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To cite this article: Yumiko Arai-Sanoh, Tsutomu Ishimaru, Akihiro Ohsumi & Motohiko Kondo (2010) Effects of Soil Temperature on Growth and Root Function in Rice, Plant Production Science, 13:3, 235-242, DOI: [10.1626/pps.13.235](https://doi.org/10.1626/pps.13.235)

To link to this article: <https://doi.org/10.1626/pps.13.235>



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Published online: 03 Dec 2015.



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Effects of Soil Temperature on Growth and Root Function in Rice

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Abstract: The objective of this study was to clarify the effects of soil temperature in the stage from late tillering to panicle initiation (SI) and during the grain-filling stage (SII) on grain setting, dry matter production, photosynthesis, non-structural carbohydrate (NSC), xylem exudation and abscisic acid (ABA) levels in rice (*Oryza sativa* L. cv. Koshihikari). Rice plants were exposed to four different soil temperatures during SI or SII: 17.5, 25, 31.5 and 36.5°C (ST18, ST25, ST32 and ST37, respectively). The yield, yield components, grain filling and quality in SI were negatively influenced by high soil temperature of 37°C. On the other hand, there was no significant difference in those characters among temperature treatments in SII. The root/shoot ratio was smallest in the ST37 plants in both SI and SII, mainly due to their lighter root weight. At 7 days after initiation of treatment (DAT) in both SI and SII, the photosynthetic and xylem exudation rate tended to increase slightly as soil temperature increased up to 32°C. At 21 DAT, however, the photosynthetic rate was lowest in ST37, with concurrent decrease of diffusion conductance and SPAD value. In addition, decrease of NSC concentration in stem and xylem exudation rate, and increase of ABA level in leaves and xylem exudate were observed in ST37 plants at 21 DAT. These results suggested that high soil temperature before heading especially influenced yield, grain quality and plant growth. Possible mechanisms of the effect of soil temperature are discussed.

Key words: Abscisic acid (ABA), Non-structural carbohydrate, Photosynthesis, Rice (*Oryza sativa* L.), Root/shoot ratio, Soil temperature, Xylem exudation.

Plant growth is affected by many environmental factors such as temperature and solar radiation. Many studies on the effects of low temperature on rice plants (*Oryza sativa* L.) have shown how cold temperatures degrade plant growth, panicle formation and grain filling (Nishiyama, 1985; Wada, 1992); these studies have helped to improve the low-temperature tolerance of rice. Recently, however, the threat derived from high temperatures is becoming more important since air temperature has been gradually increasing, especially in temperate regions, possibly due to human anthropogenic global climate change (IPCC, 2001). Recent studies have shown that high temperatures cause a deterioration of rice yield and grain quality in temperate regions (Kondo et al., 2005; Morita, 2008). The chalkiness of the grain increased when the average air temperature for 20 days after heading was above 26–27°C (Morita, 2005). Development of agronomic techniques and genotypes adapted to minimize the stress caused by high temperatures as well as low temperatures will be a crucial target in rice research. The water and surface soil temperatures in paddy fields increase as air temperature increases. Soil temperature is more influential than air temperature on plant growth, photosynthesis and

respiration in wheat (*Triticum aestivum* L.) (Kuroyanagi and Paulsen, 1988) and in grass (*Agrostis palustris* Huds.) (Xu and Huang, 2000a, 2000b). Nevertheless, little information is available on the effects of soil or root temperature on plant growth, yield and quality in rice though such information is critical for the development of countermeasures against high-temperature stress.

