

# Genotypic Variation in Response of Rainfed Lowland Rice to Prolonged Drought and Rewatering

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**Abstract** : Duration of the drought period is important for plant response during drought and after rewatering. We hypothesized that, if drought duration is extended, (1) high seedling vigor and rapid development of a deep root system will not be advantageous, and (2) osmotic adjustment will be more important. Six diverse rice (*Oryza sativa* L.) genotypes were selected from rainfed lowland germplasms to examine the development of a deep root system and osmotic adjustment, and their relationship with biomass production during drought and after rewatering, under two different drought durations (shorter and prolonged) in the greenhouse. NSG19 and KDML105 had greater seedling vigor (larger seedling biomass), developed a deep root system earlier in response to drought, extracted soil water more quickly, and their pre-dawn leaf water potential declined more rapidly during the prolonged drought period. These two genotypes showed superior drought recovery even after a prolonged drought period in which they suffered a greater reduction in transpiration, water use efficiency, and biomass production. The superior recovery ability was associated with larger plant size by the end of the drought period rather than with plant water status during drought, such as osmotic adjustment or leaf water potential. Osmotic adjustment was greater during prolonged drought periods (ca. 0.7 MPa) than during shorter drought periods (ca. 0.5 MPa), and lower osmotic adjustment was mostly associated with a higher leaf water potential. Genotypic variation in osmotic adjustment was observed, but there was no clear relationship between osmotic adjustment and biomass production during drought periods. These patterns of response of rice seedlings to drought and rewatering in the greenhouse should help to explain the patterns of adaptation of rainfed lowland rice in the field. Selection for drought recovery ability should be an advantageous strategy for early season drought.

**Key words** : Drought, Drought recovery, Osmotic adjustment, Rainfed lowland rice, Root.

Heterogeneous and variable drought environments have prevented rapid improvement of grain yield in varieties of rainfed lowland rice. Physio-morphological traits that are expressed under drought conditions and that may improve adaptation to drought environments have been studied (O'Toole, 1982; Fukai and Cooper, 1995; Fukai et al., 1998). However, the extent of their contribution to an increment in biomass production and yield is not clear.

A deep root system and osmotic adjustment have been studied as putative traits for drought avoidance with scope for marker-assisted selection (Nguyen et al., 1997). A deep root system could improve the adaptation of rice during drought through greater capacity for water extraction, thus maintaining high plant leaf water status. Lilley and Fukai (1994a) showed that cultivars of upland rice with greater root length density extracted more soil water during drought. Kamoshita et al. (2000) showed a positive

correlation between deep root length density and rate of water extraction from deeper soil layers among rainfed lowland rice genotypes during the drought period in a pot experiment. The advantage of a deep root system for adaptation to drought conditions may depend on duration of the drought period and water-holding capacity of the soil. Genotype by environment interaction for deep root characters was reported by Kamoshita et al. (2002a), who emphasized the importance of characterizing drought environments in which root traits and water extraction are quantified, and relating this to the target population of environments.

Osmotic adjustment could help plants to retain a higher relative water content at a given level of water potential. Although greater biomass or yield production due to higher capacity for osmotic adjustment has not been reported in rice, evidence is available in other crops (Zhang et al., 1999). If

Table 1. Six rice genotypes adapted to rainfed lowlands were evaluated for water-use efficiency and biomass production under drought. (a) Characteristics of each growth period used in the experiment; (b) sampling times (days after sowing; DAS) and cumulative transpiration under drought (kg); and (c) according to genotype, the five sampling occasions (1-5) in terms of DAS, and the intervals (in days) between samplings for each growth period.

(a)									
Characteristic	Growth period <sup>a</sup>								
	DR <sub>i</sub>	DR <sub>s</sub>	RW <sub>s</sub> /DR <sub>pr</sub>	RW <sub>pr</sub>					
Interval (days)	11–15 <sup>b</sup>	9–12 <sup>b</sup>	7	7					
Shorter stress	DR <sub>i</sub>	DR <sub>s</sub>	RW <sub>s</sub>	-					
Prolonged stress	DR <sub>i</sub>	DR <sub>s</sub>	DR <sub>pr</sub>	RW <sub>pr</sub>					
Transpiration rate during drought (mm d <sup>-1</sup> )	5.1	5.7	2.9	-					

(b)					
Parameter	Sampling occasion				
	1	2	3	4	5
Sampling time	21	32–36 <sup>b</sup>	43–45 <sup>b</sup>	50–52 <sup>b</sup>	57–59 <sup>b</sup>
Cumulative transpiration	0	2.0	3.9	4.3–4.6 <sup>b</sup>	-

(c)									
Genotype	Sampling occasion					Intervals <sup>a</sup>			
	1	2	3	4	5	DR <sub>i</sub>	DR <sub>s</sub>	RW <sub>s</sub> /DR <sub>pr</sub>	RW <sub>pr</sub>
CT9993	21	36	45	52	59	15	9	7	7
IR62266	21	33	44	51	58	12	11	7	7
IR58821	21	32	44	51	58	11	12	7	7
IR52561	21	35	45	52	59	14	10	7	7
KDML105	21	32	43	50	57	11	11	7	7
NSG19	21	32	43	50	57	11	11	7	7

<sup>a</sup>DR<sub>i</sub> = initiation of drought, whether the shorter or prolonged period; DR<sub>s</sub> = shorter drought period; RW<sub>s</sub> = rewatering after shorter drought period; DR<sub>pr</sub> = prolonged drought period; RW<sub>pr</sub> = rewatering after prolonged drought period. <sup>b</sup>Differs according to genotype.

drought duration were extended, a higher capacity for osmotic adjustment may be advantageous for biomass production or even survival.

Drought recovery is important, particularly after early season drought. Mitchell et al. (1998) showed that recovery after drought was related not to plant resistance during the drought period, but to leaf area at the end of the drought period. After exposure to a progressive drought of about 20 days in the greenhouse, genotypic variation in recovery following rewatering was associated with greater seedling vigor (Wade et al., 2000). If the drought period were further prolonged, however, genotypes with higher seedling vigor may be more severely injured, and so may not show superior drought recovery.

The objective of this study was to examine genotypic

variation and its interaction with drought duration for deep root development, osmotic adjustment, and drought recovery. We hypothesized that (1) genotypes with greater seedling vigor and faster water extraction during drought will be more damaged during prolonged drought and show inferior recovery after rewatering, and (2) osmotic adjustment will be greater during a prolonged drought period and will have greater effects on biomass production.

## Material and Methods

### 1. Cultural details

Six diverse rainfed lowland rice genotypes were tested in the 1999 dry season in the greenhouse at the International Rice Research Institute, Los Banos, Philippines (14°11N, 121°15E, 23 m altitude) for

their expression of physio-morphological traits under progressive drought and their capacity to recover afterwards. Two periods of drought were used: 22-24 days and about 30 days. A split-plot design with three replicates was used, with three water regimes (well-watered, shorter stress, and prolonged stress treatments) as the main plots and six rice genotypes as subplots. In the shorter stress treatment, ponded water was drained at 21 days after sowing (DAS) and no water was supplied until transpiration was about 3.9 kg of water loss at 22 to 24 days after drainage depending on genotype (shorter drought period). After the shorter drought period, 4 kg of water was replenished, and then water was added daily for 7 days to keep the level of ponded water the same as in the well-watered treatment (rewatering period). In the prolonged stress treatment, drought was extended for another 7 days. Plants were then rewatered for 7 days as for the shorter stress treatment. Ponded water with about 2- to 4-cm depth was always maintained in the well-watered treatment.

Six rice genotypes differentially adapted to rainfed lowlands were used: CT9993-5-10-1-M (CT9993; tall semi-upland from South America), IR62266-4-2-6-2 (IR62266; semi-ground cover from Philippines), IR58821-2-3-B-1-2-1 (IR58821; semi-erect from Philippines), IR52561-UBN-1-1-2 (IR52561; tall from Philippines), Khao Dawk Ma Li 105 (KDML105; weak stem from Thailand), and Nam Sa Gui 19 (NSG19; Thailand). These genotypes were among eight that were selected from diverse rainfed lowland rice germplasm and differed for root system and osmotic adjustment (Shashidhar et al., 1994; Samson et al., 1995; Lilley and Ludlow 1996; Ray et al. 1996; Sarkarung et al., 1997; Azhiri-Sigari et al., 2000; Kamoshita et al., 2000), and in patterns of adaptation (Wade et al., 1999).

