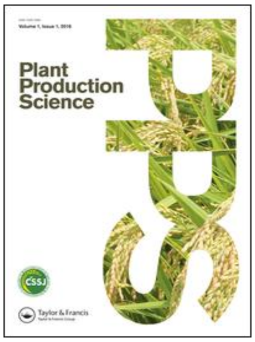

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Effects of Soil Moisture Conditions before Heading on Growth of Wheat Plants under Drought Conditions in the Ripening Stage: Insufficient Soil Moisture Conditions before Heading Render Wheat Plants More Resistant to Drought during Ripening

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Abstract : Plants growing on soil with insufficient moisture need deep and dense roots to avoid water stress. In crop plants, the production of dry matter during ripening of grains is critically important for grain yield. We postulated that shoot growth would be suppressed but root growth would continue under an insufficient soil moisture condition before heading, while shoot growth would be more vigorous than root growth under a sufficient soil moisture condition. We anticipated that the plants growing under an insufficient soil moisture condition before heading would produce more dry matter and grain under an insufficient soil moisture condition during ripening. In order to examine our hypotheses and to determine the fundamental conditions for improving grain yield and efficient use of irrigated water under limited irrigation, we grew wheat plants (*Triticum aestivum* L., cv. Ayahikari) in pots (30 cm in diameter, 150 cm in height) with insufficient soil moisture (PD-D pots) or sufficient soil moisture (PW-D pots) for six weeks before heading followed by full irrigation, and then insufficient soil moisture condition during ripening. The growth of shoots was suppressed significantly but that of roots was not before heading in PD-D plants, with a higher resultant ratio of root to shoot than in PW-D plants. The former retained a high leaf water potential and, therefore, were able to produce more dry matter and grain during soil moisture depletion during ripening as compared with the latter plants. We also obtained similar results with field-grown plants.

Key words : Drought avoidance, Dry matter production, Grain yield, Irrigation efficiency, Leaf water potential, Root, Soil water potential, Wheat.

A water deficit significantly decreases both growth and yield of crop plants (Gallagher, 1976; Boyer, 1982; Loomis and Conner, 1992; Kramer and Boyer, 1995; Martin et al., 2006). Irrigation, applied properly, can significantly improve both crop yield and quality (Martin et al., 2006). Irrigation in the field is required in many regions of the world and the extent of irrigated fields has increased significantly over the last fifty years (Yamaoka and Ochii, 2003). However, the availability of water for irrigation water is limited and increases in use of irrigation water are likely to be small in the 21st century (Hirasawa, 2007). In some regions, the availability of water for irrigation is decreasing and the supply of water may disappear altogether (National Research Council, 1989). Thus, many efforts are being made to increase irrigation efficiency by improving irrigation scheduling and by use of indicators of successful irrigation (e.g., Ehrler, 1973; Jackson et al., 1981; Fiscus et al., 1984; Proffitt et al., 1985; Stanhill, 1986; Cohen, 1988; Oweis et al., 2000; Sato et al., 2006).

Plants have many characteristics that enable them to resist drought (Loomis and Conner, 1992). In particular, deep and dense roots help plants to withstand drought and to maintain high dry-matter production and high yield in drying soil (Hirasawa, 1995; Hirasawa et al., 1998). In efforts to introduce such rooting characteristics into plants, the genetics of rooting are being studied extensively (Kamoshita et al., 1999; Shen et al., 1999; Hirota et al., 2007).

Deep and dense roots develop in soil under an insufficient soil moisture condition while shoot growth is more limited (Kramer, 1983; Kramer and Boyer, 1995). Plants with better-developed root systems might be expected to produce heavier grain under an insufficient soil moisture condition during ripening than plants with shoot growth that is more vigorous than root growth because the former plants can absorb larger amounts of water from deeper soil layers and can produce more dry matter than the latter. Indeed, soybean plants, grown under an insufficient soil moisture condition before flowering for a month during the rainy season known as “Baiu”, produced heavier grain in the relatively dry soil in summer

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than did plants grown with sufficient soil moisture before flowering (Hirasawa et al., 1994). These results indicate that humid conditions before flowering enhance the drought stress on plants during ripening in the relatively dry summer in Japan.

Wheat plants are grown widely in temperate regions of the world, where annual precipitation averages between 254 and 1780 mm (Martin et al., 2006), from semi-arid to humid regions. In humid regions, such as many regions of Japan with the exception of Hokkaido, appropriate drainage is required for reliable high yields (Nakamura et al., 2003; Nakagami et al., 2004). In semi-arid regions, wheat and fallow years are alternated to preserve sufficient rainwater in soil (Brengle, 1982; Martin et al., 2006), and plants are irrigated during the growing season in, for example, parts of western Asia, such as Afghanistan. It is important for the efficient use of irrigation water and associated labor to determine how irrigation should be scheduled. Considerable researches have been conducted on the effects of drought stress and irrigation on wheat growth and yield (Proffitt et al., 1985; Kobata et al., 1992; Musick et al., 1994; Zhang et al., 1998; Oweis et al., 1998; 2000; Foulkes et al., 2001; Yang et al., 2001; Xue et al., 2003). While soluble carbohydrate reserves before heading might contribute to grain yield to some extent (Yang et al., 2001; Foulkes et al., 2002), grain yield is mainly determined by dry matter production after heading (Schnyder, 1993; Gebbing and Schnyder, 1999). We can postulate, then, that drought avoidance during ripening might be important for higher grain yield. A deep root system at the ripening stage might be an important trait for drought avoidance that enables plants to maintain high dry-matter production and achieve relatively high grain yield when water supply is low.

Plant breeding is expected to be an effective strategy for introduction of deep root systems. Thus, for example, a drought-resistant cultivar of upland rice was generated by screening for root-system development (Hirasawa et al., 1998), but no similar examples have been reported for wheat to our knowledge. Root systems develop effectively in deeper soil layers when wheat plants are grown under an insufficient soil moisture condition for a month before heading, as compared with plants with sufficient soil moisture (Nakamura et al., 2003; Nakagami et al., 2004). We postulate that plants with a well-developed root system and, therefore, a high capacity for drought resistance, might be generated by an appropriate cultivation method with appropriate irrigation. In the present study, to test this hypothesis and to clarify factors that lead to improved irrigation efficiency, we compared the effects of soil drought during ripening on dry matter and grain production between wheat plants with better-developed root systems after growth under an insufficient soil moisture condition before heading, and plants, with poor root systems after growth under sufficient soil moisture conditions.

