Effects of High Temperature on Growth, Yield and Dry-Matter Production of Rice Grown in the Paddy Field

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Abstract: The effect of high temperatures on growth, yield and dry-matter production of rice growing in the paddy field was examined during the whole growth period in a temperature gradient chamber (TGC) from 2002 to 2006. Experimental plots, TG1 (control), TG2, TG3 and TG4, were arranged along the temperature gradient (from low to high temperature) in TGC. The mean and maximum air-temperatures in TG4 were 2.0−3.6ºC and 4.0−7.0ºC higher, respectively, than those in TG1. The plant height was taller and the maximum tillering stage was earlier in TG2, TG3 and TG4 than in TG1. Plant dry weight at maturity in TG2 and TG3 was 12.8−16.4% heavier than that in TG1. In TG4, the increase in the panicle dry weight during the ripening period was smallest and plant dry weight at maturity was 11−16% heavier than that in TG1. The increase in plant dry-matter during the ripening period was smallest in TG4. The decrease in the dry weight of stem and leaf during the ripening period, which represents the amount of assimilate translocation to the panicle, was also larger in TG2-4 than in TG1. The increase in the dry weight of stem in TG2-4 at maturity was also larger than that in TG1. The photosynthetic rate in TG2-4 was up to 35.6% lower than that in TG1 because of the acceleration of leaf senescence. Brown rice yield in TG4 was 6.6−39.1% lower than that in TG1. This yield decline was due to the decrease in the percentage of ripened grains and increase in the percentage of sterile spikelets. The relation between brown rice yield and mean air-temperature during 20 days after heading showed that the brown rice yield declined when mean air-temperature exceeded 28ºC.

Key words: Grain yield, High temperatures, Photosynthetic rate, Rice (Oryza sativa L.), Spikelet sterility.

The report of the Intergovernmental Panel on Climate Change (IPCC), predicted the global long-term climatic variation and estimated in 1990 that the mean global air-temperature would increase 1.4−5.8ºC by 2100 although the increase during the twentieth century was about 0.6ºC (IPCC, 2001). In Okayama City, in the Seto Inland Sea region, the mean air-temperature has increased 0.5ºC during the 100 years from 1890 to 1990 (Okayama Local Meteorological Observatory, 1991). The increase in CO₂ concentration, which is considered as the main cause of the global warming, may decrease stomatal conductance, which improves the water-use efficiency through the transpiration control (Morison and Gifford, 1983), depress the photorespiration, which promotes photosynthetic capacity, and thus increase the dry-matter production. This seems to be advantageous for the biomass production in C₃ plants (Imai, 1988; Sakaigaichi et al., 2004).

Although the productivity of crops becomes high with rising temperature, it declines due to the heat stress when the temperature exceeds the optimal range. In rice production, the occurrence of sterile spikelets caused by high temperatures during flowering is a constraint factor of yield (Kim et al., 1996a, b). The long-term (whole growth season) as well as short-term (flowering and ripening period) effect of high temperatures on the productivity of crops needs to be clarified urgently. In previous studies on the effect of high temperatures, plants grown in pots or small-scale fields were used and high-temperature treatments were not applied continuously. Only limited data are available for the effect of long-term temperature treatment on field-grown crops.

Kim et al. (1996a, b) clarified the effects of high-temperature and doubled CO₂ concentration on the growth and yield of rice grown in the temperature gradient chamber (TGC), but not on the leaf photosynthesis and dark-respiration. In this study, TGC was installed in paddy fields to clarify the effect of high temperatures during the whole growth period on growth, yield and dry-matter production of rice.

Materials and Methods

1. Temperature gradient chamber (TGC)

The experiments were carried out for five years from 2002 to 2006. TGC (30m length, 2.1m width, 2.1m height) was installed in an east-west direction referring to Homma and Arakawa (1996), Horie et al. (1995) and Mihara (1971), in the paddy field of Field...
weights were measured. Plants grown in the field near were oven-dried at 80ºC for 48 hours, and their dry sheath, leaf blade, dead leaf and panicle. All samples were divided into four parts, i.e. culm plus leaf and 2, 3, 7, 9, and 120 DAT in 2003, respectively. Tillering, heading, middle ripening and maturity, 0, 37, 77, 98 and 120 DAT in 2003, respectively. The photosynthetic rate of upper fully-expanded leaf was measured using a portable photosynthesis measurement system (CIRAS-1, Kioito, Japan) from the maximum tillering stage to maturity at about a two-week interval in each plot. One standard plant was dug up from TGC and replanted in a plastic pot with sufficient water in the evening on the day before the measurement. The plant was covered with transparent vinyl bag to prevent drying. The measurement was started at 0800 and repeated three times at PAR of higher than 1500 μmol m⁻² s⁻¹. Leaf temperature was maintained at 28ºC, and CO₂ concentration changed in the range of 370–390 μL L⁻¹.