PVC pots with an internal diameter of 20 cm and height of 55 cm were used as the experimental unit to control water stress development and allow measurement of secondary physio-morphological traits with less error. Previous studies in the field had large error terms, because of the heterogeneous nature of the rainfed lowlands, which tended to mask genotypic variation in physio-morphological traits such as root length or leaf water potential (Jongdee et al., 1997; Pantuwan et al., 1997).

Twenty kg of sieved air-dried sandy loam soil, pH 5.7, was placed in a plastic sleeve inside each PVC pot. The outside of the pots was covered with aluminum foil to minimize increase in soil temperature. The soil surface was covered with small cubic polystyrene after drainage and the tops of all the pots were covered with aluminum foil to minimize evaporation, so that any changes in pot weight could be attributed to transpiration from plants and/or watering. The distance between any two neighboring pots was more

than 40 cm and the effects of mutual shading were negligible. An adequate amount of fertilizer was supplied, with 2.73 g of urea for nitrogen, 1.84 g of solophos for phosphorus, and 1.04 g of muriate potash for potassium. Four to five pre-germinated seeds were sown in each pot on 29 January 1999, and thinned to one seedling per pot at 12 DAS. Green algae were removed daily from the ponded water. No disease, insect, or weed damage was observed.

## 2. Measurements

### (1) Meteorological data

The minimum and maximum daily air temperatures were collected by a hygrothermograph and evaporation was measured with seven pan evaporimeters with 20-cm diameter randomly placed inside the greenhouse. The average daily minimum and maximum air temperatures during the experiment were 26.5 and 34.4 °C, respectively, and average evaporation was 4.8 mm d<sup>-1</sup>. Average daily solar radiation during the experiment was 17.1 MJ m<sup>-2</sup> at the weather station 500 m from the greenhouse.

### (2) Transpiration and plant sampling

Daily transpiration was calculated from 21 DAS until the end of the experiments by measuring weight loss in the drought treatment and water added in the well-watered treatment. Cumulative transpiration after 21 DAS was calculated by the sum of daily increments in each water regime. In both the shorter and prolonged stress treatments, pot weight was measured 3, 6, and 24 hours after replenishing 4 kg of water to estimate how rapidly transpiration recovered after rewatering.

Plants were sampled at different times, according to genotype (Table 1):

1. At 21 DAS, before water was withheld from drought treatments;
2. When cumulative transpiration was about 2.0 kg, between 32 and 36 DAS;
3. When cumulative transpiration was about 3.9 kg, between 43 and 45 DAS;
4. At 7 days after sample 3, that is, between 50 and 52 DAS; and
5. At 7 days after sample 4, that is, between 57 and 59 DAS.

Different dates were chosen for each genotype on the second and third samplings to examine the genotypic differences when all the genotypes used the same amount of water, thus minimizing the confounding effects of different potential growth under the well-watered treatment. In the fourth and fifth samplings, response of all the genotypes to the same duration of 7 days of prolonged drought or rewatering was examined. To assess plant response during each stage of drought development and rewatering, growth periods during the experiment were divided into

- Initial drought period (between samples 1 and

- 2),
- Shorter drought period (between samples 2 and 3),
  - Prolonged drought period (between samples 3 and 4 in the prolonged stress treatment), and
  - Rewatering period (between samples 3 and 4 in the shorter stress treatment and between samples 4 and 5 in the prolonged stress treatment).

Transpiration rate during each drought period was calculated. Plants in both water regimes were sampled at the same time. At each sampling, total shoot biomass and green leaf biomass were determined. Incremental biomass changes were calculated as the differences of shoot biomass between the consecutive plant samplings.

### (3) Root parameters

After each sampling of above-ground plant parts, the soil mass within the plastic sleeve was slowly pulled from the PVC pots and divided into layers of 0-5, 5-10, 10-20, 20-30, 30-40, and 40-50 cm from the soil surface. Roots were carefully separated from the soil on a 1-mm sieve screen. Root length was measured by the COMAIR Root Length Scanner (Hawker De Havilland Victoria Limited) and the root length density for each soil layer was calculated. Root dry matter in each soil layer was measured, and total and deep root dry matter below the 30-cm soil layer were calculated. Root to shoot ratio was estimated from total root dry matter divided by total shoot biomass. Deep root ratio was calculated as the proportion of deep root dry matter to total root dry matter (Yoshida 1981). Root thickness was measured by micrometer from the 0-10-cm layer for seven randomly chosen nodal roots.

### (4) Soil water content

Soil water status was monitored daily from 36 DAS until the end of the prolonged drought period, using a 1502 Metallic Time Domain Reflectometer (TDR; Tektronix Inc., Wilsonville, Oregon USA). Five pairs of stainless-steel waveguides were inserted horizontally into the soil from holes drilled in the sides of pots at depths of 5, 15, 25, 35, and 45 cm from the soil surface. The waveguides were connected with the TDR unit using an extension cable and electronic wavelength was recorded daily. The dielectric constant,  $k$ , was calculated from the TDR readings according to the equation of Cassel (1992) adjusted by the constant of the machine used in this experiment:

$$k = 4.08 (\text{TDR reading})^2$$

The three-degree polynomial equation between the dielectric constant and volumetric soil water content (VWC) (Topp et al. 1980; Cassel 1992) was recalibrated as below:

$$\text{VWC (m}^3 \text{ m}^{-3}\text{)} = 0.12782 + 0.02575 k - 0.0018824 k^2 + 0.00005856 k^3$$

On a few occasions, when VWC exceeded 0.5, a value of 0.5 was used, which is consistent with the

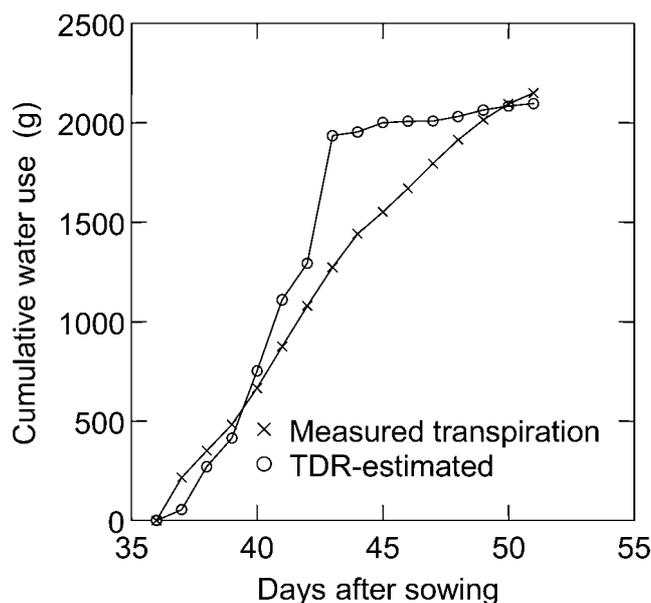


Fig. 1. Comparison of time course of transpiration (g) measured by daily weight loss of pots with soil water extraction (g) estimated by time domain reflectometry (TDR) from 36th day after sowing.

estimated value of VWC just after drainage (Kamoshita et al. 2000).

The amount of soil water extraction (WE; g) at each measured depth was calculated by multiplying the difference between VWC and soil water content just after drainage (0.50) by the dissected area of the pot in the following equation:

$$\text{WE (g)} = (0.50 - \text{VWC}) \times 3.14 \times 10^2 \times 1$$

The amount of soil water extraction (WE10) in the 10-cm layer around each measured depth (i.e., 0-10-, 10-20-, 20-30-, 30-40- and 40-50-cm layers) was calculated according to the following equation:

$$\text{WE10 (g)} = \text{WE} \times 10$$

This equation converted the measured TDR values to the water content of the soil mass from 5 cm above to 5 cm below each probe. The total amount of water extracted from all the soil layers was estimated by summing the WE10 at each depth. The daily rate of soil water extraction before and after the third sampling (43-45 DAS depending on genotype) was calculated from changes in WE10 over 6 days before and after the third sampling (36 to 42 and 42 to 48 DAS, respectively).