Materials and Methods

1. Cultivation of plants and moisture treatment

Wheat plants (*Triticum aestivum* L., cv. Ayahikari) were grown in pots (pot experiment) and in the field (field experiment).

(1) Pot experiment

Seeds were sown on November 15, 2006, in porous pots (30 cm in diameter and 150 cm in height) filled with alluvial soil from the Tama River at a density of three hills per pot and eight seeds per hill. The bottom of each pot was covered with a sheet of black polyester fibers (BDK; Yunichika, Tokyo) through which water can penetrate but not roots. The pots were placed in a field on a line from east toward west with the bottom of each pot 80 cm from the soil surface. After emergence, plants were thinned to five plants per hill. Chemical fertilizer was applied as a basal dressing at a rate of 1 g, 1 g and 1 g per pot of N, P_2O_5 and K_2O, respectively.

All plants were grown in pots under natural conditions until February 28. From March 1, some plants were grown under an insufficient soil moisture condition (PD-D pots) and other plants were grown with sufficient soil moisture (PW-D pot) until April 8. For PW-D pots, plants were irrigated with one to four liters of water per pot every 2 days and the PD-D plants were watered with five liters of water per pot every 10 days in order to prevent extreme reductions in shoot and root growth. The total amount of irrigated water was 41L and 20L per pot for PW-D and PD-D plants, respectively, during the soil moisture treatment from March 1 to April 8. At the end of the treatment, 9L and 30L of water in total amount was irrigated for PW-D and PD-D plants, respectively, for 3 days from April 9 to 11, in order to provide soil moisture to the level of field capacity. Ammonium sulfate was top-dressed at a rate of 5 g per pot on April 11, 2007. Thereafter, irrigation water was withheld from all plants until May 7. All plants were covered with a rain-out shelter whenever it rained after March 1. The shelter moved automatically to cover the plants when the amount of rain reached 1 mm and moved away from the plants when it did not rain for 30 min. Heading started on April 4, 2007.

Ten pots were prepared for each soil moisture treatment and pots of both treatments were arranged randomly. Measurements were taken for plants from 5 pots of each treatment.

(2) Field experiment

Field experiments were conducted in a 2003-2004 season (Field Exp. I) and a 2005-2006 season (Field Exp. II) at the University Farm (35°41'N latitude, 139°29'E longitude) in alluvial soil from the Tama River. The inter-row space was 30 cm and plants were thinned to 4 plants per 10 cm (2.5 cm distance between plants) in each row after emergence. From 0 to 34 cm below the surface, the soil in the field was classified as loam to clay loam; that from 34 to 44 cm as light clay; that from 44 to 71 cm as sandy loam; and that from 71 to 120 cm as light clay. The level of the underground water at this site is considered to be far more than 1.5 m below the soil surface. The experimental field, 114 m^2 in area, was divided into four parts, and plastic boards that expanded 1 m below the soil were installed in order to isolate the parts hydraulically. Moisture treatments were arranged randomly with respect to the parts and each part was subdivided, to yield four replicates for each treatment.

1) Field Exp. I : Seeds were sown on November 15 in 2003. Manure was applied at a rate of about 10 t ha^{-1}. Chemical fertilizer was applied as basal dressing at a rate of 60, 100 and 100 kg ha^{-1} of N, P_2O_5 and K_2O, respectively. Heading started on April 4 in 2004. All plants were grown under natural conditions until April 29. Then, some plants were grown without irrigation (FW-D plot) and other plants were grown with irrigation (FW-W plot) until harvest. The plants in the FW-W plot were watered at three-day intervals with the equivalent of 12, 14 and 15 mm of rain in April, May and June, respectively, with an irrigation tube (Everflow; Sunrex Industry, Yokkaichi, Japan) delivered on the soil surface at every two interrows. No fertilizer was supplied as top-dressing. All plants were covered with the rain-out shelter whenever it rained after April 30. Plants were harvested on June 18 in 2004.

2) Field Exp. II : Seeds were sown on November 15 in 2005. Manure and chemical fertilizer were applied at the same level as in Field Exp. I. All plants were grown under natural conditions until March 3 in 2006. During the period from March 4 to April 17, some plants were grown under an insuifficient soil moisture conditions without irrigation (FD-D plot) and other plants were grown under conditions of sufficient soil moisture with irrigation of 12 and 15 mm at three-day intervals in March and April, respectively (FW-D plot) with the irrigation tube. The plants in the FD-D plot were irrigated for three days at 150 mm of water at the total amount on April 17, 18 and 19 to provide soil with moisture to the level of field capacity. Thereafter, irrigation was withheld from the plants in both plots until harvest. Nitrogen was supplied as top-dressing to the plants in both plots at a rate of 40 kg ha^{-1} on April 19. All plants were covered with the rain-out shelter whenever it rained after March 4. Heading started on April 20 and plants were harvested on June 16.

2. Measurements of soil moisture

Both in pot and field experiments, soil moisture tension at high soil water potential (higher than –0.09 MPa) was measured with a tensiometer (2710AR; Soilmoisture Equipment, Santa Barbara, CA, USA; or DIK-3162; Daiki Rika Kogyo, Konosu, Japan). At low soil water potential, soil electric resistance was measured with a gypsum block. Gypsum blocks with identical properties in terms to the response to a reduction in soil moisture were used. Measurements were made every few days for the pot and field experiments. Soil water content was determined at harvest, on a dry weight basis, by drying soil at 105°C in an oven for 3 days. Soil water potential was estimated from the relationship between soil water content and soil matric potential, determined for the soil of each layer in the field and for the soil used for the pot experiment.

3. Measurements of growth of above-ground parts and roots

(1) Leaf area, dry weight and grain yield

Dry weight and leaf area were measured at the start and end of the soil moisture treatment and at harvest. In the pot experiment, leaf blade was dried at 80ºC in a ventilated oven for several days after the leaf area was measured with an area meter (AAM-9; Hayashi Denko, Tokyo, Japan). Roots were taken out from pots and soil attaching on roots was washed away with tap water gently. Plants were separated into root, leaf sheath plus stem and spike, and were dried at 80°C similarly.

In the field experiments, stem number was counted in the area of approximately 2 m^2 for each replicate and plants with an average number of stems were sampled from two of a 50 cm segment of a row for each replicate. After measurements of the area of leaf blade, leaf sheath plus stem and spike were dried at 80ºC as well as leaf blade. The sampling yield per unit area was determined for plants from an area of approximately 0.9 m^2 for each replicate.

(2) Root length and root surface area

At the end of the soil moisture treatment in the pot experiment, root length and root surface area were measured. After roots of plants grown in pots were washed as mentioned above, root length and root surface area of plants from two pots of each treatment were measured with an image-analysis system (WinRHIZO; Regent Instruments, Quebec, Canada) before drying.

