ELSEVIER

Field Crops Research 46 (1996) 21–39

Field Crops Research

Drought-stress responses of two lowland rice cultivars to soil water status

M.C.S. Wopereis [a,b,*], M.J. Kropff [a,b], A.R. Maligaya [b], T.P. Tuong [b]

[a] *Department of Theoretical Production Ecology, Wageningen Agricultural University, P.O. Box 430, 6700 AK Wageningen, Netherlands*
[b] *International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines*

Received 17 October 1994; accepted 11 October 1995

Abstract

The physiological and morphological responses of two semi-dwarf lowland rice cultivars to transient drought were studied in three greenhouse experiments. These responses were related to root-zone soil water status for use in a rainfed-rice simulation model. Results were very similar for both varieties. Drought responses in young plants occurred at a lower soil water status than in older plants. The first observed effect in a drought period in the vegetative phase was a decline in leaf expansion rate compared to well-watered plants. Leaf expansion stopped completely with root-zone soil water pressure potential h in the range -50 to -250 kPa, depending on crop age and growing season. The rate of transpiration, corrected for differences in LAI, remained roughly equal to that of well-watered plants in the range $0 > h > -100$ kPa, depending on crop age. As the soil water status declined further, relative transpiration rate decreased with increasing values of $\log(|h|)$, following a logistic function. Leaf rolling and early senescence started at $h < -200$ kPa or lower and were linearly related with $\log(|h|)$. Yield differences between plants that were transiently stressed in the early vegetative phase and well-watered plants were not significant. However, flowering and maturity were delayed. Severe drought in the reproductive phase resulted in large yield reductions, mainly caused by an increase in the percentage of unfilled grains and also in grain weight.

Keywords: Drought; Modelling; Morphology; *Oryza sativa*; Physiology; Rice

1. Introduction

Rainfed rice is grown under lowland and upland conditions. Lowland rice is direct seeded or transplanted in bunded fields and soils are often puddled by plowing at water-saturated conditions, followed by harrowing and levelling. Upland rice is always direct seeded and usually grown in unbunded fields of often naturally well-drained soils without surface accumulation of water. Rainfed lowland rice comprises approximately 37 Mha (harvested area) or 25% of total world rice area. With a total of 92 million t year^{-1} it produces 17% of global rice supply. Upland rice covers about 19 Mha, and contributes 4% to world production, with average yields of 1 t ha^{-1} or less (IRRI, 1993). Despite the problems of uncertainty and risk in rainfed environments, most research has been focused on irrigated rice (IRRI, 1989) and relatively little attention has been paid to quantitative interpretation of experimental

* Corresponding author. West Africa Rice Development Association, B.P. 96, Saint-Louis, Senegal.

0378-4290/96/$15.00
SSDI 0378-4290(95)00084-4

data using process-based simulation models. Especially in rainfed environments, such models can be very helpful in getting a better understanding of the system, as has been shown for many other crops (e.g., Van Keulen et al., 1987; Muchow et al., 1991).

Quantification of physiological and morphological responses of rice to drought stress is essential to predict the impact of soil and weather conditions on rice production using process-based crop simulation models. Drought may delay the phenological development of the rice plant (Puckridge and O'Toole, 1981; Turner et al., 1986; Inthapan and Fukai, 1988), and affect physiological processes like transpiration, photosynthesis, respiration and translocation of assimilates to the grain (e.g., Fukai et al., 1985; Turner, 1986). Drought strongly affects the morphology of the rice plant. Leaf area development may be hampered due to reduced leaf expansion, leaf rolling and early senescence, and tillering and panicle development may be reduced (e.g., O'Toole and Cruz, 1980; O'Toole and Baldia, 1982). On the other hand, drought may induce more rapid root growth (e.g., O'Toole and Chang, 1979; O'Toole and Moya, 1981).

Based on interpretation of experimental data with simulation models, it has been suggested that upland rice crops continue to transpire at high rates during severe drought periods (Woodhead et al., 1991). However, O'Toole and Baldia (1982) found that transpiration of stressed plants grown in non-puddled clay soil differed significantly from control plants when the soil water potential was in the range -0.02 to -0.15 MPa. This may have been partly or completely due to a reduction in leaf elongation rate of the stressed plants, i.e., a morphological rather than a physiological response to drought. Shiina and Hasegawa (cited by Hasegawa and Yoshida, 1982) reported soil water pressure potentials of -100 kPa and -60 kPa as minimum values for optimum growth of upland rice crops. Kamota et al. (cited by Hasegawa and Yoshida, 1982) found that transpiration of upland rice grown in pots, decreased at soil water potentials below -20 kPa. Hasegawa and Yoshida (1982) studied water uptake by upland rice in the field and reported that evapotranspiration was still at a potential rate when the soil water potential at 10–15 cm and 40–50 cm had dropped to -1 MPa and -0.7 MPa respectively. Discrepancies in critical soil water potentials reported in literature may be due to differences in rooting patterns (Hasegawa and Yoshida, 1982).

For lowland rice, grown in puddled soil, hardly any information on the relation between root-zone soil water status and physiological and morphological responses to drought is available. Because of the lack of such data, rainfed-rice simulation models often use standard relationships that have been derived for other crops (Penning de Vries et al., 1989).

Three greenhouse experiments were conducted to study the physiological and morphological responses of two semi-dwarf lowland rice varieties, grown in puddled clay soil and non-puddled sandy soil, to transient drought at various growth stages. Responses were investigated during the drought period itself and after re-irrigation. The experiments aimed at finding relationships between root-zone soil water status and drought-stress responses of the plant, for incorporation in rainfed-rice simulation models.

2. Material and methods

2.1. Plant and soil material and growing conditions

Three experiments were conducted in greenhouses at the International Rice Research Institute (IRRI) in Los Baños, Philippines (14°30′N, 121°15′E). The climate at the study area is characterized by two pronounced seasons: a dry season (DS) from December to May and a wet season (WS) from June to November, which mainly differ in the levels of radiation and rainfall.

Experiment 1 was conducted from 30 January to 6 June 1992 (DS1992); Experiment 2 from 26 September 1992 to 26 January 1993 (WS1992) and Experiment 3 from 13 April 1994 to 29 July 1994 (DS1994). Two cultivars of rice (*Oryza sativa* L.), IR20 and IR72 were grown in polyvinyl chloride (pvc) pots (20 cm diameter and 25 cm height). Three seedlings (DS1992: 21-day old; WS1992: 22-day old; DS1994: 21-day old) were planted in the center of each pot. In 1992, all pots were filled with saturated puddled Maahas clay soil (saturated volumetric water content θ_s: 0.73 cm^3 water cm^{-3} soil) taken from a submerged field at the IRRI farm that was plowed and harrowed 5 days before. The soil material comprised 13% sand, 39% silt and 48% clay. In 1994, pots were filled with non-puddled sandy soil, comprising 70% sand, 17% silt and 13% clay (θ_s: 0.42 cm^3 water cm^{-3} soil).

A hygrothermograph was used to continuously record temperature and relative humidity in the greenhouse. Solar radiation was determined at a nearby agrometeorological station. Average daily minimum temperature in dry and wet seasons was 25.3°C and 23.3°C respectively. Average daily maximum temperature was 35.0°C in the dry season and 29.0°C in the wet season. Average daily minimum relative humidity in dry and wet seasons was 49% and 65% respectively, with maximum values close to 100% in both seasons. Solar radiation was highest in the dry season, ranging from 5.4 to 26.0 MJ m^{-2} day^{-1}, with an average of 20.0 MJ m^{-2} day^{-1}. Corresponding values in the wet season were: 2.7 (minimum), 24.9 (maximum) and 15.9 (average) MJ m^{-2} day^{-1}.

High fertilizer inputs were imposed to ensure that growth of stressed plants was reduced by drought only. A basal application equivalent to 100 kg N, 40 kg P and 40 kg K ha^{-1}, was mixed into each pot one day before transplanting. Additional ammonium sulphate equivalent to 60 kg N ha^{-1} was added at mid-tillering and panicle initiation (exact timing depending on drought treatment) and 40 kg N ha^{-1} at flowering. During the experiments, occasional spraying of insecticides against whorl maggot and green leaf hopper was needed to avoid damage.

2.2. *Intensity and timing of drought stress*

In each of the three experiments, drought was imposed at different growth stages by withholding water application and by removing any ponded water from the soil surface. In 1992, drought was induced at transplanting (A), two weeks after transplanting (B), mid-tillering (D), panicle initiation (E) and first flowering (F). In 1994, the number of drought treatments was restricted to drought at three weeks after transplanting (C) and first flowering (F). For comparison, a well-watered treatment (WW) was included in each of the three experiments. Panicle initiation was defined as the first day when a white feathery cone was present inside the leaf sheath of the rice plant. First flowering was defined as the moment when 90% of the plants subjected to a certain treatment had at least one flowering panicle. The degree of leaf rolling was monitored as a stress indicator. A 0 to 5 rolling factor was used (O'Toole and Cruz, 1980). A leaf rolling factor of 1 indicates a first sign of leaf rolling, whereas score 5 means that the leaf has rolled completely.

