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Effect of Root-Zone Temperature on the Growth and Fruit Quality of Hydroponically Grown Strawberry Plants

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Abstract

It has been reported that soil temperature modulates the growth and quality of many leafy vegetables and some fruit vegetables; however, this effect has not been sufficiently reported for strawberry plants. Here using a deep flow technique hydroponic system, we investigated the effect of various root-zone temperatures (10 °C, 20 °C, and 30 °C) on the plant growth and fruit quality of strawberry plants grown at an air temperature of 20 °C. The high root-zone temperature treatment (30 °C) decreased oxygen consumption and cell viability of the roots, resulting in withering of most of the plants after 2 months of treatment. In contrast, roots exposed to low temperature (10 °C) showed higher biomass production than those exposed to ambient condition (20 °C), whereas leaf growth was only slightly influenced. The biomass of reproductive organs, such as inflorescences and fruits, were increased in plants treated with a low root-zone temperature, suggesting the activation of reproductive growth by low temperature. However, the contents of ascorbic acid and sugar in fruits were not significantly influenced by the cooling of the root-zone, although the fruit maturation period was significantly prolonged by low temperature. These data indicate that manipulation of root-zone temperature could alter the vegetative and reproductive growth of hydroponically grown strawberry plants.

Keywords: root-zone temperature, strawberry, hydroponics, reproductive organs, fruits

1. Introduction

Plant growth and development are affected by various environmental factors, including light and temperature (Fankhauser & Chory, 1997; Porter & Gawith, 1997). In June-bearing strawberry cultivars, low temperature and short-day photoperiod are required for the development of reproductive organs, such as flowers, fruits, and inflorescences (Heide, 1977; Verheul et al., 2006). In Japan, fruits are usually produced by these cultivars from winter to spring when the air temperature generally decline below 20 °C. Because flower bud induction of June-bearing cultivars can occur in response to a longer photoperiod if the temperature is generally under 15 °C (Sonsteby, 1997), the thermal condition might be a more fundamental factor in regulating strawberry fruit production.

The air temperature is one of the most important environmental elements for the alternation of plant secondary metabolite production (Kaplan et al., 2004; Zobayed et al., 2005; Ramakrishna & Ravishankar, 2011). The development and quality of strawberry fruits are also influenced by the air temperature (Kumakura et al., 1994a, 1994b; Miura et al., 1994; Wang & Camp, 2000). For instance, low air temperature conditions after flower blooming prolonged the fruit maturation period and increased sugar content in fruits (Kumakura et al., 1994a; Wang & Camp, 2000). Fruit size was also increased by low air temperature during the period of flower bud initiation (Mori, 1998). In contrast, high air temperatures reduced the size of strawberry fruits and decreased the fruit anthocyanin production (Ikeda et al., 2011).

The temperature at the root-zone also influences the growth and chemical composition of many plants (Adebooye et al., 2010; Malik et al., 2013; Yan et al., 2013; Sakamoto & Suzuki, 2015a, 2015b). We have previously shown that using deep flow technique (DFT) hydroponics root-zone temperatures modulate the production of sugar and polyphenols in carrots and red leaf lettuce (Sakamoto & Suzuki, 2015a, 2015b). In strawberry plants, heating of cultivation media enhanced the development of flower bud initiation during the low temperature season, and finally increased fruit yield (Kim et al., 2009). Using nutrient film technique (NFT)

hydroponics, cooling of the nutrient solution resulted in the reduction of fruit biomass production (Udagawa et al., 1989). Conversely, the fruit set was increased by low temperature treatment of supplied water (Ikeda et al., 2007). Although these experiments have partially revealed the thermal effects to the root-zone in strawberry plants, the precise impacts of root-zone temperature on fruit growth and development are uncertain because the plants used in previous experiments were grown in a greenhouse where uncontrolled environmental factors, such as light and air temperature, could have altered the root-zone temperature. It has previously been shown that the air temperature influences the soil temperature under temperature regulated experiments (Sigeno et al., 2001; Kinoshita et al., 2011). In addition, the determination of the precise temperature at the root cells is difficult as methods of thermoregulation are not applied directly to the roots. Therefore, we examined the effect of low and high root-zone temperatures on the growth and fruit quality of strawberry plants using a DFT hydroponic system which could directly transduce the thermal effect on the roots, under a controlled light and air temperature condition.