4. Measurements of leaf water potential, chlorophyll content and the rate of photosynthesis

(1) Leaf water potential

We measured leaf water potential with a pressure chamber (model 3005; Soil Moisture Equipment, Santa Barbara, CA, USA) both in pot and field experiments at the interval of several days, using leaves on primary tillers under direct sunlight at time from of 1130−1300 on a fine day. Each leaf was enclosed in a moist polyethylene bag immediately prior to excision. The cylindrical inner wall of the pressure chamber was covered with wet filter paper to prevent water loss by transpiration.

(2) Chlorophyll content and the rate of photosynthesis

Chlorophyll content and the rate of photosynthesis of a leaf on a main stem were measured in the pot experiment. Chlorophyll content of leaves on a main stem was estimated with a chlorophyll meter (SPAD-502; Minolta, Tokyo, Japan) and expressed as a relative value (SPAD value) at the interval of several days.

The rate of photosynthesis was measured with a portable closed gas-exchange system (LI-6200; LI-COR, Lincoln, NE, USA) during ripening in the pot experiment. Measurements were made under artificial white light (LA-100; Hayashi Tokei Kogyo, Tokyo, Japan) with a light intensity of about 2,000 μmol m^{-2} s^{-1} of PAR at the leaf surface. Measurements were started at a CO_2 concentration of 370 μL L^{-1} in the chamber and were repeated three times. The mean of the three readings was used as the measured value.

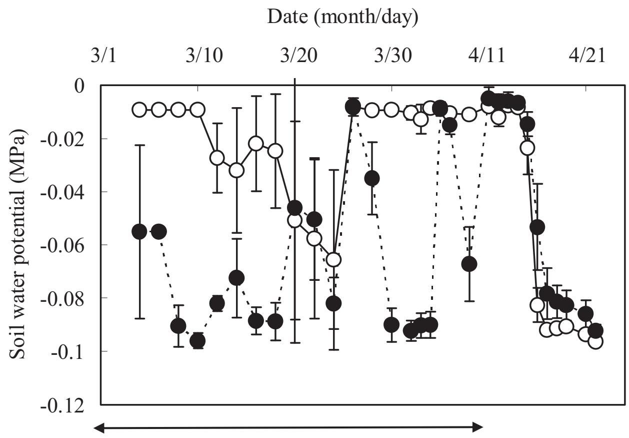

Fig. 1. Changes in soil water potential at a depth of 30 cm in pots. Open and solid circles represent PW-D and PD-D pots, respectively. The arrow indicates the duration of soil moisture treatment. Vertical bars represent standard deviations (n=5), which is applied to Figs. 2 to 7 correspondingly.

Results

1. Pot experiment

(1) Soil moisture and plant growth

Water potential of the soil at a depth of 30 cm during the soil moisture treatment was kept within the range of –0.01 to –0.03 MPa except during the period from March 20 to March 24 in the PW-D pots (Fig. 1). By contrast, water potential fell below –0.05 MPa, except on a few days just after irrigation, in the PD-D pots.

There were small differences in total dry weight, leaf area and root weight (data not shown) between PD-D and PW-D plants at the commencement of soil moisture treatment on Feb. 28, 2007. After different soil moisture treatment (April 9), total dry weight (62.4 g hill^{-1}) of PD-D plants was smaller than that of PW-D plants (78.2 g hill^{-1}). The reduction in growth of PD-D plants was larger in the shoot than the root. That is, the dry weight of above-ground parts and leaf area of PD-D plants were 21% and 25% lower, respectively, than those of PW-D plants at the end of the soil moisture treatment (Table 1). By contrast, root weights of PD-D plants were 16% lower than those of PW-D plants. The root length and root surface area of PD-D plants were only approximately 10% and approximately 4%, respectively, smaller than those of PW-D plants and the differences between the PD-D and PW-D plants were not significant. As a result, the ratios of root weight to weight of above-ground parts (C/A), of root length to leaf area (D/B), and of root surface area to leaf area (E/B) were larger in PD-D plants than in PW-D plants. In particular, the ratios of root length to leaf area and of root surface area to leaf area were significantly larger in PD-D plants.

After irrigation of all pots on April 11 at the end of soil moisture treatment, soil water potential increased significantly in the PD-D pots and there was no difference in soil water potential between the PD-D and PW-D pots (Fig. 1). Soil moisture at a depth of 30, 50 and 100 cm decreased significantly from April 15, when irrigation was withheld from the plants in both PD-D and PW-D pots (Figs. 1, 2). The soil

Table 1. Growth of shoot and root and ratio of root to shoot parameters in wheat plants grown in pots, as determined on April 9, 2007.

Plots	Total weight (g hill^{-1})	Shoot weight A (g hill^{-1})	Leaf area B (m^2 hill^{-1})	Root weight C(g hill^{-1})	Root length D (m hill^{-1})	Root surface area E (m^2 hill^{-1})	C/A (mg g^{-1})	D/B (m m^{-2})	E/B (m^2 m^{-2})
PW-D (1)	78.2±5.3	73.6±5.2	0.559±0.035	4.57±0.39	472.3±47.9	0.430±0.041	62.4±6.3	844.7±74.1	0.769±0.061
PD-D (2)	62.4±7.9	58.5±7.5	0.421±0.033	3.85±0.38	422.9±44.2	0.411±0.041	65.7±2.9	1007.8±115.8	0.980±0.111
(2)/(1)	0.8	0.79	0.75	0.84	0.9	0.96	—	—	—
t-test	**	**	*	**	ns	ns	ns	*	**

Means±SD (n=5). Plants grown in five pots were used for measurements. Root length and root surface area of plants grown in two pots were measured for each treatment and root length and root surface area of the plants in the other three pots were estimated from the ratios of length and surface area to weight of roots for each treatment. * and ** represent significant differences at 5% and 1%, respectively, between PW-D and PD-D plants (Student's t-test), and ns indicates the absence of a significant difference between PW-D and PD-D plants, which is applied to Table 2 correspondingly.

