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Fruit Development and Quality of Hot Pepper (*Capsicum annuum* L.) under Various Temperature Regimes

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Abstract

Hot pepper (*Capsicum annuum* L.) originated in South America and is cultivated worldwidely in many temperate regions as well as subtropical and tropical regions. During the growing season, various climatic and soil factors, including air temperature, light intensity, precipitation, and soil conditions, affect the growth and development of hot pepper plants. Temperature is one of the major environmental factors affecting processes such as flowering, fruit set, and fruit growth. This study investigated the effects of temperature on the vegetative growth, fruit development, and fruit quality of hot pepper cultivar 'Muhanjilju' to develop a cropping system for producing high-quality fruit in temperate regions. The temperature range of 20 - 25°C was favorable for vegetative growth and fruit development. However, a temperature of 30°C reduced fruit development, including fruit set and fruit growth, although it enhanced vegetative growth, and a temperature of 15°C caused short plant height, a small number of branching nodes on the main branch, and elongated fruit. At 20 - 25°C and 30°C, the fruit development period was shortened by 9 - 16 and 22 days, respectively, compared with that of plants grown at 15°C. In addition, the change in fruit color was advanced significantly at 20 - 25°C and 30°C. A high temperature of 30°C not only reduced the total number of fruit but also caused the formation of short or malformed fruit. Furthermore, the total free-sugar content of red ripe fruit increased significantly at 20 - 25°C, while the capsaicinoid content of red ripe fruit increased as temperatures increased in the range of 15 - 30°C. These results indicate that the temperature range of 20 - 25°C is favorable for the vegetative growth, fruit development, and fruit quality of hot pepper.

Additional key words: capsaicinoid content, *Capsicum* crop, fruit development, fruit quality, optimal temperature, vegetative growth

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Introduction

Hot pepper (*Capsicum annuum* L.), a vegetable crop in the family Solanaceae, is economically important in Korea, and is consumed worldwide as spices. Most varieties of red pepper produce capsaicinoids, which are responsible for their characteristic hot pungent taste. Hot pepper is also rich in phenolic-derived compounds with strong physiological and pharmacological properties, benefitting health (Loizzo et al., 2015). The capsaicinoid and phenolic-derived compound contents of hot pepper depend on the cultivar, maturity and postharvest manipulation (Ghasemnezhad et al., 2011; Giuffrida et al., 2013) as well as a variety of growing condtions (Jeeatid et al., 2017; Selvakumar et al., 2018). Furthermore, hot pepper has high antioxidant activity (Topuz and Ozdemir, 2007), which increases the consumer demand for hot pepper fruit. During growth (flowering, fruit set, fruit development, and fruit ripening), hot pepper plants are constantly exposed to changes in temperature that limit plant growth and productivity in a number of ways. Therefore, strategies are required to increase fruit yields and fruit quality through specific cropping systems.

Hot pepper originated from tropical regions and requires high temperatures for vegetative growth and fruit development. Favorable temperatures for the growth of hot pepper are in the range of 25 - 28°C during the day and 18 - 22°C during the night. When the temperature falls below 15°C or exceeds 32°C, growth is usually retarded and the yield is decreased (Mercado et al., 1997; Erickson and Markhart, 2002). Temperatures below 15°C reduce overall plant growth as well as flowering and fruit set, whereas temperatures above 30°C severely increase the incidence of small, diseased, or deformed fruit, resulting in low quality fruit (Song et al., 2014, 2015). Furthermore, the capsaicinoid content of hot peppers is known to decrease at high temperatures (Gurung et al., 2011).

When considering the attributes that define quality, the chemical composition of fruit is of prime importance. However, the importance of chemical composition, including capsaicinoids, is often neglected in comparison with characteristics of external appearance, such as fruit size, weight, color, etc. Therefore, to develop a cropping system of red pepper for producing high-quality fruit, it is necessary to analyze the qualitative characteristics of hot pepper fruit grown under various temperature conditions.

In this study, we investigated the effects of temperature on the vegetative growth, fruit development, and fruit yield of hot pepper cultivar ‘Muhanjilju’ and determined the contents of free sugars and capsaicinoids of the fruit under various temperature regimes.