### (5) Plant water status

At the second, third and fourth samplings and at 47 and 54 DAS, leaf water potential and osmotic potential at full turgor were measured at pre-dawn. One leaf blade of the second-youngest fully expanded leaf on the main stem or on a primary tiller with similar size was inserted into a long plastic bag, severed just below the ligule, and covered with a wet cloth. The leaf blade was immediately taken to the pressure chamber (Soil

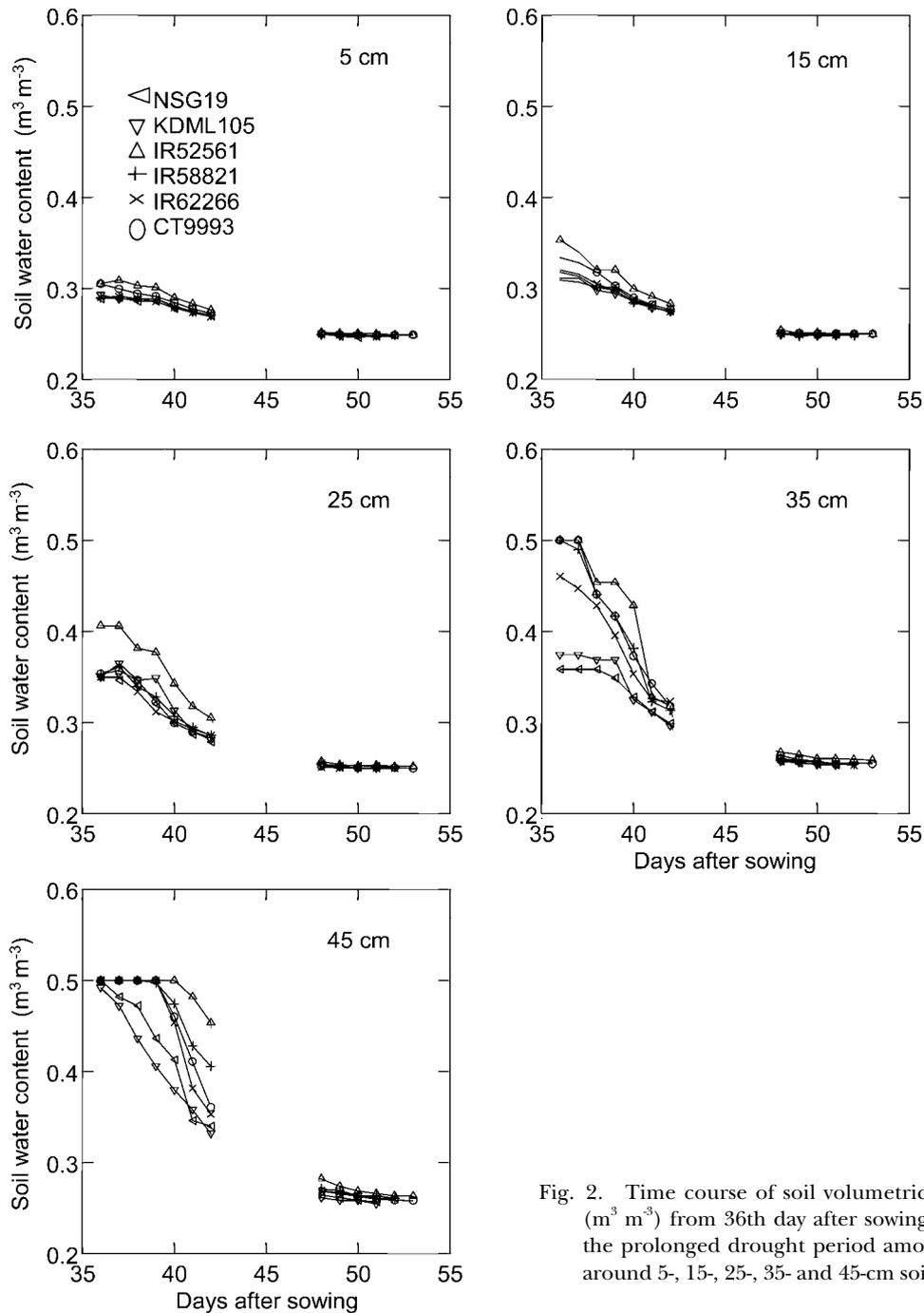


Fig. 2. Time course of soil volumetric water content ( $\text{m}^3 \text{m}^{-3}$ ) from 36th day after sowing till the end of the prolonged drought period among 6 genotypes around 5-, 15-, 25-, 35- and 45-cm soil depth.

Moisture Equipment Corp., USA) for measurement of leaf water potential. Another leaf blade of the second-youngest fully expanded leaf, taken in the same way, was soaked in water in the refrigerator for 24 hours to fully rehydrate the leaf tissue, then placed in an eppendorf tube, frozen with liquid nitrogen for 30 s to stop the physiological function of its cells, and stored in the deep freeze. Osmotic potential at full turgor was measured with the freezing-point osmometer, micro-Osmette (Precision System Inc., USA). Osmotic adjustment was calculated as the difference between

the turgid osmotic potential in the well-watered treatment and in the stress treatment on the same sampling date (Babu et al., 1999).

#### (6) Leaf elongation

Length of the youngest expanding leaf on three tillers was measured daily over three consecutive days from one day before to one day after the end of initial drought, shorter drought, and prolonged drought periods in well-watered and stress treatments. The daily rate of leaf elongation was calculated both during drought and after rewatering.

Table 2. Cumulative transpiration in shorter and prolonged water stress treatments during each growth period for each rice genotype.

Genotype	Transpiration (kg) <sup>a</sup>				
	DR <sub>i</sub>	DR <sub>s</sub>	RW <sub>s</sub>	DR <sub>pr</sub>	RW <sub>pr</sub>
CT9993	2.03	1.82	5.57	0.76	4.62
IR62266	1.95	1.96	5.32	0.65	5.06
IR58821	1.93	1.91	5.73	0.48	5.60
IR52561	1.97	1.89	5.67	0.77	5.18
KDML105	1.95	1.99	6.05	0.63	6.70
NSG19	1.98	1.92	6.32	0.53	7.14
LSD <sub>0.05</sub>	ns	ns	ns	0.10*	1.60**

<sup>a</sup>See footnote a, Table 1.

\*\* = significant at P = 0.01; \* = significant at P = 0.05; ns = not significant at P = 0.05.

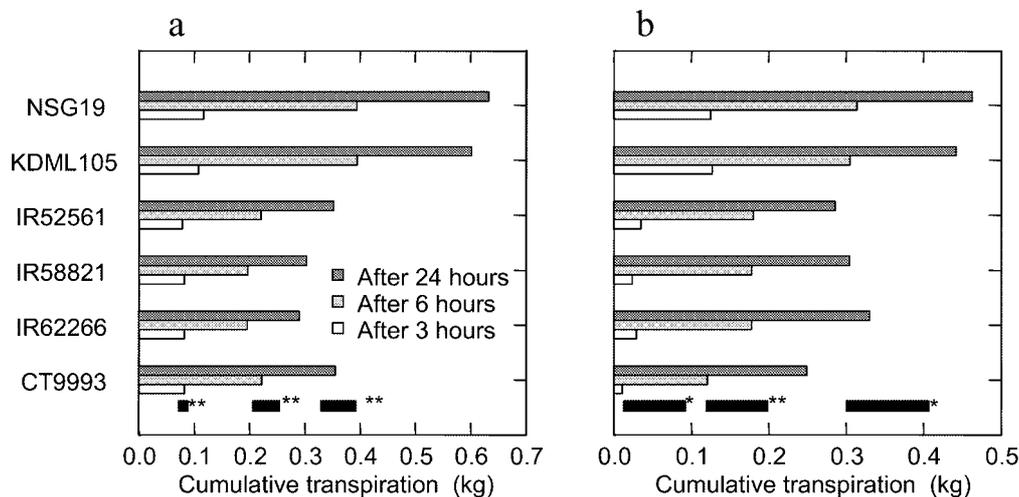


Fig. 3. Increase in cumulative transpiration (kg) measured at 3, 6, and 24 hours after rewatering in shorter (a) and prolonged (b) stress treatments. Bars represent LSD<sub>0.05</sub> for transpiration measured at 3, 6, and 24 hours after rewatering, respectively, from the left, with P=0.05 (\*) and 0.01 (\*\*).