In several field crops such as grass, wheat, cucumbers (*Cucumis sativus* L.), tomatoes (*Lycopersicon esculentum* Mill.), and apple trees (*Malus sylvestris* Mill.), supraoptimal root temperature caused negative effects on shoot and root growth (Du and Tachibana, 1994a; Gur, et al., 1972; Lyons et al., 2007; Xu and Huang, 2000a), photosynthesis and carbohydrate metabolism (Du and Tachibana, 1994b; Xu and Huang, 2000b), and water and nutrient uptake (Huang and Xu, 2000; Klock et al., 1997; Tahir et al., 2008). The production of cytokinins and abscisic acid (ABA) in roots has been suggested to have a significant role in regulating shoot growth and photosynthesis under high soil temperature in wheat and grass (Liu and Huang, 2005). In this study, we aimed at (1) comparing the effect of soil temperature at the stage from late tillering to panicle initiation (SI) and the grain-filling stage (SII), on

dry matter production of shoots and roots, yield and grain quality, and (2) clarifying the effect of soil temperature on the photosynthetic rate, xylem exudation rate and ABA level in rice.

Materials and Methods

1. Plants grown in soil

Pot experiments were conducted under controlled soil temperatures using the rice cultivar "Koshihikari" (*Oryza sativa* L. cv. Koshihikari). Seedlings at the fourth leaf stage were transplanted to Wagner pots (1/5000 a) with paddy soil on May 15, 2005, with one plant per pot. The pots were placed into four containers (5 m length×0.6 m width×0.6 m depth) in a water bath with temperature control. All measurements were made in four replicated pots. The soil temperature was kept constant at 17.5, 25, 31.5 and 36.5°C (ST18, ST25, ST32 and ST37) during the stage from late tillering to panicle initiation (SI, July 5-July 25) and during the grain-filling stage (SII, Aug. 13-Sep. 15). The average water temperature at 5 cm depth during treatments was 18.8, 23.2, 28.5 and 33.0°C in ST18, ST25, ST32 and ST37 respectively. Except for these treatment periods, plants were grown under ambient temperature conditions. The average air temperature during treatments was 25.7 and 26.5°C in SI and SII, respectively. Depth of standing water was maintained at 5 cm above soil surface throughout the growing period. Fertilizer was applied as a basal dressing at the rate of 0.3 g of N, P and K per pot. Top dressing of N was applied at the rate of 0.2 g per pot at the tillering stage and heading stage. Heading (50% heading) occurred on Aug. 7.

2. Measurements of plant growth and yield

Plants were sampled at 21 days after initiation of treatment (DAT), 27 days after heading (DAH) and at physiological maturity in both SI and SII. Dry weight was determined after drying plants for 3 days at 70°C in a ventilated oven. Grain yield and yield components were determined at physiological maturity. The ripening rate was calculated by dividing the number of brown rice grains >1.6 mm thick by the total number of grains. The percentage of chalky grain, defined as white-core, white-backed, white-belly and white-based rice kernels, was determined by a grain-quality testing machine (SATAKE, RGQI20A).

3. Measurements of photosynthetic rate and diffusion conductance

The photosynthetic rate and diffusion conductance were measured in four plants per replication using a portable photosynthesis system (LI-6400; LI-COR Inc., Lincoln, NE) in the topmost fully developed leaf on the main stem from 0900 to noon on a clear day before the marked mid-day depression occurred. The diffusion

conductance was calculated with this system according to the method of von Caemmerer and Farquhar (1981). The quantum flux density at the leaf surface, relative humidity and flow rate in the chamber, and leaf temperature were maintained at 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 60-70%, 180 $\mu\text{mol s}^{-1}$ and 30°C, respectively. The rate of CO_2 assimilation was measured at an ambient CO_2 concentration of 360 $\mu\text{L L}^{-1}$.

4. Measurement of non-structural carbohydrates

Dried samples of leaf sheath and culm were powdered for the measurement of soluble sugar and starch. Samples were treated with 80% ethanol at 80°C to extract soluble sugar. After centrifugation, the supernatants were dried with a rotary evaporator and dissolved in water. The residues were treated with boiled water to extract starch. After cooling, phosphate buffer containing amylase (from *Bacillus subtilis*) and amiloglucosidase (from *Rhizopus mold*) was added and incubated at 40°C for 20 hr. Level of soluble sugar was determined by high-performance liquid chromatography, using RI detector and column (Shodex, SUGER SP0810; Showa Denko K., Tokyo, Japan). Level of starch was determined according to the phenol-sulfuric acid method (Dubois et al., 1956) using glucose as standard.

