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Growth and Yield of Lowland Rice in Response to Shade and Drainage

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Rice (Oryza sativa L.) is most susceptible to yield reduction by shade and water deficit during panicle emergence and flowering. Effects of shade before and after flowering on the growth and development of lowland rice and their interactions with drainage effects during panicle emergence and flowering were studied in a field experiment during the 1987 wet season with three rice cultivars — IR46, IR64, and Mahsuri. Postflowering shade (50% reduction of incident radiation) 5 to 20 days after panicle emergence (DAPE) had a more adverse effect on yield than preflowering shade from 10 to 25 days after panicle initiation (DAPI). Preflowering shade resulted in reduced leaf area, tiller number, and spikelets/panicle, whereas postflowering shade reduced filled spikelet fraction and grain weight. Crop growth rate (CGR) was reduced more by preflowering than by postflowering shade, but CGRs of both shade treatments were less than those of unshaded controls. Drainage from 20 DAPI to 10 DAPE, which resulted in maximum soil moisture tension of 30 kPa, reduced leaf area and all yield components. When shade and drainage stresses were combined, the effects were mostly additive. As compared to IR64 and Mahsuri, IR46 had the highest CGR and dry weight of leaf blade and sheath, and the least reduction in yield. It was concluded of the cultivars tested, IR46 had the greatest shade and drainage tolerance during panicle emergence and flowering owing to its ability to form and set spikelets using accumulated assimilates.

Key words: Oryza sativa, water deficit, carbohydrate remobilization, drought resistance

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In South and Southeast Asia, about 70% of all rice is grown during the rainy season when the light intensity is about half that in the dry season. Failure of monsoons is frequently associated with overcast skies and low solar radiation (Venkateswarlu and Visperas, 1987). Thus, reduced light intensity, coupled with water deficit, is a typical constraint to yield of rainfed lowland rice in the tropics.

Rice sensitivity to water deficit has been reported to change with developmental stage and to be most sensitive to stress at flowering (Namuco and O'Toole, 1986; Venkateswarlu et al, 1977). The pattern of yield reduction at different growth stages brought about by drought is similar to that brought about by low light intensity for rice (Chandra et al, 1986) and maize (Fischer and Palmer, 1980). Intercepted radiation during flowering is a dominant factor in determining grain number in rice (Evans and De Datta, 1979) and maize (Tollenaar, 1977).

Effects of low light intensity and water deficit on rice growth have been studied separately (Chandra et al, 1986; Namuco and O'Toole, 1986), but little information is available on their interaction. A field experiment was conducted to determine the relationships among nonstructural carbohydrate levels, crop growth, yield, and yield components of lowland rice under wet and drained soil conditions. Shade and water deficit at different times of reproductive growth reduced levels of accumulated assimilates and yield but increased apparent translocation of carbohydrates to grain. Varietal differences in ability to accumulate, remobilize, and translocate carbohydrates in response to stress were related to varietal differences in drought resistance during reproductive growth.

MATERIALS AND METHODS

A field experiment was conducted during the 1987 wet season under lowland conditions at the experimental farm of the International Rice research Institute in Los Baños, Laguna, Philippines. Plots were 5m x 2m. Two to three 20-day-old seedlings per hill were transplanted with 20-cm x 20-cm hill spacing on 20 August 1987. A total of 100 kg N (as urea)/ha was applied, 2/3 broadcast and incorporated before transplanting and 1/3 topdressed 20 days after transplanting (DT).

Eight replicates of two water treatments were imposed as mainplots of a split-plot design: 1) wet, continuously flooded, and 2) drained from 20 days after panicle initiation (DAPI) to 10 days after panicle emergence (DAPE). Within mainplots, subplots were factorial combinations of three cultivars–IR64, IR46, and Mahsuri–and three shade treatments–no shade (control), preflowering shade (10 to 25 DAPI), and postflowering shade (5 to 20 DAPE). Thus, nine treatment combinations were randomly imposed as subplots.

Details of shade construction, weather and soil moisture parameters, and field management were described by Chaturvedi and Ingram (1988). Light intensity underneath the shade was about 50% that of natural light.

Panicle initiation was determined by dissecting main tillers and examining the growing points under a microscope. As panicle initiation and emergence occurred at different times for the three cultivars, shade and drainage treatments were imposed at different times as shown in Table 1.