## (7) Statistical analysis

Analysis of variance was conducted for each water regime and the least significant difference at a probability of 5 % was determined using Systat 7.0 (SPSS 1997).

## Results

### 1. TDR estimation of soil water extraction

The TDR-estimated water extraction from the 0-50 cm soil profile in pots matched well with estimates of transpiration obtained from sequential weighing of pots during the drying cycle, except for days 43 to 47 (Fig. 1). The reason for TDR failure in this period is not known, but may be related to soil cracking, separation of the soil mass from the pot, and the consequent reduction in soil volume, thus

lowering the dielectric constant in measurement by TDR. Consequently, values of soil water extraction are only shown for days 36 to 42, and days 48 to 50 in subsequent sections (Fig. 2). Values for upper and lower limits of plant available soil water of 0.50 and 0.25 from these TDR data match well with previous reports for this soil by Kamoshita et al. (2000).

### 2. Transpiration

In the initial drought period in which average daily transpiration among six genotypes was 5.1 mm d<sup>-1</sup>, NSG19, KDML105, and IR58821 transpired about 2 kg of water 3 and 4 days earlier than IR52561 and CT9993, respectively (cf. Table 1). In the shorter drought period with an average daily transpiration of 5.7 mm d<sup>-1</sup>, CT9993 and IR52561 transpired about

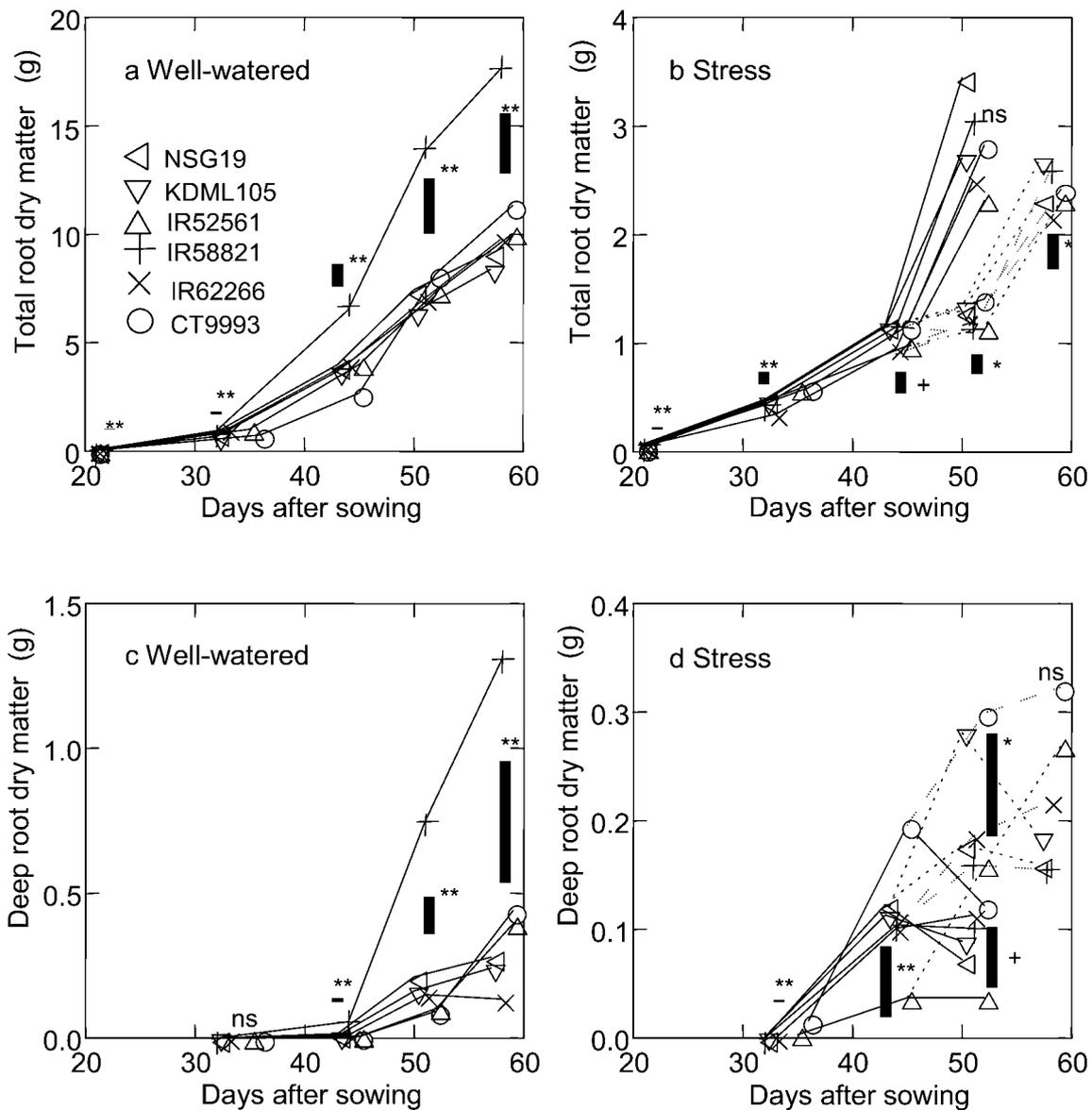


Fig. 4. Time course of total and deep root dry matter (g) in well-watered (a, c) and stress (b, d) treatments among 6 genotypes. In (b) and (d), shorter and prolonged stress treatments were represented by solid and dotted lines, respectively. Bars represent  $LSD_{0.05}$  for total or deep root dry matter at each sampling occasion, with  $P=0.10$  (\*),  $0.05$  (\*), and  $0.01$  (\*\*).

1.9 kg of water 3 and 2 days earlier than IR58821, respectively. During the 7 days of prolonged drought ( $0.64 \text{ kg}$ ) with an average daily transpiration of  $2.9 \text{ mm d}^{-1}$ , IR58821 and NSG19 transpired the smallest amount of water, whereas CT9993 and IR52561 transpired the largest amount (Table 2). During the 7 days of rewatering in both the shorter stress ( $5.78 \text{ kg}$ ) and prolonged stress ( $5.71 \text{ kg}$ ) treatments, NSG19 transpired the greatest amount of water, followed by KDML105, whereas CT9993 and IR62266 transpired the least amount of water, and this genotypic variation was larger in the prolonged stress treatment (Table 2). The increment in transpiration was higher for NSG19 and KDML105 from 3 hours after rewatering, and this

was more marked in the prolonged stress treatment (Fig. 3).

