Effects of Low Root Temperature on Dry Matter Production and Root Water Uptake in Rice Plants

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Abstract: Chilling is a major constraint in rice production in cool climates. In rice (Oryza sativa L.) plants, both the air temperature and the water (soil) temperature affect various growth processes independently, and low root zone temperature (thus, root temperature) can inhibit rice growth and yield. In this study, we investigated the effect of low root temperature on rice growth in relation to dry matter production and root water uptake. Plants were grown in hydroponic solutions at two temperatures, one equivalent to air temperature and the other 14ºC for 15 d starting 11 d after germination. Low temperature of the solution (low root temperature) inhibited dry matter production of rice plants by decreasing leaf area rather than photosynthetic rate. The response of leaf area was affected by changes in plant water status, that is relative water content (RWC) of stem was decreased by low root temperature resulting in reduced leaf area. The decrease in RWC caused by low root temperature was related to that in root hydraulic conductance (Kr). The responses of transpiration (E) and Kr to the low root temperature depended more on root surface area than on changes in hydraulic conductance per unit root surface area (Lp/r). These results suggest that dry matter production under the low root temperature condition is controlled mainly by quantitative growth parameters such as leaf area and root surface area.

Key words: Dry matter production, Lateral roots, Leaf area, Low root temperature, Root hydraulic conductance, Root surface area, Water uptake.

Chilling is a major constraint in rice production in cool climates. In the Tohoku region (37º N to 42º N), one of the coldest rice-producing areas in the world, rice production per unit area is relatively high due to high levels of solar radiation and appropriate technical inputs. However, year-to-year fluctuation is large due to the yearly change in temperature. Therefore, improving tolerance to low temperatures by means of breeding or agricultural techniques is a major target of research on rice in this region.

There are many studies on the response of rice (Oryza sativa L.) plants to low temperature that includes the temperatures of air and water (soil) in the root zone. However, it is important to investigate the effects of air and water temperatures on rice plants because they have great effect on various growth processes individually and the flooded water temperature often differs from the air temperature. The magnitude and direction of the differences varies with weather conditions and the growth stage of rice (Shimono et al., 2007a, b; Kuwagata et al., 2008). In addition, successive water supply to the paddy field and excessive water drainage from the soil often decreases the flooded water temperature even on sunny days. Quantitative investigation on the effect of the temperature in the root zone should contribute not only to understanding the mechanism of rice plant resistance to low temperature more clearly but also to the improvement of rice cultivation in cool climate area.

During the vegetative period, a lower flooded water temperature reduces the rate of tillering, delays leaf number, and reduces leaf elongation (Takamura et al., 1960, Matsushima et al., 1964, Shimono et al., 2002). In some cases, these changes are accompanied by leaf yellowing (Kondo and Okamura, 1931). Grain yield can also be reduced by physiological changes, such as nutrient absorption by root system, that occur during the vegetative period (Shimazaki et al., 1963). Since the low temperature of flooded water greatly affects biomass and grain yield,
several studies have been conducted to identify the underlying mechanisms (Takamura et al. 1960; Matsushima et al. 1964; Satake, 1976; Shimono et al., 2002). However, it is still unclear whether these mechanisms were caused by the integrated effects of low temperature on the root zone and shoot meristem near the soil surface or the effect on the root system (root temperature) alone, because in many studies flooded water was cooled in the paddy field accompanied with a decrease in air temperature. Leaf growth, which is important for dry matter production, is strongly affected by environmental factors such as temperature (Sato, 1972; Shimono et al., 2002). The reduction of dry matter production by the low temperature of flooded water might be a direct effect of low temperature on the shoot growth. On the other hand, Shimono et al. (2004) indicated that the water content of plant and bleeding from the plant after shoot excision were lower under a low flooded water temperature condition, suggesting that the low temperature of flooded water inhibits water uptake by the root and thereby reduces dry matter production. It is important to evaluate the effect of a low root temperature on water uptake separately from that on other processes to better understand the mechanism of rice plant resistance to low temperature.