In 1992, the duration of drought was also varied to investigate the responses and the ability of the rice plant to recover from different drought intensities. In the short-duration treatments (or early recovery, ER), stressed plants were recovered when plants reached leaf rolling score 5. In the long-duration treatment (or highly stressed, late recovery: LR) plants were recovered when they were close to dying, i.e., leaf rolling score 5 and roughly 50% dead leaves. Recovery was achieved by re-irrigating the pots to bring the dried soil to saturation. In 1994, only treatment ER was included. After the onset of the recovery period, plants were kept well watered until maturity. In the 1992 experiments, drought was maintained in a number of pots (i.e., no recovery).

2.3. *Experimental layout*

To mimic field conditions, pots of the same treatment and of one variety were concentrated in one block. Total number of blocks in Experiments 1 and 2 was 20 (10 treatments, 2 varieties: IR20 and IR72). In Experiment 3 three blocks were used (3 treatments, one variety: IR72). Pots were placed side by side on a wooden tray of 10 cm height, with no space in between, to simulate a 20 × 20-cm planting density. To avoid any influence of placing on plant growth, blocks were rotated weekly and pots were rotated daily within the blocks. Each block was surrounded by one row of border pots to simulate field conditions. Border pots received the same treatment as the centre pots within a block, but were not used for any measurement. A large number of pots was used in each experiment to allow for periodic destructive sampling of four pots per treatment per sampling time. The total number of pots used was 716 (Experiment 1), 794 (Experiment 2) and 90 (Experiment 3).

2.4. Plant and soil sampling

The well-watered treatments were sampled every two weeks. Plants in the drought treatments were sampled at the start of recovery and at final harvest. Four pots per treatment were removed for each sampling. Plant components (i.e., green and dead leaves, stem, roots, panicles and grains) were detached and oven-dried for one week at 70°C. Green leaf area was determined immediately after sampling, using a Delta-T meter. Leaf Area Index (LAI) was calculated based on a 20 × 20-cm spacing. To obtain the actual leaf area of stressed plants, leaves were not unrolled during measurement. At harvest a yield component analysis was conducted based on four pots (four replications) per treatment. Plant height was determined from the ground level to the tip of the tallest leaf, and for mature plants from ground level to the tip of the tallest panicle. Height measurements were conducted daily during the early stage of growth and weekly at the later stage. For all treatments the moment of first and 50% flowering (50% of panicles flowering) was recorded. In the dry season of 1992 this was done daily by estimating the percentage of flowering panicles per treatment block. In the wet season of 1992, a more accurate approach was followed, i.e., the actual number of flowering panicles per pot was recorded daily. A visual estimate of the degree of leaf rolling and the percentage of dead leaves was made daily at midday. Leaf rolling is usually associated with soil water deficits as an effective way to reduce transpiration losses. Even irrigated rice, however, may exhibit leaf rolling due to water deficits at midday (O'Toole, pers. commun.). Leaf scores and estimates of the percentage of dead leaves were given daily to stressed plants only. Average leaf rolling scores and percentages of dead leaves per treatment were calculated and translated into stress factors ranging from 1 (no leaf rolling, 0% dead leaves) to 0 (complete leaf rolling, 100% dead leaves).

The four pots removed for plant sampling at the start of recovery for a specific drought treatment were also used to determine root-zone soil water status. This was done gravimetrically at three depths (0–5, 5–10 and 10–15 cm) using 5 cm height and 5 cm diameter cylinders. Fresh weight and oven-dry weight (48 h at 105°C) of each cylinder were measured to calculate volumetric moisture content and bulk density.

2.5. Actual and potential transpiration rates

In each pot, soil and water evaporation losses were minimized by round polyethylene cover sheets, with an adjustable hole in the centre to allow for optimal tillering. Pots of treatments A (drought at transplanting) and B (drought two weeks after transplanting) were left uncovered for approximately 2 weeks to speed up incidence of drought stress through the combined effect of transpiration and soil evaporation. All pots with well-watered and stressed plants (except for border pots) were weighed daily (early morning) to estimate transpiration losses, using a balance with a resolution of 1 g. Transpiration rate was calculated as the difference in pot weight between successive days.

Sinclair and Ludlow (1986) defined relative transpiration rate (RT) of stressed plants as the ratio between weight loss of stressed pots and that of well-watered pots. To account for differences in plant size and microenvironmental variation, they normalized RT data by dividing individual values by the mean of all RT values for a plant, obtained when the soil was still relatively moist. In this way, the normalized values of RT were centered around 1. In our study this approach was not followed, because of large differences in leaf area development in plants from well-watered and drought-stress treatments. If drought stress results in a reduction of LAI, the measured potential transpiration of well-watered plants will be higher than the potential transpiration rate of stressed plants. Radiation interception is the main driving force for differences in transpiration between the well-watered and stressed canopies. The potential transpiration of the stressed plants was, therefore, calculated from the transpiration of the well-watered plants, using the ratio of calculated absorbed fraction of global radiation in stressed and well-watered plants as a weighting factor:

$$T_p(\mathrm{D}) = T_p(\mathrm{WW}) \frac{1 - \exp[-0.4\mathrm{LAI}(\mathrm{D})]}{1 - \exp[-0.4\mathrm{LAI}(\mathrm{WW})]} \quad (1)$$

where: $T_p(\mathrm{D})$ is the potential transpiration rate of stressed plants, $T_p(\mathrm{WW})$ the potential transpiration rate of well-watered plants, LAI(D) the LAI of stressed plants, and LAI(WW) the LAI of well-watered plants.

The factor 0.4 used in Eq. (1) is the extinction coefficient for global radiation in rice plants (Kropff, 1993). Relative transpiration (RT) used here is the ratio of the actual transpiration of stressed plants, $T_a(D)$, over that of well-watered plants corrected for differences in LAI using Eq. (1), Eq. (), i.e., $T_a(D)/T_p(D)$.

2.6. Soil water status

Drought-stress responses observed in the three experiments were related to soil water content measured in the pots through daily weighing. To make results more widely applicable, these soil water contents were converted to soil water pressure potentials. For this purpose, the water retention curve, relating soil water status to soil water potential h was determined for both the non-puddled sandy soil and the puddled clay soil. A complication in these measurements was the shrinkage of the puddled soil volume upon drying.

For the non-puddled sandy soil, the water retention characteristic was determined using a combination of two techniques: (i) the evaporation method for -100 kPa $< h < 0$ kPa (Bouma et al., 1983) and (ii) pressure plates for $h < -100$ kPa (Klute, 1986).

For the puddled clay soil, a different methodology was used to allow for the change in soil volume upon drying. Four pots of 20 cm diameter and 25 cm height were filled with water-saturated puddled clay soil. The initial (saturated) volumetric water content was determined gravimetrically using 100 cm^3 cylinders from extra pots filled with the same soil. Three rice seedlings were transplanted in each pot and were watered daily until 40 days after transplanting, to ensure that roots were distributed throughout the pots. Drought stress was imposed as described earlier using polyethylene sheets, to avoid non-uniform drying of the soil surface due to evaporation. Four tensiometers were installed at 5-cm depth intervals. Tensiometers and decrease in pot weight were monitored approximately four times daily until the air-entry value of all tensiometers was exceeded. Soil water status in each pot was expressed as a function of the volume of the solid phase (Bronswijk, 1988):

$$\upsilon = V_w/V_s \tag{2}$$

where υ is soil moisture ratio, V_w is volume of water and V_s is volume of the solid phase. The void ratio e is defined as the volume of pores V_p over the volume of solid phase (Bronswijk, 1988):

$$e = V_p/V_s \tag{3}$$

The sum of V_p and V_s is equal to the volume of the soil matrix. The shrinkage characteristic relates υ to e at different soil water pressure potentials h, and can be used to convert soil moisture ratios into soil pressure potentials (Bronswijk, 1988). Values for e were calculated from measurements of bulk density at several depths within the soil columns after the air-entry of the tensiometers was exceeded, assuming a density of the solid phase of 2.5 g cm^{-3}.

For each stressed plant, grown in pots filled with puddled clay soil, the soil moisture ratio υ at the start of the day was calculated taking into account the transpiration losses incurred during the previous days:

$$\upsilon_{pot} = (\theta_{sat} * V - W)/(1 - \theta_{sat}) * V \tag{4}$$

where: υ_{pot} is the soil moisture ratio of the pot (cm^3 water cm^{-3} solid phase), θ_{sat} is the saturated moisture content (cm^3 water cm^{-3} soil), W cumulative loss of water due to transpiration (cm^3), and V pot

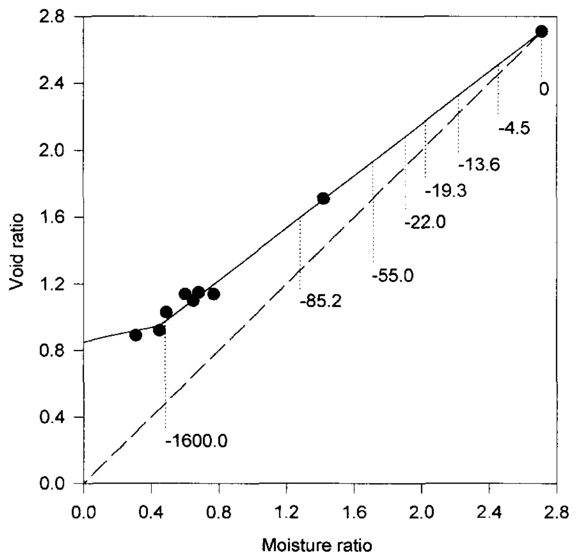


Fig. 1. Soil shrinkage characteristic of the puddled clay soil used in Experiments 1 and 2. Values in the diagram indicate soil pressure potentials (kPa).

