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Responses of Root Growth to Moderate Soil Water Deficit in Wheat Seedlings

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Abstract: In the field, plants show better root growth in drying soil than in wet soil. However, the root growth enhancement has not been demonstrated clearly in the laboratory. In this study, the root growth response of wheat seedlings to moderate soil water deficits was characterized quantitatively in an environment-controlled chamber. Germinated seeds of wheat were grown for 15 days in the soil with a water potential ranging from field capacity (FC) to approximately –0.08 MPa. The leaf area decreased with reduction in soil water potential. By contrast, the root surface area increased upon reduction of the soil water potential to –0.04 MPa while it decreased significantly in soil with a water potential of –0.08 MPa. The increase in surface area was obvious in the roots with a diameter of 0.2 to 0.4 mm and larger than 0.7 mm. Root weight increased with the reduction of soil water potential to –0.04 MPa. While specific root length decreased significantly with the reduction of water potential to –0.06 MPa, the specific root surface area did not. Assimilates transported from shoot might be used in roots to increae the surface area mainly by increasing the diameter rather than the length in response to a moderate soil water deficit in wheat seedlings. This might result from the drought tolerance mechanism of osmotic adjustment in roots.

Key words: Assimilates, Root length, Root surface area, Shoot growth, Soil water potential, Transpiration, Wheat.

A water deficit significantly decreases both the growth and yield of crop plants (Gallagher, 1976; Boyer, 1982; Loomis and Conner, 1992; Kramer and Boyer, 1995; Martin et al., 2006 and references therein). Crop growth is strongly influenced by the availability of moisture during the growing season (Kramer, 1983; Kramer and Boyer, 1995). Rooting depth and root length density are very important for the avoidance of water stress under conditions of depleted soil moisture (Loomis and Conner, 1992; Hirasawa et al., 1994). Plant breeding is an effective strategy for generation of deep and dense root systems (Gaur et al., 2008; Richards, 2008). Thus, for example, a drought-resistant cultivar of upland rice was generated by screening for root-system development (Hirasawa et al., 1998b).

In soybean (Hirasawa et al., 1998a), wheat (Nakamura et al., 2003; Nakagami et al., 2004; Saidi et al., 2008) and upland rice (Hirasawa et al., 2005), the plants with a better developed root system performed well by keeping a higher rate of leaf photosynthesis during ripening under deficient soil moisture conditions and also even under sufficient soil moisture conditions. These plants also could improve the use efficiency of irrigated water (Hirasawa et al., 1998a, 2005).

The growth reduction of root in response to soil moisture deficit is not so large compared with that of shoot (Kramer and Boyer, 1995). Root systems of soybean (Hirasawa et al., 1998a), wheat (Nakamura et al., 2003; Nakagami et al., 2004; Saidi et al., 2008) and upland rice (Hirasawa et al., 2005) developed more effectively in deeper layers of soil when plants were grown in the field with deficient moisture than in the field with adequate moisture. A high capacity for developing a better root system might be achieved by appropriate management of soil (Kawata et al., 1969; Zhang et al., 2004), irrigation (Xue et al., 2003; Saidi et al., 2008) and drainage (Hirasawa et al., 1998a; Nakamura et al., 2003; Nakagami et al., 2004).

For the establishment of appropriate management of irrigation and drainage, information on quantitative root growth in response to soil moisture conditions is required. Observations in the field indicated that root growth was better in soil with a moisture deficit than in soil with sufficient moisture, for example, in wheat (Nakamura et al., 2003; Xue et al., 2003; Nakagami et al., 2004; Zhang et al., 2004; Saidi et al., 2008), soybean (Hida et al., 1995a, b; Hirasawa et al., 1994, 1998a) and upland rice (Hirasawa et al., 2005). However, quantitative research on the growth response of root to soil moisture in wide ranges of moisture has been very limited even in the laboratory. To

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our knowledge, increase in the root elongation rate has not been observed with reduction in the water potential of soil or vermiculite in the laboratory. For example, the elongation rate of seminal roots of wheat in vermiculite decreased even at a water potential of –0.15 MPa and it fell markedly at a water potential below –0.55 MPa (Akmal and Hirasawa, 2004). The water potential of vermiculite at which the rate of root elongation fell to half of the original rate was between –0.4 MPa and –0.5 MPa. In maize, the growth rate of the seminal root decreased when the water potential of vermiculite was reduced to approximately -0.1 MPa, and the water potential of vermiculite at which the root elongation rate fell by half was estimated to be between –0.2 MPa and –0.3 MPa (Sharp et al., 1988). The enhancement of root elongation has been observed in the laboratory in some cases, for example soybean (Hida et al., 1995b), *Arabidopsis* (van der Weele et al., 2000) and maize (Sharp and Davies, 1979). Sharp and Davies (1979) observed enhanced elongation of maize roots only a few days after irrigation was discontinued. Hida et al. (1995b) also observed an increase in total root length in soybean in soil with a water potential of approximately –0.05 MPa. However, they did not examine the growth response of roots to step-down changes in soil water potential, and they did not estimate the range of soil water potentials that enhanced root elongation.

A root system consists of various kinds of roots such as seminal, nodal and branch roots. We do not know in which kind of roots the growth is enhanced in response to the reduction of soil moisture. Root surface area is important when considering root functions of water and mineral absorption. However, the enhancement of root growth has not been studied in respect to root surface area to our knowledge.