Materials and Methods

Plant Material and Growth Environments

Seeds of hot pepper (*Capsicum annuum* L.) cultivar ‘Muhanjilju’ (Syngenta Korea, Seoul, Korea) were sown in 50-cell plug trays filled with commercial bed soil and germinated under natural light and approximately 20/15°C day/night temperatures in a greenhouse. Seventy days after sowing, the seedlings with 8 - 10 true leaves were transplanted into 35 L rectangular plastic pots (35 × 35 × 28 cm) and acclimated for 10 days in walk-in growth chambers (2.7 × 5.0 × 2.2 m, GR96, Environmental Growth Chambers, Inc., Chagrin Falls, OH, USA) controlled to 20 ± 1°C, 60 - 70% relative humidity, and 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ light (16 h light/8 h dark). Then, 10 randomly selected pots were transferred to each of the above-mentioned walk-in growth chambers controlled at 15°C, 20°C, 25°C, or 30°C under the same humidity and light conditions. The chamber experiment was conducted using a completely randomized design. During the experiment, the air temperatures within the chambers were kept constant for each temperature regime, and plants were watered twice daily and fertilized weekly with 1 L of 0.1% vegetable fertilizer (Hanbang; Coseal, Korea), including macro- and micro-nutrient elements. Most data were obtained from 10 independent experiments in each temperature regime. The growth characteristics (i.e. plant height, root length, node number, total fruit number, fresh and dry weight, etc.) of plants were obtained from 5 or 6 individual plants in each temperature regime.

Gas Exchange Measurements

Eighty days after transferring the plants to the various temperature regimes, the morphological characteristics (length, width, and thickness) of leaves on the $5^{th}/6^{th}$ node of the main branch were estimated under each temperature regime using digital Vernier calipers with 0.01 mm resolution. Subsequently, gas exchange was measured on the fully-expanded leaves using a portable gas exchange system ($LCpro^{+}$, ADC Bioscientific, Hoddesdon, UK) equipped with a light-emitting diode light source. The net photosynthetic rate (*A*), stomatal conductance (*gs*), and transpiration rate (*E*) were determined at the ambient CO_2 concentration and a photon flux density of 1,200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The leaves were allowed to equilibrate to these conditions for 5 min before the gas exchange measurements. The instantaneous water-use efficiency (WUE) was calculated by dividing *A* by *gs*. The dark respiration rate (R_d) was also determined in the dark under the same conditions as those for the determination of net photosynthetic rate.

Analysis of Fruit Development and Characteristics

To analyse the phenological development of the red pepper plants, we recorded the periods from fully-opened flowers to mature green fruit and from mature green fruit to deep-red fruit, targeting flowers on the $5^{th}/6^{th}$ node of the main branch. After 80 days under each temperature regime, we recorded the morphological characteristics (length, diameter, weight, and skin color) of fruit attached on the $5^{th}/6^{th}$ node of the main branch. The fruit skin color, averaged across three regions of the surface on each fruit, was measured using a CE-310 Chroma-meter (Minolta, Tokyo, Japan) to generate the three Hunter color coordinates (L, lightness; a, redness; and b, yellowness).

Analysis of Plant Growth and Fruit Yield

After 100 days under each temperature regime, the plants were harvested and plant growth parameters, such as plant height, root length, number of nodes per main branch, and total fruit number per plant, were estimated. The number of branching nodes were obtained by counting the number of main branches developed per plant, and the number of fruit were obtained by counting the number of fruits produced per plant. The plant dry weights of the stem, leaf, root, and fruit were determined after oven drying at 60°C for 5 days. Plant water content was derived as (FW-DW)/FW × 100%, where FW and DW are the fresh and dry weight of the plant, respectively.