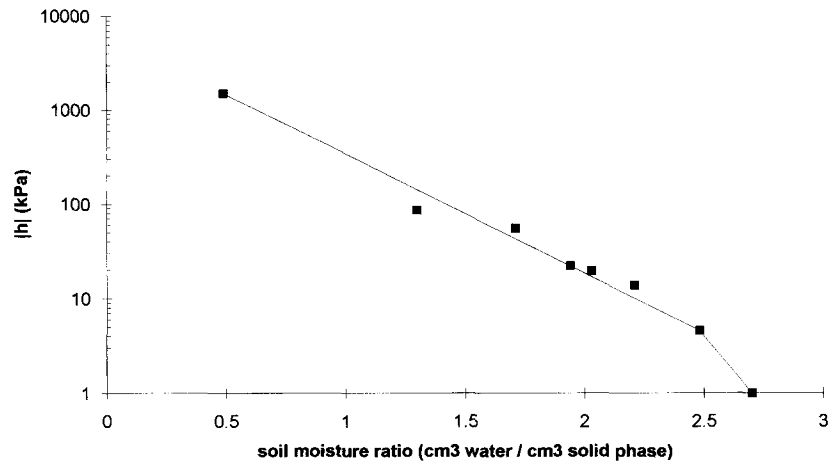


Fig. 2. Soil-water retention characteristic of the puddled clay soil material used in Experiments 1 and 2 (|h|: soil water pressure potential).

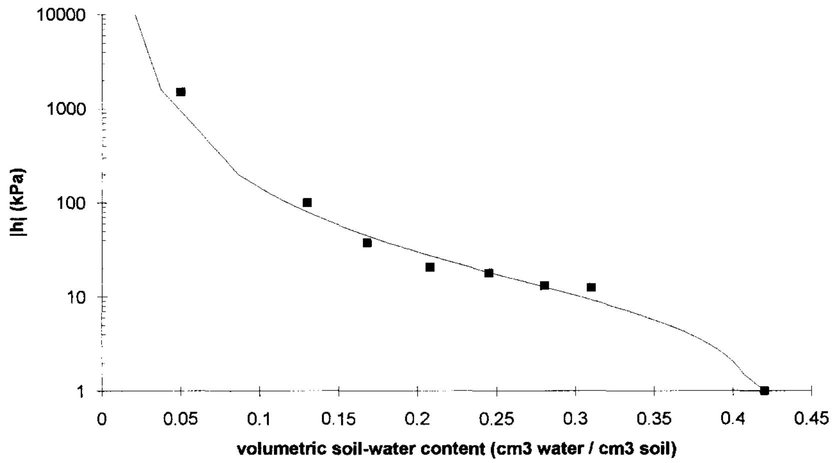


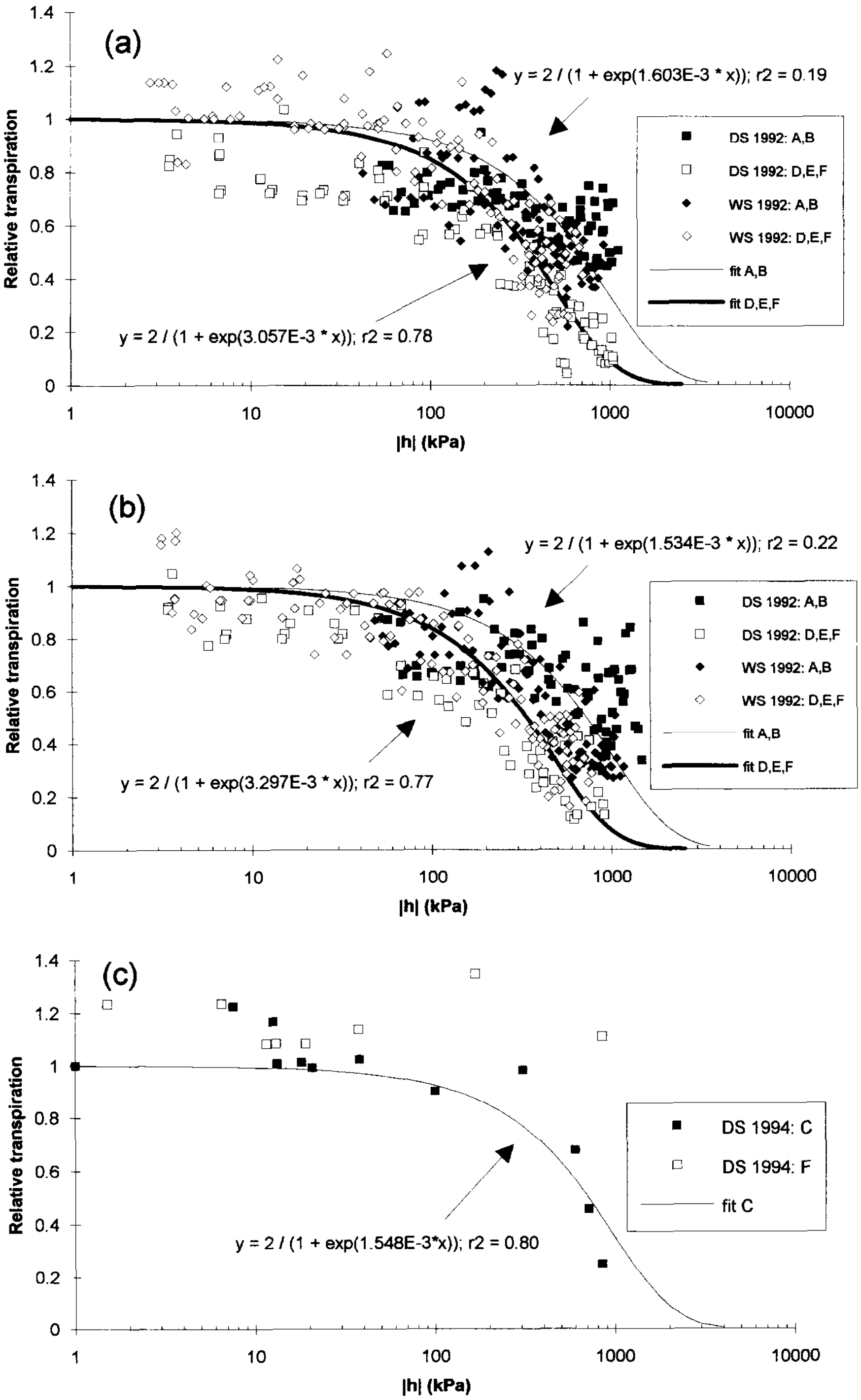
Fig. 3. Soil-water retention characteristic of the non-puddled sandy soil material used in Experiment 3 (|h|: soil water pressure potential).

volume (cm^3). The volume of solid phase in Eq. (4) equals $(1 - \theta_{sat}) * V$ (see Eq. (2)).

The soil shrinkage curve, determined for the puddled clay soil is shown in Fig. 1. Total shrinkage is very high: the initial void ratio of 2.7 cm^3 pores cm^{-3} solid phase decreases to about 0.9 cm^3 pores cm^{-3} solid phase upon drying. Air-entry occurs almost immediately if soil water status drops below saturation. Similar observations were made by Bronswijk and Evers-Vermeer (1990) for a subsoil in the Netherlands. The soil water retention curve, relating υ to h, that was derived from Fig. 1 is shown in Fig. 2.

The soil water retention curve of the non-puddled sandy soil showed a typical 'chair-shaped' relationship between soil water content θ in cm^3 water

Fig. 4. Relative transpiration rates of IR20 in Experiments 1 and 2 (a), IR72 in Experiments 1 and 2 (b) and IR72 in Experiment 3 (c) as a function of soil water pressure potential |h|, resulting from drought at different growth stages. A: drought at transplanting, B: drought two weeks after transplanting, C: drought three weeks after transplanting, D: drought at mid-tillering, E: drought at panicle initiation; F: drought at first flowering.