It has been shown that low root temperature inhibits water uptake by roots (reviewed by Kramer and Boyer, 1995). Since the water movement throughout a plant is strongly regulated by that in the root system, the inhibition of water uptake by low root temperature should affect plant water content and, as a result, dry matter production. Water uptake is controlled by both the water permeability of the root surface and the root volume. Low root temperature inhibits root growth, although there are wide differences among species in the optimal temperature for root growth (reviewed by Kramer and Boyer, 1995). However, there are few studies on the relationship between low root temperature and root volume in rice plants. On the other hand, Murai-Hatano et al. (2008) reported that root hydraulic conductivity in rice ($L_p$), which relates to its permeability, decreased with decreasing root temperature, and that $L_p$ decreased dramatically at temperatures below 15°C. Such phenomenon has been reported in several other plant species (Clarkson, 1976; Markhart et al., 1979; Wan et al., 2001; Lee et al., 2004b). It is necessary to clarify which of these factors is mainly affected by a low root temperature.

In the present study, we hypothesized that low root temperature would inhibit rice dry matter production resulted from water stress caused by reduced water uptake by the root. To test this hypothesis, we investigated the effects of long-term low root temperature on dry matter production, leaf area, root water uptake, and root morphology in rice plants in hydroponic culture. To avoid a direct effect of low temperature on the meristem of the rice shoots, we held the shoot meristem more than 3 cm above the hydroponic solution and maintained moderate growth conditions except for the root temperature.

Materials and Methods

1. Plant material

Rice seedlings (cv. ‘Akitakomachi’) were grown for 26–27 days including the time for germination. This cultivar is adapted to cold condition, and is often used in Tohoku region.

2. Growth conditions

Rice seeds were germinated in tap water in the dark for 1 d at 25°C. Thereafter, the germinated seeds were transplanted into small holes in an expanded polystyrene cap of a 200-mL glass bottle filled with the hydroponic solution. This solution contained 0.71 mM nitrogen (NH₄NO₃), 0.32 mM phosphorus (NaH₂PO₄), 0.26 mM potassium (K₂SO₄), 0.25 mM calcium (CaCl₂), and 0.41 mM magnesium (MgSO₄), 0.036 mM iron (Fe(III)-EDTA), and 0.0091 mM manganese (MnCl₂); the solution pH ranged from 5.5 to 6.0.

When roots had elongated to 2 cm (5 d old including germination), we gradually lifted the shoot meristem and held it more than 3 cm above the surface of the hydroponic solution. This was to avoid the direct effect of the low temperature given to the root system on the growth of the shoot, and to keep the root base dry and hard. These precautions were also necessary for the $L_p$ measurements described later (Murai-Hatano et al., 2008). The rice seedlings were grown in a PGW36 controlled-environment growth chamber (Conviron, Canada) at 25°C during the day and 20°C at night for 12 days. The light intensity (photosynthetically active radiation) was held at 250 μmol m⁻² s⁻¹ for 23 d, until the measurements.

3. Low temperature treatment of root

At 12 d after the start of germination (12 d old), we began the low temperature treatment of root. The seedlings were transferred into glass containers with fresh hydroponic solution and were set in a foamed polystyrene water bath (14 L) in the growth chamber. The root temperature was maintained at 14.0 ± 0.1°C (mean ± S.D.; low root temperature) by circulating cooled water in the polystyrene water bath using a recirculating chiller (CTP-1000, EYELA, Japan). Water temperature in the polystyrene water bath for control plants was equivalent to air temperature and the root temperature of control plants was 27°C/19°C (day/night). However, the temperature around the shoot meristem was 26°C/19°C (day/night) in both low temperature treated and control plants.

4. Growth analysis

Plants at 27 d after the start of germination (27 d old) were sampled for growth analysis. We sampled three to
four plants in each of four experiments, and calculated the means of the values in each experiment (n=4). We measured total leaf area (A) with aWinRhizo scanner and imaging software (Regent Instruments Inc., Canada), and then separated the plants into leaf blades, stems (including leaf sheaths and culms), and roots. The dry weight of each part was measured after oven-drying for more than 72 hr at 80°C. We calculated the mean of single leaf area by dividing A by the number of leaves. Net assimilation rate (NAR, mg m⁻² d⁻¹) was calculated as follows:

$$NAR = \frac{1}{A} \times \int_{t_0}^{t+\Delta T} \left( \frac{dTW}{dT} \right) dt,$$

where \(T_0\) is the time when the low temperature treatment of root started, \(\Delta T\) is the duration of this treatment, \(A\) is total leaf area and \(TW\) is the total dry weight. In calculating NAR we assumed that \(A\) increased exponentially with time.

