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Contributions of Capacity for Soil Water Extraction and Water Use Efficiency to Maintenance of Dry matter Production in Rice subjected to Drought

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Abstract: Dry matter production rate in plants is indicated by transpiration rate (Tr) multiplied by water use efficiency (WUE). Our objectives were to establish which of WUE or Tr is dominant in contributing to maintenance of dry matter production of rice cultivars in drought conditions. Four rice cultivars with different drought resistance rankings (from susceptible to resistant) were grown in upland field conditions and suffered soil desiccation during the reproductive stage. Dry matter production of the shoot (SDP) when irrigation was withheld was different for each cultivar; SDP was higher in drought resistant cultivars and lower in sensitive cultivars. There was a close relationship between SDP and the consumption of soil water between 0 and 40 cm below the soil surface during the soil drying period. Water consumption showed a high correlation with root density in deep soil layers. There were not, however, large cultivar differences in WUE, calculated from the transpiration rate which was estimated from the soil water consumption minus the soil evaporation rate. When three cultivars selected from these field tested cultivars were grown in pots and suffered different degrees of soil desiccation during the early reproductive stage, there were also scarcely any differences in WUE between the three cultivars.

We suggested that the high dry matter production of those rice cultivars known to be drought resistant under field conditions is caused not by high WUE, but by high ability to maintain Tr, which is supported by deep root systems.
Key words: Drought, Dry matter production, Rice, Transpiration, Water use efficiency.

干ばつ下におけるイネ乾物生産への土壌からの水吸収能力および水利用効率の貢献度：小葉田　亨・奥野友美・山本孝信（島根大学生物資源科学部）

要　旨：作物におけるある期間中の乾物生産量は土壌水分の吸収量すなわち蒸散量と吸収した水の乾物への変換効率（水利用効率）との積で表せる．そこで，本報告では干ばつ下でイネが高い乾物生産量や収量をあげるためには，土壌水分の吸収能力と水利用効率のどちらの性質がより貢献しているのかを，耐乾性のきわめて異なる4品種のイネを用いて明らかにしようとした．降雨を遮断した圃場条件下で，生殖生長期開始頃から43日間にわたって潅がいを停止すると，葉身水ポテンシャルや気孔伝導度の低下の仕方が異なり，その結果乾物生産量と収量は従来耐乾性の優れるとみなされている品種ほど高かった．さらに，この間の土壌水分消費量と乾物生産量との間には密接な直線関係があった．そして，地表10 cm以下の根重密度が高い品種ほど土壌水分の消費量が多かった．また，この土壌水分消費量から土面蒸発推定量を除した蒸散量から計算した水利用効率には大きな品種間差はなかった．さらに圃場実験に用いた品種の中から3品種を選んでポット栽培したものに，幼穂分化期初期に給水を5段階に変えて約2週間異なる土壌乾燥を与え，水利用効率を比較したところ，やはり土壌乾燥強度，品種間でほとんど違いがなかった．以上から，これまで耐干性の強いと見なされているイネは，深く発達した根によって多くの水を吸収することで干ばつ下での乾物生産を維持しており，水利用効率の品種間差が乾物生産の違いに強く寄与することは極めて少ないとみなされた．
キーワード：イネ，干ばつ，根系，水利用効率，陸稲．

There are considerable differences in the drought resistance of rice cultivars under field conditions[4,17]. When rainfall and irrigation are limited, it is very important that water conserved in soils is used more efffectively for plant growth. The reduction of soil evaporation, high soil water availability for transpiration by greater rooting depths and high water use efficiency are all key factors[7,23] towards more effective use of water. In upland rice, high root density may contribute to the amount of soil water available for transpiration[8,26]. Drought resistant rice cultivars may have higher water use efficiency (WUE) calculated from gas exchange of a leaf[6], or from dry matter production/transpiration rate of a whole plant[16] under dry soil conditions although there was no difference in WUE among diverse cultivars under wet soil conditions[8]. However it has not been established what characteristics relating to water use in rice contribute to high biomass or grain yield under drought conditions.

Dry matter production in plants can be determined by transpiration (Tr) multiplied by WUE[3,28]. Our objective was to establish whether WUE or Tr is chiefly responsible for maintenance of dry matter production in rice cultivars under drought conditions.

Materials and Methods

1. Field experiments

Four rice (*Oryza sativa* L.) cultivars were grown in a silty clay loam at an upland site on the Experimental Farm of Shimane University. The four cultivars differ in their origins and agronomic requirements: Nipponbare is an improved wetland-adapted Japonica rice, Senshou is a traditional upland-adapted Japonica rice and Tachiminori is an improved upland-adapted Japonica rice grown in Japan, while Dular is a traditional lowland-adapted Indica rice grown in India. Dular and Senshou are drought resistant cultivars, Tachiminori is a moderately susceptible cultivar, and Nipponbare is a drought susceptible in field tests [4,13,14].