In the field, soil moisture decreases gradually from the surface to deeper layers after rain or irrigation. Even though soil moisture tends to decrease considerably at the soil surface, moisture sometimes remains at close to field capacity (FC) in deeper soil. Thus, the soil water potentials examined in previous studies in the laboratory might have been far lower than the actual water potential encountered by roots in the field, in particular, at the start of a dry season or at the start of withholding irrigation. If we could identify the appropriate soil moisture for root growth enhancement in the laboratory, this would be a basic understanding of the irrigation and drainage management and the mechanisms of the growth enhancement of root would be adopted to the breeding for improving root system development.

In the present study, focusing on the increase in root surface area as well as on root elongation, we examined the actual root growth in response to the reduction in soil water potential quantitatively in wheat seedlings grown under the controlled conditions of soil water potentials higher than those examined in previous research (Akmal and Hirasawa, 2004) in the laboratory.

Materials and Methods

1. Plant material and treatments

The wheat (*Triticum aestivum* L.) cultivar Ayahikari was used in all experiments. Seeds were washed in a 0.25% sodium hyperchlorite solution for 10 min, rinsed with deionized water, and placed on wet filter paper in a glass Petri dish. The seeds were allowed to germinate at 25ºC in darkness in an incubator for approximately 30 hr. Thereafter, four germinated seeds were planted in a plastic tube10.6 cm in diameter and 30 cm in height that had been filled with alluvial soil from the Tama River. The bottom of each tube was covered with a styrofoam plate 0.5 cm in thickness. A slit of a few millimeters in width was made between the wall of the tube and the styrofoam through which excess water drained. As fertilizer, N, P_2O_5 and K_2O, was applied to each tube at a rate of 0.2, 0.2 and 0.2 g per tube, respectively.

In the first experiment (Exp. I) conducted in the period from 26 January to 9 Februry 2007, soils with FC moisture and a water potential of approximately –0.02 MPa, –0.04 MPa and –0.06 MPa were prepared. In Exp. II conducted in the period from 23 October to 9 November 2007, soils with a water potential of approximately –0.04 and –0.08 MPa were prepared in addition to investigate the effects of the further decreased soil moisture on the growth. The tubes with a soil moisture of FC, –0.02 MPa, –0.04 MPa, –0.06 MPa and –0.08 MPa are referred to as FC, –0.02 MPa, –0.04 MPa, –0.06 MPa and –0.08 MPa plots, respectively. For preparation of soils, soil moisture was reduced to a given water potential in a greenhouse over the course of several days. Water potential was monitored with a tensiometer (2710AR; Soilmoisture Equipment, Santa Barbara, CA, USA, or DIK-3162; Daiki Rika Kogyo, Konosu, Japan). When tubes were filled with soil, the soil was mixed well with fertilizer. For the FC plots, sufficient water was introduced one day before planting and excess water drained from soil. The open top surface of the soil in each tube was covered with thin plastic film to prevent loss of moisture by evaporation during growth. Plants were thinned to two plants per tube three days after planting. Five tubes were used per soil moisture treatment. Plants were grown in a growth chamber [temperature, 23/17ºC (12 hr day/12 hr night); relative humidity, 60/80% in Exp. I and 50/60% in Exp. II; light intensity, approximately 500 μmol m^{-2} s^{-1} of PAR].

2. Measurements of soil moisture content and the rates of transpiration and water uptake

The soil water potential at a depth of 20 cm was measured every day with a tensiometer as noted above. The soil in each tube was collected at depths of 5, 15 and

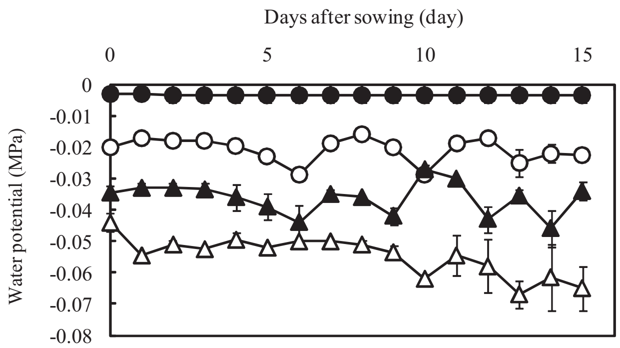

Fig. 1. Changes in soil water potential at a depth of 20 cm (Exp. I). Symbols ●, ○, ▲ and △ represent FC, –0.02 MPa, –0.04 MPa and –0.06 MPa plots, respectively. Bars represent standard deviations (n=5) in this and subsequent Figures.

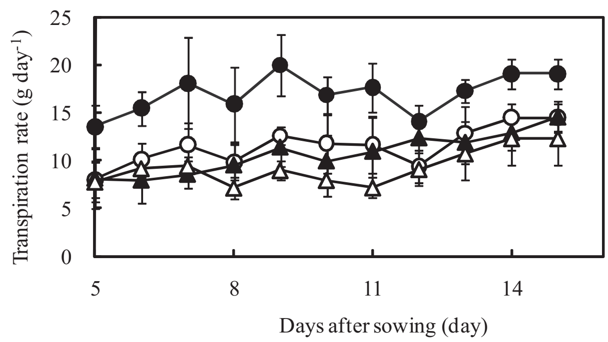

Fig. 2. Changes in transpiration rate per pot in wheat seedlings. Symbols ●, ○, ▲ and △ represent FC, –0.02 MPa, –0.04 MPa and –0.06 MPa plots, respectively.