5. ABA concentration in leaf and xylem exudate

For collection of xylem exudate, stems were cut with a sharp cutter 10 cm above the soil surface, and polyethylene bags containing pre-weighed cotton wool were attached to the cut ends with paper tape. After approximately 3 hr, the cotton wool was collected and weighed to calculate the weight of collected root exudate. Collected exudates were stored at -80°C until ABA determination. Leaf samples were taken and quickly frozen with liquid nitrogen, then stored at -80°C until ABA determination.

Determination of ABA in leaf and root exudates basically followed the procedures of Chono et al. (2006). Briefly, freeze-dried and powdered plant tissues were extracted with 80% (v/v) methanol. Solutions of xylem exudate in 80% methanol were prepared by soaking the cotton wool containing the exudates in a given volume of 100% methanol. $^2\text{H}_6$ -labeled ABA (purchased from Plant Biotechnology Institute, National Research Council of Canada) was added as an internal standard. The extract was purified using Sep-pak C18 cartridges (Waters, Milford, MA), which were rinsed with 80% methanol. After the effluent was evaporated under a vacuum, the residue was dissolved in 100% methanol and added to an equal volume of water. This sample was subjected to LC/MS/MS analysis using a quadruple tandem mass spectrometry (TSQ7000, Thermo Electron Corporation, Waltham, MA, USA) coupled with a liquid chromatograph (HP1100, Agilent Technology, Palo Alto, CA, USA) equipped with a column of CAPCELL PAK C18 MG (2.0 mm i.d.×150 mm; Shiseido Fine Chemicals, Yokohama, Japan). ABA was

Table 1. Yield components, grain quality and sterility in rice.

Cultivation term	Soil temperature (°C)	Grain wt. (g hill ⁻¹ pot ⁻¹)	Panicle no. (hill pot ⁻¹)	Spikelet no. (panicle ⁻¹)	1,000-kernel wt. (g)	Filled spikelets (%)	Sterility (%)	chalky grain (%)
SI	ST18	39.7 a	19.2 b*	92.6 a	21.1 a	80.8 a	12.8 b	15.6 b
	ST25	39.7 a	19.5 b	95.5 a	21.1 a	81.1 a	13.0 b	12.8 b
	ST32	39.2 a	17.9 b	98.1 a	21.1 a	86.1 a	10.7 b	17.1 b
	ST37	6.6 b	36.1 a	32.1 b	16.4 b	15.5 b	53.6 a	89.1 a
SII	ST18	38.2 a	16.8 a	109.2 a	21.4 a	87.4 a	8.8 a	16.9 a
	ST25	41.1 a	17.3 a	113.1 a	21.8 a	84.8 a	7.9 a	16.7 a
	ST32	41.2 a	16.9 a	112.1 a	21.0 a	87.2 a	8.4 a	19.3 a
	ST37	38.6 a	16.9 a	108.7 a	21.2 a	85.6 a	9.2 a	20.1 a

The grain weight and 1,000-kernel weight are given for a water content of 14%. 1000-kernel weight and percentages of filled spikelets refer to brown rice with a grain thickness of more than 1.6 mm. The percentage of filled spikelets was calculated by dividing the number of filled spikelets by the number of total spikelets. * Means followed by the same letters in the same stage are not different at the 5% level by LSD test (n=4).

SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage.

identified in a selected reaction monitoring mode using electrospray ionization which monitors negative daughter ions of m/z 153 and 159 derived from parental negative ions of m/z 263 (ABA) and 269 (²H₆-ABA), respectively.

In 2006, a similar pot experiment under controlled soil temperatures was repeatedly conducted and showed similar results in yield components, shoot and root growth, and root/shoot ratio as those in 2005. Therefore, we show only the results obtained in 2005.