2. Method

2.1 Plant Material and Growth Condition

For acclimation to hydroponics, pot-grown strawberry plants (*Fragaria ananassa* cv. Tochiotome) were transferred to the DFT hydroponic system with continuous aeration under 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ *PPF* (12/12 h light/dark) at 20 °C air temperature and were grown for 1 month. During the acclimation period, the root-zone temperature was ambiently maintained at 20 °C. The nutrient solution was based on a half-strength culture solution of the Otsuka House A-recipe (Otsuka Chemical Co. Ltd., Japan). Inflorescences were removed just as they emerged from the crown during the acclimation period. After the acclimation to hydroponics, root-zone temperature treatments were initiated under the same light and air temperature condition. Root-zone heating (30 °C) was applied with an IC auto heater (DS 150; DEX Co. Ltd., Japan). Low root-zone temperature (10 °C) was maintained by cooling the nutrient solution using a cool water circulator (Coolman pal C-307, Shibata Co. Ltd., Japan). Continuous aeration enabled the circulation of nutrient solution, resulting in the uniform temperature distribution to the root-zone. Six plants were subjected to each temperature treatment. Root-zone heating examination was repeated and obtained similar results.

2.2 Measurement of Plant Growth and Fruit Development

Examination of plant growth variables [leaf length, width, and number and soil-plant analyses development (SPAD) value] were measured at every month. Leaf size (length and width) data were obtained from fully expanded youngest leaves. After 4 months of temperature treatment, plants were harvested for dry weight analysis. Wilted plants obtained from the high root-zone temperature treatment after 2 months were immediately analyzed for dry weight of each organ. For the measurements of fruit dry weight, ascorbic acid, and sugar, maturated fruits were weighed and cut in half. One half of each fruit was used for dry weight estimation, whereas the remaining half was used for the measurements of ascorbic acid and sugar content. Examination of fruit weight, achene number, days from anthesis to harvest, and fruit qualities were conducted in 1^{st}–3^{rd} fruits from each inflorescence.

2.3 Measurement of Root Oxygen Consumption

Fresh roots (80 mg) were washed with distilled water and submersed in a 40 mL oxygen-saturated nutrient solution for 1 h. The initial and final dissolved oxygen (DO) concentrations were measured using a DO meter (DO-5509, Lutron, Taiwan), for the calculation of depleted DO.

2.4 Measurement of Root Cell Viability

Root cell viability assay using Evans blue uptake was spectrophotometrically conducted as described previously (Baker & Mock, 1994), with slight modifications. Fresh roots (50 mg) were washed with distilled water and submersed in 1 mL 0.25% Evans blue solution for 20 min. Roots were rigorously washed with distilled water until no more blue stain was eluted. Roots were then homogenized with 1 mL 1% sodium dodecyl sulfate (SDS). The sample was then centrifuged at 6,000× g for 5 min at room temperature. Five-fold diluted supernatant was spectrophotometrically measured at 600 nm.

2.5 Measurement of Ascorbic Acid (AsA) Content

AsA content was measured as described previously (Leja et al., 2013), with slight modifications. Fresh fruits (1.5 g) were homogenized with 13.5 mL 5% (w/v) metaphosphoric acid. The sample was then centrifuged at 6,000× g for 5 min. AsA was measured in the supernatant using a reflectometer (RQflex plus, Merck, Germany) and analysis strips (Ascorbic Acid Test, Merck).

2.6 Measurement of Sugar Content

Fresh fruits were homogenized using a mortar and pestle, and the homogenates were filtered using filter paper (No. 1, Whatman plc., United Kingdom) to remove tissue debris. The soluble solids concentration (SSC) was measured using an Atago PAL-1 Handheld Digital ºBrix Refractometer (Atago, Japan).