Plant sampling (4 hills/plot) for dry weights of leaf blade, culm, leaf sheath, and panicle was done at 10 and 25 DAPI, 5 and 20 DAPE, and at maturity. Crop growth rate (CGR) was calculated as the rate of change of total above ground dry weight in sequential samples from 10 DAPI to 20 DAPE. At maturity, grain yield was estimated from a 3.12-m^2 portion in the center of each plot and yield components were determined from a subsample of four hills randomly selected from the final harvest area.

Table 1. Shading schedule and rice cultivars used in the experiments.

Variety	PI[a]	Shade-1 (Preflowering shade at 10-15 DAPI)	Shade-2 (Postflowering shade at 5-20 DAPE)
IR64	57	67 - 82	91 - 106
IR46	67	77 - 92	101 - 116
Mahsuri	77	87 - 102	112 - 127

[a]PI = panicle initiation, DAPI = days after panicle initiation, DAPE = Days after panicle emergence, DAS = days after seeding.

RESULTS AND DISCUSSION

Dry matter distribution

Both pre- and postflowering shade significantly reduced dry weight of different plant parts under wet and drained conditions (Fig. 1, 2, 3). Preflowering shade reduced rates of dry matter increase in the vegetative plant parts whereas postflowering shade appeared to stimulate senescence. In all treatments, total dry matter of IR46 was greater than those of IR64 and Mahsuri.

Confirming observations that IR46 remobilized and translocated more nonstructural carbohydrates from vegetative plant parts to grain than did the other cultivars (Chaturvedi and Ingram, 1988), reduction of culm dry weight by postflowering shade was greatest in IR46.

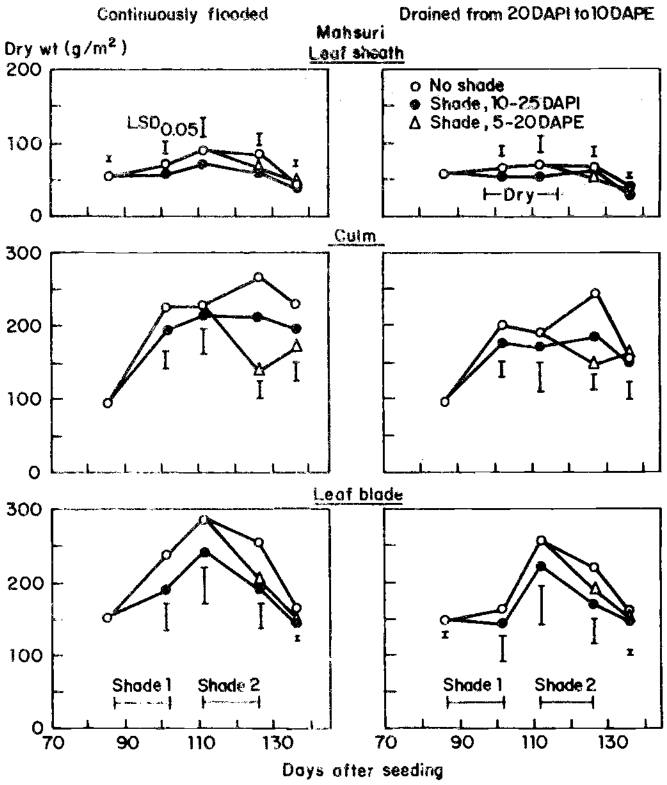

Fig. 1. Effect of shade and drainage on dry weight of leaf blade, culm, and leaf sheath of Mahsuri.

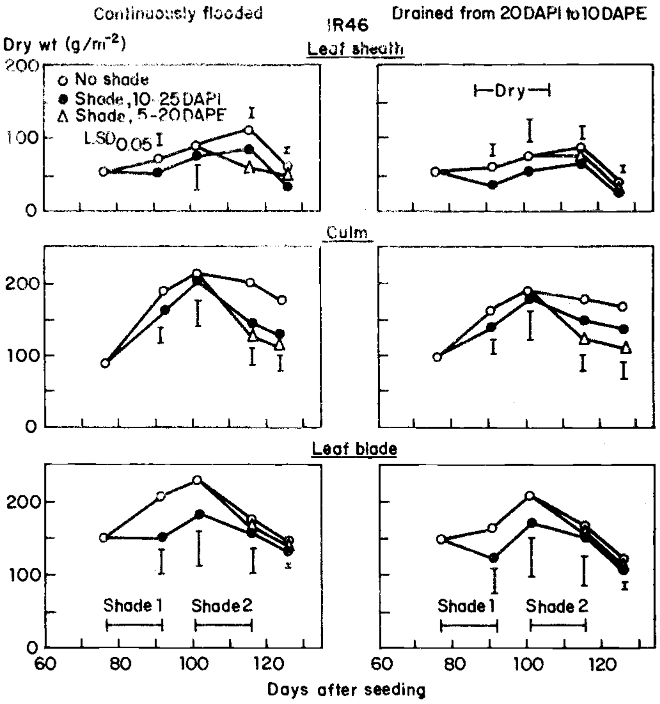

Fig. 2. Effect of shade and drainage on dry weight of leaf blade, culm, and leaf sheath of IR46.