On 17 April, 14 May and 20 May 1991, Nipponbare, Senshou and Tachiminori, and Dular seeds were sown in seed beds (60 × 30 × 3 cm) containing seedling soil (Green Soil, Izumo Green Epoch Co.) and grown in a non-temperature controlled glasshouse. The sowing date of each cultivar was changed to synchronize growth stages. On 13 May, 30 May, and 5 June 1991, seedlings at the four-leaf stage were transplanted to an upland site on the farm in rows 0.40 m apart with 0.05 m spacing between plants. Three g N m^{-2} (as ammonium sulfate), 10 g P m^{-2} (as superphosphate of lime) and 19 g K m^{-2} (as potassium chloride) were applied at transplanting and an additional 3 g and 2 g N m^{-2} (as ammonium sulfate) was applied at the early tillering stage and also at the flower initiation stage. Each of the cultivars occupied a plot 2.5 × 2.0 m. The plots were placed inside a vinyl covered house (3.5 m × 11.0 m) to prevent plants receiving water from rainfall. All cultivars were initially irrigated every two or three days. Irrigation was discontinued from 22 July 1991.

Volumetric soil water content was measured in 0.1 m layers between 0.1 m and 0.4 m soil depth on days 0 and 43 of the soil drying treatment, using a core soil sampler of 2 cm diameter. Soil moisture was determined by weighing, oven-drying at 105°C and then weighing again to estimate soil water content. Soil evaporation rate to know effects of soil desiccation in the evaporation was monitored using a micro lysimeter (0.05 m diameter and 0.15 m in height) with several 0.5 cm holes. The lysimeter was set up at soil surface level in the center between rows for each cultivar (2 lysimeters were set for each cultivar). Shoots in an area of each plot measuring 0.5 × 0.4 m were harvested on days 0 and 43 (full ripening period) after withholding irrigation. Harvested shoots were divided into straw and unhulled rice (at the last harvest only) and ripened unhulled rice was selected by ammonium sulfate solution with 1.06 of specific gravity. Roots were harvested from each cultivar using a soil core of 0.01 m^2 (soil surface area) × 0.30 m depth and divided into 0.1 m layers between 0.1 and 0.3 m soil depth and recorded as volumetric root dry weight density (g cm^{-3}). Obtaining root samplings at soil layers deeper than 0.3 m soil depth was very difficult because hard clay soil layers dominated subsoil layers. Plant materials were dried at 80°C for 48 hours and then weighed.

Leaf water potential (ψ_l), abaxial diffusive conductance (Cs) and transpiration rate for upper expanded leaves on main culms or lower tillers were measured at midday in sunny conditions (1200-1400 JST) throughout the treatment using a pressure chamber (Model 3005, Soil Moisture Equipment Co.)[12] and a steady state porometer (LI-1600, LI-COR Co.). Air temperature, humidity, radiation and wind speed were monitored with a weather station, which was set near the vinyl covered house throughout the soil drying treatment period. The data of every hour were stored in a data logger and mean of data during day time was calculated.

2. Pot experiments

Two seedlings of three rice cultivars, Nipponbare, Senshou and Dular, were transplanted into pots with a diameter of 14 cm and a depth of 30cm, and filled with rice seedling soil (Green Soil, Izumo Green Epoch Co.), on 25 May 1994. The two seedlings were reduced to one after establishment of roots. Methods for sowing and growing seedlings were the same as those used in the field experiments. Zero point one g N pot^{-1} (as ammonium sulfate), 0.2 g P pot^{-1} (as superphosphate of lime) and 0.3 g K pot^{-1} (as potassium chloride) were applied at transplanting and an additional 0.06 g and 0.1 g N pot^{-1} (as ammonium sulfate) was applied at early tillering stage and also at flower initiation stage.

Five sets of soil water status conditions were set by varying the amounts of irrigation water. Each set applied to three or four pots. At the start of the treatments, flooded water in all pots was leaked gravitationally for 24 hours. Abundant water was immediately added to one pot to maintain flooded conditions as a control. A reduced amount of water (0.5～0.6, 0.3, 0.25 and 0 times (irrigation factor) of transpirational loss per day in the flood control) was added every evening to maintain the intended level of soil desiccation (desiccated 1, 2, 3 and 4). Soil desiccation treatments started from the early flower initiation stage and were continued for 15 days under a non-temperature controlled glasshouse to prevent the plants receiving rainfall. Air temperature and humidity were monitored with a thermo-hygrometer (RHD-J, Nihonshintech Co.) throughout the soil drying treatment period. The soil surface of the pot was covered by a plastic plate and oil clay to prevent soil evaporation.

Transpiration rates (Tr) for each treatment pot were calculated from the difference in pot weight between the beginning and end of the soil desiccation treatment, and the amounts of water added during the treatment period. The latter was determined by multiplying the irrigation factor by the transpiration rate of the flooded control. Shoots from three or four replicate pots in each soil drying treatment were harvested, dried in an oven at 80°C for 48 hours, then weighed to find the shoot dry matter production (SDP). Water use efficiency (WUE) was calculated from[5)]

$$WUE = \frac{SDP}{Tr} \qquad (1)$$

Abaxial leaf conductance in the second fully expanded leaf was measured with a diffusion porometer (AP4, DELTA-T DEVICES LTD.) at morning and midday at intervals of several days to monitor the degree of stress. Drying of the bulk soil in pots was monitored by weighing the pots, at intervals of 3～5 days, during the treatment period. Volumetric soil water content was calculated from changes in weight.