7. Yield and yield components of brown rice

At the physiological maturity, 24 plants were harvested from each plot. After air-drying for about three weeks, the yield and yield components of brown rice were measured. The brown rice with a thickness of over 1.8 mm was defined as a ripened grain and the percentage of ripened grains was calculated. The moisture content was measured using a grain moisture tester (Riceter J, Kett, Japan) and grain weight was converted to that with 14.5% moisture content.

The percentage of sterile spikelets was determined in the plants used for the measurement of growth characteristics. The longest three panicles were selected from a hill, and after shattering the grains, the standards of sterile spikelets were examined.

Results

1. Weather and air temperature in TGC

The annual mean temperature in Okayama City in the five years were in the order of 2005 (26.5ºC) > 2004 (26.4ºC) > 2002 (25.9ºC) > 2006 (25.8ºC) > 2003 (25.6ºC) > 2001 (25.5ºC).
The mean temperatures in each year were 0.8 to 1.4°C higher than normal year except in 2003 (Table 1). It was rainy weather in 2006, and dry weather in 2002 and 2005 compared with a normal year. The sunshine duration was 9% longer in 2002 and 19% shorter in 2003 than in a normal year.

The mean and maximum air-temperature in TGC gradually increased from the intake side (TG1) to the exhaust side (TG4), (Table 2). In TG4, the mean and the maximum air-temperatures were 2.0−3.6°C and 4.0−7.0°C, respectively, higher than those in TG1 in the five years. Because of the ventilation at night, the minimum air-temperature was almost the same in all plots. The difference in mean and maximum air-temperature between TG1 and Outside were 0.2−0.6°C and 0.9−1.0°C in 2004−2006, respectively. The temperature difference did not vary with the season.

The air-temperature on a fine day was lowest at 0500, and highest at 1300 (Fig. 1). The temperature gradient in TGC was observed from 0800 to 1900, and the temperature difference between TG4 and TG1 was about 4.1°C from 1000 to 1400.

On a cloudy day, the difference in air-temperature between TG4 and TG1 was smaller than that on a fine day, and was only 1.1°C from 0800 to 1200. The temperature gradient of each plot suddenly increased during sunny intervals after 1300.

2. Growth
The plant elongated vigorously until 30 DAT, then slowly, and stopped to elongate at the heading time (Fig. 2). The plant height tended to be larger in TG2-4 than in TG1 during the whole growth period, especially in the early growth period (20 DAT-50
DAT). Plant height at maturity was in the order of TG2 (118.5 cm) > TG4 (115.3 cm) > TG1 (114.8 cm) ≧ TG3 (114.7 cm), in 2002, TG4 (128.8 cm) > TG2 (127.7 cm) > TG3 (126.9 cm) > TG1 (121.3 cm) in 2003, and was TG4 > TG1 > OS in 2004, 2005 and 2006.

In 2002, the number of tillers per m² in TG1 increased rapidly from 9 DAT, and reached the maximum at 37 DAT, then gradually decreased (Fig. 3). In TG2-4, it increased more steeply than in TG1 during the early growth period, and reached the maximum at 30 DAT, which was earlier than in TG1. At maturity, the number of stems was lower in TG2-4 than in TG1.

In 2003, the number of tillers tended to be higher than in 2002 throughout the growth period. In TG2-4, it reached the maximum at 32 DAT, which was earlier than TG1. At maturity, the number of stems was lower in TG2-4 than in TG1.

In 2004, the number of tillers tended to be higher than in 2002 throughout the growth period. In TG2-4, it reached the maximum at 32 DAT, which was earlier than TG1. Thereafter, the number of tillers decreased rapidly, the rate being in the order of TG2 ≧ TG3 > TG1 > TG4.

The percentage of productive tillers in 2002 and 2004 was in the order of TG2 (80.4%) > TG1 (78.5%) > TG4 (76.5%) > TG3 (74.7%) and TG1 (82.0%) > TG2 (81.4%) > TG4 (79.7%) ≧ TG3 (79.6%), respectively. It tended to be lower in TG2-4 than TG1 except for TG2 in 2002.

The heading time in 2002 was nine days later than that in 2003 (Table 3). The heading time in five years were one or two days earlier in TG2-4 than in TG1.