25 cm at the end of each experiment and was dried at 105°C in an oven for about 72 hr.

The weight of the tube in which plants were growing was measured every morning with an electric balance (E5500S; Sartorius, Tokyo, Japan). The reduction in weight was regarded mainly as the loss of transpired water during the day because the loss of soil moisture by evaporation was prevented by covering the surface of the soil in the tube with plastic film. The daily transpired water can also be regarded as the amount of water absorbed by the plants from the soil.

3. Measurements of the length and surface area of roots, leaf area and dry weight

After washed gently with tap water, the root length (RL) and root surface area (RA) of each plant were measured with an image-analysis system (WinRHIZO; Regent Instrument, Quebec, Canada). Leaf area was measured with an area meter (AAM-9; Hayashi Denko, Tokyo, Japan). Dry weights of roots (RW) and shoots were recorded after drying at 80°C in a ventilated oven. Specific root length (SRL) and specific root surface area (SRA) were calculated as follows:

SRL=RL/RW

SRA=RA/RW

4. Statistical analysis of data

Five replicates were taken for all measurements and the mean values for moisture treatment in Exp. I were compared using Tukey's test (n=5) and the mean values for the two moisture treatments in Exp. II, using Student's t-test (n=5).

Results

1. Experiment 1

(1) Soil moisture and the rate of transpiration

Figure 1 shows changes in the water potential of soil at a depth of 20 cm during the 15-day soil moisture treatment. The FC plot was irrigated every day with water equivalent to the amount of water lost in the previous day. As a result, the soil water potential in the FC plot remained within the range of –0.003 MPa to –0.005 MPa. In the –0.02MPa plot, water equivalent to the amount lost after the most recent irrigation was applied whenever the soil water potential fell to –0.03 MPa. As a result, the soil water potential remained within the range of –0.02 MPa to –0.03 MPa during the experiment. In the –0.04MPa plot, irrigation was applied when the soil water potential fell to –0.045 MPa, and the soil water potential remained in the range of –0.035 MPa to –0.045 MPa. In the –0.06 MPa plot, the soil water potential fell from –0.04 MPa, reaching –0.065 MPa 10 days after sowing, and irrigation that was equivalent to the amount of water lost during the most recent 9 days was applied. At 14 days after sowing, irrigation that was equivalent to the amount of water lost during the most recent 4 days was also applied. As a result, the soil water potential in this plot remained in the range of –0.05 MPa to –0.07 MPa during the entire soil moisture treatment.

The daily water loss by transpiration increased during the moisture treatment because of the leaf growth (Fig. 2). The water loss was the largest in the plants in the FC plot followed by the plants in the –0.02 MPa and –0.04 MPa plots. The rate was the smallest in the plants in the –0.06 MPa plot.

The soil moisture content, on a dry weight basis, at the depth of 5, 15 and 25 cm at the end of the moisture treatment was 75.0%, 80.4% and 88.8%, respectively, on the average in the FC plot; 57.6%, 57.5% and 57.8%, respectively, on the average in the –0.02 MPa plot; 55.6%, 54.2% and 55.0%, respectively, on the average in the –0.04 MPa plot; and 48.1%, 51.2% and 51.3%, respectively, on the average in the –0.06 MPa plot.

(2) Leaf area

Total leaf area at the end of the treatment was largest in the FC plot, followed by the –0.02 MPa and –0.04 MPa plots (Fig. 3). The leaf area of the plants in the –0.06 MPa plots was the smallest.

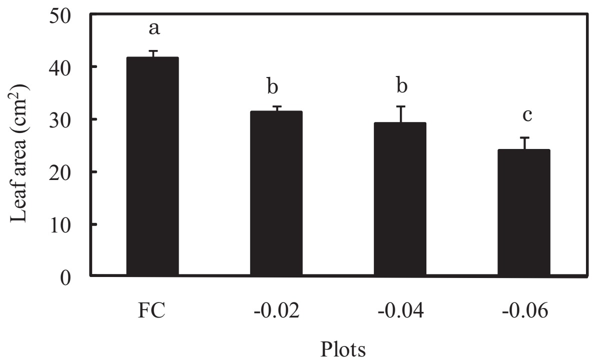

Fig. 3. Leaf area per plant in wheat seedlings (Exp. I). Letters (a, b and c) indicate statistically significant differences between treatments (Turkey-Kramer test; $P=0.05$) in this and subsequent Figures.

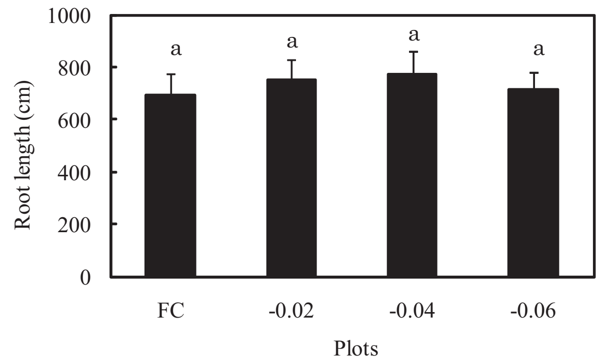

Fig. 4. Total root length per plant in wheat seedlings (Exp. I).