Analysis of the Free Sugar and Capsaicinoid Contents

For the analysis of free sugar and capsaicinoid contents, the fruits on the $5^{th}/6^{th}$ node of the main branch were selected after 80 days under each temperature regime and dried to a constant weight in an oven at 60°C for 5 days. The fruit tissues were ground in a commercial blender, and the powder (1.0 g) was extracted for 1 day after a 30-min immersion in 10 mL of extraction solution (80% ethanol for free sugars; 100% methanol for capsaicinoids). After centrifugation at 3,000 × *g* for 10 min, the supernatant was filtered through a 0.45-μm membrane filter and a Sep-Pak C_{18} cartridge (Waters, MA, USA). The free sugars were analyzed using high-performance anion exchange chromatography coupled with pulse amperometric detection (HPAEC- PAD). The HPAEC analysis was performed using a Dionex ICS-3000 ion chromatography system (Dionex, Sunnyvale, CA, USA) equipped with a CarboPac PA1 (250 × 4.0 mm, Dionex, Sunnyvale, CA, USA) column and an ED 40 pulse amperometric detector (model ED 40, Dionex, Sunnyvale, CA, USA). A mobile phase consisting of 100 mM

NaOH was used at a flow rate of 1.0 mL·min^{-1}. The injection volume was 10 μL. The capsaicinoids were analyzed using ultra-performance liquid chromatography (UPLC; Waters, MA, USA) equipped with an ACQUITY UPLC HSS T3 column (100 × 2.1 mm, Waters, MA, USA). A mobile phase consisting of methanol and water (70:30, V/V) was used at a flow rate of 0.25 mL·min^{-1}. The injection volume was 5 μL.

Data Analysis

The statistical analyses were performed using SPSS 18.0 software (SPSS, Chicago, IL, USA). Statistical variance analysis of all data was performed using one-way analysis of variance (ANOVA), and subsequent comparisons among temperature treatments were performed with Duncan's multiple range test at the $p < 0.05$ level of significance.

Results

Photosynthesis

Eighty days after transferring the plants to the various temperature regimes, leaf length, width, and thickness were measured and subsequently leaf gas exchange was measured on the fully-expanded leaves. Leaf length and width reached maximums at 20°C, and leaf thickness at 15°C, whereas leaf length and width were small and leaf thickness was thin at 30°C relative to the other temperature regimes (Table 1). The net photosynthetic rate (A) was highest in hot pepper plants grown at 15°C (21.5

Table 1. Effect of temperature on morphological characteristics of leaves at the 5th/6th node of the main branch in hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju' grown for 80 days under different temperature regimes

Leaf morphological characteristics^z	Temperature regimes			
	15°C	20°C	25°C	30°C
Leaf length (cm)	8.70 ab^y	9.76 a	9.05 ab	8.01 b
Leaf width (cm)	4.60 ab	4.87 a	4.45 ab	4.22 b
Leaf thickness (mm)	0.60 a	0.51 b	0.45 bc	0.44 c

^{z}The values of leaf morphological characteristics are represented as means of 10 independent measurements.

^{y}The different letters in the same row indicate statistically significant differences among different temperature regimes ($p < 0.05$).

Table 2. Comparison of photosynthetic characteristics in leaves at the 5th/6th node of the main branch in hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju' grown for 80 days under different temperature regimes

Photosynthetic characteristics^z	Temperature regimes			
	15°C	20°C	25°C	30°C
Net photosynthetic rate (A, μmol CO_2·m^{-2}·s^{-1})	21.5 a^y	15.2 b	13.0 b	8.0 c
Dark respiration (R_d, μmol CO_2·m^{-2}·s^{-1})	- 1.89 a	- 2.07 a	- 2.19 a	- 2.25 a
Stomatal conductance (g_s, mol H_2O·m^{-2}·s^{-1})	0.25 a	0.17 b	0.17 b	0.12 c
Transpiration rate (E, mmol H_2O·m^{-2}·s^{-1})	3.56 a	2.78 b	2.60 b	2.56 b
Intrinsic water-use efficiency (WUE, μmol CO_2·mmol H_2O)	6.05 a	5.43 a	5.02 a	3.25 b
Carboxylation efficiency (CE, mol·m^{-2}·s^{-1})	0.08 a	0.06 b	0.06 b	0.03 c

^{z}The values of photosynthetic characteristics are represented as means of 10 independent measurements.