Results

1. Yield components, grain quality and sterility

Grain yield, yield components and sterility rate are shown in Table 1. Compared with treatments at other temperatures, ST37 in SI showed an increase in the number of panicles per hill, but decreases in the grain weight, spikelet number per panicle, 1000-kernel weight and ripening rate, resulting in the lowest yield among treatments. In addition, the percentage of chalky grain and sterility rate were higher in ST37 in SI. There was no clear difference in yield and quality up to 32°C in SI. On the other hand, there was no significant difference in yield, yield components and quality among the treatments in SII. The effects of soil temperature on the final yield and grain quality were greater with the temperature treatments in SI than in SII.

2. Dry weight of shoot and root, and root/shoot ratio

Dry weight of shoot and root at 21 DAT in SI tended to be higher in ST25 and ST32 than in the other treatments (Fig. 1). The dry weight of ST37 root was remarkably lower, resulting in the smallest root/shoot ratio among SI treatments. While there were no significant differences in dry weight of shoots at the end of treatment among SII treatments, the dry weight of root and the root/shoot

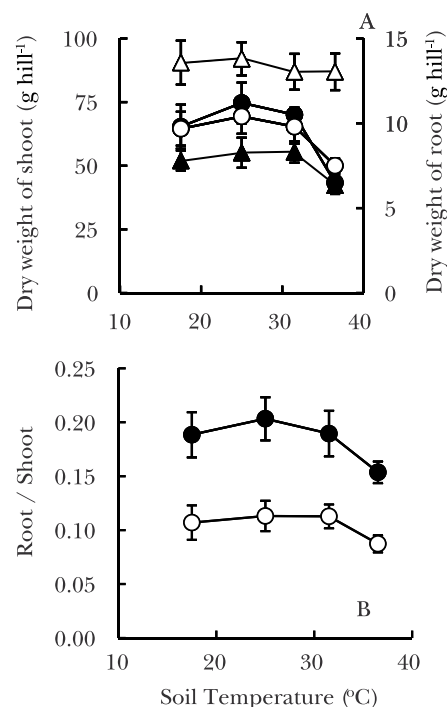


Fig. 1. Dry weight of shoot and root (A), and root/shoot ratio (B) at the end of treatment with various soil temperatures in SI and SII in rice.

Vertical bars represent standard deviation (n=4).

SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage.

(A) ● : SI, Root, ▲ : SI, Shoot, ○ : SII, Root, △ : SII, Shoot.

(B) ● : SI, ○ : SII.

ratio were smallest in ST37 among SII treatments.

3. Photosynthetic rate

The photosynthetic rate, diffusion conductance and SPAD value tended to increase as soil temperature increased up to 32°C at 7 DAT in SI and SII (Fig. 2).