### 3. Soil water extraction during drought

Data on soil water extraction are shown for each of 5 depth increments in Fig. 2. By day 36, much of the available soil water estimated from TDR measurements was already extracted from the surface layers, while extraction was just commencing at 45 cm depth. Extraction commenced earliest in KDML105 and NSG19, and latest in IR52561, with IR62266, IR58821 and CT9993 intermediate. The rate of extraction was more rapid in the 35 and 45 cm soil layers, as more of the available soil water had already been removed from

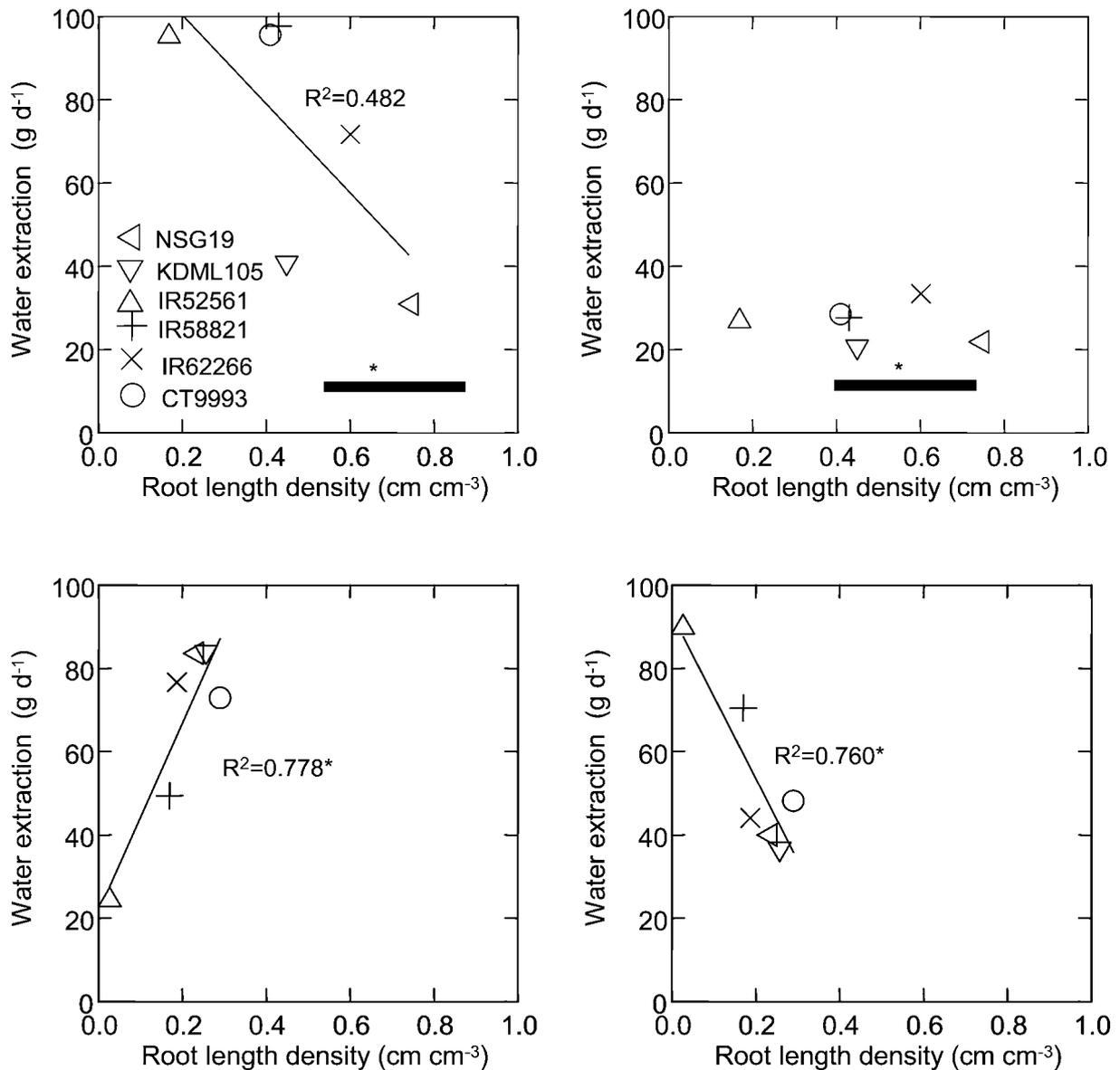


Fig. 5. Relationship between root length density ( $\text{cm cm}^{-3}$ ) at the third sampling (end of shorter drought period) and rate of soil water extraction ( $\text{g d}^{-1}$ ) from 36 to 42 and from 42 to 48 days after sowing in 30-40-cm (a, b) and 40-50-cm (c, d) soil depth. Bars represent  $\text{LSD}_{0.05}$  for root length density, with  $P=0.05$  (\*).

shallower layers. The graphs indicate the upper and lower limits of transpirable soil water (field capacity and wilting point) as 0.50 and 0.25, respectively, with extraction close to the lower limit in all cultivars at 5 and 15 cm, in most cultivars except IR52561 at 25 cm, and with significant differences among cultivars in available water remaining at 35 and 45 cm soil depths. By day 48, almost all of the plant-available soil water had been removed at all depth increments, with just a little remaining in the deepest soil layer, especially for IR52561.

#### 4. Root growth

In the well-watered treatment, IR58821 had a significantly higher total and deep root dry matter

than the others (Fig. 4a,c). At 51 DAS, the root to shoot ratio of IR58821 was 20% and at 58 DAS the deep root ratio was 7.3% (data not shown). Among the other five genotypes, NSG19 and KDML105 increased deep root dry matter at an earlier growth stage, whereas CT9993 and IR52561 developed deep roots at a later stage.

In the stress treatments, IR58821 had the smallest root to shoot ratio (5.7%) at the end of the prolonged drought period (data not shown) and IR52561 had the smallest total root dry matter during the drought periods (Fig. 4b). CT9993 always had the highest values of root to shoot ratio (9.7% at the end of the prolonged drought period) (data not shown) and largest total root dry matter by the end of the