2.7 Data Analysis

The data obtained for each variable were analyzed using the statistical package JMP (SAS Institute, Cary, NC, USA). Differences among treatments were determined by one-way analysis of variance (ANOVA). Mean comparisons were conducted using the Tukey's multiple comparison test at $p < 0.05$.

3. Results

3.1 Plant Growth

Strawberry plants acclimated to DFT hydroponics at 20 °C root-zone temperature were transferred to three different root-zone temperature conditions (10 °C, 20 °C, and 30 °C). After 7 days of treatment, thermal effects to the root cells were estimated by measuring root oxygen consumption. Root-zone heating at 30 °C significantly reduced root oxygen consumption compared with that at 10 °C and 20 °C root-zone temperature condition (Figure 1), suggesting the decrease of root cell respiration. To determine the damage to roots, Evans blue uptake by root cells was measured after 10 days of treatment. The uptake of Evans blue was increased in roots exposed to high temperature (Figure 2). This indicated the severe damage to roots accompanied with cell death in roots exposed to high temperature. In accordance with this, 83% of plants treated with root-zone heating resulted in wilting after 2 months (Table 1). The time-course observation of plant growth variables revealed that leaf sizes of newly emerged leaves were time-dependently decreased in plants of all temperature treatments (Figures 3A and 3B). The number of leaves and SPAD value tended to be increased by root-zone cooling (Figures 3C and 3D). The SPAD value of the surviving plant from the high root-zone temperature treatment was decreased at 4 months (Figure 3D). During the 4 month temperature treatment, the number of newly emerging leaves from the crowns tended to be increased in plants treated with root-zone cooling, although no significant difference was observed (Table 2). In accord with this, the total number of inflorescences and flowers tended to increase in the root-zone cooling treatment (Table 2). The flower number of the 1st florescence was not changed between the plants treated at 10 °C and 20 °C but that of the 2nd florescence in plants treated at 10 °C was significantly increased.

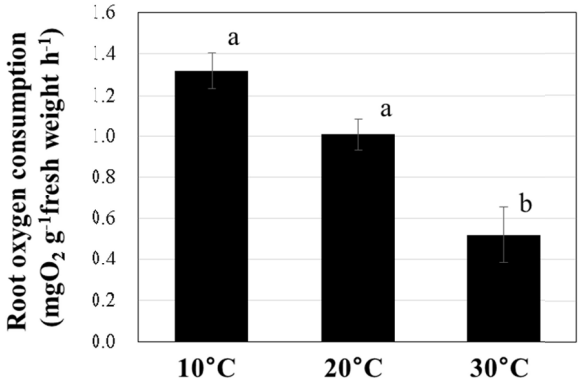

Figure 1. Effect of root-zone temperature on root oxygen consumption of hydroponically grown strawberry plants. Vertical bars represent ± SE. Different letters indicate significant differences by Tukey's multiple comparison test ($p < 0.05$)

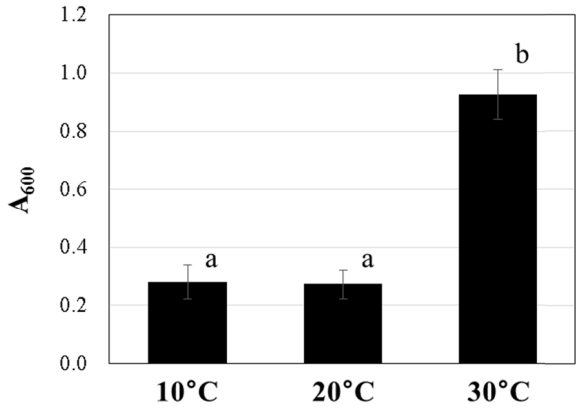

Figure 2. Effect of root-zone temperature on uptake of Evans blue by hydroponically grown strawberry plant roots. Evans blue was spectrophotometrically monitored at 600 nm (A_{600}). Vertical bars represent ± SE. Different letters indicate significant differences by Tukey's multiple comparison test ($p < 0.05$)