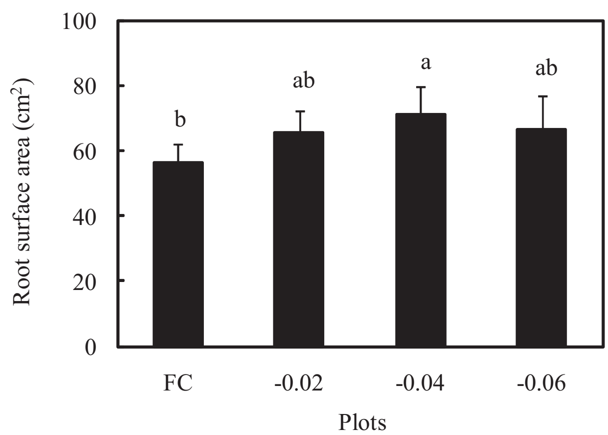

Fig. 5. Root surface area per plant in wheat seedlings (Exp. I)

(3) Root length and root surface area

Total root lengths of plants grown in soil with various water potentials are shown in Figure 4. The lengths in the FC plot tended to be shorter than in other plots, although there were no significant differences among treatments. In comparison with –0.02 MPa, –0.04 MPa and –0.06 MPa plots, the plants in the –0.04 MPa plot tended to have longer roots.

Significant differences in root surface area were found among the soil moisture treatments. The root surface area was largest in the –0.04 MPa plot, followed by the in the –0.06 MPa and –0.02 MPa plots (Fig. 5). The surface area of roots was the smallest in the FC plot.

(4) Relation of the lengths and surface area of roots with root diameter

We classified the roots into ten classes with different lengths at 0.1 mm intervals. Root length was the longest in the roots with a diameter of 0.1–0.2 mm decreased with the increase in root diameter in all plots (Fig. 6A). Root length tended to be large in plants grown in soil with a low water potential in the case of roots with diameters greater than 0.7 mm.

The surface area was largest in the roots with diameters from 0.1–0.2 mm in all plots, and decreased with the increase in the diameter to 0.9 mm (Fig. 7A). The surface area of the roots with diameters of 0.2–0.4 mm tended to be larger in the –0.02 and –0.04 MPa plots. The surface area of the roots with diameters larger than 0.7 mm tended to be larger in the –0.04 MPa and –0.06 MPa plots than in the FC and –0.02 MPa plots.

The ratio of the length (Fig. 6B) and surface area (Fig. 7B) in the roots with a diameter smaller than 0.6 or 0.7 mm to those in all roots tended to be larger in the FC plot than in the –0.04 MPa and –0.06 MPa plots. By contrast, the ratio of these values in the roots with a diameter larger

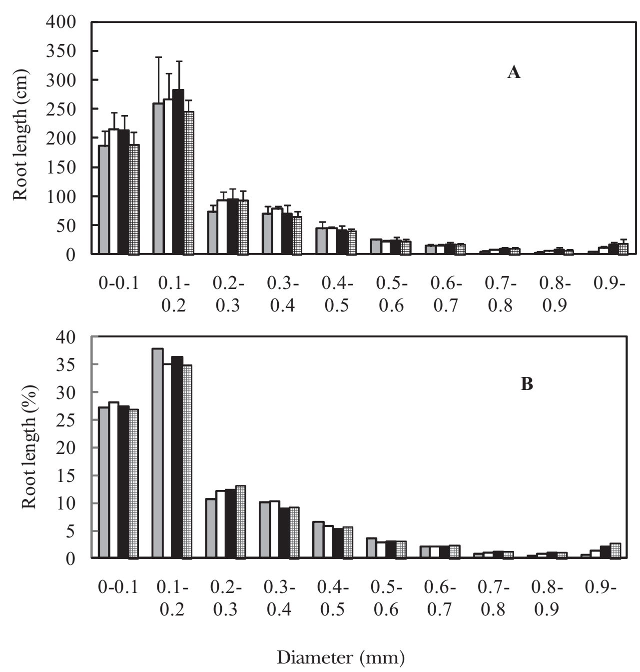

Fig. 6. Distribution of the lengths of roots with different diameters in wheat seedlings (Exp. I). A: length, B: percentage to total length. Gray, white, black and hatched columns represent FC, –0.02 MPa, –0.04 MPa and –0.06 MPa plots, respectively.

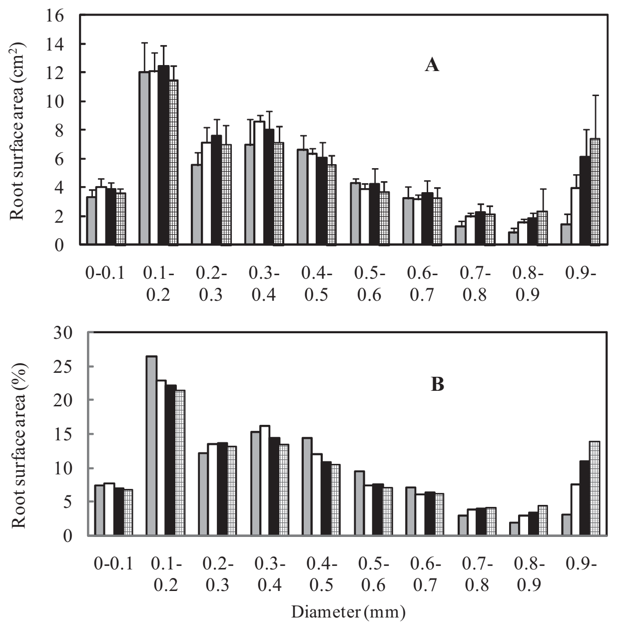

Fig. 7. Distribution of the surface area of roots with different diameters in wheat seedlings (Exp. I). A: length, B: percentage to total length. Gray, white, black and hatched columns represent FC, –0.02 MPa, –0.04 MPa, and –0.06 MPa plots, respectively.