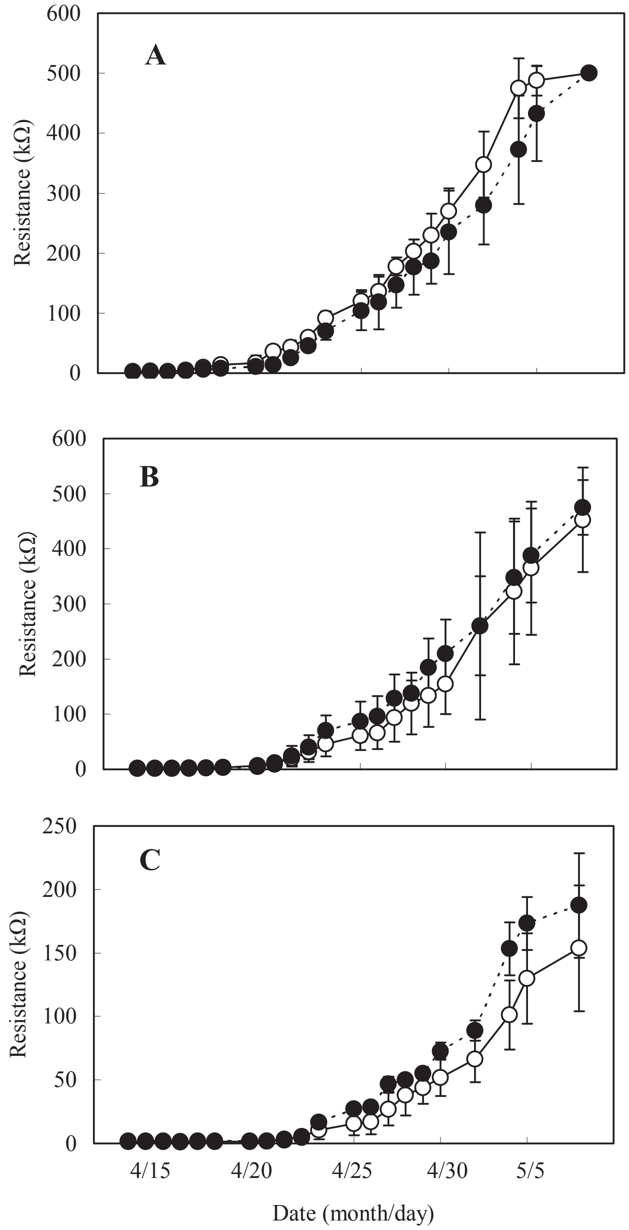

Fig. 2. Changes in soil electric resistance of a gypsum block at a depth 30 cm (A), 50 cm (B) and 100 cm (C). Open and solid circles represent the PW-D and PD-D pots, respectively.

water content (water potential) was approximately 25% (approximately –0.9 MPa as estimated from the relationship between soil moisture content and soil water potential), approximately 26% (approximately –0.8 MPa) and approximately 34% (approximately –0.15 MPa) at depth of 30, 50 and 100 cm, respectively, on May 7. After April 20, the soil moisture at a depth of 30 cm tended to decrease more rapidly in the PW-D pots than in the PD-D pots. By contrast, the soil moisture at a depth of 100 cm tended to decrease more rapidly in the PD-D pots than in the PW-D pots (Fig. 2).

Leaf water potential in the daytime on fine days

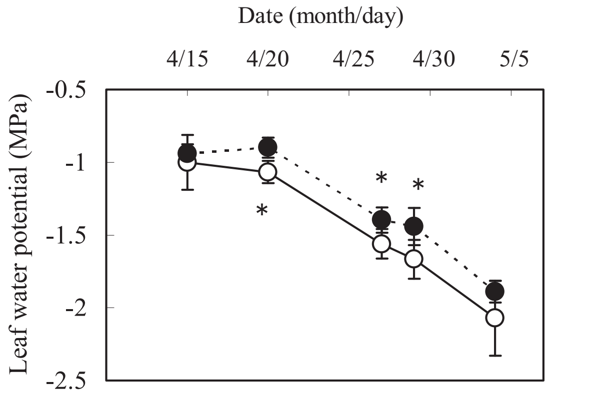

Fig. 3. Changes in leaf water potential of flag leaves of plants grown in pots. Water potential was measured from 1130 −1300 on a fine day. Two or three leaves per pot were used for one measurement, which is applied to Fig. 4 correspondingly. Open and solid circles represent the PW-D and PD-D plants, respectively. * represents significant differences at 5% level between PW-D and PD-D plants (Student's t-test).

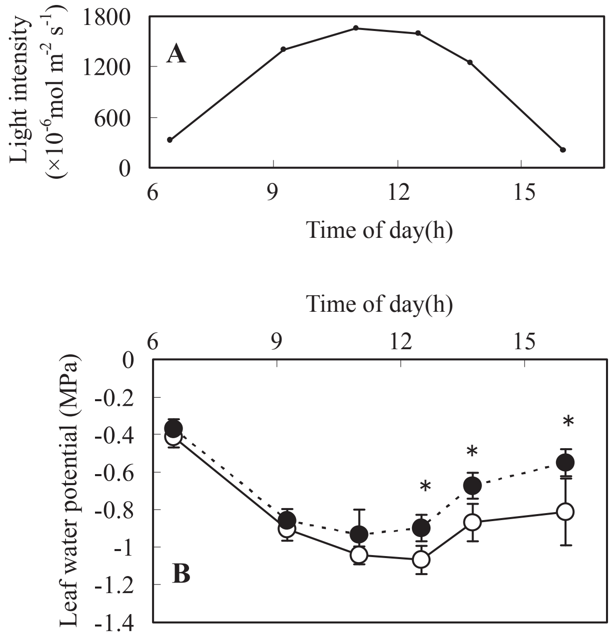

Fig. 4. Diurnal changes in solar radiation (A) and leaf water potential of plants grown in pots (B) on a fine day (April 20, 2007). Flag leaves were used for measurements. Open and solid circles represent PW-D and PD-W plants, respectively. * represents significant differences at 5% level between PW-D and PD-D plants (Student's t-test).

started to decrease on April 20 and the reduction in leaf water potential was more marked in the PW-D plants than in the PD-D plants (Fig. 3). Fig. 4 shows the diurnal changes in leaf water potential on April 20 when a difference in daytime leaf water potential was first observed. The leaf water potential decreased in the morning and reached its lowest value in both PW-D and PD-D plants at noon. The leaf water potential was

