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Quantifying lowland rice responses to soil-water deficit

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Management of drought-prone rainfed lowland rice ecosystems requires quantitative understanding of rice plant responses to water deficit. A greenhouse experiment was conducted to study the physiological and morphological responses of two rice varieties, PSBRC14 and IR72, to drought as influenced by crop establishment methods (dry seeding in non-puddled soil, wet seeding and transplanting in puddled soil). Temporary drought was imposed at tillering, panicle initiation, and flowering, by withholding water until the plants registered a leaf rolling score of 5. Leaf elongation stopped when the soil moisture tensions exceeded 40-60 kPa in all establishment methods. Leaf rolling started at a lower soil water tension in dry-seeded rice than in wet-seeded or transplanted rice. Leaf rolling could reduce the leaf area index by almost 50% compared with unrolled leaves. This was the primary cause for the decline in transpiration rate in the initial stages of drought imposition. Further decline in transpiration was caused by stomata closure at soil water tensions of 10^3 kPa irrespective of establishment methods. Dry-seeded rice had more uniform water extraction pattern, which allowed it to withstand drought for a longer period than wet-seeded and transplanted rice. Statistically significant interactions existed between establishment method and drought imposition at various stages for grain yield.

Almost one quarter of the total area under rice in the world is classified as rainfed lowland rice ecosystem. Rice grown in this ecosystem is always associated with uncertainty due to the unpredictability of rainfall (IRRI 1992). Rainfed lowland rice has many challenges to offer, as during any season the crop may be exposed alternately to drought and floods, in addition to pests and diseases. Even a moderate increase in the productivity of this ecosystem will have a large impact on total rice production.

One of the major problems under rainfed conditions is proper establishment of the crop. Quite often, transplanting and wet seeding of pre-germinated seeds on puddled soils can be delayed due to insufficient rainwater for land preparation (Saleh et al 1993). Dry seeding has the advantage that rice can be sown in non-puddled dry conditions which allows utilization of early season rainfall (Tuong et al 1993). The soil environment under non-puddled and puddled conditions is totally different. The method of establishment may therefore affect the response of rice to drought.

Very limited attempts have been made to quantify the physiological and morphological responses of lowland rice to drought. When available, data are generally confined to transplanted rice (Wopereis 1993, Singh et al 1994, Wopereis et al 1995). Information on how establishment methods might influence the drought response of rice is lacking (Shad and De Datta 1986), but is needed to parametrize crop simulation models which can be used to select optimum management strategies and to identify areas suitable for particular crop establishment practices.

The effects of drought can be manifested in reduction of transpiration (Tanguilig et al 1987), leaf area index (Cruz et al 1986), leaf elongation (Tanguilig et al 1987), increase in leaf senescence (Malabuyoc et al 1985) etc. Linking such parameters to soil water potential is needed to predict crop responses to drought in different soil and climatic environments. This study reported here was therefore carried out with the following objectives:

1. To compare the response of rice to drought as affected by the method of establishment.
2. To derive functional relationships between soil water status and relative transpiration, leaf rolling score, and early leaf senescence.

Materials and methods

Experimental conditions

The experiment was conducted in a greenhouse at the International Rice Research Institute (IRRI) located at Los Baños, Philippines (14°30' N, 121°15' E) during the dry season, from January to May 1994.

Two rice cultivars (*Oryza sativa* L.), PSBRc14 and IR72, were grown in PVC pots (20 cm diameter and 25 cm height). The soil used for the experiment was clay loam in texture having an average sand, silt, and clay content of 27, 42, and 31%.

Methods of establishment

PSBRc14 was established by dry seeding (DSR), wet seeding (WSR), and transplanting (TPR). IR72 was established by DSR and WSR only. For dry seeding, the soil was air dried, passed through a 4-mm mesh sieve before being packed at a bulk density of 1.1 g/cm^3 into the pots up to a height of 20 cm. The soil was kept dry until seeding was done. For wet seeding and transplanting, a plot in the field from where the soil was taken for dry-seeded treatment was puddled. Pots were filled with this puddled soil. The soil in the pots was puddled again thoroughly using an electric stirrer before wet seeding and transplanting were done.

