through similar modifications in canopy architecture.

An increase in the length of vegetative phase, due to the delayed PI, increased the dry matter produced at flowering. A 10-day delay in flowering was equivalent to an increase of 260 g m⁻² in total dry matter. This increase was associated with various morphological changes; a 10-day delay in flowering resulted in a mean increase of 43 cm in stem length and a 17% increase in leaf number. This confirms our earlier results that the potential for subsequent leaf area development, radiation interception and dry matter production is dependent upon growth prior to PI (ICRISAT, 1978).

Besides modifying assimilate production, the dwarfing gene and the delayed PI treatment modified assimilate partitioning. PNGDW per panicle at maturity was increased by 39% in all hybrids, owing to delayed PI. This increase in the potential sink capacity was proportional to the time to flowering, indicating that the allocation of biomass to panicles was closely tied to the duration of pre-flowering stage. Using supplementary light, rather than altering the duration of panicle development stage, as done in the present work, Stockman et al. (1983) showed similar responses in wheat.

However, neither the dwarfing gene nor a delay in PI had any effect on assimilate partitioning when PNGDW was expressed on unit area basis. This contrasting response of PNGDW per panicle and PNGDW m⁻² to delayed PI. was due to the reduction in panicles m⁻². The dwarfs neither allocated more assimilates to the panicles nor improved the reproductive efficiency compared to the talls. But a consistent relative difference in assimilate partitioning between panicles and stem was clearly evident between them. However, as suggested by Brooking and Kirby (1981) and Fischer (1983), the key to the differences in the relative allocation of assimilate to panicles and stems lies not in a stronger panicle sink, but rather in less competition from the growing stem which is the major alternative sink. This difference in partitioning of assimilates in favour of the panicles in the dwarfs was clearly evident under ED, where the stems were the alternate sinks competing for the assimilates (Table 4). Setting up of different patterns of competition within the plant by ED was clearly evident in the present work also, confirming the suggestions of Kirby (1969).

Yield and yield components

The increase in duration of vegetative and panicle development led to an increase in grain number per panicle. This was closely related to both the length of the vegetative period and the assimilate partitioning to the panicle during panicle development stage. The former relationship has been reported in wheat (Rawson, 1970; Wall and Cartwright, 1974; Midmore et al., 1982); the latter for both wheat (Brooking and Kirby, 1981) and maize (Fischer and Palmer, 1983).

The increase in grain number per panicle due to delayed PI could either be caused by a larger apex size at PI leading to more grain sites and/or, as suggested by Fischer (1983) for wheat, by assimilate competition becoming less critical for component survival because of increased assimilate availability. However, it is not possible from the present work to determine the cause although it could be argued that both factors operated jointly.

Delayed vegetative development reduced the panicle number in both talls and dwarfs. Delayed development reducing fertile tillers has been recorded in barley (Guitard, 1960) and also in wheat (Hammes and Marshall, 1980). Low panicle number per plant is a common feature of West African landrace pearl millets which flower in 60—80 days. The reason for such a relationship is not clear. In a comparison of 2- and 6-row barley, Kirby and Riggs (1978) concluded that low head numbers at maturity in 6-row barley appeared in part to be a consequence of bigger apex size at any equivalent leaf stage and to a bigger panicle at anthesis, leading to a more intense competition for assimilates by main shoots. Similarly, the panicle meristem of pearl millet was larger and the dry weight of the panicles at anthesis was increased by delayed PI. The growing stem was also larger due to the delayed PI treatment. At the flowering stage, on average the stem weight per shoot increased by 135% and the weight per panicle increased by 53% due to delayed PI. Such circumstantial evidence in the present study suggests that reduction in panicle numbers due to delayed PI might be due to an increased intraplant competition for assimilates. However, there is no unequivocal experimental evidence to prove this hypothesis from the present study.

The increase in grain number per panicle in response to delay in PI was not equally reflected in overall grain yield per panicle in the dwarfs and talls. The failure of yield per panicle to respond to changes in grain number per panicle in the dwarfs was due to reduction in grain size, which appeared to be associated with an increase in grain packing. Grain packing increased in both the talls and dwarfs with delayed PI, but absolute values were higher in magnitude in the dwarfs (Table 5). For every unit of increase in grain packing, the 100 grain weight decreased by 0.2 g in dwarfs only (Fig. 4). This physical constraint appeared to have restricted the normal grain growth and led to grain deformity. The potential grain size in rice is known to be physically restricted by hull size (Yoshida, 1983). It also appears that this reduction in potential grain size led to the severe reduction in the values of e (the efficiency of conversion of intercepted radiation) during the grain filling period in the dwarfs. Whether this inverse relationship between grain packing and 100 grain weight is associated with the seed parent 81A or is common to the d_2 character needs further study.

Considering the conversion of intercepted radiation, e values until flowering compare reasonably with others for pearl millet (Azam-Ali et al., 1984; Huda et al., 1984). The ontogenetic decline in the present work (Fig. 5) has been reported in wheat (Doyle and Fischer, 1979) and in pearl millet (Huda et al., 1984). The decline in post-flowering e values was greater in the dwarfs than in talls, despite the fact that dwarfs, as a group, did not differ from talls in terms either of the maximum percent light interception that occurred before flowering or in the accumulated intercepted radiation during growing season. One reason for the greater decline could be the failure of grains to fill normally in the dwarfs.

It was thus possible to increase grain numbers per panicle and total crop dry matter by increasing the length of the vegetative period. However, this was not reflected in increased grain yield. The increase in grain number per panicle was offset by the decrease in panicle number. The increase in dry matter was primarily due to an increase in stem weight. The dwarfing gene did not result in an increased panicle dry weight during the panicle development phase, and it (or the background of the dwarfing gene) affected grain filling, when grain numbers per panicle were increased by delayed PI. These unfavourable associations need to be broken before the possibility of greater grain yields through either longer duration of vegetative stage or the dwarfing gene can be utilized.

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