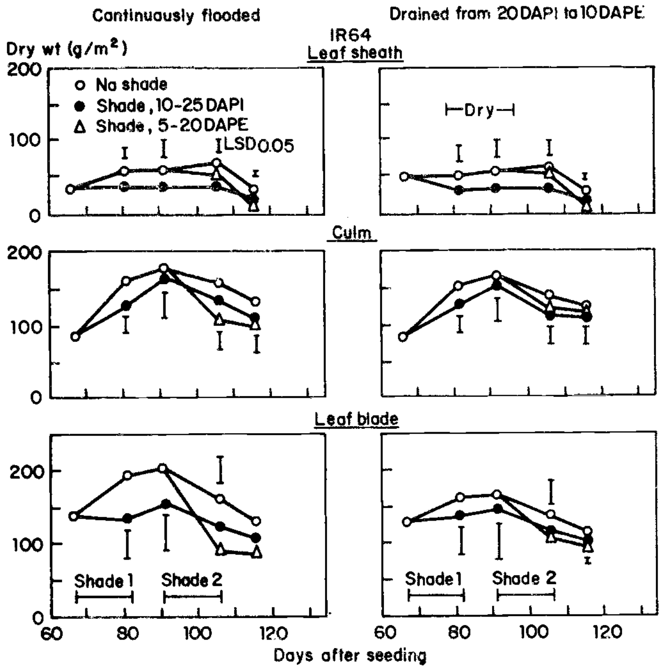

Fig. 3. Effect of shade and drainage on dry weight of leaf blade, culm, and leaf sheat of IR64.

Culm dry weight of Mahsuri continued to increase even after flowering in the no-shade treatments, confirming that this cultivar did not translocate appreciable amounts of assimilate from culms to panicles during grain growth. On the contrary, net translocation of assimilates to Mahsuri culms was positive and resultant grain yields were low. This observation may be explained by one of two mechanisms: either culms of Mahsuri were a stronger sink for assimilates than were panicles or some other factor reduced grain set and demand for assimilate by panicles.

Although Mahsuri was relatively susceptible to stress in this experiment, it is widely planted in stress-prone, rainfed lowland areas of eastern India, Bangladesh, and Southeast Asia. It is possible that farmers use other criteria to select a cultivar, but it is more likely that the performance of Mahsuri in Los Baños does not reflect its performance in other rainfed lowland rice-growing areas.

Dry matter distribution at maturity (Fig. 4, 5, 6) showed that both shade timings reduced the fraction of dry matter in panicles as compared with controls for all cultivars, but reduction was more pronounced in the post than in the preflowering shade treatment. Under drained conditins, IR46 had the highest fraction of dry weight in panicles; under wet conditions, IR64 had the highest fraction. Of the three cultivars, Mahsuri had the lowest fraction of dry weight in panicles for all treatments. For all cultivars, the proportion of dry matter in panicles was higher under drained than under wet conditions.

Under low light intensity (such as what rice experiences during the wet season), reduction of crop dry matter is related to impaired photosynthesis (Murty et al, 1975; Nayak et al., 1978; Sircar and Dass, 1974; Chandra et al, 1986; Tanaka and Kawano, 1966). Previous experiments showed that shade effects on dry matter accumulation of rice are more critical after than before panicle initiation (Venkateswarlu et a, 1977). In wheat, Wang and Nakaseko (1986) found that postflowering shade resulted in greater reduction in dry weight of panicles, culm, and roots than did preflowering shade. In this experiment, however, dry matter content of vegetative plant parts did not significantly differ regardless of shade treatment, although a fraction of dry matter in the panicles was reduced more by the post- than by the preflowering shade treatment.

Canopy development

Maximum leaf area index (LAI) and maximum tiller number were observed in unstressed treatments of all cultivars at 25 DAPI and near panicle emergence (Fig. 7, 8). Thus, the end of tillering and leaf area development coincided with the end of the preflowering shade; leaf area and tiller number were already fully established before postflowering shade was imposed.