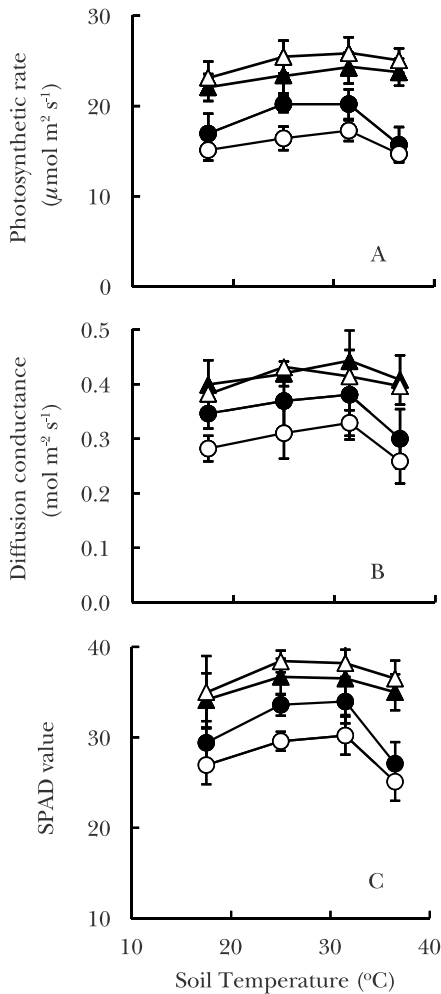


Fig. 2. Photosynthetic rate (A), diffusion conductance (B) and SPAD value (C) at 7 and 21 DAT in SI and SII at various soil temperatures in rice. DAT, days after initiation of treatment. Vertical bars represent standard deviations ($n=4$). SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage. \blacktriangle : SI, 7 DAT, \bullet : SI, 21 DAT, \triangle : SII, 7 DAT, \circ : SII, 21 DAT.

Similar photosynthetic rates were obtained for ST 32 and ST37. However, at 21 DAT in SI and SII, the photosynthetic rate tended to be lower in ST18 and ST37 than in the other treatments. The decrease in photosynthetic rate was associated with the lower diffusion conductance and SPAD values.

4. Starch and soluble sugar concentrations in leaf sheath and culm

Among SI treatments, the starch and soluble sugar concentrations in leaf sheath and culm were lowest in ST37 at 21 DAT, but highest in ST37 at 27 DAH (Fig. 3). In SII, these concentrations were slightly lower in ST37 than in the other treatments at 21 DAT.

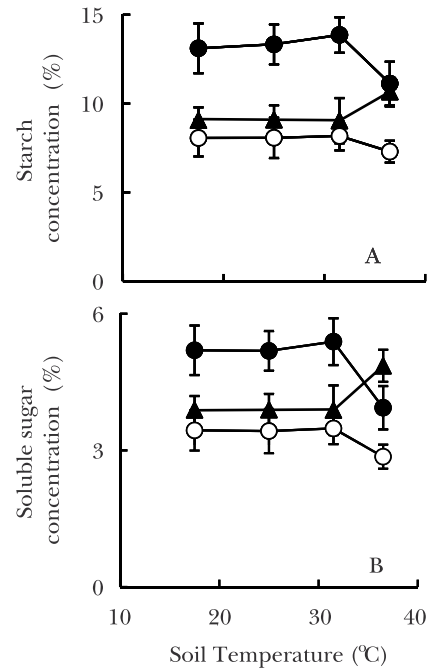


Fig. 3. Starch (A) and soluble sugar (B) concentrations in leaf sheath and culm at 21 DAT in SI and SII, and at 27 days after heading (DAH) in SI in rice. DAT, days after initiation of treatment. Vertical bars represent standard deviation ($n=4$). SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage. \bullet : SI, 21 DAT, \blacktriangle : SI, 27 DAH, \circ : SII, 21 DAT.

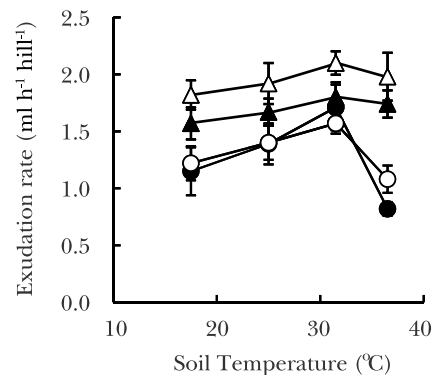


Fig. 4. Exudation rate at 7 and 21 DAT in SI and SII at various soil temperatures. DAT, days after initiation of treatment in rice. Vertical bars represent standard deviations ($n=4$). SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage. \blacktriangle : SI, 7 DAT, \bullet : SI, 21 DAT, \triangle : SII, 7 DAT, \circ : SII, 21 DAT.

5. Xylem exudation rate

In both SI and SII, the rate of xylem exudation increased at a higher soil temperature up to 32°C at 7 DAT (Fig. 4). The tendency among treatments changed at 21 DAT. The exudation rate in ST37 was markedly lower in 21 DAT in both treatments.