5. Measurement of photosynthetic rate and related parameters

We measured the light-saturated photosynthetic rate (\(P_{sat}\)), stomatal conductance (\(G_s\)), and the \(CO_2\) concentration inside the leaf (\(C_l\)) simultaneously for the uppermost fully-expanded leaf on the main stem of three to four 27-d-old plants using an LI-6400 portable gas-exchange system (LI-COR, Lincoln, NE, USA). All measurements were made at a \(CO_2\) concentration of 400 \(\mu L L^{-1}\) and an irradiance (photosynthetic photon flux density) of 2000 \(\mu L L^{-1}\ s^{-1}\) under artificial light, an air temperature of 25°C, a root temperature of 25°C (control) or 14°C, and a vapour pressure deficit of 1.54±0.11 kPa. To evaluate the maximum leaf photosynthetic potential, we made the measurements within a 3 hr period in the morning (09:00 to 12:00). In addition, the high irradiance illuminated only the leaf being used for the photosynthetic measurements, and the other leaves were kept at ambient irradiance to avoid excess plant water stress.

6. Measurement of relative water content (RWC) and plant transpiration

We transferred the 26-d-old seedlings into 100-mL plastic bottles (with the surface covered by aluminum foil to prevent evaporation) filled with the hydroponic solution at either 14°C or 27/19°C (day/night, the control) in the chamber, and weighed them for 1 d to determine the transpiration per plant. RWC of leaf blade and stem were measured in the morning and afternoon on the same day. RWC (\%) was calculated as follows:

$$RWC=\left(\frac{FW-DW}{TW-DW}\right) \times 100$$

where \(FW\) is the fresh weight, \(DW\) is the dry weight, and \(TW\) is the turgid fresh weight. \(TW\) was determined as the fresh weight after soaking in water for more than 5 hr (Hirasawa and Ishihara, 1978, Kohata, 1984).

7. Measurement of xylem sap exudation (bleeding) under pressure and determination of the hydraulic conductance and conductivity of the root system

Root hydraulic conductance (\(K_r\)) and root hydraulic conductivity (\(L_p\)) of 26-d-old seedlings were measured in both low temperature-treated and control plants using pressure chambers (Nihon ANS Co., Japan) that were modified as described by Murai-Hatano et al. (2008).

To measure these parameters, we carefully threaded the plant shoot through a silicon rubber stopper that fit in the hole at the centre of the pressure chamber’s metal lid so that the root system could be enclosed in the chamber under a static pressure.

We monitored the vertical temperature profile of the root medium at two points using an RTR-52 thermorecorder (T&D, Japan) so that the roots could be maintained at the desired temperature. The vertical temperature variation was within ±0.2°C. The stability of the temperature was also within ±0.2°C for most of the measurements.

To measure root hydraulic conductance, we excised the shoot with a razor blade at the root base. We collected the exuded xylem sap using a #702 microliter syringe (Hamilton Co., Nevada) for 30 to 180 s. \(K_r\) (m s⁻¹ MPa⁻¹) and \(L_p\) (m s⁻¹ MPa⁻¹) were calculated as follows:

$$K_r = \frac{V}{\Delta P} \quad L_p = \frac{K_r}{A}$$

where \(V\) is the flow rate of xylem sap (m³ s⁻¹), \(\Delta P\) is the applied pressure, and \(A\) is the total root surface area. There was a linear relationship between \(V\) and \(\Delta P\) (from 0.02MPa to 0.2 MPa above atmosphere), and \(K_r\) was calculated as the slope of the \(V\) versus \(\Delta P\) relationship. We characterized the root morphology (e.g., \(A\) and the number of lateral roots) using the WinRhizo scanner and imaging software.