Results of other studies confirm that maximum LAI occurs near panicle emergence, but they differ in finding the maximum tiller number near panicle initiation (Nayak and Murty, 1980). These data do not preclude that tiller numbers may have been greater before than during the sampling period, but the consistent upward trend from 10 to 25 DAPI suggests that tiller numbers did indeed increase after panicle initiation in unstressed treatments.

Draining shaded plots reduced tiller numbers more than did shade alone, but there were no significant differences among shade treatments in drained. For both water regimes and all cultivars, LAI was lowest in the preflowering shade treatment even though differences in leaf dry weight were small by 10 DAPE.

Yoshida and Parao (1976) reported that vegetative shade resulted in smaller leaves and lower LAI. Venkateswarlu et al, (1977) observed that rice growing at about 0.5 natural light intensity also produced as many tillers as did rice growing in full sunlight. In this experiment, LAI was more susceptible to reduction by shade than were tiller numbers, whereas tiller numbers were more susceptible to reduction by drainage than was LAI.

Crop growth rate

In most cases, CGR decreased with time during the sampling period (Fig. 9). In general, CGR was highest in IR46. Shade, as has been observed by Wang and Nakaseko (1986), decreased CGR. Drainage also reduced CGR in unshaded treatments, but CGR in drained

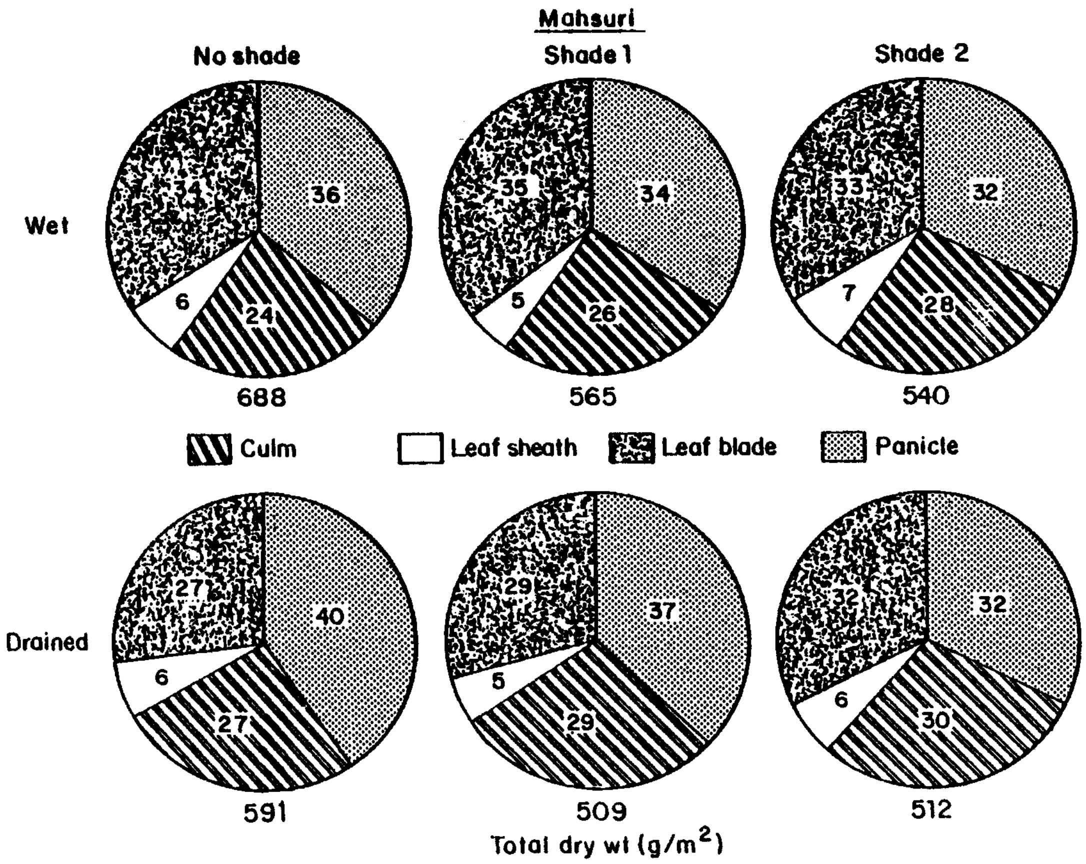

Fig. 4. Effect of shade and drainage on dry matter distribution at harvest of Mahsuri.