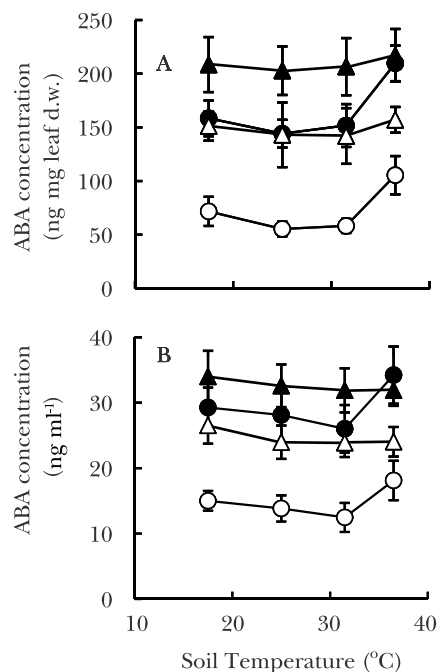


Fig. 5. ABA contents of leaf (A) and exudate (B) at 7 and 21 DAT in SI and SII at various soil temperatures in rice.

DAT, days after initiation of treatment. Vertical bars represent standard deviations ($n=4$).

SI: the stage from late tillering to panicle initiation, SII: the grain-filling stage.

▲ : SI, 7 DAT, ● : SI, 21 DAT, △ : SII, 7 DAT, ○ : SII, 21 DAT.

6. ABA levels in leaf and xylem exudate

In both SI and SII, ABA levels in leaf and xylem exudate were not significantly different among treatments at 7 DAT (Fig. 5). At 21 DAT, however, the ABA levels in leaf and exudates in ST37 were significantly higher than those for other treatments in both SI and SII.

Discussion

1. Yield and grain filling

The results showed that the effects of soil temperature on final yield and grain quality were greater in SI than in SII (Table 1). Panicle formation is assumed to be sensitive to water and soil temperature, because young panicles are located within or near the water level. It is well established that a water temperature below approximately 19°C at panicle initiation causes a decrease in the number of spikelets per panicle, delayed heading and increased sterility in rice (Nishiyama, 1985; Wada, 1992). There was no effect on panicle formation in ST18. This was due to the fact that soil temperature treatment finished by 16 d before heading and water temperature during the day time was higher than 19°C. On the other hand, a marked negative effect on yield and quality was observed in ST37. The soil temperature of 37°C in SI increased the panicle number, but decreased the number of spikelets per panicle

thereby increasing the sterility rate. In addition, the 1000-kernel weight and ripening rate were decreased in ST37 in SI. The high water temperature of 37°C caused an increase in the number of the tillers emerged later and killed the young panicle inside the tiller (Tsunoda, 1964; Matushima and Tsunoda, 1959). A high soil temperature in SI at panicle initiation would affect the grain filling process in addition to the grain setting process. For grain quality, the increased rate of chalky grain in ST37 in SI also supports the possibility that a high soil temperature before the heading stage would significantly affect the grain filling. Grain filling is supported by photosynthesis after heading and also by accumulated non-structural carbohydrate in the leaf sheath and culm before heading. Reduced grain size and deteriorated grain quality occur when the carbohydrate supply to the grain is insufficient (Kobata et al., 2004; Sato et al., 1973). In this study, non-structural carbohydrate concentrations in the leaf sheath and culm (Fig. 3) and its contents per grain (data not shown) were smaller in ST37 at 21 DAT in SI. Then, insufficient carbohydrate supply to the panicle inhibited grain filling, especially at the early ripening stage. It would be interesting to investigate the mechanisms by which the soil temperature treatment before heading affects non-structural carbohydrate accumulation in vegetative organs and the starch synthesis ability of spikelets.