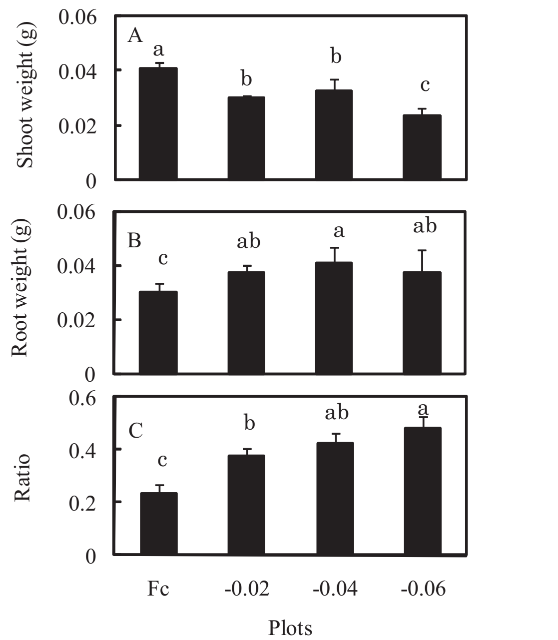

Fig. 8. Shoot weight (A), root weight (B), and the ratio of root weight to shoot weight (C) in wheat seedlings (Exp. I).

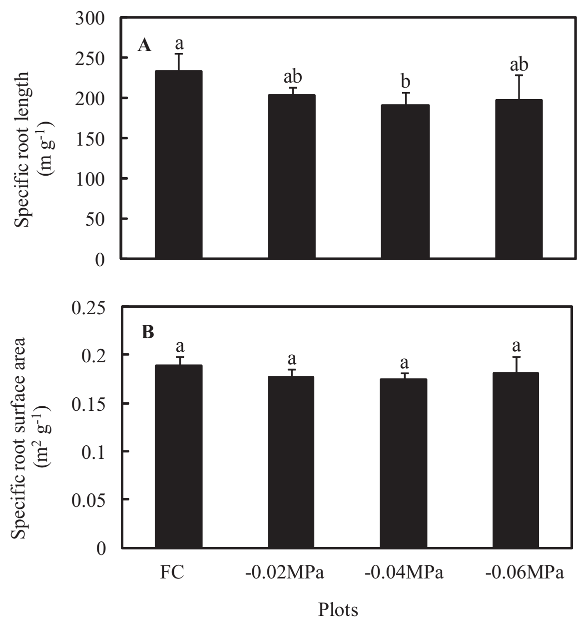

Fig. 9. Specific root length (A) and specific root surface area (B) in wheat seedlings (Exp. I).
Specific root length = Root length/Root weight
Specific root surface area = Root surface area/Root weight

than 0.7 mm to those in all roots tended to be larger in the latter plots than in the former plot. This tendency was clearer in root surface area (Fig. 7A, B).

(5) Shoot weight, root weight and their ratio

The dry weight of above-ground parts was heaviest in the FC plot, followed by the –0.02 MPa and –0.04 MPa plots (Fig. 8A). It was lightest in the –0.06 MPa plot. By contrast, the dry weight of roots was lightest in the FC plot (Fig. 8B). There were no significant differences in root weight among plants in the –0.02 MPa, –0.04 MPa and –0.06 MPa plots. Thus, the ratio of root to shoot weight was largest in the -0.06MPa plot, followed by the –0.04 MPa and –0.02 MPa plots (Fig. 8C). The ratio was smallest in the FC plot.

(6) Specific root length and specific root surface area

Specific root length decreased with the reduction in soil water potential (Fig. 9A). However, the specific root surface area did not decrease with the reduction in soil water potential to –0.06 MPa.

(7) Transpiration and water uptake rates

Even when the soil water potential decreased to approximately –0.06 MPa, the rate of transpiration per unit leaf area did not decrease (Fig. 10A). This means that the relative stomatal conductance was kept high by the treatment. However, the rate of water uptake per unit root surface decreased significantly when the soil water potential decreased to approximately –0.02 MPa, and tended to decrease with further decrease in soil water potential to approximately –0.06 MPa although the difference in the rate between the –0.02 MPa and –0.06 MPa plots was not significant (Fig. 10B).

2. Experiment II

The growth of the plants in the FC, -0.04MPa and –0.06

MPa plots was examined. The values of leaf area, total root length, root surface area and shoot weight were significantly lower in the –0.08 MPa plot than in the –0.04 MPa plot (Table 1). The root weight tended to decrease in the –0.08MPa plot. The root-shoot ratio increased significantly in the –0.08 MPa plot compared with the –0.04 MPa plot (Table 1). Specific root length decreased further in the -0.08 MPa plot and specific root surface area was significantly smaller in the –0.08 MPa plot than in the –0.04 MPa plot (Table 1).

Transpiration rate per unit leaf area as well as water uptake rate per unit root surface area decreased significantly in the –0.08 MPa plot compared with the –0.04 MPa plot (Table 2).