8. Statistical analysis

We tested for significant differences (P<0.05) between the treatments in dry matter production, leaf photosynthesis, water content, and root water uptake by \(t\) tests using the data of individual experiments from 3 - 4 separate plants in each experiment (n=4) except for 2 experiments (n=6 or 7) for \(K_r\) and \(L_p\) measurements as implemented by the software (Excel for Windows).

Results

1. Effects of low root temperature on dry weight, leaf area, and leaf photosynthesis

Figure 1 shows the total dry weight and total leaf area of the treated and control plants. Although all the plants grew under the same air temperature, total dry weight of the plants whose root system was exposed to a low temperature (simply called treated plants, hereafter) was
55.2 mg, which was about 70% of that in the control plants (77.0 mg, Fig. 1A), and this was significantly different from the control. \( A_l \) was also about 40% lower in the treated plants (2.98 m\(^2\)) than in the control (5.01 m\(^2\); Fig. 1B). Although the leaf number was also significantly lower in the treated plants (Table 1), this reduction was relatively small compared with the reduction in total leaf area (Fig. 1B) and specific leaf area (SLA, leaf area per unit leaf dry weight; Table 1). In addition, a low temperature treatment of root significantly decreased leaf dry weight (66% of control) and dry matter allocation to the leaves (93% of control, Table 1). SLA and single-leaf area were both significantly lower in the treated plants (Table 1). On the other hand, \( NAR \) was only slightly (and not significantly) lower than that in the control plants (Fig. 2). Similarly, there was no significant difference in \( P_{\text{max}} \) at 15 d after the start of low temperature treatment between the treated and control plants (Table 2).

### 2. Effects of low root temperature on water transport and related parameters

Table 3 compares the RWC of the treated and control plants. RWC of leaf blade on the treated plants was almost equal to that on the control plants, and daytime depression of RWC of the leaf blade was not seen in either treated or control plants (Table 3). However, the RWC of the stem

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**Table 1.** Leaf number, dry weight, dry matter allocation to the leaf (Allocation), specific leaf area (SLA) and single leaf area of rice plants as affected by a low root temperature.

|                      | Leaf number | Leaf dry weight (mg plant\(^{-1}\)) | Allocation (%) | SLA (×10\(^{-3}\) m\(^2\) g\(^{-1}\)) | Single leaf area (×10\(^{-4}\) m\(^2\) plant\(^{-1}\)) |
|----------------------|-------------|------------------------------------|----------------|------------------------------------------|--------------------------------------------------|
| Control              | 5.23 ± 0.20 | 21.9 ± 4.23                        | 28.2 ± 1.82    | 24.5 ± 2.76                              | 0.95 ± 0.13                                      |
| Low root temperature | 4.80 ± 0.10 | 14.5 ± 2.43                        | 26.3 ± 1.44    | 20.8 ± 1.97                              | 0.62 ± 0.06                                      |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown. * indicates significance at the 5% level.

**Table 2.** Light-saturated photosynthetic rate \( (P_{\text{max}}) \), stomatal conductance \( (G_s) \) and CO\(_2\) concentration inside the leaf \( (C_i) \) of rice plants as affected by a low root temperature.

|                  | \( P_{\text{max}} \) (\( \mu \)mol m\(^{-2}\) s\(^{-1}\)) | \( G_s \) (mol m\(^{-2}\) s\(^{-1}\)) | \( C_i \) (ppm) |
|------------------|-----------------------------------------------------|--------------------------------------|----------------|
| Control          | 13.0 ± 1.97                                         | 0.25 ± 0.03                          | 270 ± 30.7     |
| Low root temperature | 13.3 ± 3.34                                    | 0.27 ± 0.06                          | 285 ± 31.6     |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown. ns, not significant.
length (30% of control), total root surface area (48% of control) and specific area of the roots (67% of the control, Table 5). Although there was no statistical difference in allocation rate of dry matter to the root between the treated and control plants, the mean value was lower in the low-temperature-treated plants than in the control plants. (Table 5). In both treated and control plants, the number of primary roots was the same, but the total number of lateral roots and the number of lateral roots per primary root were significantly lower (less than 40% of control, decreased in the afternoon, and was significantly lower in the treated plants (to 85.6%) than in the control plants (89.7%) (Table 3). Transpiration (E) per plant in the treated plants was less than 50% of that in the control plants (Table 4). The E per leaf area but not that per root surface area was also significantly lower in the treated plants than in the control (Table 4). Similarly, Kr decreased to less than 50% of the control value, but Lp (= Kr/Ar) (Table 4).