(a)
y = 2 / (1 + exp(1.603E-3 * x)); r2 = 0.19
y = 2 / (1 + exp(3.057E-3 * x)); r2 = 0.78
DS 1992: A,B
DS 1992: D,E,F
WS 1992: A,B
WS 1992: D,E,F
fit A,B
fit D,E,F
Relative transpiration
|h| (kPa)
(b)
y = 2 / (1 + exp(1.534E-3 * x)); r2 = 0.22
y = 2 / (1 + exp(3.297E-3 * x)); r2 = 0.77
DS 1992: A,B
DS 1992: D,E,F
WS 1992: A,B
WS 1992: D,E,F
fit A,B
fit D,E,F
Relative transpiration
|h| (kPa)
(c)
y = 2 / (1 + exp(1.548E-3*x)); r2 = 0.80
DS 1994: C
DS 1994: F
fit C
Relative transpiration
|h| (kPa)

Table 1
Duration of drought stress (Du, in days) and leaf area index (LAI) of rice cultivars IR72 and IR20 at the start of drought at different growth stages

Treatment	Experiment 1				Experiment 2				Experiment 3	
	IR20		IR72		IR20		IR72		IR72	
	Du	LAI	Du	LAI	Du	LAI	Du	LAI	Du	LAI
Drought at transplanting (A)										
AER	38	0.04	38	0.04	38	0.05	40	0.03	n.a.	
ALR	41	0.04	41	0.04	46	0.05	46	0.03	n.a.	
Drought two weeks after transplanting (B)										
BER	23	0.3	23	0.4	27	0.5	27	0.4	n.a.	
BLR	26	0.3	26	0.4	31	0.5	31	0.4	n.a.	
Drought three weeks after transplanting (C)										
CER	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	11	0.7
Drought at mid-tillering (D)										
DER	13	3.0	15	3.2	24	1.7	22	1.7	n.a.	
DLR	17	3.0	20	3.2	27	1.7	27	1.7	n.a.	
Drought at panicle initiation (E)										
EER	12	6.5	14	6.4	22	2.8	19	3.3	n.a.	
ELR	14	6.5	16	6.4	24	2.8	23	3.3	n.a.	
Drought at first flowering (F)										
FER	8	6.9	12	6.6	17	5.2	17	5.5	9	5.3

Drought induced at A: transplanting; B: two weeks after transplanting; C: three weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering.
ER: early recovery, i.e. drought ended at leaf rolling score 5; LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves.
n.a.: not applicable.

cm^{-3} soil and soil pressure potential h (Fig. 3). Van Genuchten's closed form equation (Van Genuchten, 1980) was fitted to the data, yielding $\alpha = 0.0145$ cm^{-1} and $n = 1.498$ ($r^2 = 0.98$). The water content at a soil pressure potential h of -100 kPa is low: 0.13 cm^3 water cm^{-3} soil.

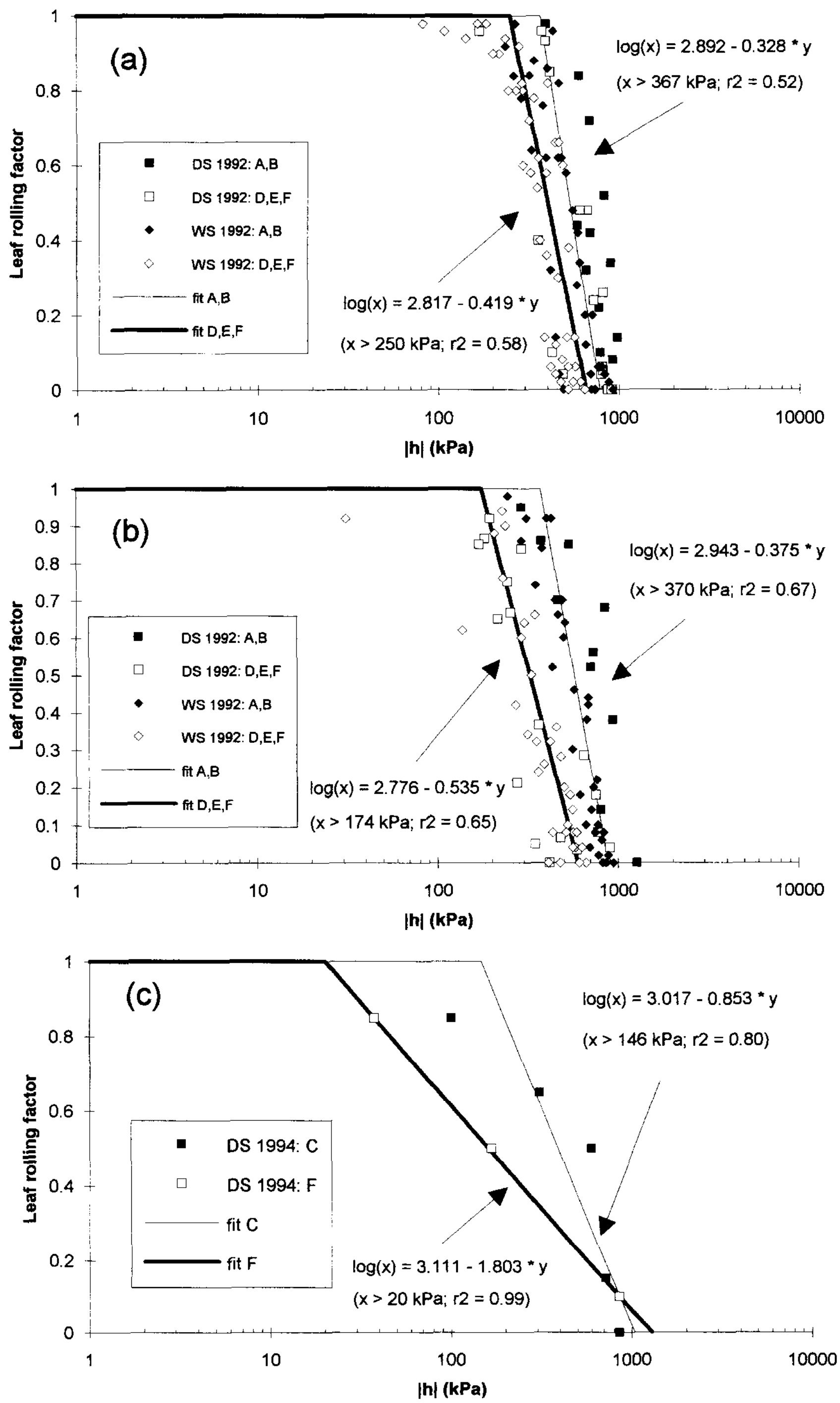
The total initial amount of water in each pot (volume: 5.7 l) can be calculated from the saturated volumetric water content of both soil types. For the sandy non-puddled soil used in 1994 this was: $5.7 * 0.42 = 2.4$ l of water, for the puddled clay soil used in 1992 a much larger volume of water was available for transpiration: $5.7 * 0.73 = 4.2$ l of water.

3. Results and discussion

3.1. Evaporative demand of the air

The evaporative demand of the air in the various experiments was estimated from the transpiration rates of the well-watered plants between 40 and 80 days after transplanting (closed canopy condition).

Fig. 5. Leaf rolling factors of IR20 in Experiments 1 and 2 (a), IR72 in Experiments 1 and 2 (b) and IR72 in Experiment 3 (c) as a function of soil water pressure potential $|h|$, resulting from drought at different growth stages. A leaf rolling factor of 1 indicates no leaf rolling, a leaf rolling factor of 0 indicates that leaves are completely rolled up. A: drought at transplanting, B: drought two weeks after transplanting, C: drought three weeks after transplanting, D: drought at mid-tillering, E: drought at panicle initiation; F: drought at first flowering.


(a)
Leaf rolling factor
|h| (kPa)
DS 1992: A,B
DS 1992: D,E,F
WS 1992: A,B
WS 1992: D,E,F
fit A,B
fit D,E,F
log(x) = 2.892 - 0.328 * y
(x > 367 kPa; r2 = 0.52)
log(x) = 2.817 - 0.419 * y
(x > 250 kPa; r2 = 0.58)
(b)
log(x) = 2.943 - 0.375 * y
(x > 370 kPa; r2 = 0.67)
log(x) = 2.776 - 0.535 * y
(x > 174 kPa; r2 = 0.65)
(c)
DS 1994: C
DS 1994: F
fit C
fit F
log(x) = 3.017 - 0.853 * y
(x > 146 kPa; r2 = 0.80)
log(x) = 3.111 - 1.803 * y
(x > 20 kPa; r2 = 0.99)

Average transpiration rate in DS1992 was 16 mm day^{-1} (standard deviation, SD: 3 mm day^{-1}), in WS1992: 6 mm day^{-1} (SD: 2 mm day^{-1}) and in DS1994: 11 mm day^{-1} (SD: 3 mm day^{-1}). These values were slightly higher than transpiration rates observed in the field by Wopereis et al. (1993).

3.2. Impact of drought on physiological processes

Transpiration rates of stressed and well-watered plants were converted into relative transpiration rates (RT) using Eq. (1) and Eq. () and expressed as a function of soil water pressure potential h. Variation of RT below and above 1 at low absolute values of h (moist soil) can be explained by micro-environmental variation in and between experiments and error in estimating daily LAI values for well-watered and stressed plants from a limited number of observations.

3.2.1. Experiments 1 (DS1992) and 2 (WS1992)

Relative transpiration rates (RT) for IR20 and IR72 are shown in Fig. 4. Observations for the A and B treatments start at pressure potentials near -100 kPa only, because the pots were initially left uncovered. Logistic curves fitted the data reasonably well. A similar result was obtained by Sinclair and Ludlow (1986) for four tropical grain legumes, relating fraction of transpirable soil water (FTSW) to RT, defining total transpirable soil water as the difference between initial pot weight and its weight when RT reached 0.1.

Differences between dry and wet season data for similar drought treatments were relatively minor given the contrast in evaporative demand between both seasons. Plant age had a more pronounced effect on the relation between RT and soil water pressure potential h. Differences in rooting pattern may have had some influence in the early drought treatments (A, B). However, at the moment of recovery, roots extended throughout the (shrunken) soil volume for all treatments, indicating no restriction on availability of soil water at greater depths in the pots.