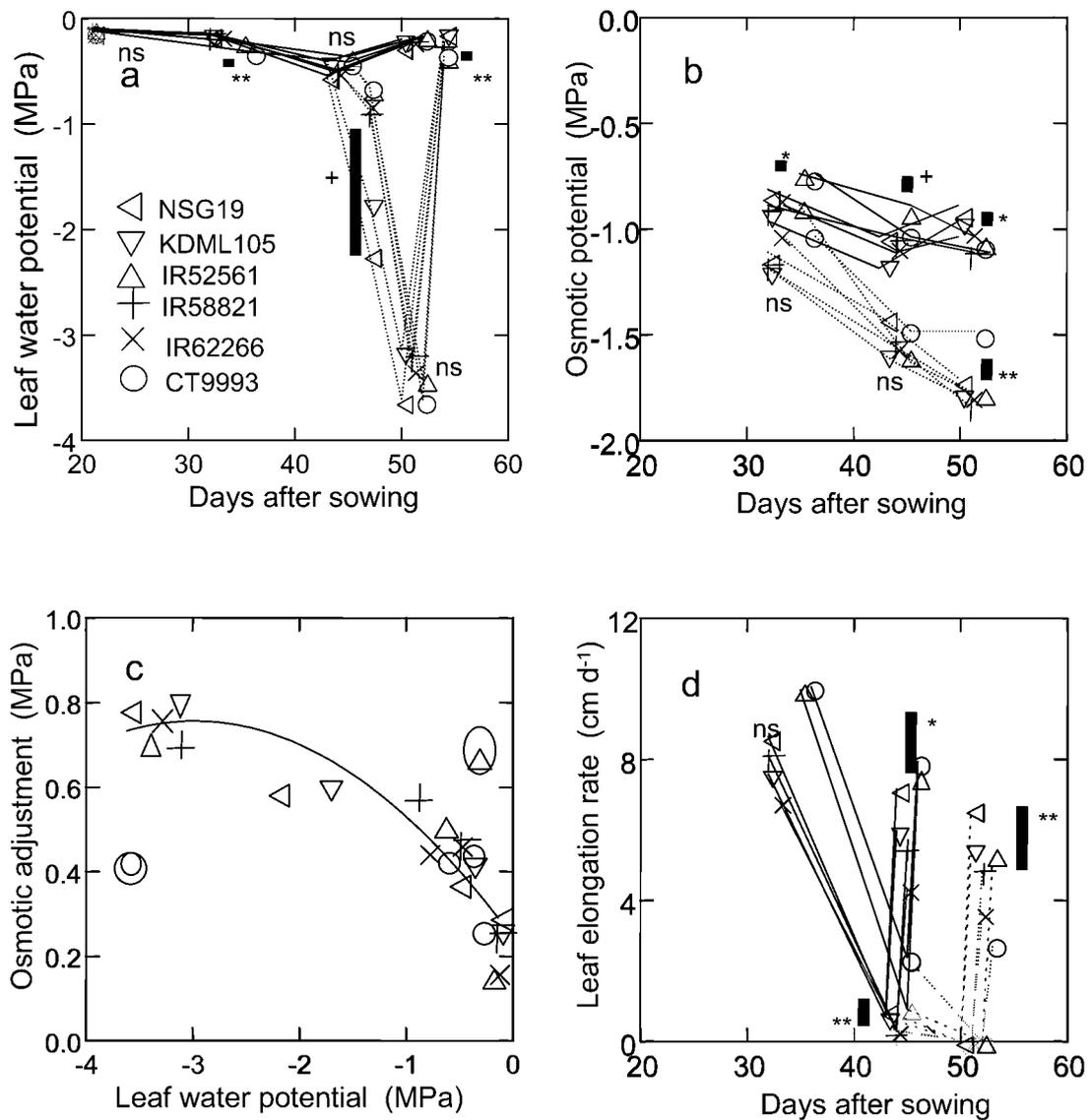


Fig. 6. Time course of pre-dawn leaf water potential (a) and leaf elongation rate (d) in shorter (solid lines) and prolonged (dotted lines) stress treatments, and time course of osmotic potential (MPa) in well-watered (solid lines) and stress (dotted lines) treatments (b), among 6 genotypes. Relationship between pre-dawn leaf water potential (MPa) and osmotic adjustment (MPa) among 6 genotypes (c), with quadric regression line excluding the high and low values of IR52561 and CT9993 (encircled), was drawn:  $y = 0.2439 - 0.3435 x - 0.05755 x^2$ . Bars represent  $LSD_{0.05}$  at each sampling occasion, with  $P=0.10$  (+),  $0.05$  (\*), and  $0.01$  (\*\*).

prolonged drought period. After rewatering, the increment in total root dry matter and root to shoot ratio was generally higher in IR58821 and CT9993 (data not shown) in both the shorter and prolonged stress treatments. The increment in root dry matter and root length density (data not shown) occurred in the shallower soil layers (shallower than 30-cm depth) before 33 DAS. The deep root ratio was 10% and 17% at the end of the shorter and prolonged drought periods, respectively, while it was less than 3% in the well-watered treatment at the corresponding times. Deep root dry matter increased the fastest in CT9993, followed by NSG19 and KDML105, and the

slowest in IR52561 by around 44 DAS (Fig. 4d). During the prolonged drought period, KDML105, CT9993, and IR52561 increased deep root dry matter sharply, while the increment of the other genotypes was intermediate.

##### 5. RLD and rate of water extraction

The relationship between root length density at the third sampling (43-45 DAS depending on genotype) and average rate of soil water extraction over 6 days before (36-42 DAS) and 6 days after (42-48 DAS) the third sampling was examined in both 30-40-cm and 40-50-cm depths (Fig. 5). These intervals were chosen

Table 3. Shoot biomass (g) in six rainfed-lowland rice genotypes before stress imposition and at the end of the experiment under a well-watered treatment, and increment of shoot biomass (g) during each growth period under water stress treatments for each genotype.

Genotype	Shoot biomass (g)						
	Well-watered		Stress <sup>a</sup>				
	First sampling	Fifth sampling	DR <sub>i</sub>	DR <sub>s</sub>	RW <sub>s</sub>	DR <sub>pr</sub>	RW <sub>pr</sub>
CT9993	0.38	86.4	6.6	6.2	13.8	3.5	7.5
IR62266	0.59	104.5	4.9	9.7	12.6	3.3	9.2
IR58821	0.78	115.5	5.5	10.1	14.5	3.0	8.2
IR52561	0.52	97.4	6.8	7.9	14.7	3.8	7.4
KDML105	0.68	117.1	5.8	11.3	15.2	2.6	11.7
NSG19	0.87	123.0	6.5	10.7	17.0	1.5	10.9
LSD <sub>0.05</sub>	0.20**	10.1**	1.3 <sup>+</sup>	3.8*	4.8 <sup>+</sup>	ns	2.1**

<sup>a</sup>See footnote a, Table 1.

\*\* = significant at P = 0.01; \* = significant at P = 0.05; <sup>+</sup> = significant at P = 0.10; ns = not significant at P = 0.10.

as the calibration of TDR values with cumulative transpiration were correct on days 36, 42 and 48 (Fig. 1). From 36-42 DAS in the 30-40-cm depth, genotypes with a greater root length density such as NSG19 and KDML105 extracted water more slowly than genotypes with a lower root length density such as IR52561 (Fig. 5a). From 42-48 DAS, the rate of water extraction was much lower in all the genotypes regardless of the difference in root length density (Fig. 5b). At 36-42 DAS in the 40-50 cm depth with smaller root length density than in the 30-40-cm depth, genotypes with a slightly greater root length density such as NSG19 and KDML105 extracted water more rapidly than genotypes with a lower root length density such as IR52561 (Fig. 5c). In the 40-50-cm depth at 42-48 DAS, IR52561 had a greater rate of water extraction (Fig. 5d). As discussed later, these outcomes relate to the amounts of water remaining available for extraction by the different cultivars for the various soil layers during these periods.

## 6. Plant water status and leaf growth

By the end of the shorter drought period, NSG19 had the lowest pre-dawn leaf water potential (-0.54 MPa) and IR52561 and CT9993 had the highest values (-0.36 and -0.41 MPa, respectively) (Fig. 6a). A more rapid decline in pre-dawn leaf water potential was recorded at 47 DAS in NSG19 (-2.23 MPa) and KDML105 (-1.75 MPa). At the end of the prolonged drought period, KDML105 (-3.15 MPa) had a higher leaf water potential than NSG19 (-3.62 MPa) and IR52561 (-3.42 MPa) had a higher leaf water potential than CT9993 (-3.62 MPa). Pre-dawn leaf water potential recovered to -0.3 to -0.1 MPa after rewatering depending upon genotype and

duration of drought. Genotypic variation was observed in osmotic potential under both drought and well-watered conditions (Fig. 6b). By 45 DAS, IR52561 had the highest osmotic potential under well-watered conditions (-0.75 and -0.93 MPa at 35 and 45 DAS, respectively). At the end of the initial drought period, NSG19, KDML105, and IR58821 had the lowest osmotic potential (-1.2 to -1.1 MPa). During the shorter drought period, IR52561 and IR62266 reduced their osmotic potential to a greater extent. By the end of the prolonged drought period, osmotic potential was highest in CT9993 (-1.50 MPa) and lowest in IR62266 (-1.79 MPa). Osmotic adjustment increased with the slight decline in leaf water potential and then increased more slowly as leaf water potential declined further in all the genotypes (Fig. 6c), with the average osmotic adjustment among six genotypes being 0.2, 0.5, and 0.7 MPa by the end of the initial, shorter, and prolonged drought periods, respectively. The exception was the high osmotic adjustment of IR52561 at the end of the shorter drought period (0.67 MPa) and the low osmotic adjustment of CT9993 at the end of the prolonged drought period (0.42 MPa).

The leaf elongation rate was higher in CT9993 (10.1 cm) and IR52561 (10.0 cm) at the end of the initial drought period and this genotypic ranking was retained by the end of the shorter drought period when the leaf elongation rate declined sharply (Fig. 6d). All the genotypes stopped leaf elongation by the end of the prolonged drought period. Leaf area decreased slightly during the prolonged drought period because of leaf rolling and leaf death. In the shorter stress treatment, the leaf elongation rate after rewatering was the highest in CT9993, followed by IR52561 and NSG19. In the prolonged stress