Results

1. Growth and water use from soils of four rice cultivars subject to drought under field conditions

(1) Leaf water potential (ψ_l) and leaf conductance (Cs) under drought conditions

After irrigation was terminated, the midday ψ_l of all the cultivars decreased (Fig. 1). However, there were large differences in reduction of ψ_l between the cultivars.The lowest ψ_l in Nipponbare was observed but in Senshou, Dular and Tachiminori ψ_l was higher than in Nipponbare by 0.6 MPa or more, while that in Tachiminori was a little lower than in Senshou and Dular. The Cs in all cultivars started to decrease shortly after withholding irrigation, although there was a difference in the levels of the reduction between the cultivars ; Cs in Nipponbare decreased to near zero, in Senshou, Cs remained higher and then decreased, and in Dular and Tachiminori, Cs decreased but slightly recovered at the last phase of the soil drying treatments. Trends of change in transpiration rate from leaves near the top of the plant were similar to those of Cs in the four cultivars (Fig. 1).

(2) Dry matter production and soil water use

Shoot dry matter increase in drought resistant cultivars, Dular and Senshou, was larger than in the susceptible Nipponbare or the moderately susceptible Tachiminori under drought conditions (Fig. 2). Soil water use from 0 to 40 cm soil depth during the soil drying treatments, which was estimated from reduction of soil water content, was also higher in Dular and Senshou ; in Tachiminori it was moderate, and in Nipponbare it was lowest. When all data were combined, a close relationship between shoot dry matter increase and soil water use during non-irrigated conditions was evident (Fig. 2).

Soil water use in deep layers between 10 to 40 cm soil depth was higher in Dular and Senshou than in Tachiminori, and noticeably

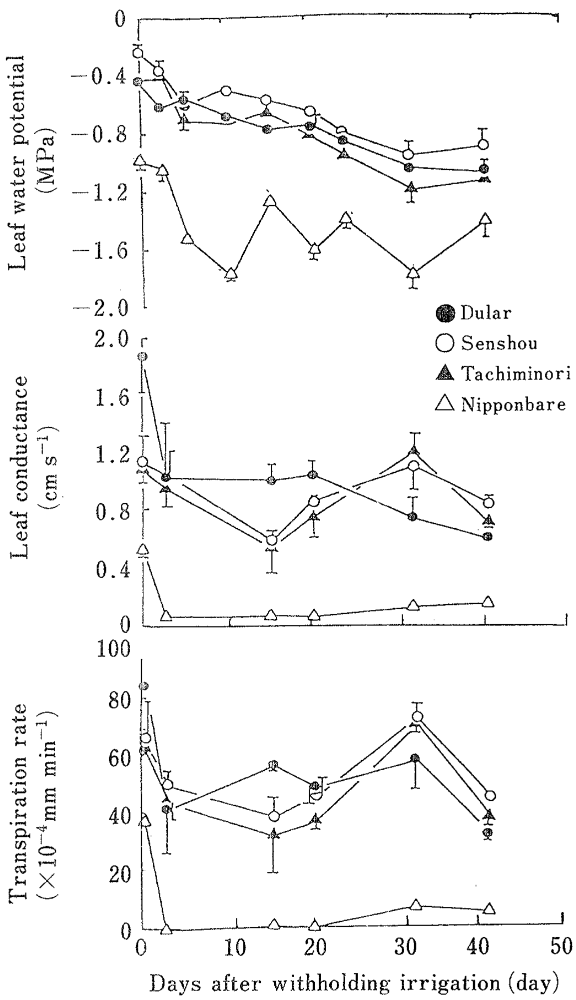

Fig. 1. Leaf water potential, leaf conductance and transpiration rate at midday after withholding irrigation. Irrigation was stopped for a period of 43 days during the last part of the growing season under field conditions. Each value represents the mean and standard error of three observations. Error bars smaller than symbols were omitted for clarity.

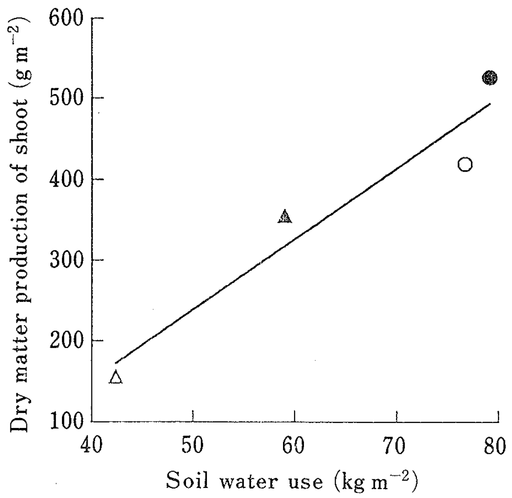

Fig. 2. Relationship between dry matter production (SDP) of the shoot and soil water taken up from soil layers between 0 and 40 cm depth (SWU) by four cultivars during 43 of days drought treatment under field conditions. The average vapor deficit in the day time during the treatment period was 6.9 g m^{-3}. See Figure 1 for treatments and symbols. $SDP = -199.4 + 8.8SWU$, ($r^2 = 0.923$, $P < 0.01$).