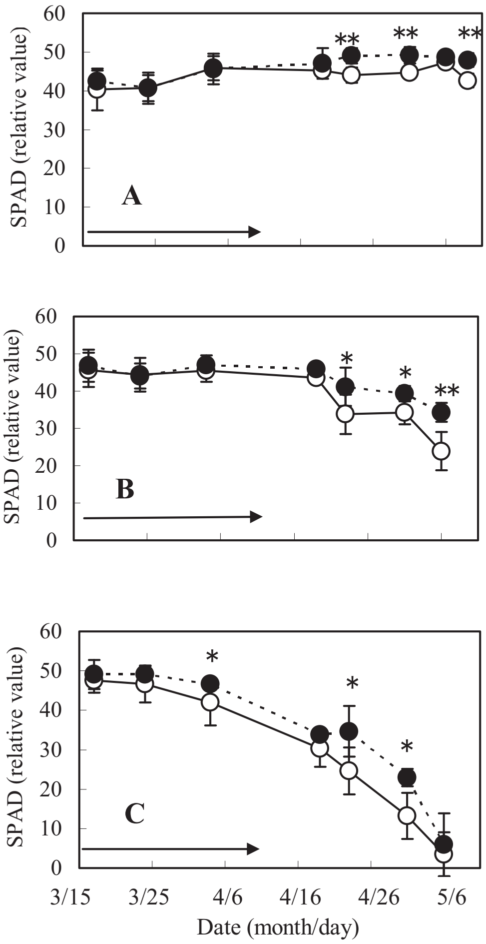

Fig. 5. Changes in SPAD values (level of chlorophyll) of the flag (A), second (B) and third leaves (C) of PW-D (○) and PD-W (●) plants. Leaves on all main stems were used for measurements. * and ** indicate the significant differences between the PW-D and PD-D at 5% and 1 %, respectively (Student's t-test). Arrows represent the duration of soil moisture treatment for PW-D and PD-D plants.

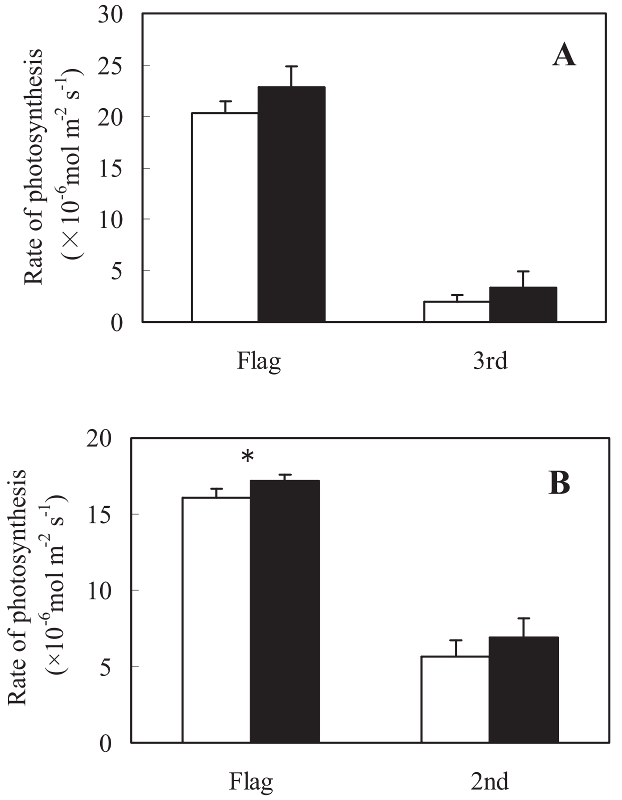

Fig. 6. The rate of photosynthesis in PW-D and PD-D plants on April 21 (A) and April 29 (B), 2007. White and black bars represent PW-D and PD-D plants, respectively. * represents significant difference between PW-D and PD-D plants (Student's t-test).

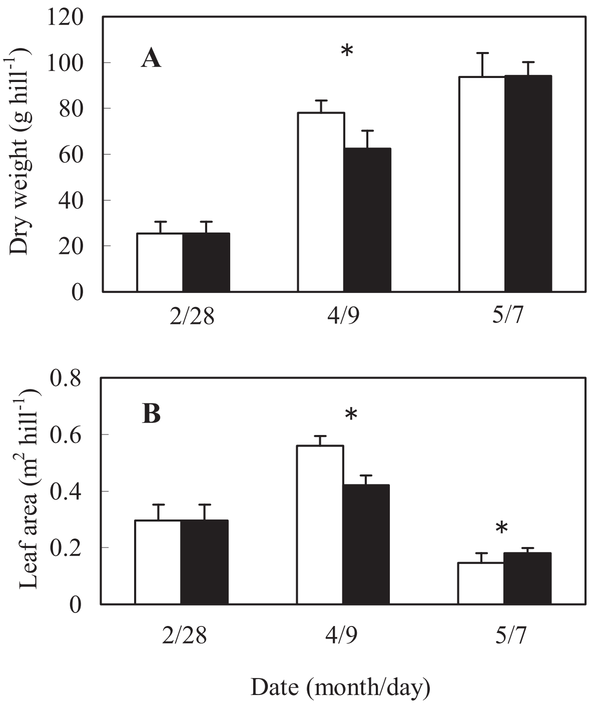

Fig. 7. Changes in dry weight (A) and leaf area (B) of PW-D (□) and PD-D (■) plants. * represents significant differences between PW-D and PD-D plants (Student's t-test).

lower in the afternoon than in the morning, even at same level of solar radiation. The difference in leaf water potential between PW-D and PD-D plants was significant at noon and in the afternoon.

These results indicate that the PD-D plants were able to absorb considerable water from the deeper soil layers in pots and could maintain a high leaf water potential even when the moisture level in the surface soil had fallen significantly.

(2) Leaf chlorophyll content and the rate of photosynthesis after soil moisture treatment

During soil moisture treatment, there were no differences in SPAD values (levels of chlorophyll) of the flag and second leaves between PW-D and PD-D plants, but values of PW-D plants tended to be lower for the third leaf from the flag leaf than in PD-D plants (Fig. 5). During senescence, after this treatment, SPAD values of the PD-D plants remained higher in the flag and second leaves, as well as in the third leaf, than

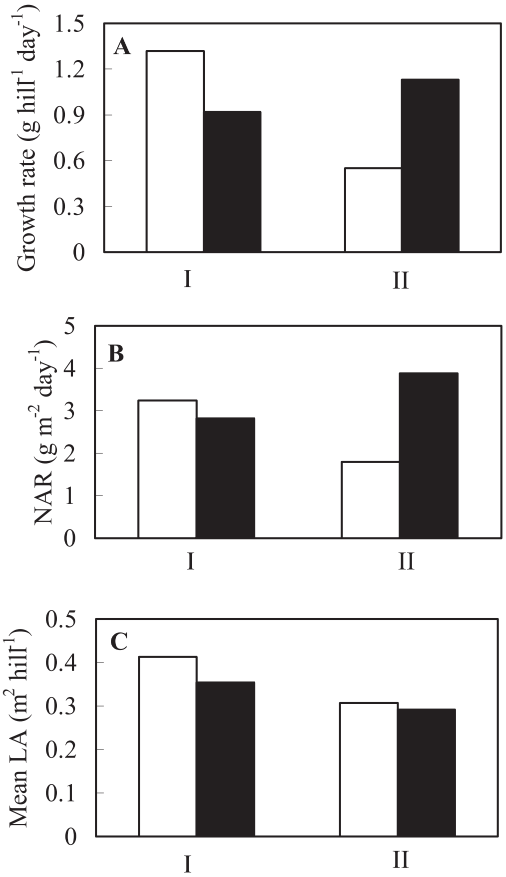

Fig. 8. Plant growth rates (A), net assimilation rates (NAR; B) and mean leaf areas (mean LA; C) of PW-D (□) and PD-D (■) plants. I, The period from February 28 to April 9, 2007; II, the period from April 9 to May 7, 2007.