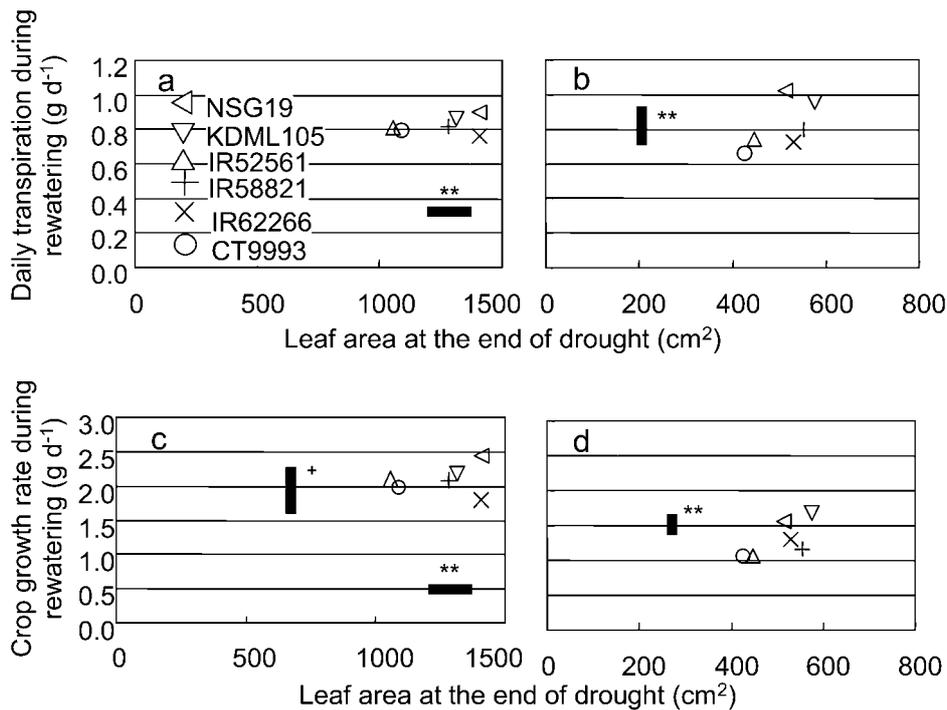


Fig. 7. Relationship between leaf area ( $\text{cm}^2$ ) at the end of shorter drought period and daily transpiration ( $\text{g d}^{-1}$ ) (a) and crop growth rate ( $\text{g d}^{-1}$ ) (c) during rewatering, and between leaf area ( $\text{cm}^2$ ) at the end of prolonged drought period and daily transpiration ( $\text{g d}^{-1}$ ) (b) and crop growth rate ( $\text{g d}^{-1}$ ) (d) during rewatering.

treatment, the leaf elongation rate after rewatering was lower than in the shorter stress treatment, and NSG19 and KDML105 had the highest values.

### 7. Shoot biomass production

Before stress imposition, significant genotypic variation occurred in shoot biomass at 21 DAS, with the order from high to low being NSG19, IR58821, KDML105, IR62266, IR52561, CT9993 (Table 3), and NSG19, IR58821 and KDML105 were regarded as having higher seedling vigor. This genotypic ranking was retained in a similar order by the end of the experiment in the well-watered treatment. During the initial drought period, shoot biomass increment was higher in IR52561 and CT9993 (cf. with  $\text{DR}_i$  14 and 15 days in Table 1c) than in IR62266 and IR58821 (cf. with  $\text{DR}_i$  12 and 11 days in Table 1c), although all genotypes transpired about the same amount of water. During the shorter drought period, shoot biomass increment was higher in KDML105 and NSG19 (cf. with  $\text{DR}_s$  11 days in Table 1c) than in CT9993 and IR52561 (cf. with  $\text{DR}_s$  9 and 10 days in Table 1c), and again all genotypes transpired about the same amount of water. During the 7 days of the rewatering period in the shorter stress treatment, shoot biomass increment was the highest in NSG19, followed by KDML105, and the smallest in IR62266. During the 7 days of the prolonged drought period, NSG19 and KDML105 had the smallest increase in shoot biomass, while

IR52561 and CT9993 had the greatest. During the 7 days of the rewatering period in the prolonged stress treatment, KDML105 and NSG19 had the greatest shoot biomass increment while it was the least in CT9993 and IR52561. KDML105 and NSG19 retained a larger leaf biomass and leaf area at the end of the shorter and prolonged drought periods, which was related with their higher daily transpiration and crop growth rate during rewatering periods (Fig. 7a,b,c,d), though there was an exceptional case that recovery ability of IR62266 was inferior in spite of its largest leaf area at the end of the shorter drought period (Fig. 7a,c). Water use efficiency calculated by the increment in shoot biomass divided by the increment in transpiration (both from 21 DAS) in the well-watered treatment was  $2.58 \text{ g kg}^{-1}$  during the experiment. Water use efficiency was higher under drought, with values of 3.06, 3.95, and  $4.04 \text{ g kg}^{-1}$  at the end of the initial drought, shorter drought, and prolonged drought periods, respectively. In response to rewatering, water use efficiency declined to  $3.10 \text{ g kg}^{-1}$  in the shorter stress treatment and dropped to  $2.68 \text{ g kg}^{-1}$  in the prolonged stress treatment.

### Discussion

#### 1. Trait expression under two different lengths of drought and recovery

Previous studies have examined how deep root development, water extraction, leaf growth, osmotic

adjustment, and shoot biomass production are affected by drought and rewatering (Azhiri-Sigari et al., 2000; Banoc et al., 2000a,b; Wade et al., 2000; Kamoshita et al., 2000, 2001). In the present study we compared these plant responses under two different lengths of drought periods (shorter and prolonged) and after rewatering. The level of stress intensity before the end of the shorter drought period (daily average transpiration  $5.7 \text{ mm d}^{-1}$ ) was comparable with the values reported by Kamoshita et al. (2000) (ca.  $7.6 \text{ mm d}^{-1}$ ). The stress further intensified during the prolonged drought period and average daily transpiration declined severely ( $2.9 \text{ mm d}^{-1}$ ). Proliferation of deep roots was enhanced, with the deep root ratio increasing to 10 and 17 % at the end of the shorter and prolonged drought periods, respectively. These values were much greater than those previously reported by Azhiri-Sigari et al. (2000) (3% and 4%). Although the reason is not clear, it may be because of the slower rate of stress development in this study because of the polystyrene cover above the surface soil that must have minimized water loss from the surface soil by evaporation. It may also be due to the use of 1 kg less of dried soil packed in each pot in this study, which might result in a slightly lower bulk density and might create a greater gap between the soil and plastic sleeves during drought. As deep root ratio in the well-watered treatment by the end of the shorter drought period (0.3 %) was comparable with the values of Azhiri-Sigari et al. (2000) (0.4% and 1.2%), the adaptive response of deep root development may be more greatly affected by the characteristics of drought development and soil physical characteristics. Osmotic adjustment increased gradually but not dramatically from the end of the shorter drought period (about 0.5 MPa) to the end of the prolonged drought period (0.7 MPa). Babu et al. (1999) showed that rice plants required a longer time for solute accumulation for a greater expression of osmotic adjustment. However, this increase in osmotic adjustment during the prolonged drought period was not apparently associated with the maintenance of the leaf elongation rate, which declined sharply during the shorter drought period. The rapid reduction in pre-dawn leaf water potential occurred after leaf elongation stopped, as was reported by Lilley and Fukai (1994b). Water use efficiency increased slightly from the end of the shorter drought to the end of the prolonged drought period ( $3.95$  and  $4.04 \text{ g kg}^{-1}$ , respectively), and hence shoot biomass production during the prolonged drought was lower than during the shorter drought, and was almost proportional to the reduction in transpiration. There was no difference in the recovery period between the two stress treatments in the rate of transpiration, but the increment in shoot biomass after rewatering in the prolonged stress treatment was 63% of that of the

shorter stress treatment, thus showing greater damage to the physiological function of the shoot because of the prolonged drought period

## 2. Genotypic variation

### (1) Water extraction and deep root development during drought

This study demonstrated that genotypes with a larger plant size before stress initiation and with quicker development of a deep root system after stress imposition suffer a greater suppression of growth when the drought period is further extended. Genotypes with higher seedling vigor such as NSG19 and KDML105 developed a deep root system and started extracting soil water from deeper layers earlier, as reported by Kamoshita et al. (2000). NSG19 and KDML105 showed a decreased leaf water potential earlier after exhausting the extractable soil water, and had a lower transpiration rate and water use efficiency during the prolonged drought period, which suggested that growth of these two genotypes was damaged most severely in the prolonged stress treatment. These genotypes still retained a higher shoot biomass by the end of the drought periods. Passioura (1982) argued that vigorous genotypes should exhaust soil water earlier and be damaged more severely when drought is extended. In terms of shoot biomass, however, genotypic ranking was not affected by the duration of drought in this study.