For both varieties and for all treatments, plants transpired roughly at potential rate, corrected for differences in LAI, until the soil water pressure potential h reached the range -70 to -100 kPa (Fig. 4a and b). At lower soil pressure potentials, RT declined rapidly, especially if drought was induced at a later growth stage (D, E, F). RT values declined more or less linearly with $\log(h)$. Decline in RT started earlier for the D, E, F treatments than for the A, B treatments. This is probably due to the larger size and higher transpiration demand of the older plants.

3.2.2. Experiment 3 (DS1994)

In the C treatment (drought three weeks after transplanting) plants showed signs of a decline in RT if the soil water pressure potential h dropped below -200 kPa (Fig. 4c), i.e., a result similar to the A and B treatments in Experiments 1 and 2. For plants of the F treatment (drought at first flowering), RT did not decline at all. This may be explained by the short duration of stress (9 days, see Table 1), caused by rapid extraction of water from the pots. which quickly emptied the low available water volume (2.4 l) of the sandy soil. Soil water pressure potentials fell below -100 kPa during the last two days of drought only.

Tanguilig et al. (1987) monitored responses of another semi-dwarf rice variety (IR36) to drought stress in the vegetative phase, grown in non-puddled Maahas clay. Their data show that transpiration rate of stressed rice plants (not corrected for differences in LAI) started to deviate from the control after 7 days of stress, corresponding to a soil water content of 0.34 cm^3 cm^{-3}. This soil water content occurs for non-puddled Maahas clay at a soil water potential of about -30 kPa (Wopereis et al., 1993). Because stressed plants showed reduced leaf elongation rates well before that time, transpiration rate corrected for differences in leaf area must have been still close to the control. Differences were however significant after 9 days of stress, corresponding to a soil water content of 0.29 cm^3 cm^{-3}, i.e., a soil water potential

Fig. 6. Dead leaves factors of IR20 in Experiments 1 and 2 (a), IR72 in Experiments 1 and 2 (b) and IR72 in Experiment 3 (c) as a function of soil water pressure potential $|h|$, resulting from drought at different growth stages. A dead leaves factor of 1 indicates that no dead leaves are present, a dead leaves factor of 1 indicates that all leaves are dead. A: drought at transplanting, B: drought two weeks after transplanting, C: drought three weeks after transplanting, D: drought at mid-tillering, E: drought at panicle initiation; F: drought at first flowering. No curves were fitted through the data for Experiment 3 as plants were recovered early: dead leaves factors did not decrease below 0.5.

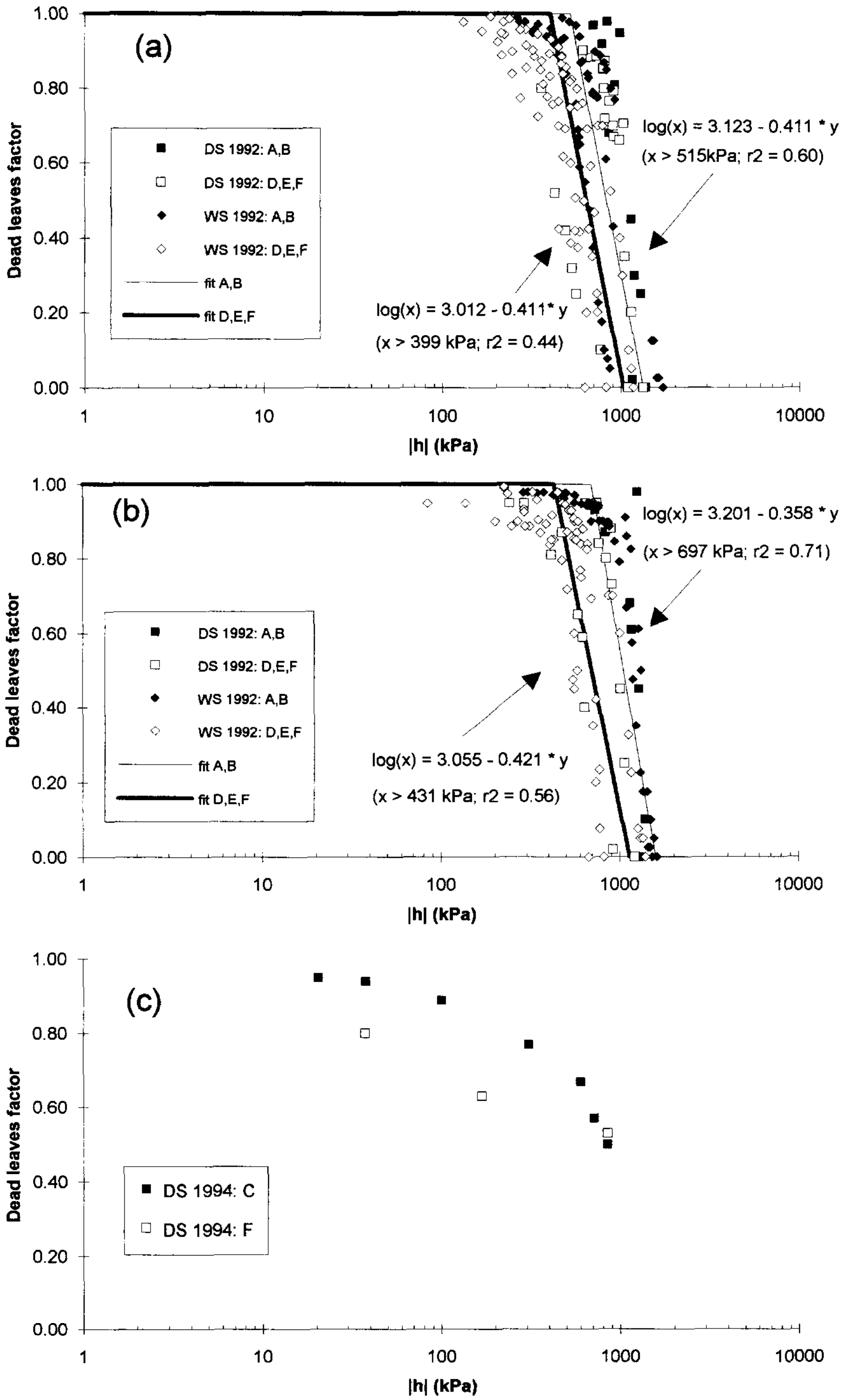

(a)
DS 1992: A,B
DS 1992: D,E,F
WS 1992: A,B
WS 1992: D,E,F
fit A,B
fit D,E,F
log(x) = 3.123 - 0.411 * y
(x > 515kPa; r2 = 0.60)
log(x) = 3.012 - 0.411* y
(x > 399 kPa; r2 = 0.44)
Dead leaves factor
|h| (kPa)
(b)
log(x) = 3.201 - 0.358 * y
(x > 697 kPa; r2 = 0.71)
log(x) = 3.055 - 0.421 * y
(x > 431 kPa; r2 = 0.56)
(c)
DS 1994: C
DS 1994: F

Table 2
Critical soil water pressure potentials (kPa) below which leaf expansion stopped for rice cultivars IR20 and IR72 in Experiments 1 and 2. Data are averages of at least four replicates

Treatment	Experiment 1		Experiment 2	
	IR20	IR72	IR20	IR72
Drought at transplanting (A)				
AER	−97	−120	−252	−262
ALR	−86	−144	−126	−234
Drought two weeks after transplanting (B)				
BER	−74	−161	−157	−157
BLR	−77	−101	−145	−147
Drought at mid-tillering (D)				
DER	−91	−68	−130	−159
DLR	−86	−51	−221	−141
Drought at panicle initiation (E)				
EER	n.a.	n.a.	−86	−76
ELR	n.a.	n.a.	−109	−54
Drought at first flowering (F)				
FER	n.a.	n.a.	n.a.	n.a.

Drought induced at A: transplanting; B: two weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering. ER: early recovery, i.e. drought ended at leaf rolling score 5; LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves.
n.a.: not applicable.

of about −100 kPa (Wopereis et al., 1993), which is similar to the results obtained in this study.

3.3. Relationships between leaf morphology and soil water status

3.3.1. Experiments 1 (DS1992) and 2 (WS1992)

Leaf elongation rate of plants stressed in the vegetative phase decreased rapidly after an initial period of normal growth. Tanguilig et al. (1987) also found an abrupt decrease in leaf elongation rate 11 days after initiation of drought stress in IR36. The critical soil water pressure potential at which leaf expansion in the vegetative phase stopped completely (zero leaf expansion) was estimated from graphs of plant height. Because plant height measurements were made at weekly intervals, results (Table 2) should be interpreted as rough estimates only. In the dry season of 1992, critical pressure potentials ranged from −50 kPa (IR72, DLR) to −160 kPa (IR72, BER). Critical pressure potentials were lower in the wet season of 1992, ranging from −50 kPa (IR72, ELR) to −260 kPa (IR72, AER), probably due to the lower evaporative demand in the wet season. For younger plants, leaf expansion stopped at lower pressure potentials, which may also be attributed to a lower evaporative demand of a small leaf canopy.