Table 2. Spike number and dry weight of grains in plants grown in pots, measured on May 7, 2007.

Plots	Spike no. ($hill^{-1}$)	Grain wt. ($g\ hill^{-1}$)
PW-D	30.8±4.7	10.2±0.8
PD-D	33.9±2.6	12.3±1.1
t-test	ns	*

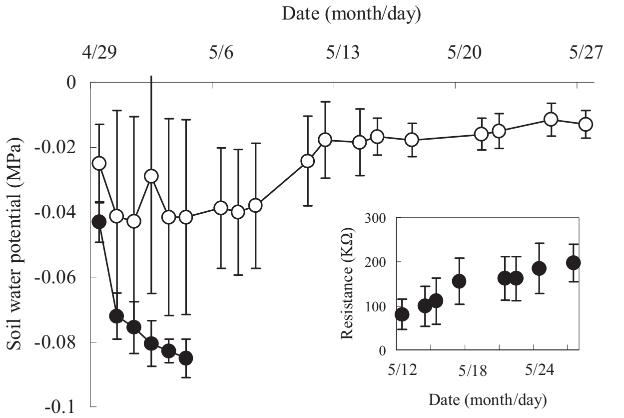

Fig. 9. Changes in soil water potential and electric resistance of a gypsum block (inserted figure) in the FW-W (○) and FW-D (●) plots at a soil depth of 30 cm in 2004. Vertical bars represent standard deviations (n=4), which is applied to Figs. 10 to 13 correspondingly.

those of PW-D plants. The difference between SPAD values tended to be larger in the lower leaves.

The rate of photosynthesis in the flag and third leaves, measured on April 21, and the rates in the flag and second leaves, measured on April 29, tended to be larger in the PD-D plants than in the PW-D plants (Fig. 6). In particular, the rate of photosynthesis differed significantly between the flag leaves of the PW-D and PD-D plants on April 29.

(3) Increase in dry weight after soil moisture treatment

Dry weight of PD-D plants was significantly lower than that of PW-D plants at the end of the soil moisture treatment. However, there was no difference in dry weight between the two types of plant on May 7 after growth without irrigation (Fig. 7A). Leaf area was also significantly smaller in PD-D plants than in PW-D plants at the end of the soil moisture treatment, but that of PD-D plants was significantly larger than that of PW-D plants on May 7 (Fig. 7B).

During the soil moisture treatment, the growth rate of PD-D plants was lower than that of PW-D plants as a result of lower net assimilation rate (NAR) and smaller mean leaf area (mean LAI) (Fig. 8). However, under the conditions of deficient soil moisture, without irrigation, after the soil moisture treatment, the growth rate of PD-D plants was far higher than that of PW-D plants. This result was not due to a larger mean LAI but to a larger NAR in the case of PD-D plants. The greater dry-matter production resulted in greater grain production and the dry weight of grain during ripening was approximately 20% higher in PD-D plants than in PW-D plants on May 7 (Table 2).

2. Field experiment

(1) Effects of soil moisture reduction during ripening on the dry weight of above-ground parts and grain yield (Field Exp. I)

Precipitation in April 2004 was very low compared with the average of recent 30 years. At the commencement of soil moisture treatment on April 29, 2004, soil water potential had already decreased to –0.04 MPa. Soil moisture continued to decrease from the start of the soil moisture treatment (Fig. 9) and soil water potential in the FW-D plot at a depth of 30 cm was between –0.8 to –0.9 MPa, as estimated from the relationship between resistance of a gypsum block and soil water potential at the end of May. Leaf water potential of plants in the FW-D plot was also significantly lower than that of the plants in the FW-W plot and was close to -2 MPa on May 15 (Fig. 10).

Grain yield was significantly lower in the FW-D plot than in the FW-W plot. There was no significant difference in dry weight of above-ground parts between the FW-W and FW-D plants, but the harvest index tended to be lower in the FW-D plot than in the FW-W plot (Table 3).

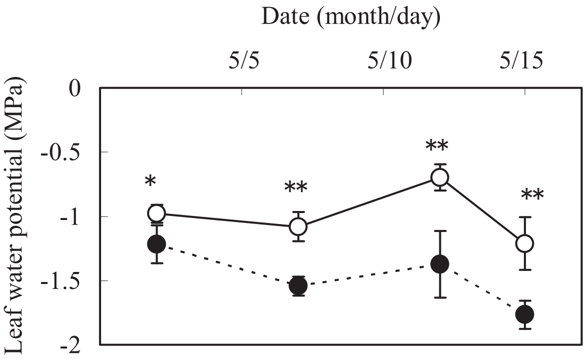

Fig. 10. Changes in leaf water potential of flag leaves of plants in FW-W (○) and FW-D (●) plots in 2004. * and ** represent significant differences at 5% and 1%, respectively (Student's t-test).

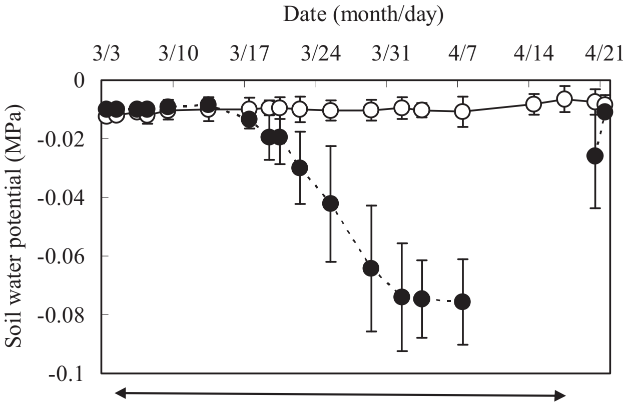

Fig. 11. Changes in soil water potential, measured with a tensiometer at a depth of 30 cm during soil moisture treatment. Open (○) and closed (●) circles represent values for FW-D and FD-D plots, respectively. The arrow represents the duration of soil moisture treatment.