higher than in Nipponbare (Fig. 3). There was scarcely a difference in soil water use in shallow layers over 10 cm from the soil surface among the four cultivars. Root weight density in Dular and Senshou in soil layers below 10 cm from the soil surface was higher than in the other cultivars at final harvest, while that in Nipponbare was the highest in shallow soil layers over 10 cm. High root density in the shallow soil layers did not affect soil water use under drought conditions. Thus there was a close relationship between deep root density (below 10 cm soil depth) at harvest time and soil water use during withholding of irrigation (Fig. 4).

(3) Dry matter of shoot at harvest time and grain yield

The following percentages of total shoot weight at final harvest were produced during the drought treatment period (Table 1) ; 70% for Dular, 55% for Senshou, 41% for Tachiminori, and 31% for Nipponbare. Grain yield (absolute dry weight) of four cultivars varied from 255.8 g m^{-2} for Dular to 3.7 g m^{-2} for Nipponbare, which suffered the effects of drought. Harvest indices (grain yield/shoot dry weight) for Dular, Senshou, Tachiminori and Nipponbare were 0.33, 0.31, 0.25 and 0.01, respectively. The lowest harvest index, for Nipponbare, was caused by a serious lack of fertility (data are not provided). Cultivars which indicated higher dry matter production during the period of drought conditions also had higher grain yields and harvest indices.

2. Water use efficiency under soil drying conditions in pot grown plants

The soil water content of the pots decreased from 50 to 10% of field capacity in relation to the amounts of irrigation water on the last day of the treatments, although the levels of soil desiccation varied slightly between cultivars (Fig. 5). Cs of the most severely desiccated

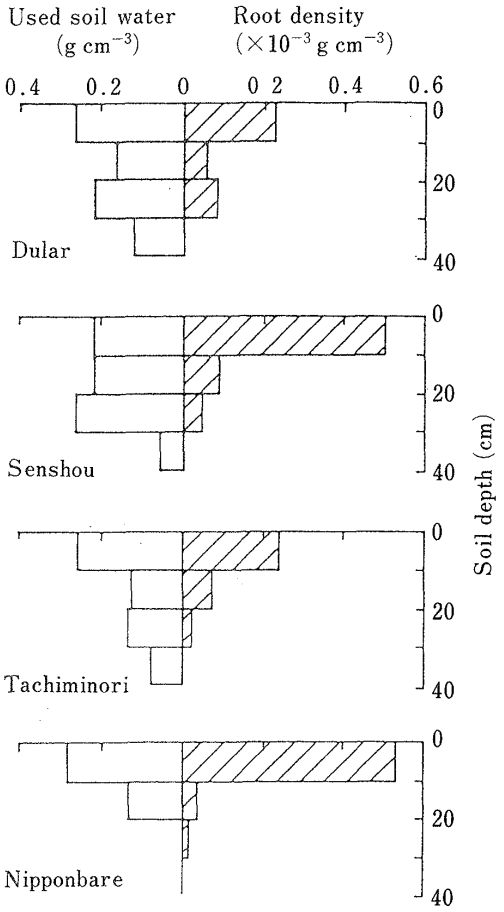

Fig. 3. Soil water use (SWU) and root density of four rice cultivars in various soil depths under drought conditions in a field experiment. See Figure 1 for treatments.

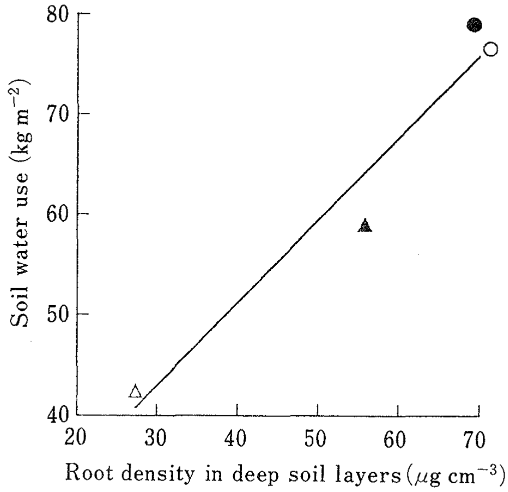

Fig. 4. Soil water use (SWU) and root density of deep soil layers (RDD) between 10 to 30 cm from the soil surface in a field experiment. See Figure 1 for treatments.
$SWU = 18.20 + 8.24RDD$,
($r^2 = 0.949$, $P < 0.001$).

plants decreased by 50～60% compared with the well-watered control (Table 2). These depression indicated that the plants suffered degrees of water stress ranging from mild to severe. Soil desiccation reduced both shoot dry matter increase and transpiration rate in each cultivar during the treatment period, and there was a close relationship between these reductions (Fig. 6). The WUE of each cultivar did not change significantly due to soil desiccation, as the average WUE for Nipponbare, Senshou and Dular in five soil drying treatments was 1.75 ± 0.10, 1.59 ± 0.08 and 1.87 ± 0.11 × 10^{-3} g g^{-1} (mean ± standard error of five soil drying treatments), respectively. When data for all soil drying treatments were compared, there was little difference in WUE between the three cultivars, except that WUE for Dular under flood conditions was high. The slope of the regression (Fig. 6) indicates a mean WUE (1.74 × 10^{-3} g g^{-1}) for all data.