Our results suggested that there was no significant effect of soil temperature treatment in SII on yield and grain quality. After heading, water and soil temperature hardly affected grain filling in rice (Morita et al., 2004; Tsunoda, 1964). This is contrary to previously reported results in other crops. In wheat, it is reported that high root temperature at 30–38°C during ripening had a significant effect in reducing the weight of the kernels (Guedira et al., 2000; Guedira and Paulsen, 2002; Kuroyanagi and Paulsen, 1988), the duration of grain filling, the contents of sucrose and starch, and the activities of starch synthesis-related enzymes in grain (Guedira and Paulsen, 2002). Also, senescence occurred at the high root temperature of 35°C in wheat during the ripening stages (Kuroyanagi and Paulsen, 1998). In this study with rice, although photosynthesis decreased in ST37 at the later ripening stage (Fig. 2), grain filling was insensitive to high root temperature (Table 1). As mentioned above, carbohydrates accumulated before heading provided a complementary supply of carbon to grain filling, when the supply of carbohydrates from photosynthesis was not sufficient. The carbohydrate supply from other organs to the panicle might have compensated in the grain filling, resulting in stable grain filling across various soil temperatures. It should be noted that the adverse effect of extreme soil temperature during ripening on grain filling would be more prominent if the sink demand were large, as in the case of high spikelet numbers.

2. Root and shoot growth

The dry weight of shoot (Fig. 1) and plant height decreased, and the number of tiller (data not shown) increased in ST37 as compared with other treatments at 21 DAT in SI. This result seemed consistent with previous reports that root temperature treatment of $> 35^{\circ}\text{C}$ at tillering resulted in increased tiller number and decreased leaf area (Sasaki, 2002; Matsushima et al., 1964). Decreased shoot weight and plant height can be explained by the effect of water and soil temperatures on the apical meristem of shoot located at the base of the plant.

It should be noted that the root/shoot ratio decreased in ST37 in both SI and SII (Fig. 1). Decrease of root weight and root/shoot ratio at high soil temperatures compared with control temperatures of $22\text{--}24^{\circ}\text{C}$ has been reported in other crops: grass at 35°C (Xu and Huang, 2000a), wheat at 35°C (Tahir et al., 2008) and tree of heaven (*Ailanthus altissima*) at 34°C (Graves et al., 1991). The optimum soil temperature for root growth ranges from $10\text{--}18^{\circ}\text{C}$ in most cool-season grasses (Fly and Huang, 2004), and is about 20°C in cucumbers (Tachibana, 1982). In this study, optimum soil temperatures for root development in rice was approximately 25°C (Fig. 1). The optimal temperature for root growth appears to be higher in rice than in some other field crops.

The decrease in root/shoot ratio caused by high soil temperature may be attributed to inhibition of the formation and elongation of the main root (Sattelmacher et al., 1990), decreased distribution of carbohydrates to root (Xu and Huang, 2000b) and increased respiration (Du and Tachibana, 1994b). In this study, the partitioning of the dry matter to root tended to be smaller (data not shown). This would be related to lower carbohydrate distribution to root or increased respiration. To clarify the reason for the response of the root/shoot ratio to soil temperature, we need to investigate the dynamics of carbon transport from shoot to root.

3. Photosynthetic rate, non-structural carbohydrate concentration, xylem exudation rate and ABA level

Effect of soil temperature on photosynthesis varied with the duration of treatment (Fig. 2). The photosynthetic rate increased with temperature up to 32°C at 7 DAT. These results suggested that high soil temperature treatment in the short term stimulated higher water and nitrogen uptakes as indicated by a higher diffusion conductance and increased leaf nitrogen concentration (SPAD value), resulting in enhanced photosynthesis. A positive relationship between photosynthetic rate and water temperature has been reported in the range of $16\text{--}25^{\circ}\text{C}$ average daily temperature from the stage of panicle initiation to heading in rice (Shimono et al., 2004). The lower photosynthetic rate under low temperatures in that study was also associated with lower diffusion conductance.