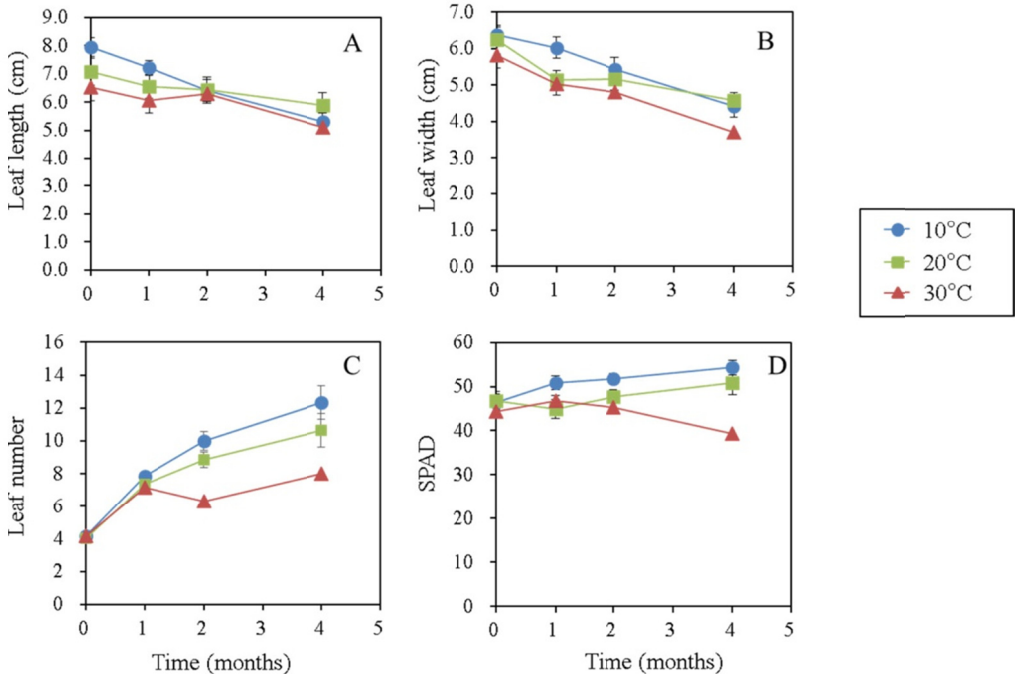

Figure 3. Time-course changes in growth variables of strawberry plants grown at three different root-zone temperatures. A, leaf length; B, leaf width; C, leaf number; and D, soil plant analysis development (SPAD) value

Table 1. Number of wilted strawberry plants by the root-zone temperature treatments

Root-zone temperature	Wilted plants		
	month 1	*month 2*	*month 4*
10 °C	0/6	0/6	0/6
20 °C	0/6	0/6	0/6
30 °C	0/6	5/6	5/6

Table 2. Effect of root-zone temperature on the emergence number of new leaves, inflorescences, and flowers of hydroponically grown strawberry plants within 4 months

Root-zone temperature	New leaf number	Inflorescence number	Flower number		
			Total	*1st Inflo.*	*2nd Inflo.*
10 °C	8.2 a	2.0 a	14.5 a	9.5 a	4.5 a
20 °C	7.0 a	1.7 ab	12.5 a	9.5 a	2.7 a
30 °C	3.0 b	0.5 b	2.3 b	2.3 a	0.0 b

Note. Different letters in the same column indicate significant differences by Tukey's multiple comparison test ($p < 0.05$).

3.2 Plant Biomass

Total plant biomass expressed as dry weight was higher in plants exposed to low root-zone temperature (Figure 4). In contrast, total plant biomass was remarkably decreased in plants exposed to the high root-zone temperature treatment (Figure 4), mainly because 83% of the plants of this treatment resulted in wilting within 2 months (Table 1). The biomass values of shoot vegetative organs (leaves, petioles, and crowns) were similar in plants subjected to 10 °C and 20 °C root-zone treatments (Figure 4). In contrast, root biomass was increased by approximately 1.3-fold by root-zone cooling treatment (Figure 4). The low root-zone temperature treatment increased the biomass of reproductive organs (fruits and inflorescences) by approximately 1.5-fold (Figure 4). Similarly, the proportion of the dry weight of reproductive organ to total plant weight was increased by the root-zone cooling treatment (Figure 5).