(2) Effects of soil moisture reduction before heading on the dry weight of above-ground parts and grain yield under an insufficient soil moisture condition during ripening (Field Exp. II)

Soil water potential at a depth of 30 cm was significantly lower in the FD-D plot in the middle of March than the FW-D plot and finally it fell below –0.08 MPa (Fig. 11). After irrigation of both plots was stopped, soil moisture at a depth of 30 cm continued to decrease until June 12 (Fig. 12), when soil water potential was estimated to be close to –0.5 MPa from the soil moisture content. The reduction in soil moisture tended to be larger in the FD-D plot than in the FW-D plot. The reduction in soil moisture at a depth of 50 cm was smaller than the reduction at 30 cm but the reduction in soil moisture was far larger

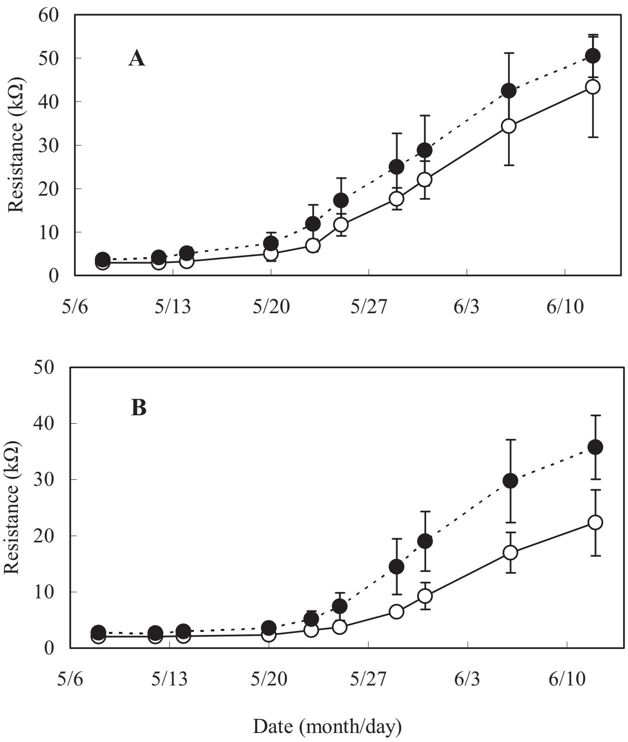

Fig. 12. Changes in soil electric resistance of a gypsum block at a depth of 30 cm (A) and 50 cm (B). Open (○) and closed (●) circles represent values for FW-D and FD-D plots, respectively.

Table 3. Yield, yield components, dry weight of above-ground parts (dry wt.) and harvest index (HI) for plants in the FW-W and FW-D plots in 2004.

Plots	No. of spike (m^{-2})	No. of spikelet ($spike^{-1}$)	No. of grain ($spikelet^{-1}$)	No. of grain (10^3 m^{-2})	One grain wt. (10^{-3} g)	Grain yield (g m^{-2})	Dry wt. (g m^{-2})	HI (%)
FW-W	537.5±42.7	14.1±0.2	1.9±0.1	15.0±0.4	40.5±1.3	672.2±41.1	1378±35	43.0±1.0
FW-D	530.0±28.0	13.6±0.1	2.0±0.0	14.6±1.3	39.5±1.5	595.0±36.1	1357±13	41.6±1.1
t-test	ns	ns	ns	ns	ns	*	ns	ns

Means±SD (n=4). Grain weight at 12.5% moisture. * represent a significance at the 5% level between the FW-W and FW-D plots (Student's t-test). ns indicates the absence of a significant difference.

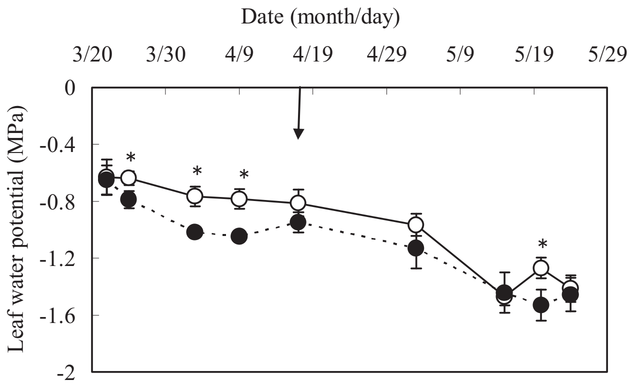

Fig. 13. Changes in leaf water potential of individual flag leaves. Open (○) and closed (●) circles represent FW-D and FD-D plants, respectively. The arrow indicates the date of heading. * represents significant differences at 5% level between FW-D and FD-D plants.

in the FD-D plot than in the FW-D plot. Actually, root length density at the deep soil tended to be large in the FD-D plants compared with the FW-D plants as Nakamura et al. (2003) and Nakagami et al. (2004) observed.

Leaf water potential of the plants in the FD-D plot was significantly lower during the period of soil moisture treatment from the middle of March to the middle of April than that of the plants in the FW-D plot (Fig. 13). However, no difference between plots in leaf water potential was found during ripening except for on May 20 after irrigation was stopped in both plots.

Dry weight of above-ground parts of the FD-D plants was higher than that of the FW-D plants at a 10% level of significance (Table 4). The harvest index also tended to be higher in the FD-D plants. However, grain yield in the FD-D plants was not significantly larger than that in the FW-D plants (P=0.13).

Discussion

Especially in grain crops, such as wheat, it would be important to enhance dry matter production during ripening to achieve greater grain production, even under drought conditions, because the contribution of dry-matter production after anthesis accounts for 60% to 80% of final grain weight (Schnyder, 1993; Gebbing and Schnyder, 1999). Efficiency of irrigation water use in grain production would be improved if the plants develop better root systems before heading, even if shoot growth is suppressed to some extent. Much research on irrigation scheduling has been performed, but almost all studies involved fixed irrigation intervals without consideration of the adaptive responses of plants to drought (Proffitt et al., 1985; Oweis et al., 1998, 2000). However, it was reported recently that irrigation a few weeks before heading, during which roots grew vigorously, encouraged plants to develop shoots and roots more effectively with increased grain yield under severe soil moisture depletion (Xue et al., 2003). Few attempts have been made to understand plant responses to drought and to exploit them in irrigation scheduling (Hirasawa et al., 1994), to our knowledge. In the regions where sufficient soil moisture is available at planting and soil moisture depletion is not severe enough to cause serious growth deterioration before heading, we might be able to improve grain yield and the efficiency of irrigation water use in grain production if plants are grown under limited irrigation that encouraged the development of deep and dense root systems (Nakamura et al., 2003; Nakagami et al., 2004).