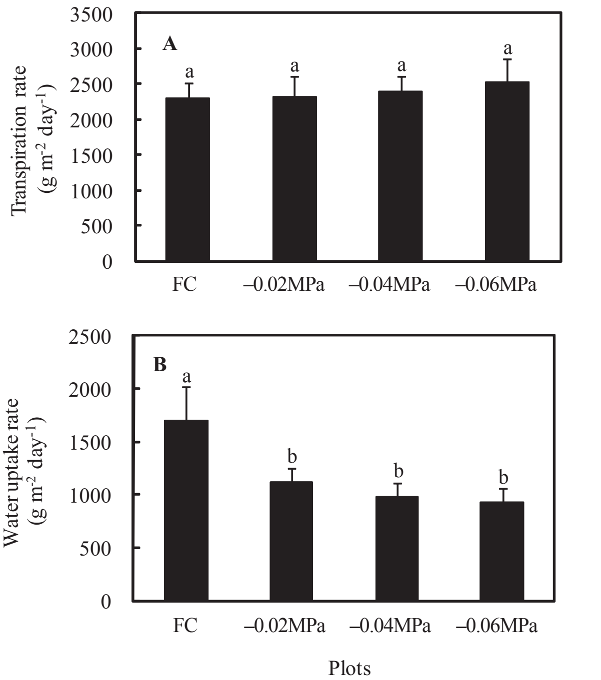

Fig. 10. Transpiration rate per leaf area (A) and water uptake rate per root surface area (B) in wheat seedlings (Exp. I). The average of the transpiration (water uptake) rate of the last two days of the experiment and the leaf area and root surface area measured at the end of the experiment were used for the calculation of the rates.

Discussion

In Exp. I, the leaf area and shoot dry weight were significantly higher in the FC plot than in the other plots with a lower moisture content (Figs. 3, 8). These results indicate that shoot growth was promoted by supplying adequate water even in wheat, which is known as a relatively drought-resistant crop plant. As observed earlier by others (Kramer, 1983; Kramer and Boyer, 1995; Lambers et al., 1998 and references therein), leaf area decreased markedly with reduction in soil water potential (Fig. 3), but the growth response of roots to the reduction in soil water potential was less marked than that of shoots (Figs. 4, 5, Table 1). As a result, the ratio of root weight to shoot weight increased with reduction in the soil water potential (Fig. 8, Table 1). In the field, the growth of wheat roots is enhanced by the reduction in soil water potential, and this makes the root system development better rather than that in the soil with sufficient moisture (Nakamura et al., 2003; Xue et al., 2003; Nakagami et al., 2004), and the same is also the case, for example, in the roots of rice (Hirasawa et al., 2005), soybean (Hida et al., 1995a) and cowpea (Angus et al., 1983) in the field.

In studies in the laboratory, the root elongation rate was not increased by a reduction in the water potential in maize and wheat grown in vermiculite (Sharp et al., 1988; Akmal and Hirasawa, 2004). Neither was the root length density increased by the reduction of soil moisture in potted rice (Asch et al., 2005). In the present study,

Table 2. Transpiration rate per unit leaf area and water uptake rate per unit root surface area in wheat seedlings in –0.04 MPa and –0.08 MPa plots (Exp. II).

	Transpiration rate per unit leaf area (g m^{-2} day^{-1})	Water uptake rate per unit root surface area (g m^{-2} day^{-1})
–0.04 MPa	1900±321 a	957.4±149.3 a
–0.08 MPa	868±134 b	433.9±66.8 b

Mean±standard deviation (n=5).

Table 1. Leaf area, total root length, root surface area, shoot and root weight, the ratio of root weight to shoot weight and specific length and surface area of roots in wheat seedlings in the plots of –0.04 MPa and –0.08 MPa (Exp. II).

Plots	Leaf area (cm^2)	Root length (cm)	Root surface area (cm^2)	Shoot wt. (g)	Root wt. (g)	Root/shoot ratio (g/g)	Specific root length (m g^{-1})	Specific root surface area (m^2 g^{-1})
–0.04 MPa	23.2 (± 2.29) a	733.0 (± 33.3) a	70.8 (± 2.3) a	0.079 (± 0.005) a	0.036 (± 0.001) a	0.46 (± 0.03) b	203.9 (±12.1) a	0.197 (±0.009) a
–0.08 MPa	11.8 (± 0.8) b	519.1 (± 50.8) b	57.0 (± 4.4) b	0.045 (± 0.003) b	0.032 (± 0.004) a	0.73 (± 0.14) a	163.7 (±12.9) b	0.180 (±0.014) b

Mean±standard deviation (n=5). Means with the same letters in a given column are not significantly different, as determined at the 5% level by Student's t-test in this and subsequent tables.

however, we found that root growth, in terms of root length and surface area, was enhanced by a reduction of soil water potential from FC (0.003–0.005 MPa) to –0.02～–0.06 MPa in wheat seedlings (Figs. 4, 5). In previous studies by Akmal and Hirasawa (2004), the water potential of the soil or vermiculite before treatment might have been too low to enhance root elongation. This might also have been the case in maize (Sharp et al., 1988) and rice (Asch et al., 2005).