For dry seeding, 20 seeds were sown in one 20 cm row per pot. 10 mm of water was added daily to each pot till constant emergence was attained. The plants were then thinned down to 15 per pot. The soil in DSR pots was kept below saturation until 3 weeks after emergence, then flooded to a depth of 2.5 cm. To ensure that the plants in all the treatments were of the same physiological age, the seeds for WSR and TPR were soaked the day DSR seeding was done in pots.

Similarly, 20 pre-germinated seeds were sown in a 20 cm row per pot for wet seeding. The seeds were initially soaked for 24 hours and incubated for 36 hours before seeding. Wet seeding was done in saturated puddled soil without standing water. As in DSR, the plants were thinned to 15 per pot after establishment.

In the transplanted treatment, three 14-day-old seedlings were transplanted in the centre of each pot containing puddled soil with ponded water. Ponded water depth of 2.5 cm was maintained in all pots when drought was not imposed.

In addition to the basal application of P and K both at 40 kg/ha, 200 kg N/ha was applied in four splits viz., complete emergence (at transplanting in TPR), maximum tillering, panicle initiation, and flowering.

Drought imposition

Drought was imposed at three stages: tillering (T), panicle initiation (PI), and flowering (FL). There was one well-watered control (C). Drought was imposed in the stress treatments by withholding water till a leaf rolling score of 5 (O'Toole and Cruz 1980) was attained. Stress was terminated by rewatering the plants. The days of stress initiation and termination in various treatments are summarized in Table 1.

Experimental layout

To simulate field conditions all the treatments were concentrated in blocks. The pots were placed on wooden supports 10 cm in height and were arranged to represent 20 cm row spacing for DSR and WSR, and 20 cm × 20 cm hill spacing for TPR. The pots on which measurements were carried out were placed in the centre of the block. All the treatment blocks were surrounded by one row of border pots treated similarly to minimize border effects. No measurements were made on these border pots. The blocks were rotated every two weeks to eliminate any differences due to variation in the microclimatic conditions within the greenhouse.

Parameters monitored

Plant. For control treatments and during nonstressed periods, measurements were carried out every 3 weeks on physiological parameters viz., dry matter production and its partitioning, and leaf area. Days of panicle initiation, flowering, and maturity were also recorded for each treatment. Yield and yield related parameters were monitored at maturity. Non-destructive parameters such as Haun index (Haun 1973) and plant height were measured every 3 days during the first 6 weeks, every 2 days during stress imposition and weekly otherwise. During stress, destructive plant sampling was done when at least three of the four observation pots showed leaf rolling scores of 1, 3, and 5. Area of both rolled and unrolled leaves was taken. The leaves were unrolled by dipping them in culture solution (Flowers and Yeo 1981). The proportion of dead leaves, if any, was also recorded.

Soil. During the period of drought imposition, soil water content and bulk density at depths 0-5, 5-10, 10-15 and 15-20 cm of the stressed pots were taken at the time of drought initiation (leaf rolling score of 1, 3, and 5) through destructive soil sampling coinciding with the plant sampling. Soil moisture tension was monitored twice daily using tensiometers installed at 2.5, 7.5, 12.5, and 17.5 cm depths from the soil surface. When the soil water tension exceeded the tensiometer range, the pF curves of the puddled and non-puddled soils were used to convert the measured soil water content into soil water tension. Soil water tensions averaged over these four depths have been used in the results section.

Table 1. Duration of water stress in the various treatments.

Establishment method	Date of planting (day of the year)	Treatments	Start of stress (day of the year)	End of stress (day of the year)
PSBRc14				
Dry-seeded rice	18	Tillering	46	59
		Panicle initiation	68	80
		Flowering	84	94
Wet-seeded rice	21	Tillering	46	59
		Panicle initiation	68	80
		Flowering	84	94
Transplanted rice	32	Tillering	52	73
		Panicle initiation	68	80
		Flowering	92	101
IR72				
Dry-seeded rice	18	Tillering	46	57
		Panicle initiation	68	80
		Flowering	92	100
Wet-seeded rice	21	Tillering	46	57
		Panicle initiation	68	77
		Flowering	92	100

Transpiration. The soil surface in the pots was covered with plastic to prevent evaporation. The pots were weighed daily to provide transpiration estimates.