**Table 3.** Relative water content (RWC, %) of leaf blade and stem in the morning (a.m.) and in the evening (p.m.) of rice plants as affected by a low root temperature.

|                | Leaf     |            | Stem     |            |
|----------------|----------|------------|----------|------------|
|                | a.m.     | p.m.       | a.m.     | p.m.       |
| Control        | 97.6 ± 0.45 | 94.7 ± 1.25 | 98.4 ± 0.56 | 89.7 ± 1.11 |
| Low root temp. | 96.6 ± 0.71 | 93.9 ± 1.01 | 97.1 ± 0.40 | 85.6 ± 0.75 |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown. ns, not significant. * indicates significance at the 5% level. RWC of a.m. and p.m. were measured just before illumination and 8 hr after illumination start, respectively.

**Table 4.** Transpiration per plant (E), plant transpiration per leaf area (E/A), plant transpiration per root surface area (E/Ar), hydraulic conductance (Kr) and hydraulic conductivity (Lpr) of a root system of rice plants as affected by a low root temperature.

|                | E (g d⁻¹ plant⁻¹) | E/A (×10⁻³ g d⁻¹ m⁻²) | E/Ar (×10⁻³ m² s⁻¹ MPa⁻¹) | Kr (×10⁻⁶ m s⁻¹ MPa⁻¹) | Lpr (×10⁻⁸ m³ s⁻¹ MPa⁻¹) |
|----------------|------------------|----------------------|---------------------------|------------------|------------------|
| Control        | 1.30 ± 0.27      | 2.56 ± 0.28          | 538 ± 101                 | 0.53 ± 0.17      | 21.7 ± 5.90      |
| Low root temp. | 0.52 ± 0.07      | 1.96 ± 0.34          | 438 ± 62                  | 0.21 ± 0.04      | 18.7 ± 4.24      |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown for E, E/A, and E/Ar. Means ± S.E. of 6–7 plants in 2 experiments are shown for Kr and Lpr. ns, not significant. ** and * indicates significance at the 1% and 5% level, respectively.

**Table 5.** Root dry weight, dry matter allocation to the root (Allocation), root length, total root surface area (Ar) and specific root surface area (SRA) of rice plants as affected by a low root temperature.

|                | Root dry weight (mg plant⁻¹) | Allocation (%) | Root length (m plant⁻¹) | Ar (×10⁻⁴ m plant⁻¹) | SRA (cm² g⁻¹) |
|----------------|-----------------------------|----------------|------------------------|----------------------|---------------|
| Control        | 19.8 ± 2.68                 | 26.0 ± 1.33    | 4.58 ± 0.40            | 25.2 ± 2.53          | 1.40 ± 0.19   |
| Low root temp. | 13.0 ± 2.00                 | ns             | 1.36 ± 0.23            | 12.2 ± 0.75          | 0.94 ± 0.09   |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown. ns, not significant. ** indicates significance at the 1% level. Allocation = root dry weight / total dry weight × 100. SRA = root surface area / root dry weight

**Table 6.** Numbers of primary roots, lateral roots and lateral roots per primary roots of rice plants as affected by a low root temperature.

|                | Primary roots | Lateral roots | Lateral roots per primary roots |
|----------------|---------------|---------------|-------------------------------|
| Control        | 12.5 ± 0.86   | 180.0 ± 129.7 | 155.0 ± 12.4                 |
| Low root temp. | 14.8 ± 2.06   | 701.3 ± 184.5 | 54.8 ± 19.5                  |

Means ± S.E. of 4 experiments with 3–4 plants in each experiment are shown. ns, not significant. ** indicates significance at the 1% level.
Discussion

Although there are many reports on rice growth at suboptimal temperatures (including air and flooded water temperatures, reviewed by Nishiyama, 1985), few researchers have reported the effect of root temperature on crop dry matter production. In addition, even though a sufficient supply of water from root to shoot is crucial for dry matter production, few studies have examined the effect of low root temperature on the water supply. In the present study, we determined the effect of low root temperature on rice growth in relation to dry matter production and root water uptake.