Discussion

Low dry matter production for Nipponbare and Tachiminori under non-irrigated condition seemed to be caused primarily by suppression of leaf assimilation activity. When conversion efficiencies[10] from the absorbed rediation by crop to the dry matter production were calculated from accumulated short wave rediation and leaf area index during the non-irrigated period, the efficiencies for Nipponbare and Tachiminori were very low, 0.51 and 0.77 g MJ^{-1}, while for Senshou and Dular 0.14 and 1.39 g MJ^{-1}, respectively. The efficiency for Nipponbare was only 36% or less of that observed under irrigated field conditions (1.4～1.6 g MJ^{-1}, calculated value for shoot)[2,10]. Very low Cs for Nipponbare suggested severe reduction of conversion efficiency through stomatal closure. Differences of leaf area among these cultivars did not appeared to cause cultivar difference in dry matter production, because leaf area indices for Senshou and Dular were between the lowest for Nipponbare (1.8, mean during non-irrigated period) and the highest for Tachiminori (4.1). Assimilation activity for Senshou and Dular seemed to be maintained by higher capacity of dehydration avoidance[19]. Senshou and Dular, which had a relatively large amount of root systems

Table 1. Shoot dry matter increase during the period of withholding irrigation, shoot dry weight at harvest time, grain yield and harvest index of four rice cultivars which suffered drought for 43 days during the last part of the cropping seasen.

Cultivar	Dry matter increase of shoot during drought ($g\ m^{-2}$)	Dry weight of shoot at harvest (TW) ($g\ m^{-2}$)	Grain yield (Y) ($g\ m^{-2}$)	Harvest index (Y/TW) (%)
Dular	526.4 (70)	756.5	255.8	0.33
Senshou	418.9 (55)	762.9	233.5	0.31
Tachiminori	355.1 (41)	873.2	213.5	0.25
Nipponbare	155.5 (31)	497.8	3.7	0.01

Data were calculated from 10 plants in an area of land measuring 0.2 m^2.
Grain yield represents the absolute dry weight of brown rice selected by specific gravity of 1.06.
Parentheses indicate the percentage of dry matter increase of shoot during drought in dry weight of shoot at harvest.

Table 2. Average leaf conductance from morning to afternoon $\pm$ standard error of measurements for four days (3, 8, 11 and 14 days after withholding water) in the plants suffered different irrigation rates under pot conditions.

Irrigation factor	Cultivar		
	Nipponbare	Senshou ($cm\ s^{-1}$)	Dular
1.0	1.20±0.26	1.78±0.24	1.63±0.31
0.5—0.7	0.74±0.14	1.69±0.18	1.34±0.23
0.3	0.71±0.15	1.26±0.35	1.22±0.21
0.25	0.57±0.20	1.08±0.22	0.91±0.31
0.0	0.46±0.22	0.72±0.36	0.61±0.28

Irrigation factor indicates a reduced amount of water of transpirational loss per day per plant in the flood control (factor=1).
See Figure 5 for treatments.

between 10 and 40 cm below the soil surface, maintained higher ψ_1 than Nipponbare having less during the non-irrigated conditions, although there was no clear difference in ψ_1 between the drought resistant cultivars and the moderately susceptible Tachiminori.

In our pot experiment WUE for three cultivars calculated from dry matter increase /transpiration rate was stable under diverse soil water conditions. And the WUE differed only very slightly between the cultivars. The stability of WUE for rice under soil desiccation was suggested for other improved rice cultivars[16], such as Nipponbare and Tachiminori, in our results. The WUE of three lowland and upland cultivars suffered soil drying hardly differed more than 20% compared to wet control plants[16]. Generally, WUE calculated from dry matter increase/transpiration rate is extremely stable regardless of soil water or nutrient conditions in other plant species[5,17], although WUE in rice measured by ratio of photosynthetic to transpiration rate in a leaf for a short time showed a definite change as a result of soil drying and leaf dehydration[6]. In a crop plant, responses of WUE to soil drying on the level of dry matter/transpiration rate for the long term, nevertheless, may be more important than the instantaneous gas exhange rate.