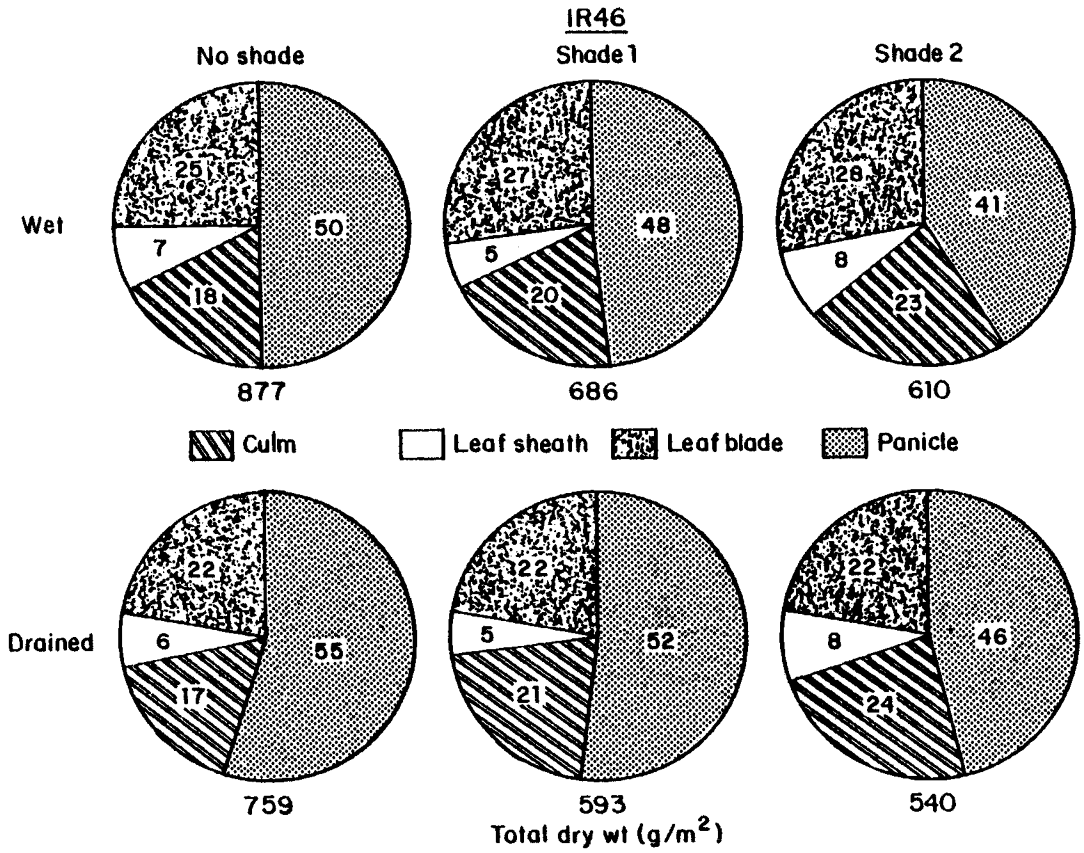

Fig. 5. Effect of shade and drainage on dry matter distribution at harvest of IR46.