Relative transpiration rates (T_r) and normalized relative transpiration rates (T_{rn}) were used to quantify the effect of water stress on plants.

$T_r = T_{rd} / T_{pw}$..... (1)

where T_{rd} is the measured transpiration rate of stressed plants, and

T_{pw} is the measured transpiration rate of well-watered plants.

Imposition of stress slows down plant growth and leaf area development, resulting in the reduction of leaf area in stressed plant as compared to the well-watered plant. The measured potential transpiration of the well-watered plants, T_{pw}, would therefore be higher than the potential transpiration of the plants having a leaf area equivalent to the stressed plant (T_{pd}).

To compare transpiration of stressed plants to that of well-watered plants having the same leaf area index (LAI) as the stressed plants, T_{rn} is used:

$T_{rn} = T_{rd} / T_{pd}$..... (2)

where T_{pd} is the potential transpiration rate of well-watered plants having the same LAI as the stressed plant.

T_{pw} has to be suitably modified by the following equation (equation 3) to obtain T_{pd} based on the LAI of the non-stressed and stressed plants (Wopereis 1993).

$T_{pd} = T_{pw} * (1 - e^{-0.4*LAI(d)})/(1 - e^{-0.4*LAI(w)})$..... (3)

where LAI(d) is the LAI of the stressed plants with rolled leaves, and

LAI(w) is the LAI of the well-watered plant.

T_{rd} and T_{pw} were measured daily, while LAI(d) and LAI(w) were measured periodically (see section on plant measurement) and linearly interpolated to obtain daily estimates of parameters used in equation 3.

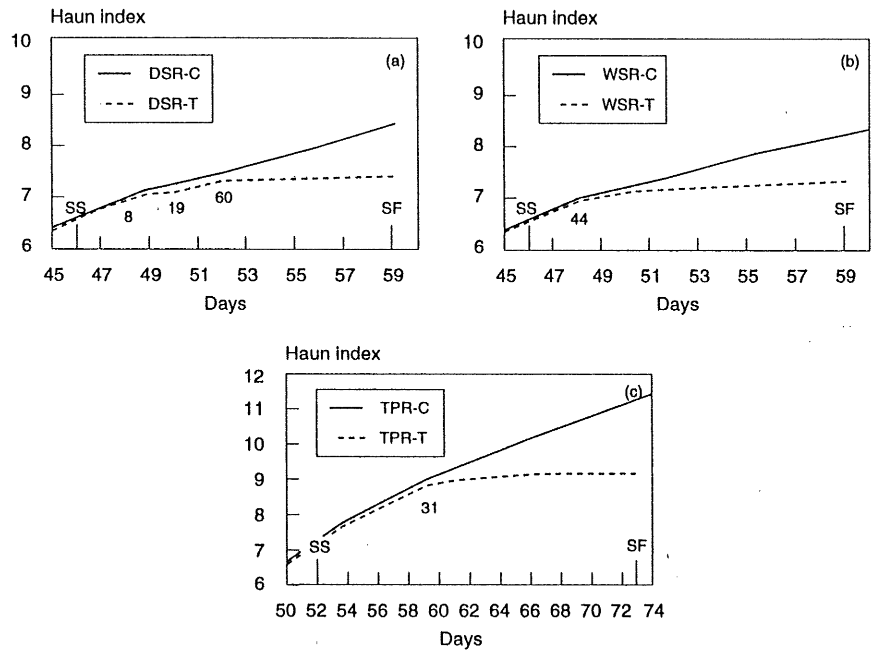
Results and discussion

Effect of water stress on physiological processes

Leaf expansion. Haun index values, derived from the leaf length measurements of the youngest and the penultimate leaf, indicated that water stress at T caused the process of leaf elongation to slow down and subsequently cease (Fig. 1). Plants, as affected by methods of establishment, responded in different ways in terms of number of days before the leaf elongation stopped: 7 days for TPR, 6 for DSR, and 3 for WSR. When expressed in terms of the soil moisture status of the root zone, however, Haun index in all methods of establishment levelled off at about 40-60 kPa of soil water tension (Fig. 1). This indicates that DSR, WSR, and TPR had different soil extraction rates and patterns to deplete the soil water reservoir to a level low enough to affect the leaf elongation rate (see subsection on soil water depletion).