To assess the effect of WUE in the crop production, we need to clarify whether WUE for four cultivars under non-irrigated field conditions was also stable. First, soil evaporation needs to be divided from the soil water use for estimation of transpiration rate. Soil evaporation rate (E_{soil}) can be shown as[25];

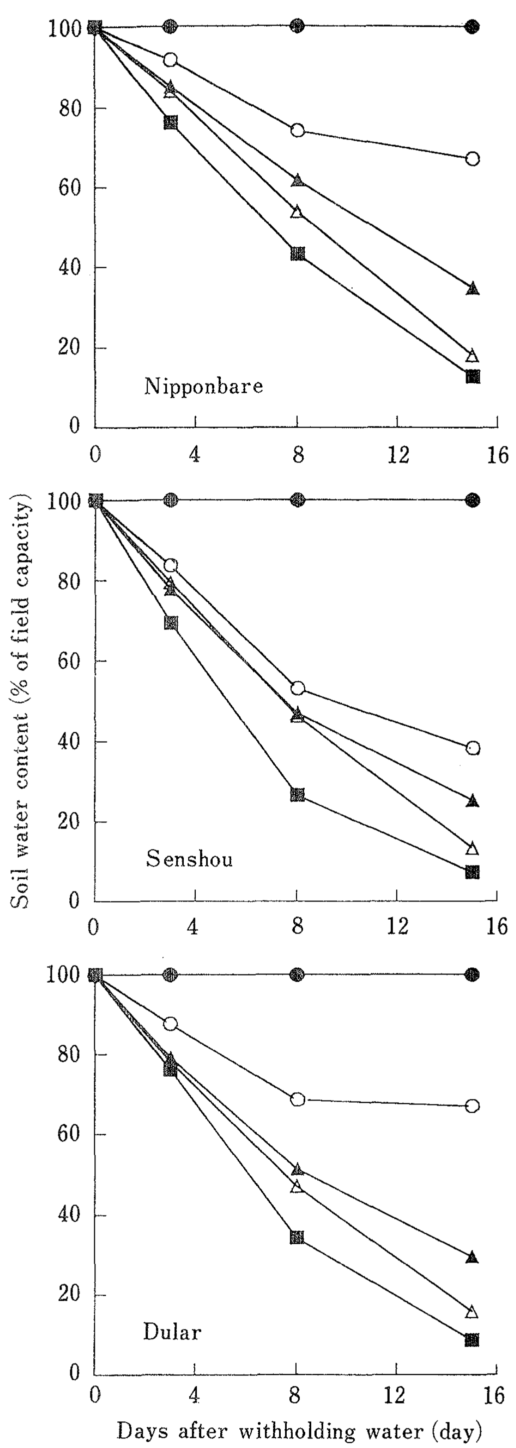

Fig. 5. Changes of soil water content (% of field capacity) of three cultivars during the early reproductive stage under pot conditions. Watering each day was reduced to 0.5～0.7 (○), 0.3 (▲), 0.25 (△) and 0 (■) times transpiration rate in the flooded control pot (●). Standard errors of three observations were less than symbols.

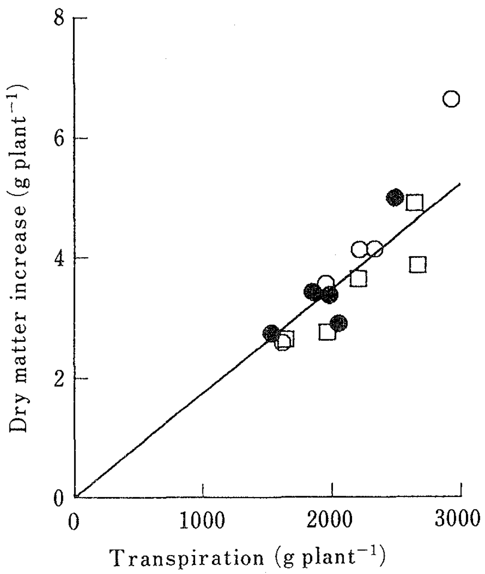

Fig. 6. The relationship between dry matter increase of the shoot (SDP_p) and transpiration rate (Tr_p) of three rice cultivars during soil drying treatments for 15 days of the early reproductive stage under pot conditions. ○ indicates Dular, □ Senshou and ● Nipponbare. The average daytime vapor deficit during the treatment period was 19.4 g m^{-3}. See Figure 5 for treatments. The line indicates a relationship between SDP_p and Tr_p, when all data were combined ($SDP_p = 1.74 \times 10^{-3} Tr_p$, $r^2 = 0.781$, $P < 0.001$).

$$E_{soil} = (E_{psoil}/E_p) \times E_p \times F \qquad (2)$$

where E_{psoil}/E_p is a ratio of potential soil evaporation to potential evapotranspiration rate, and estimated from the empirical equation[22] as a function of leaf area index (LAI) in rice[1].