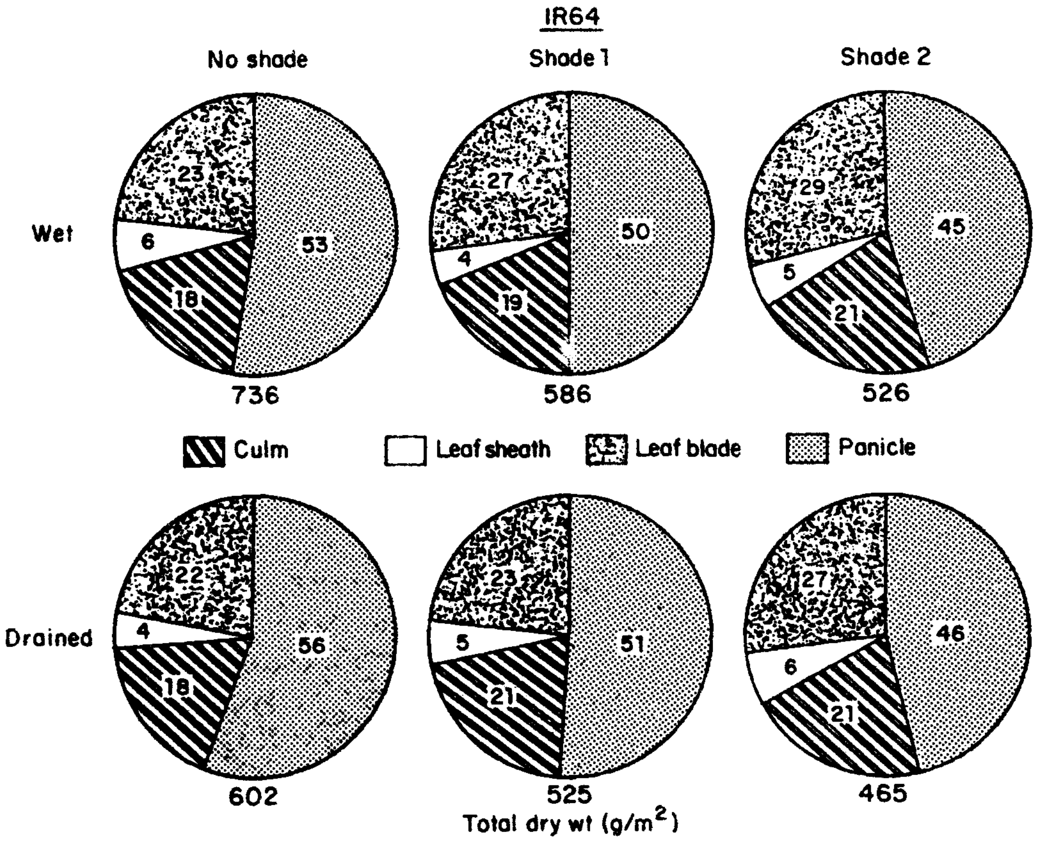

Fig. 6. Effect of shade and drainage on dry matter distribution at harvest of IR64.

plots was less affected by shade compared with that in continuously flooded plots.

Yield and yield components

The yield equation for rice may be written as:

$$\text{Grain Yield} = \frac{\text{tillers}}{\text{m2}} \times \frac{\text{panicles}}{\text{tillers}} \times \frac{\text{spikelets}}{\text{panicle}} \times \frac{\text{filled spikelet}}{\text{fraction}} \times \frac{\text{weight}}{\text{filled spikelets}}$$

These variables are presented in Table 2. In general, the crop age at which these yield components are established is earliest toward the left and latest toward the right of the equation. Tillers/m² generally increase from germination until panicle initiation with final tiller numbers being established by panicle emergence; panicles/tiller are determined during panicle emergence and anthesis; and weight/filled spikelet is determined from anthesis until maturity. Although stresses may either reduce the formation of yield components or may cause the loss of previously formed yield components, and although yield components are measured only at harvest, analysis of yield components can be used to infer treatment effects on growth and development (Yoshida and Parao, 1976). Both Nayak and Murty (1980) and Yoshida and Parao (1976) used yield components similar (but not identical) to those in our yield equation above and obtained similar results.

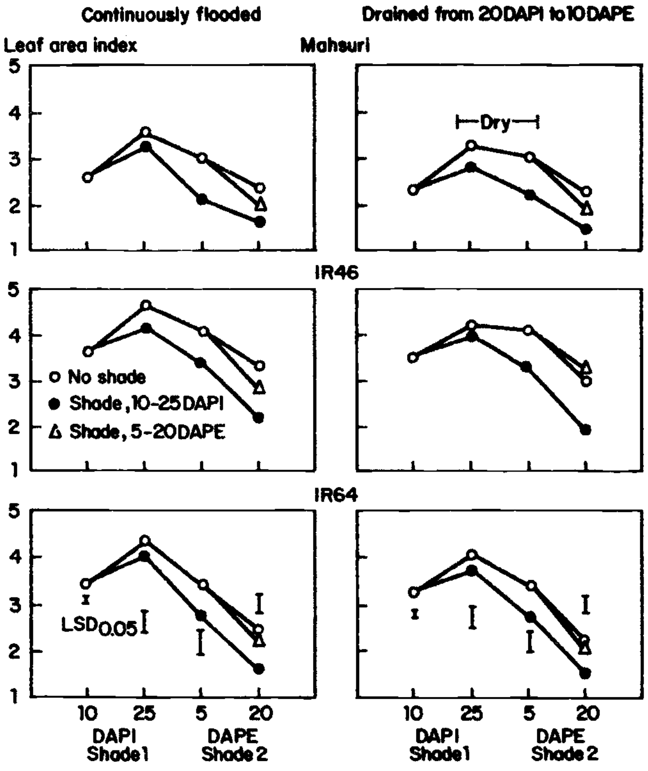

Fig. 7. Effect of shade and drainage on leaf area index of three lowland rice varieties.