Leaf rolling. As the severity of the stress increased, the leaves began to roll at a root-zone soil moisture tension generally beyond the tensiometer measurement range. Though in terms of soil water tension, leaf rolling started much earlier in DSR (< 100 kPa) than in WSR and TPR (200 kPa or more), leaf rolling score (LRS) 5 was attained at the soil water tension of around 900-1000 kPa (Fig. 2). Leaf rolling caused reductions in leaf area up to 50% (Fig. 3). The distribution of data shows that the reduction in leaf area due to leaf rolling is not influenced by either the variety or the method of establishment.

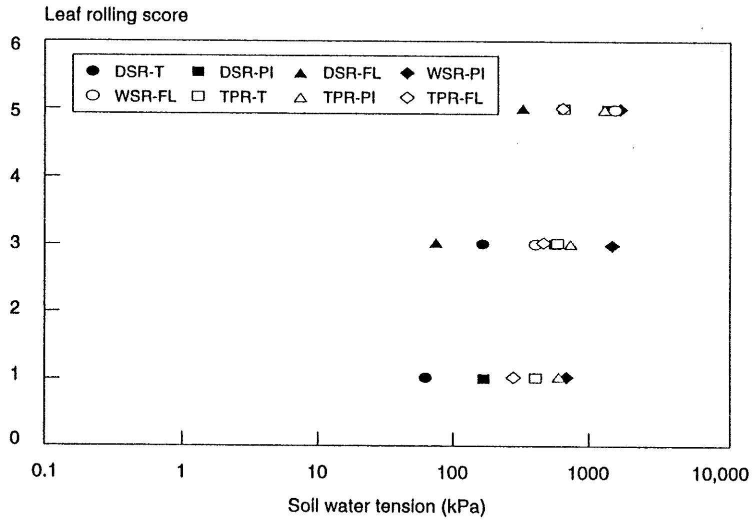
Leaf senescence. Dead leaves appeared in all treatments at LRS 3 and higher. Naturally occurring senescence around flowering time was accounted for in quantifying the senescence caused by stress only. The proportion of stress-induced dead leaves was higher when stress was imposed at PI and FL stages rather than at T. At LRS 5, the percentage of dead leaves recorded was around 50% in the PI and FL treatments. Some dead leaves could be recorded even at LRS 1 in PI and FL stress treatments. The dead leaf factor (1 representing no dead leaves and zero 100% dead leaves) could be described by a logistic function of soil water tension (Fig. 4). Dead leaves could be detected at tensions greater than 100 kPa in most treatments.



1. Haun index of PSBRc 14 in (a) dry-seeded rice in control (DSR-C) and stressed at tillering (DSR-T); (b) wet-seeded rice in control (WSR-C) and stressed at tillering (WSR-T); and (c) transplanted rice in control (TPR-C) and stressed at tillering (TPR-T) treatments. SS indicates start of stress and SF the end of stress. Numbers in the figure are the average soil water tension in kPa.

Soil water depletion

Figure 5 presents the soil water tension, measured by tensiometers installed at different depths, during stress imposition at tillering in DSR, WSR, and TPR. DSR was able to extract water rather uniformly throughout the depth of the pot (Fig. 5a), while the soil water tension of top soil layer WSR was much higher and reached air entry values faster than that of the lower soil layers WSR (Fig. 5b). Soil water tension also increased more rapidly in WSR than in DSR. WSR continued to extract water at a high rate for a few days before the effect of stress was exhibited by the plant. DSR, on the other hand extracted water more uniformly and was able to roll leaves at a relatively lower soil water tension (Fig. 2). By doing so, DSR could withstand longer drought periods.