Low root temperature decreased dry matter production during the vegetative stage, and also leaf area significantly (Fig. 1B). Total leaf area ($A_l$) is determined by tillering number, leaf appearance, and single-leaf area. Shimono et al. (2002) found that the dry matter production of rice grown in low flooded water temperature condition decreased severely with decreasing tiller number and leaf number during the vegetative period. In the present study, however, the main factor responsible for decreased $A_l$ was the reduction in single-leaf area (Table 1). This difference came from the difference in the growth stage of the plants examined, i.e., we used younger plants and sampled them just before tillering. In addition, the effect of low root temperature on leaf number in our experiment was much smaller than that in their experiment in which both root and meristem were cooled (Shimono et al., 2007c). We lifted the shoot apex (meristem) above the water surface and protected the meristem from the low temperature. In the present experiment, the reduction in $A_l$ a major factor that determines dry matter production, resulted from decreased single-leaf area (Fig. 1, Table 1). In addition, low root temperature decreased dry matter allocation to the leaves and SLA (Table 1). These changes suggested that the inhibition of allocation of photosynthates to the leaves and the leaf thickness should cause the reduction in single-leaf area and, as a result, $A_l$.

On the other hand, $NAR$ was not significantly affected by the low root temperature (Fig. 2). Under high intensity of the light, $P_{\text{max}}$ at 15 d in the treated plants (low root temperature) did not differ significantly from that in the control, indicating that photosynthetic capacity was not strongly affected by low root temperature (Table 2). Similarly, Shimono et al. (2004) found no effect of low flooded water temperature on the photosynthetic rate of rice during the vegetative stage. The reduction in total dry weight caused by low root temperature therefore could be mainly due to the reduced leaf area.

Leaf growth is sensitive to various environmental stresses such as low temperature (Sato, 1972; Shimono et al., 2002), water deficits (Boonjing and Fukai, 1996), and nitrogen deficiency (Hasegawa and Horie, 1997). Tang and Boyer (2002) indicated that leaf growth was controlled by water potential difference between xylem and expanding cells in growing parts, which was usually lower than that in the mature parts in the leaf blade, and this water potential difference is very sensitive to water supply from the roots. $RWC$ of the leaf blade was not significantly influenced by the low temperature treatment of root, but that of the stem was significantly decreased by the treatment in the afternoon (Table 3). In the present study, mature parts of the leaves were sampled to measure $RWC$ of leaf blade, and growing leaf parts were included in the stem. Damage in mature leaves by low root temperature should be lower because mature parts of the treated leaves did not show lower water condition ($RWC$ and photosynthetic capacity ($NAR$ and $P_{\text{max}}$) than those of control significantly (Fig. 2, Tables 2, 4). These observations may indicate that low root temperature decreased water potentials of the stem and growing parts of the leaves in the afternoon, causing the reduction in leaf area, but did not reduce the physiological activity of the mature leaves. The stem water was utilized complementarily as the resource for diurnal leaf transpiration in napiergrass (Nagasuga 2004). Although there were few studies on the use of stem water in rice plants, diurnal leaf transpiration might be compensated temporarily by stem water in the low root temperature condition.