As soil water status declined further ($h < -200$ kPa), leaf rolling started in all treatments and for both varieties (Fig. 5a and b). Complete leaf rolling was observed if pressure potentials dropped further to −1 MPa or lower. As drought progressed, the percentage of dead leaves increased rapidly as well (Fig. 6a and b). Both leaf rolling and dead leaves factors were linearly related with $\log(h)$. The younger the plant, the lower the soil water potential before leaf rolling started. Leaves rolled and dead leaves appeared relatively quickly if drought was initiated at flowering, probably because of the added effect of natural senescence.

3.3.2. Experiment 3 (DS1994)

If drought was induced 3 weeks after transplanting (C), leaf rolling and appearance of dead leaves started at soil water pressure potentials below −100 kPa (Fig. 5c and Fig. 6c), although some dead leaves were already visible earlier. Drought at flowering induced early leaf senescence and rolling, as was also observed in Experiments 1 and 2. These results are influenced by the short duration of drought (Table 1). Measurements of soil water status (i.e., weighing of the pots) were done in the early morning, whereas scoring for leaf rolling was done in the early afternoon. Leaf scores are therefore linked to soil water pressure potentials that are slightly too high.

Summarizing the results of the three experiments, the response of leaf morphology to drought may be separated into three more or less sequential phases:
1. decline in leaf expansion (vegetative phase only),
2. leaf rolling, and
3. early leaf senescence.

For most treatments phases 2 and 3 showed some overlap, i.e., dead leaves appeared at leaf rolling scores below 5. Results obtained for the puddled clay and non-puddled sandy soil were remarkably similar, indicating the potential of the soil water pressure potential to act as an indicator for drought in different soil types. Most drought responses started if the soil pressure potential dropped below −100 kPa.

Table 3
Delay in dates of 50% flowering of drought treatments as compared to the well-watered treatment (DEL, in days) and number of days between moment of zero leaf expansion and recovery (DIF) for rice cultivars IR20 and IR72 in Experiments 1 and 2. Data are averages of at least 4 replicates

Treatment	Experiment 1				Experiment 2			
	IR20		IR72		IR20		IR72	
	DEL	DIF	DEL	DIF	DEL	DIF	DEL	DIF
Drought at transplanting (A)								
AER	19	17	16	17	16	18	15	17
ALR	22	20	22	23	n.av.	24	20	23
Drought two weeks after transplanting (B)								
BER	18	13	15	13	10	14	10	13
BLR	21	18	19	17	16	18	15	17
Drought at mid-tillering (D)								
DER	12	8	12	10	10	11	9	10
DLR	17	13	14	12	12	13	n.av.	15
Drought at panicle initiation (E)								
EER	8	n.a.	6	10	6	11	8	12
ELR	12	n.a.	10	12	10	13	8	16
Drought at first flowering (F)								
FER	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

Drought induced at A: transplanting; B: two weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering.
ER: early recovery, i.e. drought ended at leaf rolling score 5; LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves.
n.av.: not available; n.a.: not applicable.

3.4. Impact of drought on phenology

The delay in dates of 50% flowering of all drought treatments as compared to well-watered plants in Experiments 1 and 2 is shown in Table 3. Early drought postponed flowering by a maximum of 22 days (ALR, Experiment 1). The delay in flowering was reduced if drought was induced at later growth stages. Postponement was in reasonable agreement with the number of days between the date of zero

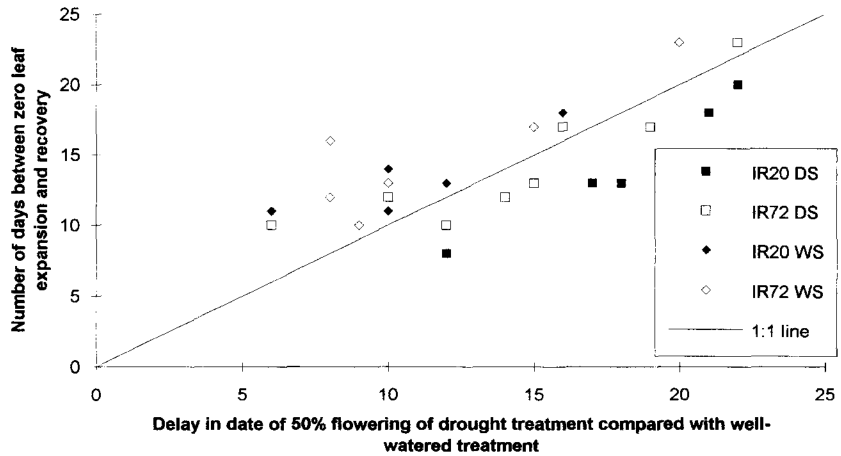


Fig. 7. Comparison between the delay in date of 50% flowering and the number of days between zero leaf expansion and recovery for all drought treatments in Experiments 1, 2 and 3.

Table 4
Mean grain yield (g m^{-2}) for rice cultivars IR20 and IR72 in Experiments 1, 2 and 3 (averages of four replicates). Means followed by a common letter are not significantly different at 5% confidence level

Treatment	Experiment 1		Experiment 2		Experiment 3
	IR20	IR72	IR20	IR72	IR72
Drought at transplanting (A)					
AER	744 [a]	830 [a]	460 [b]	454 [c]	n.a.
ALR	686 [ab]	793 [a]	289 [d]	274 [d]	n.a.
Drought two weeks after transplanting (B)					
BER	684 [ab]	724 [ab]	611 [a]	678 [a]	n.a.
BLR	701 [ab]	561 [bc]	415 [bc]	588 [ab]	n.a.
Drought three weeks after transplanting (C)					
CER	n.a.	n.a.	n.a.	n.a.	662 [b]
Drought at mid-tillering (D)					
DER	555 [bc]	666 [abc]	362 [cd]	547 [bc]	n.a.
DLR	492 [c]	504 [c]	162 [e]	240 [de]	n.a.
Drought at panicle initiation (E)					
EER	255 [d]	223 [d]	118 [ef]	145 [ef]	n.a.
ELR	148 [d]	91 [d]	62 [f]	48 [f]	n.a.
Drought at first flowering (F)					
FER	110 [d]	152 [d]	181 [e]	203 [de]	477 [bc]
Well-watered plants (WW)					
WW	827 [a]	723 [ab]	n.av.	n.av.	1011 [a]

Drought induced at A: transplanting; B: two weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering.
ER: early recovery, i.e. drought ended at leaf rolling score 5; LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves; WW: well-watered.
n.a.: not applicable; n.av.: not available because of rat damage.

Table 5
Yield components of the drought treatments and the well-watered control for both rice cultivars IR20 and IR72 in Experiment 1. Data are average of four replicates

	Number panicles per hill		Number filled grains per panicle		Unfilled % of grains per hill		1000-grain weight (g)	
	IR20	IR72	IR20	IR72	IR20	IR72	IR20	IR72
Drought at transplanting (A)								
AER	24	24	81	64	16	16	15.5	22.7
ALR	28	21	64	75	15	20	15.6	20.8
Drought two weeks after transplanting (B)								
BER	29	21	65	67	20	19	15.8	20.9
BLR	27	20	67	55	14	24	15.7	20.9
Drought at mid-tillering (D)								
DER	21	31	62	52	9	12	17.2	21.6
DLR	18	18	67	54	14	18	17.1	21.9
Drought at panicle initiation (E)								
EER	30	31	24	17	62	71	14.2	17.0
ELR	28	26	13	7	76	87	14.8	16.7
Drought at first flowering (F)								
FER	19	28	21	8	73	89	11.5	22.1
Well-watered plants (WW)								
WW	19	24	114	58	6	19	16.6	21.5

Drought induced at A: transplanting; B: two weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering.
ER: early recovery, i.e. drought ended at leaf rolling score 5; LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves; WW: well-watered.

leaf expansion and the recovery date (Fig. 7). This may indicate that if the soil is too dry to produce new leaves, the development rate of the crop stops also.

3.5. Impact of drought on yield and yield components

3.5.1. Experiment 1 (DS1992)

For both varieties, yields obtained in early drought treatments (A and B) did not differ significantly from the well-watered yields. Drought at mid-tillering, panicle initiation and flowering strongly reduced yields to below 200 g m^{-2} (Table 4).

The low yields obtained if drought was induced at panicle initiation or flowering were caused by a large percentage of unfilled grains (Table 5). Drought at tillering did not result in an increase in the percentage of unfilled grains compared with the well-watered control plants, but yield reduction was caused by fewer panicles and fewer grains per hill. The 1000-grain weight remained fairly constant among treatments, except if drought was induced at panicle initiation. Grain weight of IR20 was considerably smaller that that of IR72, but the number of grains per panicle was greater.

3.5.2. Experiment 2 (WS1992)

Plants of the well-watered treatments of both varieties suffered from rat damage and yield data are therefore not available. Yields were smaller than in the dry season experiment because of lower solar radiation levels. Drought in the reproductive phase resulted in very low yields (Table 4). Just like in Experiment 1, this was mainly caused by a large percentage of unfilled grains (Table 6). The low yield obtained for the ALR treatment is due to the small number of panicles per hill. Grain weight remained fairly constant among treatments, except if drought was induced at panicle initiation or flowering. Grain weight of IR20 was again lower than that of IR72.