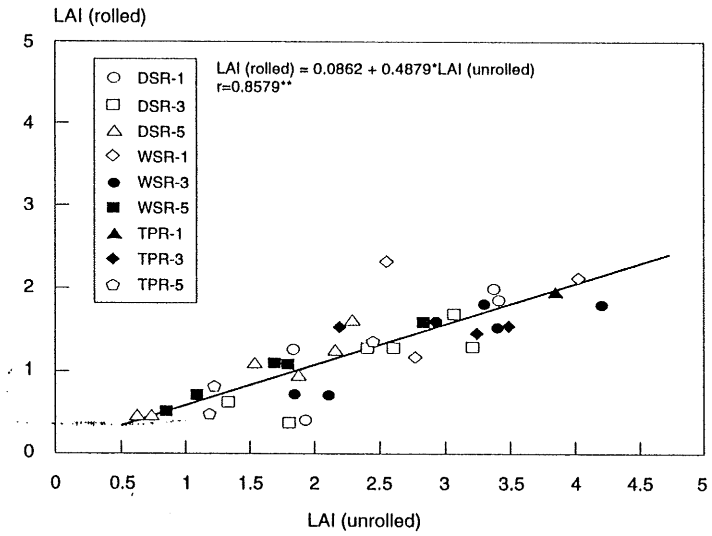
2. Effect of soil water tension on the leaf rolling score as influenced by the method of establishment in PSBRc14. DSR is dry-seeded rice; WSR is wet-seeded rice; TPR is transplanted rice; T, PI and FL refer to stress at tillering, panicle initiation and flowering.

During stress at tillering TPR extracted water at a lower rate than DSR and WSR, i.e it took longer for the soil profile to reach air entry values (Fig. 5c). This was due to lower LAI (Fig. 6) values and hence lower transpiration of TPR. The extraction rate of TPR during stress at flowering increased and was greater than that WSR and DSR (data not shown).

The differences in pattern and rate of extraction in different crop stages and different crop establishment methods indicated that the combined effect of LAI (Fig. 6) and the root length density distribution in different soil depths may play an important role in crop response to drought.

Transpiration

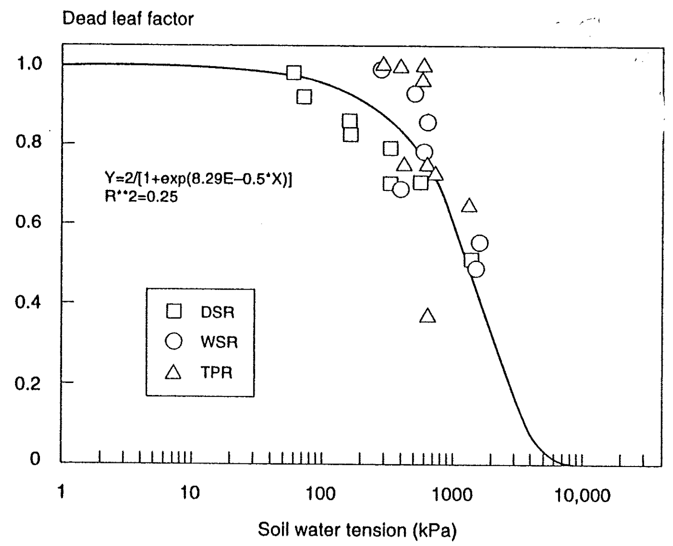
After the imposition of stress, the stressed plants continued to transpire at the same rate as the well-watered plants before the transpiration rate was reduced. Both relative transpiration rate, T_r, and the normalized relative transpiration rate, T_{rn}, can be expressed as a logistic function of the soil moisture tension of the root zone (Fig. 7a,b). They differed, however, in terms of the magnitude of the response. T_r started decreasing at soil water tensions of 10-30 kPa (Fig. 7a), while T_{rn} began falling only after the soil water tension exceeded 200 kPa (Fig. 7b). The difference in T_r and T_{rn} indicates that although the total transpiration rate of the stressed plant declined initially, it was caused by the reduction in leaf area only and the roots were able to extract soil moisture to meet the potential transpiration rate of the available green leaves of the stressed plants at soil water tensions less than 200 kPa. It is only at a later stage when the soil water tension exceeded 200 kPa that the stomata closed and contributed to reduction in transpiration.