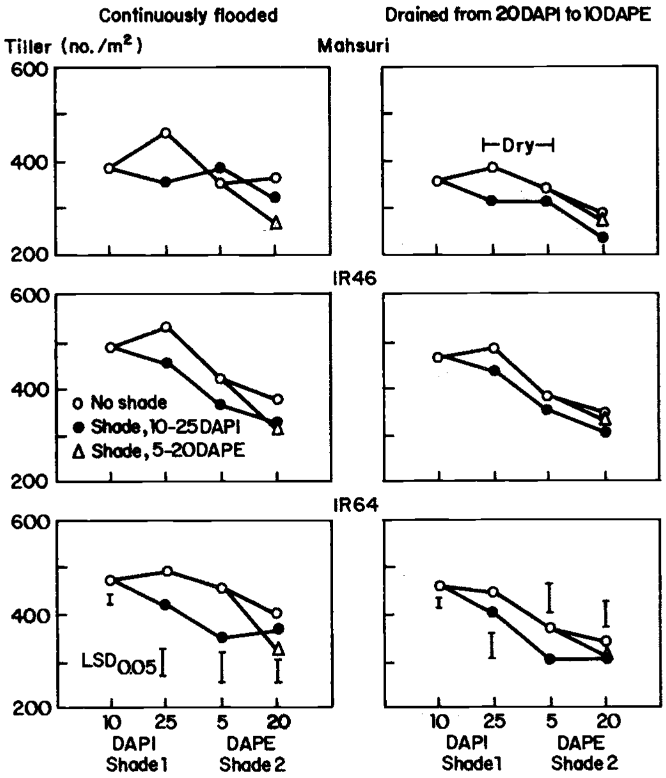

Fig. 8. Effect of shade and drainage on tiller numbers in three lowland rice varieties.

Trends in tiller numbers at harvest (Table 2) were similar to those at 20 DAPE (Fig. 5). Tiller numbers of IR46 and IR64 were not significantly different, although both were significantly greater than those of Mahsuri. Furthermore, preflowering shade reduced tiller numbers to a greater proportion in Mahsuri than in the other cultivars. The 10-25 DAPI shade treatment significantly reduced tiller numbers, but the 5-20 DAPE shade treatment did not. Drainage reduced tiller numbers in the no-shade treatments only, presumably because plant water deficit was mitigated by reduced evaporative demand under shade conditions.

It appeared that stress reduced panicles/tiller in Mahsuri and increased the same in for IR46 and IR64, but there were no significant differences in this yield component among treatments or among cultivars (Table 2). The lack of significant differences might be explained by the fact that stress treatments were not imposed until after panicle initiation. But if this were true, why then did stress treatments affect tiller number? Because panicles/tiller were very high in all treatments, the most likely explanation is that only very severe stress would significantly reduce the proportion of bearing tillers.

According to Yoshida and Parao (1976), spikelet number is directly related to photosynthate production from panicle initiation to panicle emergence; it is thus not surprising that preflowering shade significantly reduced spikelets/panicle in all cultivars (Table 2).

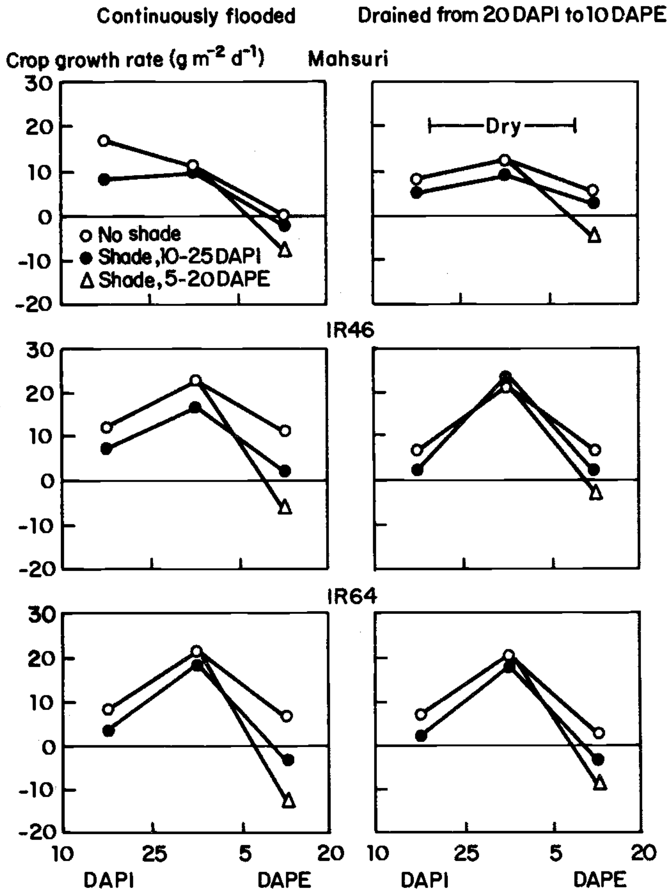

Fig. 9. Effect of shade and drainage on crop growth rate in three lowland rice varieties.