In the –0.02 MPa, –0.04 MPa and –0.06 MPa plots, the root surface area increased more significantly than root length (Figs. 4, 5). The length and surface area of roots with diameters from 0.2 mm to 0.4 mm (corresponding to lateral roots) and larger than 0.7 mm (corresponding to seminal roots) tended to increase with a reduction of soil water potential (Figs. 6, 7). Morita and Okuda (1994) reported that a reduction in soil moisture increased the production of lateral roots. The length of branch roots was longer in soybean in soil with a water potential of approximately –0.05 MPa than in soil with field-capacity moisture (Hida et al., 1995b). However, our measurements in wheat seedlings indicated that the increase in root growth was not limited to lateral roots. The axial and radial growth of seminal roots as well as lateral roots was responsible for the increase in the surface area of roots.

Hydraulic conductance of soil decreases with the reduction of soil moisture (Kramer, 1983). This causes the decrease in soil water potential at root surface. The reduction not only in water potential of bulk soil but also in soil water potential at the root surface decreased the rate of water uptake per unit root surface (Fig. 10B). However, due to the increase in root surface as well as the decrease in leaf area, the rate of transpiration per unit leaf area was kept high in the plants in the –0.02 MPa, –0.04 MPa and –0.06 MPa plots. This might make the plants maintain a high rate of leaf photosynthesis. However, in the plants in the –0.08 MPa plot, the rate of water uptake per unit root surface decreased markedly. This caused a significant reduction in the rate of transpiration per unit leaf area and, therefore, the rate of leaf photosynthesis, although the decrease in leaf area was greater than the decrease in root surface area (Table 1). These results suggest that an appropriate soil moisture regime, in which the plants with a large absorption surface of roots could be grown without any reduction of leaf productivity, might exist in wheat plants at the water potential far lower than FC.

An increase in root growth in soil with a decreased water potential might be affected by a decrease in shoot growth because of changes in carbohydrate partitioning (Richards, 2008; Yoshimura et al., 2008). Even in vermiculite with inadequate moisture, the turgor pressure of wheat roots remained high, as a result of the accumulation of solutes (Akmal and Hirasawa, 2004). Cell wall loosening was inhibited and the hydraulic conductivity of tissue fell in the wheat roots grown in soil with decreased moisture (Akmal and Hirasawa, 2004). Even though turgor pressure remained high, growth of wheat roots was suppressed in vermiculite with a decreased water potential (Akmal and Hirasawa, 2004). However, the growth might be enhanced if soil water potential was not decreased enough for decreasing cell wall loosening and the hydraulic conductivity of the root, and if enough carbohydrates for the growth were supplied to roots from the shoot (Figs. 4, 5). The reduction in soil water potential to approximately –0.04 MPa might be such conditions for the wheat seedlings in the present study. The dry weight of roots increased significantly in the plants grown in soil with a water potential of –0.04 MPa plot (Fig. 8B). As the high rate of leaf photosynthesis was expected to be maintained in the –0.04 MPa plot, excess carbohydrate might be transported to roots from leaves. This might increase root dry weight significantly in the plants in the –0.04 MPa plot. However, in the soil with water potential lower than –0.08 MPa, the reduction in root growth under water stress might have been caused by the limitation of carbohydrates, a decrease in wall loosening and a decrease in the hydraulic conductivity of tissues (Akmal and Hirasawa, 2004).

With the reduction in soil water potential to –0.06 MPa, the specific root length decreased significantly while the specific root surface area was kept constant (Fig. 9). The carbohydrates were used predominantly for increasing root diameter, and not for root elongation. Our results indicate that assimilates transported from shoots might be used mainly for osmotic adjustment of root cells and the root response to the reduction in soil moisture might be for drought tolerance rather than drought avoidance, although the absorption area of roots was certainly increased. Some regulatory mechanism(s) such as signal transduction pathway(s) might operate for the changes in carbohydrate partitioning and the use of carbohydrate for growth of the plant (Lambers et al., 1998).

In this study, we could clarify not only that the ratio of root weight to shoot weight increases with a reduction in soil moisture but also that root growth itself can be enhanced under conditions of moderately reduced soil moisture. The results might represent fundamental characteristics of the growth responses of wheat to a reduction in soil water potential. Although we performed the present study with young seedlings in the laboratory, our results indicate that the root length and root surface area can be increased by optimizing the soil water potential. A soil water potential of approximately -0.04 MPa seemed to be optimal for root growth, in terms of root length and surface area, in wheat in our case. Even though this value for the soil water potential might change with atmospheric conditions, we note that the apparently optimum soil water potential is significantly lower than field capacity. Field managements to generate appropriate soil moisture conditions, such as drainage, should be emphasized in areas where precipitation is abundant, such as Japan.

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References

Akmal, M. and Hirasawa, T. 2004. Growth responses of seminal roots of wheat seedlings to a reduction in the water potential of vermiculite. *Plant Soil* 267: 319-328.

Angus, J.F., Hasegawa, S., Hsiao, T.C., Liboon, S.P. and Zandstra, H.G. 1983. The water balance of post-monsoonal dryland crops. *J. Agric. Sci.* 101: 699-710.

Asch, F., Dingkuhn, M., Sow, A. and Audebert, A. 2005. Drought-induced changes in rooting patterns and assimilate partitioning between root and shoot in upland rice. *Field Crops Res.* 93: 223-236.

Boyer, J.S. 1982. Plant productivity and environment. *Science* 218: 442-448.

Gallagher, J.N., Biscoe, P.V. and Hunter, B. 1976. Effects of drought on grain growth. *Nature* 264: 541-542.