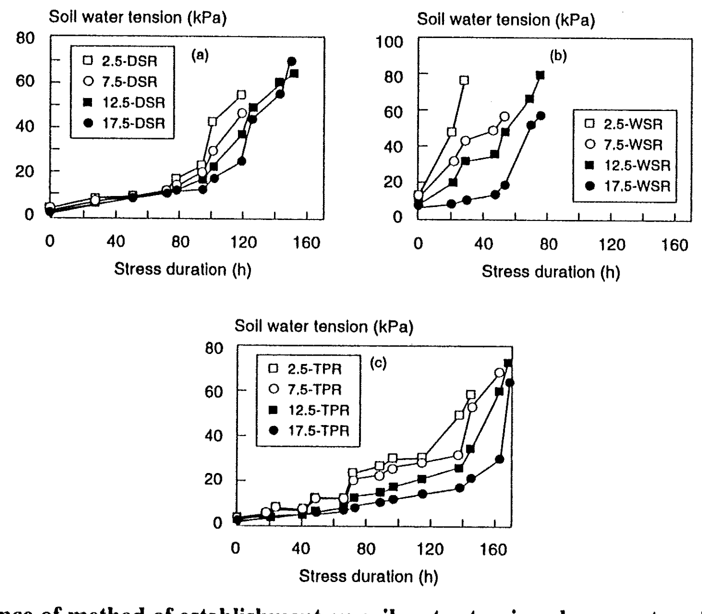
3. Effect of leaf rolling on leaf area index (LAI). DSR, WSR and TPR refer to dry-seeded, wet-seeded, and transplanted rice. 1, 3, and 5 are leaf rolling scores of 1, 3, and 5. Data of both PSBRc14 and IR72 have been pooled.

Crop phenology

Stress imposition at vegetative phases delayed panicle initiation, flowering, and maturity in both the varieties (Table 2, data for IR72 not shown). Flowering was delayed up to 2 weeks when stress was imposed at tillering. Stress at PI also delayed the flowering but to a lesser extent (6-8 days).

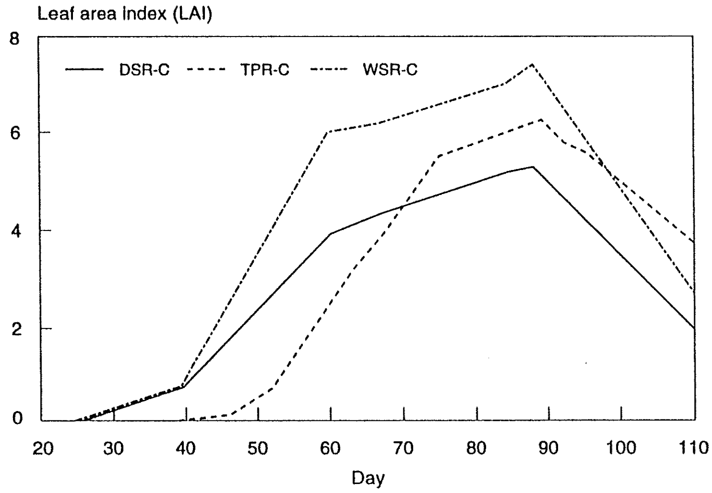


4. Effect of soil water tension on dead leaves factor in dry-seeded (DSR), wet-seeded (WSR), and transplanted (TPR) PSBRc14. A dead leaf factor of 1 indicates that no dead leaves are present and a dead leaf factor of 0 indicates that all leaves are dead.

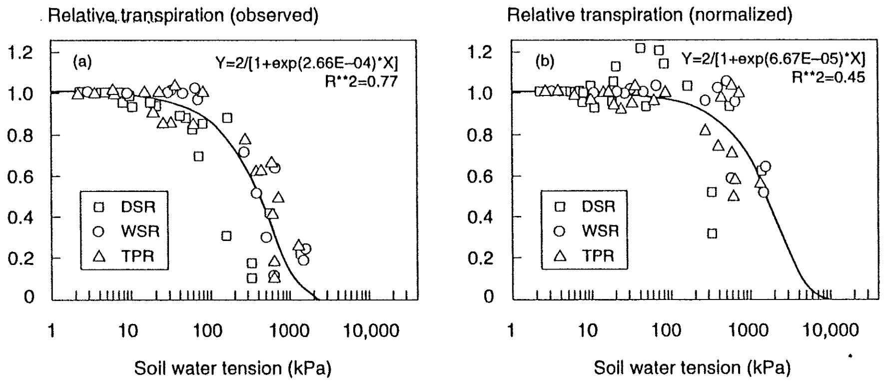


5. Influence of method of establishment on soil water tension changes at various depths during stress in PSBRc14 at tillering. 2.5, 7.5, 12.5, and 17.5 refer to depths (in cm) of soil water tension measurements; DSR, WSR, and TPR refer to dry-seeded, wet-seeded and transplanted rice, respectively.