In our pot experiment, the plants that had been grown under an insufficient soil moisture condition before heading (PD-D plants) developed roots more effectively than shoots. Ratios of root length and root surface area to leaf area were greater than those in the plants grown with sufficient irrigation (PW-D plants) (Table 1). Under drought conditions without irrigation during ripening, the former plants (PD-D plants) were able to absorb more water from soil in deeper layers and maintained higher leaf water potentials during ripening than the latter plants (PW-D plants) (Figs. 2, 3 and 4). Thus, the PD-D plant did not suffer from severe water stress even though they had been grown without irrigation, unlike the PW-D plants.

The reduction in leaf area and in the rate of photosynthesis due to senescence during ripening was smaller in the PD-D plants than in the PW-D plants (Figs. 6 and 7). As a result, the former plants were able to maintain high dry matter production even without

Table 4. Yield and yield components, dry weight of above-ground parts (dry wt.) and hervest index (HI) for plants of the FW-D and FD-D plots in 2006.

Plots	No. of spike (m^{-2})	No. of grain ($spike^{-1}$)	One grain wt. (10^{-3} g)	Grain yield (g m^{-2})	Dry wt. (g m^{-2})	HI (%)
FW-D	444.4±11.2	30.1±4.0	41.8±0.6	558±68	1317±27	37.0±4.1
FD-D	453.7±18.9	32.8±0.9	42.0±0.5	625±35	1357±27	40.3±1.7
t-test	ns	ns	ns	ns	#	ns

Means±SD (n=4). Number of grains per spike was calculated from grain yield, one-grain weight and number of spikes. Weights were determined at 12.5% moisture. ns indicates the absence of a significant difference.

irrigation and were able to produce heavier grain during ripening as compared with the latter plants (Fig. 8, Table 2).

Our results support the hypothesis that plants with better-developed root systems can tolerate water stress and produce greater grain yield under an insufficient soil-moisture condition during ripening, even when shoot growth before heading is suppressed. It seems likely that appropriate irrigation management might protect wheat plants from water stress during ripening and increase the efficiency of irrigation water use in grain production.

The increase in dry weight during ripening in the PD-D plants was approximately twice as large as that in the PW-D plants (Fig. 8). However, the final difference in grain weight was approximately 20% between the PW-D and PD-D plants (Table 2). The pot experiment was terminated in the middle of the ripening stage because the plants were dying as a result of water stress in the limited volume of soil. The shortened experimental period might be responsible for the limited effect of the soil moisture treatment on grain weight. There might be a difference in the pre-anthesis reserves of soluble carbohydrates in stems between the PW-D and PD-D plants, and this difference might be another cause of the smaller difference in grain weight than expected from the difference in increase in dry matter.

We examined whether deficient soil-moisture conditions before heading render the plants more resistant to drought during ripening in the field like in the pots mentioned above. Grain yield in the field decreased as a result of water stress if rainwater and irrigation were excluded from the field at the ripening stage even in the area with humid atmosphere in Japan such as the Kanto region (Table 3). We could confirm that even in the field under the conditions of the absence of rainwater and irrigation during ripening, plants grown under an insufficient soil moisture condition before heading produced more dry matter and grain than plants grown with sufficient soil moisture before heading (Table 4). The same results were obtained in a similar but preliminary field experiment where cv. Bandowase was used without replication (Hirasawa et al., 1993). Moreover, as noted previously (Nakamura et al., 2003; Nakagami et al., 2004), the former plants have a better developed root systems than the latter plants.

The rate of leaf photosynthesis decreases at a leaf water potential lower than approximately -1 MPa and by 50% at a leaf water potential below approximately -2 MPa (Hirasawa, 1999). We were unable to conduct the experiment in the field under the markedly decreased soil moisture condition in Field Exp. II and leaf water potential did not decrease markedly as in semi-arid regions (Proffitt et al., 1985). However, our results suggest that grain yield and the efficiency of irrigation water use might be improved by scheduling irrigation on the basis of plant responses to drought in semi-arid regions. Al-Kaisi and Shanahan (2007) recommended to avoid irrigation during early vegetative growth, although this was to prevent lodging. Growth of shoots and roots, and the ratio of root growth to shoot growth can be changed, to some extent, by the irrigation scheduling. From the results of this study and those of Xue et al. (2003), the irrigation schedule could affect grain yield and the efficiency of irrigation water use through its effects on the development of root system. Irrigation should be scheduled in specific geographic regions on the basis of the strength of water stress, the availability of irrigation water, and the responses of plants to drought, among other factors.

Finally, with respect to the responses of plants to drought, we would like to mention the growth responses of wheat roots to drought. Although we do not yet have quantitative details of the responses of rooting depth and root surface area to drought, these responses are very important in the absorption of water from soils with a low moisture content. The rate of elongation of primary seminal roots of wheat seedlings decreased at a water potential of vermiculite as high as –0.15 MPa (Akmal and Hirasawa, 2004). Our results suggest that, among the responses of roots to drought, the increase in dry weight is the most sensitive, while the increase in root surface area is less sensitive to drought than is the axial growth of roots (root length) (Table 1). The growth of finely branched roots is stimulated under insufficient soil moisture conditions (Morita and Okuda, 1994). The pattern of root growth response to soil moisture might depend on the reduction in soil moisture. The growth of wheat roots involves hydrotropism, as well as geotropism (Oyanagi et al., 1995). These responses of root growth to soil moisture affect the architecture and density of root systems in the soil. They remain to be investigated in quantitative detail.

Conclusion

A better developed root system is an important character for drought avoidance and this can enable plants to produce more dry matter under the conditions of insufficient soil moisture because plants can uptake much water from soil. Under an insufficient soil moisture condition, growth becomes more vigorous in roots than in shoots. In this research we clarified that wheat plants in which shoot growth was suppressed but roots continued to grow under moisture-depleted conditions before heading could produce more dry matter and grain during ripening under moisture-depleted conditions compared with plants that shoot growth was vigorous than root growth in sufficient moisture soil before heading. This indicates that a high capacity for drought avoidance could be generated by appropriate irrigation management. For improving drought resistance and irrigation efficiency, irrigation should be scheduled on the basis of the strength of water stress, the availability of irrigation water, and the response of plants to drought, among other factors.

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