3.5.3. Experiment 3 (DS1994)

The well-watered treatment achieved a yield above 1000 g m^{-2} (Table 4). Both drought treatments had lower yields; in case of C because of a smaller number of panicles per hill and in case of F because

Table 6
Yield components of the drought treatments and the well-watered control for both rice cultivars IR20 and IR72 in Experiment 2. Data are average of four replicates

	Number of panicles per hill		Number of filled grains per panicle		Unfilled % of grains per hill		1000-grain weight (g)	
	IR20	IR72	IR20	IR72	IR20	IR72	IR20	IR72
Drought at transplanting (A)								
AER	16	11	69	76	6	21	16.5	21.1
ALR	10	9	69	63	6	16	16.3	20.5
Drought two weeks after transplanting (B)								
BER	21	16	73	79	6	16	15.7	21.3
BLR	15	13	68	92	8	15	16.7	20.3
Drought at mid-tillering (D)								
DER	20	19	50	58	27	19	14.6	20.1
DLR	12	15	36	33	18	30	15.2	19.2
Drought at panicle initiation (E)								
EER	14	15	24	24	61	61	14.1	18.2
ELR	15	14	13	9	75	87	13.5	16.4
Drought at first flowering (F)								
FER	17	13	42	32	44	58	15.2	18.7
Well-watered plants (WW)								
WW	14	15	59	51	11	15	15.8	20.6

Drought induced at A: transplanting; B: two weeks after transplanting; D: mid-tillering; E: panicle initiation; F: first flowering.
ER: early recovery, i.e. drought ended at leaf rolling score 5, LR: late recovery, i.e. drought ended at leaf rolling score 5 and 50% dead leaves; WW: well-watered.

Table 7
Yield components of the drought treatments and the well-watered control for rice cultivar IR72 in Experiment 3. Data are average of four replicates

	Number of panicles per hill	Number of filled grains per panicle	Unfilled % of grain per hill	1000-grain weight (g)
Drought three weeks after transplanting (C)				
CER	14	100	26	20.1
Drought at first flowering (F)				
FER	21	58	43	16.6
Well-watered plants (WW)				
WW	17	105	20	23.1

C = drought three weeks after transplanting; F = drought at first flowering.
ER = early recovery, i.e. drought ended at leaf rolling score 5; WW = well-watered.

of a larger percentage of unfilled grains and a smaller grain weight (Table 7).

Results indicate that in this greenhouse experiment, rice plants were tolerant of drought stress in the vegetative phase, i.e., if drought was induced before mid-tillering. Yanbao and Ingram (1988) also reported that water deficit in the vegetative phase had no significant effect on grain yield and that a 15-day stress period in the reproductive phase resulted in yield reductions up to 88%, resulting from a reduction in the number of spikelets per plant and an increase in the percentage of unfilled spikelets.

3.6. Impact for modeling of rainfed rice production

The soil water–drought response relationships presented above may be used in models that predict rice growth and yield in rainfed environments. Both well-tested soil water balance models, like the SAWAH model (Ten Berge et al., 1992) and crop simulation models that simulate potential yield under well-watered conditions, like ORYZA1 (Kropff et al., 1993) are available. The relationships obtained in this study may be used to link both type of models. Soil water pressure potentials h, obtained from a soil water balance model may be translated into changes in leaf morphology, and relative transpiration. These responses can be defined as functions of $\log(h)$ as shown in Figs. 4, 5 and 6. A similar approach, linking stress factors to soil extractable water, was taken for other crops by Sinclair (1986) and McCree and Fernandez (1989).

Effects of water shortage on transpiration is often modeled by assuming that the ratio of actual transpiration T_a over potential transpiration T_p is a function of soil water volume (V) over the rooting zone (Penning de Vries et al., 1989). As V decreases from field capacity (V_{FC} defined at $h = -10$ kPa) to wilting point (V_{WP}, often defined at $h = -1.5$ MPa), T_a/T_p stays equal to 1 until V reaches a threshold or critical value, V_C. T_a/T_p decreases from 1 to 0 as V decreases from V_C to V_{WP}. The ratio $(V_{FC} - V_C)/(V_{FC} - V_{WP})$ is often taken between 0.5 and 0.7 for other crops than rice (Saugier and Katerji, 1991). V_C for lowland rice is often set to V_{FC} (e.g., Penning de Vries et al., 1989), assuming a very sensitive response of T_a/T_p to soil water content. Results from this study indicate that V_C should be defined at a much lower pressure potential, i.e., in the early vegetative phase at $h = -100$ kPa. This result was obtained for a puddled clay soil and a non-puddled sandy soil. Corresponding values for $(V_{FC} - V_C)/(V_{FC} - V_{WP})$ are respectively: 0.35 cm^3 cm^{-3} and 0.72 cm^3 cm^{-3}, and for the non-puddled clay soil 0.53 cm^3 cm^{-3} (using data from Wopereis et al., 1993). Relating drought responses to soil water volume is therefore risky because of the differences in soil water retention characteristics between soil types.

Results obtained from this study and from Tanguilig et al. (1987) for IR36 suggest that the decline in leaf elongation rate of semi-dwarf lowland rice varieties, stressed in the vegetative phase, is relatively abrupt. This could be tentatively modeled as a 'step function' declining from 1 (normal leaf expansion) to 0 (zero leaf expansion) if the soil water pressure head drops below its critical value for zero leaf expansion.

The reasonable good agreement between delay in flowering and the number of days between the moment of zero leaf expansion and recovery (Fig. 7) suggests that the development rate stops when the soil becomes too dry for further leaf expansion and resumes if drought stress is released. If the critical soil water pressure potential for zero leaf expansion is reached, stressed plants will still be able to produce carbohydrates for growth, as transpiration has not yet ceased. The plant therefore stores C, which may result in thickening of leaves during drought stress. This excess C may be available for leaf production as soon as drought stress is released. In a rainfed-rice model, this may be modeled as a temporary storage pool for carbohydrates during drought, as was also done by McCree and Fernandez (1989).

Plant size and evaporative demand of the air will influence the drought-stress responses to some extent, as was also shown in this study. Results reported here are, however, not as distinct as reported by Doorenbos and Kassam (1979) for C3 crops, despite the clear difference in evaporative demand of the air in the wet and dry season experiments.

Root distribution in the field is very important. Water uptake rate of rice roots from a top soil layer may decrease with decreasing soil water potential, but roots at greater depth may make up for this difference by increasing water uptake, even if the soil water potential at that depth is also decreasing (e.g., Hasegawa and Yoshida, 1982). In this experiment roots were limited to a cylinder of 25 cm height and 20 cm diameter. In reality roots may grow deeper, especially in the absence of a hard plow pan. For modeling purposes it is important to establish extraction rates at different depths in the root zone.

Results reported here are specific for two semidwarf lowland varieties. Dryland rice varieties are known to be more 'pessimistic' (Bradford and Hsiao, cited in Dingkuhn et al., 1989) in their drought

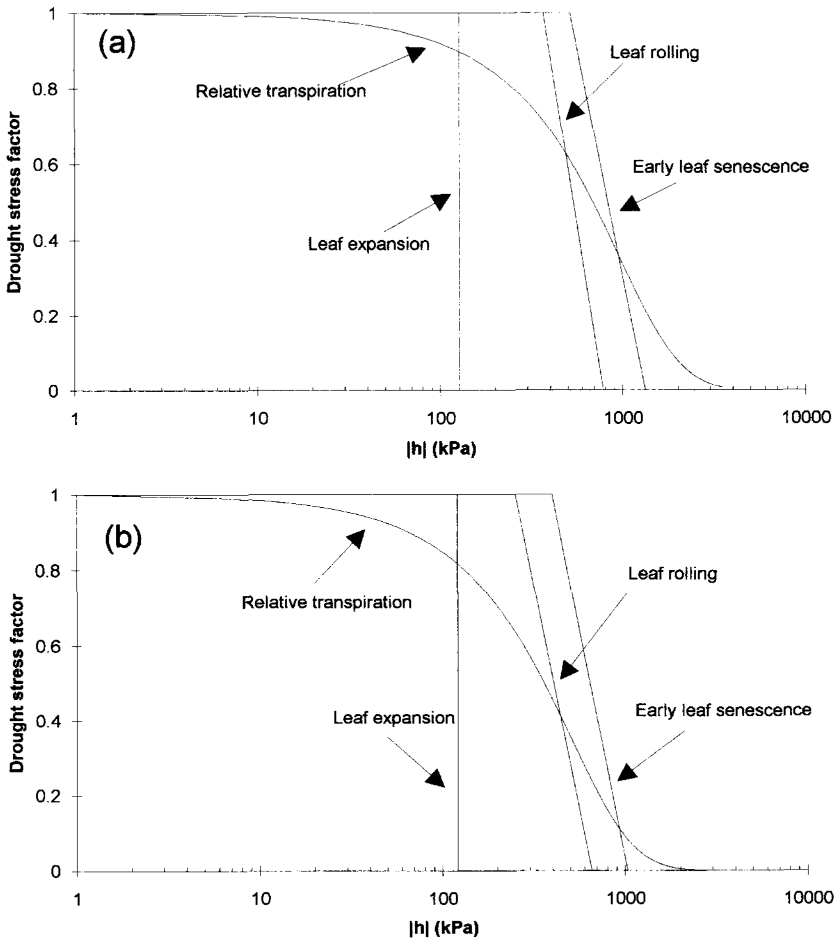


Fig. 8. Relationship between soil water pressure potential $|h|$ and drought stress factors for IR20; (a) results for treatments A (drought at transplanting) and B (drought two weeks after transplanting (a), (b) results for treatments D (drought at mid-tillering), E: drought at panicle initiation) and F (drought at first flowering).

responses as they show leaf rolling at higher leaf water potentials (e.g., Turner et al., 1986; Dingkuhn et al., 1989). They also tend to have a deeper root system than lowland rice varieties (Yoshida, 1981) and may therefore be more effective in exploring soil water resources.