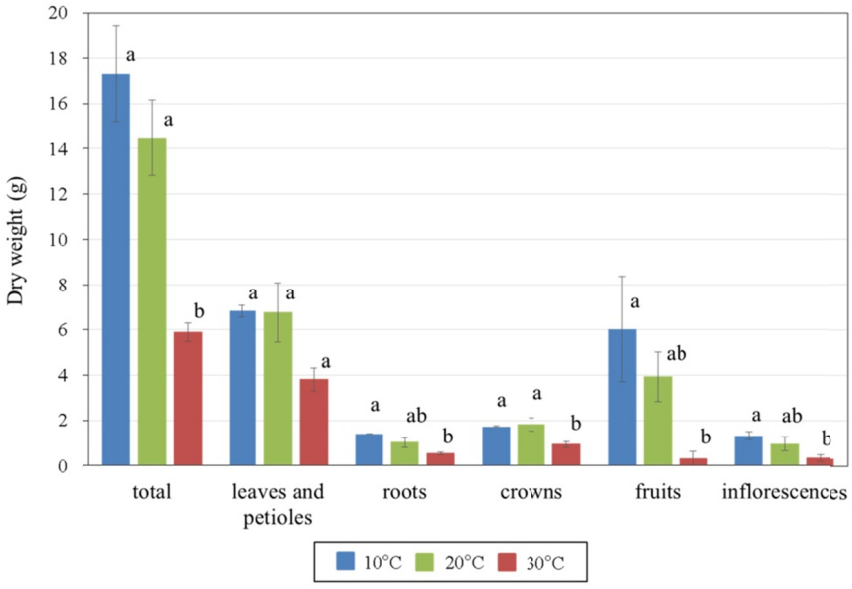

Figure 4. Effect of root-zone temperature on the dry weight of strawberry plants grown at three different temperatures. Vertical bars represent ± SE. Different letters in the same variable indicate significant differences by Tukey's multiple comparison test ($p < 0.05$)

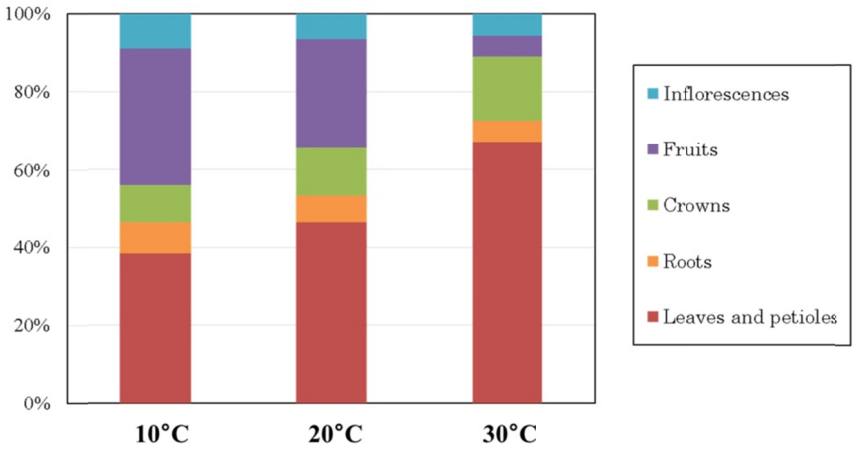

Figure 5. Effect of root-zone temperature on the proportion of plant organ dry weight to total plant dry weight of strawberry plants grown at three different temperatures

3.3 Development of Fruits

In plants exposed to the high root-zone temperature treatment, only irregular shaped fruits developed (data not shown), although inflorescence emergence and flower development were observed in some plants. Therefore, fruit development and quality were examined only in plants subjected to the 10 °C and 20 °C treatments. Among these plants, the number of fruits and fruit size (fresh weight) tended to increased by root-zone cooling treatment (Table 3). The number of achenes in the 1st–3rd fruits of each inflorescence was not affected by the 10 °C temperature treatment (Table 3). The days from anthesis to harvest was significantly prolonged in plants exposed to the low root-zone temperature (Table 3). In contrast, sugar and ascorbic acid contents in fruits were not significantly changed in plants of the 10 °C and 20 °C treatments (Table 4).