3. Dry-matter production

Plant dry weight per m² after the tillering stage was heavier in TG2 and TG3 than in TG1, and was heaviest in TG3 in 2002 and TG2 in 2003 (Fig. 4).

In 2002, plant dry weight per m² at maturity was in the order of TG3 (1825 g) > TG2 (1764 g) > TG1 (1568 g) > TG4 (1310 g). The increase in panicle dry weight during the ripening period was smallest in TG4. The total dry weight at maturity in TG4 was 16% lighter than that in TG1. The increase in dry-matter during the ripening period (ΔW) was larger in TG2 and TG3 than in TG1, and was smallest in TG4 (Table
4. The decrease in leaf sheath + culm dry weight (−ΔS), during the ripening period, which represents the amount of the dry-matter translocated to the panicle, was greater in the high-temperature plots than in TG1, and the increase in the dry weight of leaf sheath + culm (ΔS) at maturity, was largest in TG3 (200 g m⁻²) and smallest in TG1 (31 g m⁻²).

In 2003, plant dry weight per m² at maturity was in the order of TG2 (1648 g) > TG3 (1465 g) > TG1 (1461 g) > TG4 (1301 g), and that in TG2-4 was heavier than that in TG1 as in 2002. ΔW was largest in TG2, and smallest in TG4. The decrease in the dry weight of leaf sheath + culm (−ΔS) during the ripening period was greater in the order of TG1 > TG2 > TG3, but no decrease was observed in TG4. ΔS at maturity was decreased with rising temperature, and was in the order of TG2 > TG3 > TG4 as in 2002.

4. Photosynthetic rate
The photosynthetic rate of flag leaf changed in the range of 20–25 μmol m⁻² s⁻¹ from the tillering
to heading stage, and declined after heading with the progress of ripening (Fig. 5). In 2002, the photosynthetic rate at the tillering stage was significantly higher in TG4 than in the other plots, but after tillering to heading it was almost the same in all plots. At the early ripening stage (84 DAT), the photosynthetic rate in TG1 and TG2 was nearly the same as that at heading, but that in TG3 and TG4 was about 20% lower. At the middle ripening stage (98 DAT), the photosynthetic rate in TG1 was 30% lower than that at heading, but that in TG2, TG3 and TG4 was about 20% lower than that in TG1. At the later ripening stage, the photosynthetic rate in TG2-4 was 33.5% lower than that in TG1, and the difference among plots at maturity was reduced.

In 2003, the photosynthetic rate in TG2-4 started to decline earlier than in TG1, and became about 35% lower than that in TG1 at maturity as in 2002.

5. Specific dark-respiration
Specific dark-respiration (Rs) in the whole plant was low at transplanting, and reached the maximum value at the tillering stage, gradually decreasing thereafter (Fig. 6). Rs in TG1 was 0.19 mg g⁻¹ h⁻¹ higher than that in TG4 from the tillering to heading stage. However, Rs at maturity was higher in TG4 than in TG1. Rs in leaf and culm showed a change similar to that in the whole plant, and increased during the ripening period especially in TG4, though the difference with TG1 was not significant. In TG1, Rs in panicle was 0.21–0.41 mg g⁻¹ h⁻¹ higher than that in TG4 at the heading and middle ripening stage.

The number of panicles per m² in TG1 was larger than that in TG4 in 2002, 2003, 2005 and 2006 but was smaller than that in TG4 in 2004 (Table 5). The number of spikelets per panicle was not significantly different among the plots in 2004, but was lower in high-temperature plots than in TG1 in 2003, 2005 and 2006. The number of spikelets per m²

| Year | Plot | Middle ripening | Maturity |
|------|------|-----------------|----------|
|      |      | ΔW   | ΔS   | ΔW   | ΔS   |
| 2002 | TG1  | 340.6 | −25.6 | 189.4 | 30.8 |
|      | TG2  | 337.7 | −61.9 | 329.5 | 179.3 |
|      | TG3  | 368.2 | −26.7 | 336.9 | 200.2 |
|      | TG4  | 185.0 | −68.5 | 141.3 | 115.8 |
| 2003 | TG1  | 294.0 | −51.1 | 190.0 | 73.0 |
|      | TG2  | 357.7 | −41.7 | 237.2 | 147.9 |
|      | TG3  | 360.1 | −6.0  | 140.1 | 124.8 |
|      | TG4  | 284.2 | 30.2  | 102.1 | 67.3 |

Fig. 5. Ontogenic changes in photosynthetic rate of flag leaf grown in TGC during aging. Arrows show heading date, and vertical bars indicate SD of means (n = 3).
showed the same tendency.