The relationship between root length density and soil water extraction rate by the end of the shorter drought period was positive in the 40-50-cm layer, showing the advantage of deep root development for extracting water from deep soils when drought period is not extended. Similar findings were reported by Kamoshita et al. (2000). However, greater root length density did not result in greater water extraction during prolonged drought period. In fact, the negative relationship was observed between root length density and soil water extraction (cf. in the 40-50-cm layer during prolonged drought period), because of smaller amounts of extractable water remaining in deep soil layers for genotypes which had developed greater deep root system earlier and more quickly extracted soil water from depth (cf. NSG19, KDML105). Genotypes developing deep roots in response to drought can uptake water more quickly at first but, as the extractable water in the deep soil layer decreases, the amount of deep root length has little advantage for extracting water unless roots continue to proliferate in still deeper soil layers where water remains available.

### (2) Osmotic adjustment

Genotypic variation in osmotic adjustment was small except for IR52561 at the end of the shorter drought period and for CT9993 at the end of the prolonged drought period. Their ranges were 0.38-0.47 MPa and 0.71-0.81 MPa at the end of the shorter and prolonged

drought periods, respectively. Rice is reported to have a wide range in osmotic adjustment among diverse genotypes (0.1-1.7 MPa, Lilley and Ludlow, 1996; Babu et al., 1999; Zhang et al., 1999), but, partly because of the small genotypic variation in this study, a clear relationship between osmotic adjustment and shoot biomass production during the drought period was not found. The high osmotic adjustment in IR52561 at the end of the shorter drought period may be associated with its maintenance of the leaf elongation rate during the corresponding period, but it did not result in greater biomass production during the shorter drought period. In contrast, CT9993 had the lowest osmotic adjustment at the end of the prolonged drought period but its biomass production during this period was not lower than that of other genotypes. Therefore, the second hypothesis that higher osmotic adjustment will maintain higher biomass production during a prolonged drought was not supported by the evidence from this study. This result is consistent with the literature, where there have been no reports of a contribution of osmotic adjustment to biomass production in rice. The difficulty lies first in the fact that a higher expression of osmotic adjustment requires a reduction in leaf water potential, which causes an increase in stomatal resistance and a reduction in photosynthesis (O'Toole and Cruz 1980). Second, development of osmotic adjustment is confounded by the change in osmotic potential in well-watered conditions, as was discussed by Babu et al. (1999). Even in a pot experiment with consistent soil conditions, a relationship between osmotic adjustment and shoot biomass production could not be established in this study. To clearly demonstrate the effect of osmotic adjustment on growth, it may be necessary to use doubled haploids or near-isogenic lines of similar genetic background.

Genotypic variation in maintenance of leaf water potential was not clear, except that those with higher seedling vigor extracted soil water more quickly and their leaf water potential declined earlier (this study, Kamoshita et al., 2000). Osmotic potential in the stressed treatment decreased earlier in genotypes with a larger plant size before stress, but osmotic adjustment declined in IR62266 and IR52561 by the end of the shorter drought period.

### (3) Drought recovery

The first hypothesis that genotypes with higher seedling vigor and quicker water extraction during drought will show inferior drought recovery in response to rewatering after an extended drought period was not supported in this study. Although NSG19 and KDML105 were the most severely damaged during the prolonged drought period in terms of the least water use efficiency and least transpiration, these two genotypes gained a larger shoot biomass during 7 days of rewatering than the other genotypes in both

the shorter and prolonged stress treatments. This was more remarkable in prolonged stress treatment than in the shorter stress treatment.

Genotypic variation in drought recovery was related to plant water status to some extent, but was influenced to a greater extent by plant or leaf size at the end of the drought period. Blum (1999) presented the framework that drought recovery was more affected by plant water status such as relative water content, leaf water potential, or osmotic adjustment at the end of the drought period. In this study, recovery after a shorter drought seemed to be little associated with such plant water status except for the second-highest leaf water potential at the end of the drought period in KDML105 (-0.40 MPa). Osmotic adjustment in KDML105 and NSG19 was the lowest (0.42 and 0.38 MPa, respectively) and NSG19 had the lowest leaf water potential (-0.53 MPa). Leaf water potential was higher in CT9993 and IR52561 (genotypes with a slower growth rate) at the end of the shorter drought and these genotypes had a greater leaf elongation rate after rewatering, but this did not result in greater biomass production after rewatering. Recovery after prolonged drought, however, was more associated with plant water status: NSG19 and KDML105 had the highest osmotic adjustment at the end of the prolonged drought period (0.81 and 0.79 MPa, respectively) and KDML105 had the highest leaf water potential (-3.15 MPa). Although leaf water potential and osmotic adjustment differed greatly between the end of the shorter (ca. -0.5 MPa and 0.5 MPa) and prolonged (ca. -3.4 MPa and 0.7 MPa) drought periods, the time to commencement of transpiration after rewatering did not differ between the two stress treatments and a rapid increase in transpiration started in NSG19 and KDML105 as soon as 3 hours after rewatering, even in the prolonged stress treatment. This may lead to a new hypothesis that drought recovery in terms of shoot biomass production is a "passive phenomenon" in response to available water, simply depending upon plant and leaf size retained at the end of the drought period. The greater shoot biomass retained by the end of the drought periods in NSG19 and KDML105 would have been advantageous for increasing transpiration more rapidly after rewatering. Wade et al. (2000) and Mitchell et al. (1998) pointed out the importance of leaf area and leaf biomass at the end of the drought period for superior drought recovery.

### (4) Characterization of trait expression

CT9993 and IR58821 are generally grouped as deep root genotypes in terms of their large distribution of biomass to root and development of a root system in deeper soil layers. These genotypes were used as parental lines in populations created for QTL analysis of drought resistance traits (Ali et al., 2000; Zheng et al., 2000; Zhang et al., 2001; Kamoshita et al.,

2002a,b; Babu et al., 2003). Seedlings of CT9993 are less vigorous under lowland conditions, however, and hence, their development of a deeper root system is delayed if drought does not occur (this study; Azhiri-Sigari et al., 2000; Kamoshita et al., 2002a). Moreover, CT9993 had a thicker and less branched root system and its deep root length density was relatively lower compared with the amount of biomass in deep soil layers (Azhiri-Sigari et al., 2000). IR58821 was high in seedling vigor, but it did not develop a deep root system on some drought occasions (this study, Azhiri-Sigari et al., 2000). IR58821 had a consistently higher deep root dry matter and deep root ratio in well-watered conditions in this study and in a previous study (Azhiri-Sigari et al., 2000). A clearer definition of drought development (e.g., rate of soil drying) may be needed to understand genotype by environment interaction for deep root development. Genotypic variation in osmotic adjustment was to some extent consistent with the results of Kamoshita et al. (2000) that showed a high osmotic adjustment of IR52561 and low osmotic adjustment of CT9993.

Wade et al. (1999) related the trait expression of reference lines with their adaptation to diverse rainfed lowland environments. These results may help to further explain the adaptation of these rainfed lowland reference lines to early season drought. Drought recovery may be a consistent and useful trait for selection for improved adaptation to drought. The effects of secondary physio-morphological traits such as osmotic adjustment on biomass production and growth need to be quantified using genotypes with a similar genetic background.

### Conclusions

Longer drought duration caused more severe damage in terms of lower transpiration and lower water use efficiency and an earlier reduction in leaf water potential in genotypes such as NSG19 and KDML105 with higher seedling vigor, a quicker development of a deep root system, and faster extraction of available soil water during the drought period. However, recovery ability was always better in NSG19 and KDML105 even when drought period was further extended to cause greater drought injury. This recovery was associated with the retention of a larger plant size at the end of the drought period, rather than with plant water status during drought. Osmotic adjustment differed among genotypes and increased during the prolonged drought period, but the relationship with biomass production or growth was not clearly established. Selection for drought recovery ability should be useful for improved adaptation to early season drought.

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