Postflowering shade also significantly reduced spikelets/panicle compared to the unshaded control, but the effect was not as great as that of preflowering shade. Among cultivars, IR46 had the most number of spikelets/panicle and Mahsuri the least, but there was no effect of drainage. Shade treatments had relatively the least effect on spikelets/panicle in IR46, a result that may help explain the apparent reproductive stage drought resistance of IR46 as reported by Chaturvedi and Ingram (1988).

Among cultivars, the filled spikelet fraction showed trends similar to those for spikelets/panicle (Table 2). But postflowering shade reduced filled spikelet fraction more than did the preflowering shade–a result consistent with the hypothesis that grain setting depends on the level of available assimilates during initial grain growth the first few days after anthesis. As in the case of spikelets/panicle, shade treatments had less relative effect on the filled spikelet fraction in IR46 than in IR64 and Mahsuri, a further evidence of the superior reproductive phase drought resistance of IR46.

Spikelet weight was greatest in IR64 and was least in Mahsuri. Maximum spikelet weight is relatively constant in rice (Yoshida and Parao, 1976), but shade treatments significantly reduced spikelet weight (Table 2). Postflowering shade reduced spikelet weight more than did preflowering shade.

Table 2. Effect of shade and drainage on yield and yield components of three lowland rice cultivars.

Cultivar	Shade	Tillers/m^2		Panicles/tiller		Spikelets/panicle		Filled spikelet fracton		Individual spikelet weight (mg)		Grain yield (Mg/ha)	
		W	D	W	D	W	D	W	D	W	D	W	D
Mahsuri	No Shade	342 (100) [b]	324 (95)	0.97 (100)	0.95 (98)	56 (100)	55 (98)	0.81 (100)	0.80 (98)	18.6 (100)	18.6 (100)	3.0 (100)	2.9 (97)
	10-15 DAPI	230 (67)	219 (64)	0.93 (96)	0.93 (96)	49 (88)	47 (84)	0.65 (80)	0.63 (77)	16.9 (91)	16.8 (90)	2.1 (70)	2.0 (67)
	5-20 DAPE	338 (99)	329 (96)	0.93 (96)	0.93 (96)	52 (93)	51 (92)	0.55 (68)	0.55 (68)	14.9 (80)	14.8 (80)	1.8 (60)	1.7 (57)
IR46	No Shade	414 (100)	379 (92)	0.91 (100)	0.97(107)	69 (100)	69 (100)	0.85 (100)	0.83 (98)	21.6 (100)	20.9 (97)	4.6 (100)	4.4 (96)
	10-16 DAPI	343 (83)	327 (79)	0.93 (102)	0.91(100)	63 (91)	63 (91)	0.80 (94)	0.76 (90)	18.6 (86)	18.7 (87)	3.6 (78)	3.5 (76)
	5-20 DAPE	407 (98)	393 (95)	0.93 (102)	0.93(102)	67 (97)	66 (96)	0.67 (79)	0.64 (75)	18.5 (86)	17.9 (83)	3.4 (74)	3.3 (72)
IR64	No Shade	409 (100)	377 (92)	0.94 (100)	0.92 (97)	64 (100)	63 (98)	0.83 (100)	0.80 (97)	23.8 (100)	22.4 (94)	4.0 (100)	3.9 (98)
	10-15 DAPI	339 (83)	345 (84)	0.96 (102)	0.94(100)	55 (83)	53 (83)	0.74 (89)	0.74 (89)	20.8 (87)	20.0 (84)	3.1 (78)	3.1 (78)
	5-20 DAPE	398 (97)	383 (94)	0.97 (103)	0.95(101)	61 (95)	52 (81	0.57 (68)	0.54 (66)	19.0 (66)	19.3 (81)	2.8 (70)	2.8 (70)

[a] W = wet (continuously flooded); D = drained 20 DAPI to 10 DAPE.

[b] values in parentheses are percentages of no-stress treatment for each cultivar.

Combined, the above yield components explain observed differences in yield. Mahsuri had a low overall yield potential/; its susceptibility to stress was most related to reduction in tiller number by the preflowering stress. The flowering stage resistance to stress of IR46 was related to its superior ability to form spikelets and set grains under stress conditions, an ability which is related to remobilization and translocation of stored assimilates (Chaturvedi and Ingram, 1988).

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