The percentage of ripened grains in TG1 was lower than that in TG2 and TG3 (2003), but higher than that in TG4 in all years. There was no clear difference in the 1000-grain weight among the plots, but it tended to be lighter in TG4 than in the other plots.

Brown rice yield per m$^2$ tended to be lower in TG1 than in TG2 and TG3, but higher than that in TG4 (Table 5). The percentage of sterile spikelets was lower in TG1 than in the other plots and was highest in TG4 in all five years.

Discussion

1. Growth and dry-matter production

Many authors reported that plant height of rice increased with the rise of temperature within the range of 30–35ºC (Kondo and Okamura, 1931; Osada et al., 1973). The same was the case in this study (Fig. 2).

In TG2-4, the number of tillers per m$^2$ during the early growth period was larger and the maximum tillering stage was earlier than TG1 (Fig. 3). Yamamoto et al. (1985) reported that the air-temperature lower than 20ºC during the tillering stage was advantageous for the increase in the number of panicles. In this study, the number of tillers per m$^2$ in the early growth period tended to be larger in TG2-4 than in TG1. The high-temperature after the active-tillering stage seemed to decrease the number of panicles at maturity.

Plant dry weight was heavier in TG2 and TG3 than in TG1, and was lowest in TG4 (Fig. 4), which was consistent with many previous reports (Koyama et al., 1983; Ziska et al., 1997; Fukui, 2000; Newman et al., 2001). Kondo and Okamura (1931) suggested that the optimum temperature for dry-matter production was lower than or equal to that for elongation of plant height. Therefore, the temperature in TG2 and TG3 was considered to be within the optimum range for dry-matter production. However, the dry weight in TG4 at maturity was 11–16% lighter than that in TG1.

Kim et al. (1996a, b) reported that the rate of increase in dry-matter in the panicle after the heading decreased in the high-temperature plots due to the
increase in the number of sterile spikelets. Once sterile spikelet was increased by a high temperature, the dry weight of panicle did not recover even if the subsequent environment was improved, the assimilation products being accumulated in the leaf and culms (Sato et al., 1973). The plants in TG2 and TG3 exhibited higher dry-matter production before heading, but a large amount of assimilate was accumulated (ΔS) in the leaf and culms during the ripening period due to the suppression of translocation to the panicles (Table 4).

Hirai et al. (2003) indicated that Rs in the ripening period was influenced by the temperature history. However, our results showed that Rs during vegetative growth was little higher in TG1 and the effect of high-temperature during vegetative growth, i.e., the effect of temperature history on Rs, was not observed clearly. It was considered that the higher Rs in TG4 during the ripening period was associated with the increase in the amount of substrate for respiration due to the accumulation of dry-matter.

2. Factors affecting the photosynthetic rate
Photosynthetic rate in TG2-4 started to decline earlier than TG1, and was reduced by 11.2–35.6% from the heading time to the middle ripening stage (Fig. 5). A high-temperature has been reported to promote the ripening, and shorten the duration of grain filling (Satake and Yoshida, 1978). Tsuno and Yamaguchi (1987) clarified that the high-temperature depressed the photosynthetic rate through the reduction in root activity. Our study showed that high-temperature shortened the duration of grain filling and the photosynthetic rate in TG2, TG3 and TG4 was 40–60% lower than that in TG1 at the middle ripening stage, which suggested that the high-temperature during ontogeny of flag leaf enhanced the senescence.

Makino et al. (1994) showed that the photosynthetic rate per unit RuBPCase was a little lower in plants grown under low temperature, but the activity of RuBPCase was not affected by the growing temperature. They considered that this might be attributable to the starch accumulation in the chloroplasts. In our experiment, a large amount of assimilate was accumulated in the leaf and culms due to the occurrence of sterile spikelets, and consequently photosynthetic rate might be depressed by the similar mechanism with Makino et al. (1994). Badger et al.
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(1982) cultivated the plants under low- and high-temperature conditions, and reported that the optimum temperature for photosynthesis shifted to the low- and high-temperature range, respectively. Berry and Björkman (1980) also reported that the temperature dependence of photosynthesis varied with the growing temperature even if the same genotype was used. These results suggested that the temperature at the time of photosynthetic measurement in our experiment (28ºC) was not always optimum for each plot. It is necessary to clarify the temperature dependence of photosynthesis in consideration of the temperature history as same as in Rs. In our study, photosynthetic rate was measured in the laboratory by using the plants dug up from the field. Detailed field measurements using the intact plants grown in the TGC are needed.