Table 3. Effect of root-zone temperature on the fruit growth variables of hydroponically grown strawberry plants.

Root-zone temperature	Fruit number per plant	Fruit weight	Achenes number	Days from anthesis to harvest
10 °C	8.0 a	10.55 a	300.8 a	35.7 a
20 °C	7.0 a	9.08 a	304.8 a	32.2 b
30 °C	n.d.	n.d.	n.d.	n.d.

Note. Different letters in the same column indicate significant differences by Tukey's multiple comparison test ($p < 0.05$). n.d. = not determined.

Table 4. Effect of root-zone temperature on fruit qualities of hydroponically grown strawberry plants

Root-zone temperature	°Brix	Ascorbic acid
10 °C	11.5 a	78.5 a
20 °C	10.5 a	77.3 a
30 °C	n.d.	n.d.

Note. Different letters in the same column indicate significant differences by Tukey's multiple comparison test ($p < 0.05$). n.d. = not determined.

4. Discussion

4.1 Plant Withering

Heat stress causes an imbalance in plant metabolism and disruption of cellular homeostasis, resulting in deleterious damage to plant cells (Suzuki & Mittler, 2005). Heat stress to the roots also triggers significant

alternations in plant physiological processes, such as water uptake and leaf photosynthesis (Suzuki et al., 2008; He et al., 2013). In rice seedlings, high root-zone temperatures increased susceptibility to chilling stress, resulting in leaf chlorophyll bleaching and tissue necrosis (Suzuki et al., 2008). In this study, the high root-zone temperature treatment induced plant withering within 2 months (Table 1) or decreased the chlorophyll content as expressed by the SPAD value (Figure 3D). Given that in the present study, high root-zone temperature increased stress to roots and induced root cell death (Figures 1 and 2), the reduction of root organs by root cell death might be involved in the shoot stress response, including the limitation of water uptake, leading to photosynthetic impairment and death of the whole plant. In support of our results, it has been shown that high root-zone temperature (32 °C) leads to the gradual deterioration of strawberry plants grown in sandy soil under a high ammonium ion concentration condition, and finally results in complete cell death (Ganmore-Neumann & Kafkafi, 1983). Moreover, strawberry plants grown by NFT hydroponics at a 23 °C root-zone treatment exhibited enhanced root browning and reduced root elongation, whereas plants grown under a 13 °C treatment showed no obvious damage to roots (Udagawa et al., 1989). Because root rot pathogens, such as *Pythium*, can easily propagate at a high temperature condition under hydroponics (Gold & Stanghellini, 1985), we cannot rule out the possibility that the wilting of strawberry plants may partly result from root infection by soil borne pathogens under a high temperature condition.

4.2 Vegetative Growth

Root-zone temperature influences the vegetative growth and biomass of the plant (Zhang et al., 2008; Chadirin et al., 2011; Sakamoto & Suzuki, 2015a, 2015b). We had previously shown that a 10 °C root-zone temperature treatment decreased plant biomass in the leaves and roots of red leaf lettuce plants (Sakamoto & Suzuki, 2015b). In contrast, a high root-zone temperature treatment reduced plant biomass in hydroponically grown carrots (Sakamoto & Suzuki, 2015a). In general, the optimum root-zone temperature for strawberry plants is relatively lower than that for other crops (Kaspar & Bland, 1992). In the present study, compared with the 20 °C root-zone treatment, the total and root biomass of hydroponically grown strawberry plants were reduced by root-zone heating and increased by root-zone cooling (Figure 4). In agreement with this, root biomass has been shown to be increased by low air or root-zone temperature in strawberry plants (Kumakura & Shishido, 1994b; Wang & Camp, 2000; Kadir & Sidhu, 2006) and decreased by root-zone heating (Udagawa et al., 1989). Given that the air temperature at approximately 20 °C is the most suitable condition for the biomass production of strawberry plants (Wang & Camp, 2000; Kadir & Sidhu, 2006), the optimal growth temperature of roots in strawberry cultivars may be lower than that of shoots under a hydroponic condition. Therefore, differential thermal regulation of shoots and roots would be an effective strategy to increase plant growth.