$$E_{psoil}/E_p = EXP(-0.45LAI) \qquad (3)$$

The potential evapotranspiration rate was estimated from meteorological data by the Penman equation[21]. In our field experiment, E_{psoil}/E_p ranged from 0.20 to 0.45 according to cultivar, when average LAI between the start and the end of the desiccated period was used (eq. (3)). Accumulated E_p during this period was 184.6 mm. The F is a factor indicating relative suppression of soil evaporation to E_p under cessation of irrigation. The factor F was estimated as a ratio of soil evaporation rate (E_{ly}) measured with a micro lysimeter to E_p (Fig. 7). The lysimeter was set in the center between rows which scarcely received shading by leaves under experimental conditions and thus it was suggested that E_{ly} indicated the maximum evaporation rate of surface soil undergoing soil desiccation. This was supported by evidences that E_{ly}/E_p was much higher (0.7~0.8) than E_{psoil}/E_p (0.1~0.4) (eq. (3)) under wet soil conditions at the start of the cessation of irrigation regardless of cultivar (Fig. 7). Moreover the effect of LAI in E_{ly} may have been smaller after withholding irrigation because LAI of four cultivars decreased during soil desiccation treatments. There was almost no difference in E_{ly}/E_p between the four cultivars. E_{ly}/E_p was high at the start of cessation of irrigation but decreased steeply to 0.2 within two weeks after the start of soil desiccation. Thus in four cultivars, the same F (0.27) average during the non-irrigated period was used. Calculated E_{soil} dispersed from 22.3 for Nipponbare to 14.8 for Dular when these data were input in eq. (2) (Table 3). The average of E_{soil} for four cultivars (18.2 ± 1.7 mm) almost coincided with soil water use (SWU, 22.7 mm) at SPD=0 in the regression between SDP and SWU (Fig. 2), which suggested to indicated only soil evaporation. This may support reliability of the estimation for soil evaporation rate.

When E_{soil} was eliminated from soil water use and estimated transpiration (SWU-E_{soil}) was input in eq. (1), WUE showed no large difference between the four cultivars (coefficient of variance, cv=0.11) (Table 3). These results coincided with those of pot experiment (cv=0.08). The WUE in Dular or Senshou, even though these are drought resistant rice cultivars, therefore, seemed not to be necessarily much higher than that of the sensitive cultivar Nipponbare, or moderately sensitive Tachiminori under field conditions.

Transpiration rate is profoundly effected by the vapor deficit of the atmosphere. Thus absolute WUE under field experimental condi-

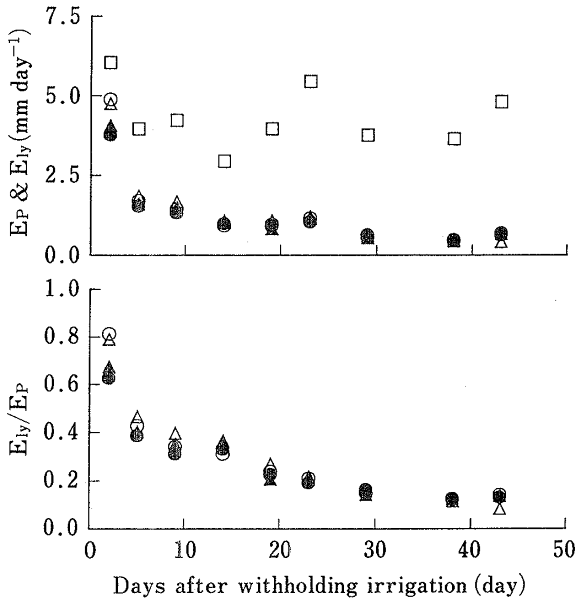

Fig. 7. Soil evaporation rate (E_{ly}) from the center position between rows for each cultivar with a micro lysimeter, potential evaporatin rate (E_p, □) calculated from the Penman equation[21], and E_{ly}/E_p in the field experiment. Accumulated E_p during desiccation treatments was 185 mm and average of E_{ly}/E_p was 0.27 for the period. See Figure 1 for symbols and treatments.

Table 3. Soil water use (SWU), estimated soil evaporation (E_{soil}), estimated transpiration (SWU-E_{soil}), shoot dry matter increase (SDP) and water use efficiency (WUE and WUEa) of four rice cultivars during withholding irrigation at the field experiment.

	Nipponbare	Tachiminori	Senshou	Dular	$\bar{X}$±se	cv
SWU (mm)	42.4	59.0	76.6	79.1	64.3 ± 8.6	0.27
E_{soil} (mm)	22.3	19.8	15.8	14.8	18.2 ± 1.7	0.19
SWU-E_{soil} (mm)	20.1	39.2	60.8	64.3	46.1 ±10.3	0.45
SDP (g m^{-2})	155.5	355.1	418.9	526.4	364.0 ±78.0	0.43
WUE (×10^{-3} g g^{-1})	7.74	9.06	6.89	8.19	7.97± 0.45	0.11
WUEa (×10^{-3} g m^{-3})	53.4	62.5	47.5	56.5	55.5 ± 3.13	0.11

E_{soil} was estimated from

$E_{soil} = (E_{Psoil}/E_P) \times E_P \times F$

where $E_{Psoil}/E_P = \exp(-0.45\ LAI)$, which indicates the ratio of potential soil evaporation to potential evapotranspiration (E_P) in rice field[1], and F is estimated from E_{ly}/E_P. E_P was calculated from the Penman equation[21]. See Figure 7 for E_{ly}/E_P.

WUEa = WUE × VD, where VD is vapor deficit in daytime.