3. Effect of high temperature on yield component

The percentage of sterile spikelets was in the order of TG4>TG3>TG2>TG1 in both 2002 and 2003 (Table 5).

The susceptibility to high-temperature-induced floret sterility is highest at the flowering stage, followed by booting stage (Sato et al., 1973; Satake and Yoshida 1978). The temperature at which sterility occurs varies with the cultivar. Sterility occurs at a temperature over 35ºC due to poor anther dehiscence, decrease in the number of pollen grains on the stigma, and poor germination of pollen on the stigma (Satake and Yoshida, 1978; Imaki et al., 1983; Matsui et al., 1997, 2001a, b).

A positive correlation (r=0.874**) was observed between the percentage of sterile spikelets and the maximum temperature during the flowering period (first heading to full heading), and the percentage of sterile spikelets exceeded 10% when the maximum temperature was around 37ºC (Fig. 7). Imaki et al. (1982, 1983) reported that the flowering time of rice differed among cultivars, and some cultivars flowered early in the morning. Such cultivars may be useful to avoid the damage by high temperatures at the flowering time.

In TG2-4, the sink capacity was lower than in TG1, due to the increase in the percentage of sterile spikelets, but the 1000-grain weight was slightly lighter than or equal to that in TG1 (Table 5). In TG2-4, the increase in sink capacity (grain-thickening growth) seemed to stop earlier than TG1, because a large amount of assimilate was accumulated in the leaf and culm. The enzymatic activity of the starch synthesis is closely related to the formation and thickening of the grain (Jeng et al., 2003). The reduction of enzymatic activity under a high-temperature condition has been reported in wheat (Keeling et al., 1993) and maize (Wilhelm et al., 1999). Jeng et al. (2003) reported that the shortening of ripening period in rice due to a high temperature was caused by the higher activity of enzyme involved in starch synthesis during the early grain growth stage. These findings suggested that the reduction in 1000-grain weight under high-temperature conditions was caused by the reduced activity of sink for starch synthesis.

The relation between grain yield and mean air-temperature for 20 days after heading time in the five years was regressed to the quadratic function upward convexity, showing that the grain yield declined steeply when the mean temperature exceeded 28ºC (Fig. 8). If
the rice cultivar Nipponbare is grown conventionally, the mean air-temperature during 20 days after heading time in a normal year is 27.0°C and when the mean temperature during 20 days after heading reaches 29°C and 30°C, 4.6% and 22.0% reduction in grain yield, respectively, is estimated.

Shifting of the cropping season and adoption of a late maturing cultivar may be probable methods to prevent the yield reduction due to high-temperature. In the plain area of Okayama Prefecture, some farmers practice rice-barley double-cropping. They mainly cultivated the late maturing cultivar Hinohikari and Akebono seeding in middle May, and transplanting in mid June. Three cultivars headed in August or early September, and were harvested in late or mid October. The normal value of the mean temperature during 20 days after heading was 26.1°C and 23.9°C in Hinohikari and Akebono, respectively, which is 1.7−3.9°C lower than Nipponbare. Therefore, it is considered that the temperature does not limit the grain yield in a normal year. Usually, the rice in Okayama Prefecture has not been cultivated under a high temperature condition during the ripening period.

If the rice cultivar Koshikari is grown conventionally in the plain area of Okayama Prefecture, the mean air-temperature for 20 days after heading time in a normal year is 28.0°C, and the yield reduction is unavoidable in a high-temperature year. In addition, the increase in the white immature grain by the high-temperature has become a serious problem recently, and the decrease in farmer’s cash income by the deteriorated grain quality has raised much concern. In the future, we are planning to examine the effects of high temperature on grain quality in rice by using TGC.

The effect of a 2−3°C rise in mean air-temperature on rice cultivation may be summarized as follows. The earlier the maximum tillering stage, the greater the increase in the number of panicles. The dry-matter production is decreased by the promotion of leaf senescence during the ripening period. The 1000-grain weight decreases due to the earlier cessation of grain thickening growth. The percentage of ripened grains decreases with the rise in the percentage of sterile spikelets. The brown rice yield decreases 6.6−35.7% by the reduced source activity and the shortage of sink capacity. The improvement of crop management technique such as topdressing and irrigation to avoid the heat damage, genetic analysis of heat tolerance and breeding of heat-tolerant cultivars, are necessary in the future.

Since the high-temperature during the ripening period deteriorates grain quality (Terashima et al., 2001), we will examine the grain quality and palatability of cooked rice produced in TGC.

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