4.3 Reproductive Growth

Temperature is a key factor in the growth transition from the vegetative to reproductive phase in strawberry plants (Heide, 1977; Verheul et al., 2006). In June-bearing strawberry plants, low air temperature is necessary for the induction of flower bud formation (Verheul et al., 2006). In this study, the high temperature treatment to the root-zone clearly reduced the ratio of the weight of reproductive organs to total plant weight, including fruits and inflorescences (Figure 5). This was partly because most of the plants exposed to the high root-zone temperature wilted before the activation of reproductive development, such as the fruit set. However, given that normal fruits were not developed in a surviving plant exposed to the high root-zone temperature, heat stress to roots is suggested to restrict reproductive development of strawberry plants. In contrast, the proportion of the biomass of the reproductive organs to total plant biomass was increased when the root-zone temperature was lowered (Figure 5). It has previously been shown that strawberry plants grown at low air temperatures result in an elevated biomass of reproductive organs (Wang & Camp, 2000; Kadir & Sidhu, 2006). Given that the air temperature also influences the root-zone temperature in these experiments that use pot-grown strawberry plants, cooling only to the root-zone may be sufficient to elevate the biomass of reproductive organs. Because cooling of a medium containing carbonized chaff and peat moss triggered the increased production of strawberry fruits (Ikeda et al., 2007), cooling of the leaves may not always be necessary for the enhancement of reproductive development in strawberry plants.

4.4 Fruit Development

High or low temperature stress is known to influence the quantities of plant organic components, including secondary metabolites (Kaplan et al., 2004; Ramakrishna & Ravishankar, 2011). In the herb *Panax quinquefolius*, high air temperature reduced photosynthesis and plant biomass and increased root secondary metabolite concentrations (Jochum et al., 2007). In strawberry plants, the ascorbic acid and sugar contents in fruits were increased in plants grown under low air temperature (Kumakura & Shishido, 1994a; Wang & Camp, 2000),

whereas fruit anthocyanin contents were decreased under a high air temperature condition (Ikeda et al., 2011). In contrast to these experiments, the low root-zone temperature treatment in the present study did not result in significant changes in the sugar and ascorbic acid contents in fruits (Table 4). Therefore, the thermoregulation of whole plants and not just the root-zone might be sufficient to modulate the production of these metabolites. The drought-responsive plant hormone abscisic acid was recently demonstrated to play a key role in the regulation of the ripening stage of strawberry fruit (Jia et al., 2011). Given that drought stress applied to the roots triggered the production of sugar in the fruits of tomato, apple, orange, and mandarin (Mills et al., 1996; Yakushiji et al., 1998; Hockema & Etxeberria, 2001; Mingchi et al., 2010; Lu et al., 2013), the induction of drought stress, such as the limitation of water supply in hydroponically grown strawberry roots, may be a useful strategy to enhance fruit quality. It has also been shown that the fruit size of strawberry plants is influenced by temperature (Miura et al., 1994; Kumakura & Shishido, 1994a; Ikeda et al., 2011). The distribution of photosynthetic products to fruits was shown to be increased under a low temperature condition (Kumakura & Shishido, 1994b). In accordance with this, the proportion of fruit biomass to total plant biomass was increased by root-zone cooling (Figure 5), although fruit size was not significantly changed (Table 3). These indicate that root-zone cooling may partially reproduce the air temperature-induced reproductive development. Under low air temperature conditions, the period of fruit maturation is prolonged (Kumakura & Shishido, 1994a; Ikeda et al., 2011). In this study, the period from flower anthesis to fruit ripening was significantly increased by the low root-zone temperature treatment (Table 3), although the changes were smaller than those reported by previous studies (Kumakura & Shishido, 1994a; Ikeda et al., 2011). By understanding the organ-specific responses to local temperature alternations, techniques for improving the yield and quality of strawberry plants with minimum stress could be developed.

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