Gaur, P.M., Krishnamurthy, L. and Kashiwagi, J. 2008. Improving drought-avoidance root traits in chickpea (*Cicer arietnum* L.) – current status of research at ICRISAT. *Plant Prod. Sci.* 11: 3-11.

Hida, Y., Hirasawa, T. and Ishihara, K. 1995a. Differences in dry matter production and root system development between soybean cultivars under deficient soil moisture conditions. *Jpn. J. Crop Sci.* 64: 573-580.

Hida, Y., Hirasawa, T. and Ishihara, K. 1995b. Comparison of root growth response of soybean seedlings to the reduction in soil moisture between cvs. Enrei and Tachinagaha. *Rep. Kanto Branch. Jpn. Soc. Crop Sci.* 10: 25-26*.

Hirasawa, T., Izumi, K. and Ookawa, T. 2005. Effects of soil moisture conditions before heading on the rate of photosynthesis and related characteristics during ripening in upland rice plants. *Jpn. J. Crop Sci.*74 (Extra 1): 106-107.

Hirasawa, T., Nakahara, M., Izumi, T., Iwamoto, Y. and Ishihara, K. 1998a. Effects of pre-flowering soil moisture deficits on dry matter production and ecophysiological characteristics in soybean plants under well irrigated conditions during grain filling. *Plant Prod. Sci.* 1: 8-17.

Hirasawa, H., Nemoto, H., Suga, R., Ishihara, M., Hirayama, M., Okamoto, K. and Miyamoto, M. 1998b. Breeding a new upland rice variety "Yumenohatamochi" with high drought resistance and good eating quality. *Breed. Sci.* 48: 415-419.

Hirasawa, T., Tanaka, K., Miyamoto, D., Takei, M. and Ishihara, K. 1994. Effects of pre-flowering soil moisture deficits on dry matter production and ecophysiological characteristics in soybean plants under drought conditions during grain filling. *Jpn. J. Crop Sci.* 63: 721-730.

Kawata, S., Oohashi, Y., Yamazaki, K. and Ishihara, K. 1969. Root system formation in rice and soil environment. *Proc. Crop Sci. Soc. Jpn* 38: 434-441**.

Kramer, P.J. 1983. Water Relations of Plants. Academic Press, New York. 1-489.

Kramer, P.J. and Boyer, J.S 1995. Water Relations of Plants and Soils. Academic Press, San Diego. 1-495.

Lambers, H., Chapin III, F.S. and Pons, T.L. 1998. Plant Physiological Ecology. Springer, New York. 1-540.

Loomis, R.S. and Conner, D.J. 1992. Crop Ecology. Cambridge University Press, Cambridge. 1-538.

Martin, J.H., Waldren, R.P. and Stamp, D.L. 2006. Principles of Field Crop Production. Pearson Prentice Hall, Columbus. 1-945.

Morita, S. and Okuda, H. 1994. Effect of soil water condition on root development of wheat seedling with special reference to branching of primary seminal root. *Jpn. J. Crop Sci.* 63: 418-422**.

Nakagami, K., Ookawa, T. and Hirasawa, T. 2004. Effects of a reduction in soil moisture from one month before flowering through ripening on dry matter production and ecophysiological characteristics of wheat plants. *Plant Prod. Sci.* 7: 143-154.

Nakamura, E., Ookawa, T., Ishihara, K. and Hirasawa, T. 2003. Effects of soil moisture depletion for one month before flowering on dry matter production and ecophysiological characteristics of wheat plants in wet soil during grain filling. *Plant Prod. Sci.* 6: 195-205.

Richards, R.A. 2008. Genetic opportunities to improve cereal root systems for dryland agriculture. *Plant Prod. Sci.* 11: 12-16.

Saidi, A., Ookawa, T., Motobayashi, T., and Hirasawa, T. 2008. Effects of soil moisture conditions before heading on growth of wheat plants under drought conditions in the ripening stage: In sufficient soil moisture conditions before heading render wheat plants more resistant to drought during ripening. *Plant Prod. Sci.* 11: 403-414.

Sharp, R.E. and Davies, W. J. 1979. Solute regulation and growth by roots and shoots of water-stressed maize plants. *Planta* 146: 319-326.

Sharp, R.E., Silk, W.K. and Hsiao, T.C. 1988. Growth of maize primary root at low water potentials. I. Spacial distribution of expansive growth. *Plant Physiol.* 87: 50-57.

van der Weele, C.M., Spollen, W.G., Sharp, R.E. and Baskin, T.I. 2000. Growth of *Arabidopsis thaliana* seedlings under water deficit studied by control of water potential in nutrient-agar media. *J. Exp. Bot.* 51: 1555-1562.

Xue, Q., Zhu, Z., Musick, J.T., Stewart, B.A. and Dusek, D.A. 2003. Root growth and water uptake in winter wheat under deficit irrigation. *Plant Soil* 257: 151-161.

Yoshimura, K., Masuda, A., Kuwano, M., Yokota, A. and Akashi, K. 2008. Programmed proteome response for drought avoidance/tolerance in the root of a C_3 xerophyte (wild watermelon) under water deficits. *Plant Cell Physiol.* 49: 226-241.

Zhang, X., Pei, D. and Chen, S. 2004. Root growth and soil water utilization of winter wheat in the North China Plain. *Hydrol. Process.* 18: 275-287.

* In Japanese.
** In Japanese with English abstract.