On the other hand, the low rates of photosynthesis for ST18 and ST37 at 21 DAT in SI and SII were associated with decreased diffusion conductance and SPAD value (Fig. 2). Suppression of photosynthesis and related characteristics by long-term high root temperature has also been reported for other crops such as grass at 35°C for 10–58 d (Xu and Huang, 2000b). The factors of lowered diffusion conductance and SPAD value for high soil temperature in this study are discussed below.

The starch and soluble sugar concentrations of leaf sheath and stem were lower in ST37 than in other temperature treatments at 21 DAT in SI and SII (Fig. 3). The decrease may be partly attributed to the limited assimilation due to the lowered photosynthesis. In addition, high soil temperature possibly reduces the distribution of assimilated carbon into non-structural components. It is possible that allocation of assimilated carbon into non-structural and structural carbon was altered by soil temperature. Further study on the regulatory mechanisms of assimilation and distribution into non-structural components is needed. At 27 DAH, the starch and soluble sugar concentrations increased for ST37 in SI (Fig. 3). This increase might be relevant to a higher sterility rate and chalky grain rate, which resulted in limited demand for translocation of carbon from leaf sheath and stem.

The xylem exudation rate increased as soil temperature increased up to 32°C at 7 DAT but was lower in ST37 at 21 DAT (Fig. 4). Exponential increase of xylem exudation and root respiration rate by increased root temperature was observed in the range from 7 to 29°C for 3 hr treatments (Yamaguchi et al., 1995). In this study, root respiration, and uptake of water and nutrients might be stimulated by high soil temperature until 7 DAT. Inhibition of water uptake by long-term elevation of soil temperature was observed in tree of heaven (Graves et al., 1991) and wheat (Tahir et al., 2008); that of root respiration was observed in tomatoes (Klock et al., 1997). The nitrogen and water absorption in rice decreased by long-term elevation of water temperature at 37°C (Baba, 1958). Therefore, suppressed photosynthesis in ST18 and ST37 at 21 DAT were probably related in part to decreased water and nutrient capture due to lower root activity and a smaller root zone.

An effect of soil temperature on ABA level was also observed. ABA levels in leaves and xylem exudate did not vary with the treatment at 7 DAT, and increased at 21 DAT in ST37 (Fig. 5). The role and physiological significance of hormones in the xylem exudate as stress signals are widely recognized (Bano et al., 1993; Davies and Zhang, 1991; Sauter and Hartung, 2002). The ABA level has been shown to be increased by water stress, and inhibit transpiration through stomatal closure (Davies and Zhang, 1991). This suggests that high ABA production in roots conducted by

xylem flow is related to a reduction in the diffusive conductance of leaves under high soil temperature conditions. A high root temperature reduced the level of cytokinins and increased the level of ABA in the xylem exudate in beans (Itai et al., 1973). In addition, increased levels of ABA and decreased levels of cytokinins in shoots were observed when shoot growth was retarded at high soil temperatures in grass (Liu and Huang, 2005). Cytokinin was associated with the maintenance of photosynthetic rate in rice (Ookawa et al., 2004; San-oh et al., 2006; Soejima et al., 1992, 1995). Then, in this study, the interactive effect of ABA and cytokinins would relate to the decrease in photosynthesis, which contribute to the decline in dry weight of shoot and root under high soil temperature stress.

The overall results in this study signify that a high soil temperature before heading is more influential on yield, grain quality and plant growth compared with a high temperature during the ripening stage. Long-term elevation of soil temperature above 32°C has a negative effect on plant growth and yield. High soil temperature would magnify stress from high air temperatures. Further investigation is needed to clarify the effect of soil temperature under field conditions. We need a deeper understanding of the physiology of the temperature-sensing mechanisms of root and the interactive responses of shoot and root growth. Since soil temperature treatments in this study included the effects of soil chemical and microbial activities, we also need to distinguish these indirect effects from the direct effect of temperature on root.

Acknowledgements

We thank Dr. Satoshi Yoshinaga for helpful suggestions on the manuscript. This work was financially supported by Japan Society for the Promotion of Science.

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* In Japanese

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