$\bar{X}$ indicates mean ± standard error of four cultivars and cv coefficient of variation.

tions could not be compared immediately with that under the pot experimental conditions, because the transpiration rate of each experiment was measured under very different environmental conditions. WUE (eq. (1)) multiplied by vapor pressure deficit (VD, g m^{-3}) or evaporation rate from a pan evaporimeter (WUEa) indicates stable rate for each cultivar regardless of humid conditions[5,11,23].

$$WUEa=\frac{W}{Tr/VD}=WUE\times VD \quad (4)$$

In the pot experiment, WUEa for Nipponbare, Senshou and Dular was 34.0 $\pm$ 1.9, 30.9 $\pm$ 1.6 and 36.3 $\pm$ 2.1 $\times$ 10^{-3} g m^{-3}, respectively, when mean VD of 19.4 g m^{-3} in the daytime was input into eq. (4). This high vapor deficit was observed by reason of a strictly dry and high temperature year in 1994. In the field experiment when mean VD for the daytime, 6.9 g m^{-3}, during the period of withholding water was input into eq. (4), WUEa for four cultivars in a the field experiment was estimated as 53.4 for Nipponbare, 62.5 for Tachiminori, 47.5 for Senshou and 56.5 $\times$ 10^{-3} g m^{-3} for Dular (Table 3). Thus the mean absolute rate of WUEa in field experiments (55.0 $\pm$ 3.1 $\times$ 10^{-3} g m^{-3}, average of four cultivars $\pm$ se) was 1.6 times as large as that in the pot experiments (33.7 $\pm$ 1.6 $\times$ 10^{-3} g m^{-3}, average of three cultivars). Two major reasons for these differences in WUEa between the field and the pot experiments may be estimated. The first reason concerned temperature effect in respiratory loss of dry matter to reduce WUEa[17] in the pot experiment, because the season of 1994 was hotter than 1991. However, WUEa for the pot experiments may never differ greatly from results observed in the field experiments. In paddy field experiments at several locations in Shimane prefecture, WUEa for Nipponbare was 32.0 $\pm$ 0.9 $\times$ 10^{-3} g m^{-3} (mean $\pm$ se of average data at three locations during the early reproductive stage)[2]. The second reason is the effect of supplementary water from the underground water table in observed soil water use under field conditions, so that the transpiration may be underestimated and thus cause overestimation of WUEa[9]. We need to monitor amounts of supplementary water to make accurate comparisons of absolute WUEa under field and pot conditions.

Larger cv in soil water use (0.27) or estimated transpiration (0.45) than in WUE (0.11) clearly indicated cultivar differences in maintenance capacity of transpiration under desiccated soil conditions (Table 3). Transpiration rate was higher, the more dry matter increased under desiccated field conditions. These results indicate that dry matter production in rice plants is maintained under drought conditions not by higher WUE, but by the use of large amounts of water from the soil, i.e. drought resistant cultivars can gather water from a larger volume of soil.

This high capacity for water use in drought resistant cultivars, such as Dular and Senshou, was caused by the high root density of deep soil layers. The susceptible cultivar, Nipponbare, had the highest density of roots in a shallow soil layer, but the roots seemed not to take up much water during long periods of drought because water in the shallow soil layers was used up by means of both high root density and soil evaporation within a short time after withholding water. It has been suggested that drought resistant cultivars extend their root systems into deep soil layers to make contact with deep wet soil[8,19,26]. The improved upland cultivar Tachiminori has a good and stable yield under irrigated conditions[18] but this cultivar seems to lack the ability to use water from deep soil layers.

Maintenance of dry matter production contributed significantly to grain yield under drought conditions, because higher dry matter production during periods of drought was reflected noticeably in grain yield and harvest indices. Moreover, there was not much difference in harvest indices except for a case of Nipponbare, where sterility increased. In addition, deep root systems which connect with wet soils may reduce sterility due to escape of reduction of ψ_1, or production of an inhibitor in the root[15], resulting in a higher harvest index.

In this experiment we used four rice cultivars with a different drought resistance ranking. A Indica type Dular is considered as a drought resistant cultivar by means of visual score, maintenance ability of leaf water potential or growth et al. under field trial at IRRI[4]. The three Japanese rice cultivars, Nipponbare, Tachiminori and Senshou, were selected from cultivars which were ranked drought susceptible to resistant with several standard varieties of IRRI[4] under drought condition in a field site[13,14]. Senshou was considered one of the most drought resistant cultivars in traditional Japanese upland rice of sixteen lines[24] (lines of Indica type, lowland origin and waxy rice were not included)[13,14]. Thus the four cultivars used in these experiments could be considered plant materials covering a wide range of cultivar responses to drought.

We suggested that high production performance by drought resistant rice cultivars under dry soil conditions is caused not by high WUE but by a superior ability to gather soil water, by distribution of roots into deep and wide soil layers. WUE may not be such a good indicator of the field drought resistance of rice as estimated for other crops[3], because the range of variation (13% or less) in WUE between different cultivars was much less than that of the ability of soil water use caused by deep root systems (200~300%).

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