Stress at tillering was responsible for delay in crop maturity by 6-8 days. Stress imposed at PI also delayed maturity by almost 2 weeks in DSR and WSR but not to that extent in TPR. Even stress at flowering delayed maturity by a few days. By delaying or slowing growth and development, the plant is able to withstand drought spells for short periods.



6. Leaf area index (LAI) as a function of time in non-stressed treatments. DSR, WSR, and TPR refer to dry seeded, wet seeded, and transplanted rice, respectively.



7. Relative transpiration rate (a), and normalized relative transpiration rate (b), as a function of soil water tension in dry seeded (DSR), wet seeded (WSR), and transplanted (TPR) PSBRc14. Relative transpiration rates of drought at all stages are plotted here. In the normalized transpiration rate, differences in Leaf Area Index between stressed and well-watered plants have been taken into account.

Table 2. Effect of stress on flowering and maturity dates in PSBRc14.

Stress treatments	Method of establishment (days after seeding/planting) Dry-seeded rice	Wet-seeded rice	Transplanted rice
		50% Heading	
Control (no stress)	64	63	60
Stress at tillering	76	77	73
Stress at panicle initiation	70	75	62
Stress at flowering	65	62	60
		Maturity (90%)	
Control (no stress)	100	98	92
Stress at tillering	108	104	100
Stress at panicle initiation	114	115	98
Stress at flowering	106	106	96

Grain yield

Yields in the control (non-stressed) treatment of DSR, WSR, and TPR were of comparable level but imposition of stress at the various stages resulted in a differential response by the crop in the three methods of establishment (Table 3). Stress at tillering affected the yield of DSR, WSR, and TPR compared with the control but the reduction in yield was much higher in WSR. Stress at PI and FL reduced yields in all the treatments very significantly. Many workers have reported that stress at vegetative phase delays the maturity but does not significantly affect grain yield of rice (O'Toole and Moya 1980, Yambao and Ingram 1988, Wopereis 1993). The duration of stress and the limited soil volume available for the roots was probably responsible for yield reduction at tillering. In WSR, the greater reduction in yield due to stress at tillering was probably brought about by the rapid removal of water from the soil profile (Fig. 5b).

Conclusion

A greenhouse study was carried out to quantify the response of two rice cultivars to soil water deficit as affected by establishment methods. When related to the average soil water tension of the root zone, the decline in leaf expansion, relative transpiration, and dead leaves factor of DSR, WSR, and TPR did not differ significantly. DSR started to roll their leaves at a lower water tension (< 100 kPa) as compared to WSR and TPR (≥ 200 kPa). Early leaf rolling and its ability to extract water more uniformly throughout the root zone allowed DSR to prolong its ability to withstand drought.

The method of crop establishment also influenced the response of rice to drought in terms of grain yield. Stress at tillering affected yield of WSR more significantly than that of TPR or DSR. Stress at panicle initiation and flowering affected yields significantly in all methods of establishment. Water stress delayed panicle initiation, flowering and maturity.

The physiological and morphological responses of the experimented cultivars could be expressed as functions of the average soil water tension in the root zone. These functions could be used in simulation models to assess the impact of climate and soil conditions to rice production in rainfed environment.

Table 3. Effect of method of establishment and water stress at various stages on yield (g/pot) of rice.

Stress	Method of establishment			Mean
	Dry-seeded rice	Wet-seeded rice	Transplanted rice	
Control (no stress)	27.56 Aa	28.06 Aa	24.50 Ab	26.71
Stress at tillering	25.02 Ba	19.90 Bb	21.62 Bb	22.18
Stress at panicle initiation	11.88 Ca	11.53 Ca	15.02 Cb	12.81
Stress at flowering	6.58 Da	8.88 Db	6.52 Da	7.33
Mean	17.76	17.09	16.92	17.26

In a column (upper case) or row (lower case), means followed by a common letter are not significantly different at the 5% level by DMRT.

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