The advantage of expressing drought-stress responses as a function of soil water pressure potential is that they can be used for any soil type, even when the soil shrinks, provided a good soil water balance model and knowledge of the soil's water retention and soil shrinkage curve, linking h to soil water content θ, is available. If such drought responses are used as an input for the rice-growth simulation model ORYZA1, predictions of rice yield under water-limited conditions can be made.

4. Conclusions

Three greenhouse experiments were conducted to investigate drought-stress responses of two lowland rice cultivars, grown in puddled clay and non-puddled sandy soil. Results for both soils were quite similar. Drought affected transpiration rates by closure of stomata and changes in leaf morphology of the rice plant. The first observed response, if drought was initiated in the vegetative phase, was a relatively abrupt decline in leaf expansion. Logistic functions could be used to describe the decline in relative transpiration, corrected for differences in LAI, as a function of $\log(h)$. Leaf rolling and rate of senescence were linearly related to $\log(h)$. An overview of the dependence of drought-stress factors on soil water potential is given in Fig. 8a and b. Such functions can be used in rainfed-rice simulation models to translate the soil water status into a crop response.

Plant age had a more distinct effect on drought-stress responses than differences in evaporative demand of the air between dry and wet seasons. Roots extended throughout the (shrunken) soil volume for all treatments. Differences in rooting pattern among drought treatments are therefore expected to be minor.

Drought in the vegetative phase, delayed phenological events but did not result in significant yield losses if drought occurred within 2 weeks after transplanting. Drought in the reproductive phase resulted in substantial yield losses, mainly caused by large percentages of unfilled grains and a reduction in grain weight.

Acknowledgements

The assistance of Mr. L. Tatad and Mr. R. Galang in the conduct of the experiments is gratefully acknowledged. This work was financed by the Netherlands' Ministry for Development Co-operation, Project 'Simulation and Systems Analysis for Rice Production' (SARP).

References

Bouma, J., Belmans, C., Dekker, L.W. and Jeurissen, W.J.M., 1983. Assessing the suitability of soils with macropores for subsurface liquid waste disposal. J. Environ. Qual., 12: 305–310.

Bronswijk, J.J.B., 1988. Modeling of water balance, cracking and subsidence of clay soils. J. Hydrol., 97: 199–212.

Bronswijk, J.J.B. and Evers-Vermeer, J.J., 1990. Shrinkage of Dutch clay soil aggregates. Neth. J. Agric. Sci., 38: 175–194.

Dingkuhn, M., Cruz, R.T., O'Toole, J.C. and Dörffling, K., 1989. Net photosynthesis, water use efficiency, leaf water potential and leaf rolling as affected by water deficit in tropical upland rice. Aust. J. Agric. Res., 40: 1171–1181.

Doorenbos, J. and Kassam, A.H., 1979. Yield Response to Water. FAO Irrigation and Drainage Paper 33, FAO, Rome, 193 pp.

Fukai, S., Kuroda, E. and Yamagishi, T., 1985. Leaf gas exchange of upland and lowland rice cultivars. Photosynthesis Res., 7: 127–135.

Hasegawa, S. and Yoshida, S., 1982. Water uptake by dryland rice root system during soil drying cycle. Soil Sci. Plant Nutr., 28: 191–204.

Inthapan, P. and Fukai, S., 1988. Growth and yield of rice cultivars under sprinkler irrigation in south-eastern Queensland. 2. Comparison with maize and grain sorghum under wet and dry conditions. Aust. J. Exp. Agric., 28: 243–248.

IRRI, 1989. IRRI Towards 2000 and Beyond. International Rice Research Institute, Manila, Philippines, 66 pp.

IRRI, 1993. Rice Research in a Time of Change. IRRI's Medium-term Plan for 1994–1998. International Rice Research Institute, Manila, Philippines, 79 pp.

Klute, A., 1986. Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods. Agronomy 9, 2nd edition. American Society of Agronomy, Madison, Wisconsin, 1188 pp.

Kropff, M.J., 1993. Mechanisms of competition for water. In: M.J. Kropff and H.H. van Laar (Editors), Modelling Crop–Weed Interactions. CAB International, Wallingford, UK, pp. 63–76.

Kropff, M.J., van Laar, H.H. and ten Berge, H.F.M. (Editors), 1993. ORYZA1, a Basic Model for Irrigated Lowland Rice Production. International Rice Research Institute, Los Baños, Philippines, 78 pp.
McCree, K.J. and Fernandez, C.J., 1989. Simulation model for studying physiological water stress responses of whole plants. Crop Sci., 29: 353–360.
Muchow, R.C., Hammer, G.L. and Carberry, P.S., 1991. Optimising crop and cultivar selection in response to climatic risk. In: R.C. Muchow and J.A. Bellamy (Editors), Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics. CAB International, Wallingford, UK, pp. 235–262.
O'Toole, J.C. and Baldia, E.P., 1982. Water deficits and mineral uptake in rice. Science, 22: 1144–1150.
O'Toole, J.C. and Chang, T.T., 1979. Drought resistance in cereals – Rice: a case study. In: H. Mussel and R. Staples (Editors), Stress Physiology in Crop Plants. Wiley-Interscience, New York, pp. 373–405.
O'Toole, J.C. and Cruz, R.T., 1980. Response of leaf water potential, stomatal resistance and leaf rolling to water stress. Plant Physiol., 65: 428–432.
O'Toole, J.C. and Moya, T.B., 1981. Water deficits and yield in upland rice. Field Crops Res., 4: 247–259.
Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M. and Bakema, A., 1989. Simulation of Ecophysiological Processes of Growth in Several Annual Crops. Simulation Monographs 29. IRRI, Los Baños and Pudoc, Wageningen, 271 pp.
Puckridge, D.W. and O'Toole, J.C., 1981. Dry matter and grain production of rice, using a line source sprinkler in drought studies. Field Crops Res., 3: 303–319.
Saugier, B. and Katerji, N., 1991. Some plant factors controlling evapotranspiration. Agric. For. Meteorol., 54: 263–277.
Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production. I. Model development. Field Crops Res., 15: 125–141.
Sinclair, T.R. and Ludlow, M.M., 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Aust. J. Plant Physiol., 13: 329–341.
Tanguilig, V.C., Yambao, E.B., O'Toole, J.C. and De Datta, S.K., 1987. Water stress effects on leaf elongation, leaf water potential, transpiration, and nutrient uptake of rice, maize, and soybean. Plant Soil, 103: 155–168.
Ten Berge, H.F.M., Jansen, D.M., Rappoldt, K. and Stol, W., 1992. The Soil Water Balance Module SAWAH: User's Guide and Outline. CABO-TPE Simulation Report Series, no. 22. CABO, Wageningen, 78 pp.
Turner, N.C., 1986. Crop water deficits: a decade of progress. Adv. Agron., 39: 1–51.
Turner, N.C., O'Toole, J.C., Cruz, R.T., Namuco, O.S. and Ahmad, S., 1986. Responses of seven diverse rice cultivars to water deficits. I. Stress development, canopy temperature, leaf rolling and growth. Field Crops Res., 13: 257–271.
Van Genuchten, M.Th., 1980. A Closed-form Equation for Predicting the Hydraulic Properties of Unsaturated Soils. US-EPA, Ada, OK, 85 pp.
Van Keulen, H., Berkhout, J.A.A., van Diepen, C.A., van Heemst, H.D.J., Janssen, B.H., Rappoldt, C. and Wolf, J., 1987. Quantitative land evaluation for agro-ecological characterization. In: A.H. Bunting (Editor), Agricultural Environments. Characterization, Classification and Mapping. CAB International, Wallingford, UK, pp. 185–197.
Woodhead, T., ten Berge, H.F.M. and de San Agustin, E.M., 1991. Modeling upland rice hydrology. In: F.W.T. Penning de Vries, M.J. Kropff, P.S. Teng and G.J.D. Kirk (Editors), Systems Simulation at IRRI. International Rice Research Institute, Los Baños, Philippines, pp. 53–60.
Wopereis, M.C.S., Kropff, M.J., Wösten, J.H.M. and Bouma, J., 1993. Sampling strategies for measurement of soil hydraulic properties to predict rice yield using simulation models. Geoderma, 59: 1–20.
Yanbao, E.B. and Ingram, K.T., 1988. Drought stress index for rice. Philipp. J. Crop Sci., 13: 105–111.
Yoshida, S. 1981. Fundamentals of Rice Crop Science. International Rice Research Institute, Manila, Philippines, 269 pp.