Plant water status depends on the balance between root water uptake and water loss (transpiration) from the shoot. Low flooded water temperature affects this relationship by decreasing both plant water content and transpiration in rice (Hasegawa et al., 1999), and similar results have been reported in cotton and bean plants (McWilliam et al., 1982). In the present study, the low root temperature decreased $E$ and $RWC$ of stem (Tables 4, 5). Plant transpiration is almost equal to water uptake by the root system during the early vegetative stage (Hirasa, 1987), and the response of $E$ to low root temperature could be regarded as that of root water uptake. Since $K_e$ also decreased significantly in the treated plants (Table 4), the reduction in $RWC$ of stem by low root temperature would be associated with that in root water uptake. Root water uptake is controlled by both the water permeability of the root surface and the root volume. $E$ and $K_e$ were lower in the treated plants, but there was no significant difference in $E/\text{NAR}$ and $P_{\text{max}}$ ($K_e/\text{A}_{l}$) between the treated and control plants (Table 4). These results suggest that the response of root water uptake to a low temperature was associated with the change in quantity of roots, such as $A_l$ and root number. In the treated plants, root dry weight was lower, $A_l$ and root surface area per unit root dry weight was larger than in the control plants (Table 5). Although the number of primary roots was not influenced, the number of lateral roots was significantly decreased by a low root temperature (Table 6). These findings suggest that the low temperature...
treatment of root decreased the root surface area through a decrease in the number of lateral roots, leading to reduced root water uptake.

Many investigators have suggested that crops must develop deep and branched roots to avoid drought stress (Hurd, 1974; Jordan and Miller, 1980; Taylor, 1980). Lilley and Fukai (1994) demonstrated that rice with a high root-length density (i.e., long root length per unit soil volume) take up more water under drought. Lateral root formation has been extensively studied using the model plant Arabidopsis thaliana, revealing that auxin played a critical role in the initiation of lateral roots (Celenza et al., 1995; Hobbie and Estelle, 1995; Reed et al., 1998; Ruegger et al., 1998; Xie et al., 2000; Fukaki et al., 2002). Although there is little information about the environmental control of auxins, the low root temperature might decrease the number of lateral roots by inhibiting auxin transport or signalling in the root system. The change in root growth under a low root temperature condition should be evaluated in the future study.

Before this study, we hypothesized that water stress induced by low root temperature would result from decreased Lp, because in a previous study with rice plants, Lp decreased drastically within 2 to 3 hr after exposure of root to a low temperature (Murai-Hatano et al., 2008). In the present study, however, Lp was not significantly changed by the low temperature treatment of root (Table 4). In addition, we observed no significant change in E/A (Table 4). Furthermore, the difference in Lp and E/A, between the treated and control plants was much smaller than the difference in A (Tables 4, 6). These results indicate that the effect of the low root temperature on Lp would be smaller than that on A.

In our previous study (Murai-Hatano et al., 2008), we measured Lp just before exposure of the root to a low temperature, and we completed our experiments within 2 to 3 hr. In the present study, the roots were exposed continuously to low temperature for about 2 weeks to 3 hr. In the present study, the roots were exposed to a low temperature for about 2 weeks. In the present study, we hypothesized that water stress induced by low root temperature would result from decreased Lp, because in a previous study with rice plants, Lp decreased drastically within 2 to 3 hr after exposure of root to a low temperature (Murai-Hatano et al., 2008). In the present study, however, Lp was not significantly changed by the low temperature treatment of root (Table 4). In addition, we observed no significant change in E/A (Table 4). Furthermore, the difference in Lp and E/A, between the treated and control plants was much smaller than the difference in A (Tables 4, 6). These results indicate that the effect of the low root temperature on Lp would be smaller than that on A.

In conclusion, low root temperature inhibited dry matter production of rice plants by decreasing leaf area rather than by decreasing photosynthetic rate. The response of leaf area to a low root temperature was affected by plant water status, since RWC of the stem was decreased by the low root temperature resulting in a reduced leaf area. The reduction in RWC caused by low root temperature was related to significantly decreased Ks. The responses of E and Ks to a low root temperature depended more on a change in root surface area than on changes in Lp. These results suggest that dry matter production during a long-term exposure of root to a low temperature is controlled mainly by quantitative growth parameters such as leaf area and root surface area.

Acknowledgements

We are grateful to Dr. Maki Katsuhara and Dr. Tomoyuki Kaneko (Okayama University) for their helpful advice on measuring root hydraulic conductance using a pressure chamber.

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* In Japanese.

** In Japanese with English summary.