^{y}The different letters in the same row indicate statistically significant differences among different temperature regimes ($p < 0.05$).

Table 3. Effect of temperature on growth characteristics of hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju' grown for 100 days under different temperature regimes

Growth characteristics[z]	Temperature regimes			
	15°C	20°C	25°C	30°C
Plant height (cm)	65.8 c[y]	71.2 bc	78.2 b	97.2 a
Root length (cm)	41.8 a	38.5 a	45.5 a	43.0 a
Branching node number/main branch	9.6 c	11.6 b	12.8 b	15.0 a
Fruit number/plant	38.8 b	47.2 b	51.6 b	70.2 a
Whole-plant dry weight (g DW/plant)	87.5 b	91.4 ab	102.5 ab	104.2 a
Fruit dry weight/plant	56.7 ab	60.6 ab	68.1 a	47.5 b
Leaf dry weight/plant	13.0 b	14.4 b	13.9 b	17.3 a
Stem dry weight/plant	13.3 b	13.6 b	17.2 b	34.2 a
Root dry weight/plant	4.54 a	2.92 b	3.38 b	3.16 b
Shoot/Root (ratio)	19.7 b	31.0 a	30.6 a	32.0 a
Plant water content (%)	82.6 a	83.2 a	78.0 b	78.9 b

[z]The values of growth characteristics are represented as means of 5 - 6 independent measurements.
[y]The different letters in the same row indicate statistically significant differences among different temperature regimes ($p < 0.05$).

μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), decreased with rising temperature, and was lowest at 30°C (Table 2). Similarly, the stomatal conductance (g_s), transpiration rate (E), and carboxylation efficiency (CE) were high in hot pepper plants grown at 15°C and decreased with rising temperature. The intrinsic water-use efficiency (WUE) was significantly lower at 30°C compared with hot pepper plants grown at 15 - 25°C. By contrast, dark respiration (R_d) increased slightly with increased temperature, but there was no significant difference among the temperature regimes (Table 2).

Plant Growth and Fruit Yield

When cultured under different temperatures for 100 days, the height and branching node number per main branch of hot pepper plants increased with increasing temperature. Root length did not differ significantly among the temperature regimes, although it was slightly longer above 25°C. The fruit number per plant was greatest when grown at 30°C, although the percentage of red fruit was highest at 25°C (data not shown). The dry weight of the whole plant increased with increasing temperature. The fruit dry weight per plant was significantly higher at 25°C than below or above 25°C. The dry weights of stems and leaves per plant were significantly higher at 30°C compared with those below 25°C. Conversely, the root dry weight per plant was significantly higher at 15°C, although it was low above 20°C. The shoot/root dry weight ratio was high above 20°C. The water content of the plants was slightly higher at 15 - 20°C than at 25 - 30°C (Table 3).

Fruit Development and Characteristics

The period of fruit maturation after flowering was shortened with increasing temperature (Table 4). The fruit development period from flowering to deep-red fruit was less than 1 month at 30°C, while it was about 1 month at 20 - 25°C and 1.5 months at 15°C. The period from flowering to mature green fruit was 21.6 and 18.5 days at temperatures of 25°C and 30°C, respectively, and it was between 25.5 and 30.1 days at temperatures of 15 - 20°C. The period from mature green fruit to deep-red fruit was 7.6 and 5.4 days at temperatures of 25°C and 30°C, respectively, and it was between 11.0 and 16.5 days at

Table 4. Effect of temperature on the fruit development of hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju'

Fruit developmental period (days)^z	Temperature regimes			
	15°C	20°C	25°C	30°C
Flowering to mature green fruit	30.1 a^y	25.5 b	21.6 c	18.5 d
Mature green to deep-red fruit	16.5 a	11.0 b	7.6 c	5.4 d
Flowering to deep-red fruit	45.6 a	36.5 b	29.1 c	23.9 d

^{z}The values of photosynthetic characteristics are represented as means of 10 independent measurements.

^{y}The different letters in the same row indicate statistically significant differences among different temperature regimes ($p < 0.05$).

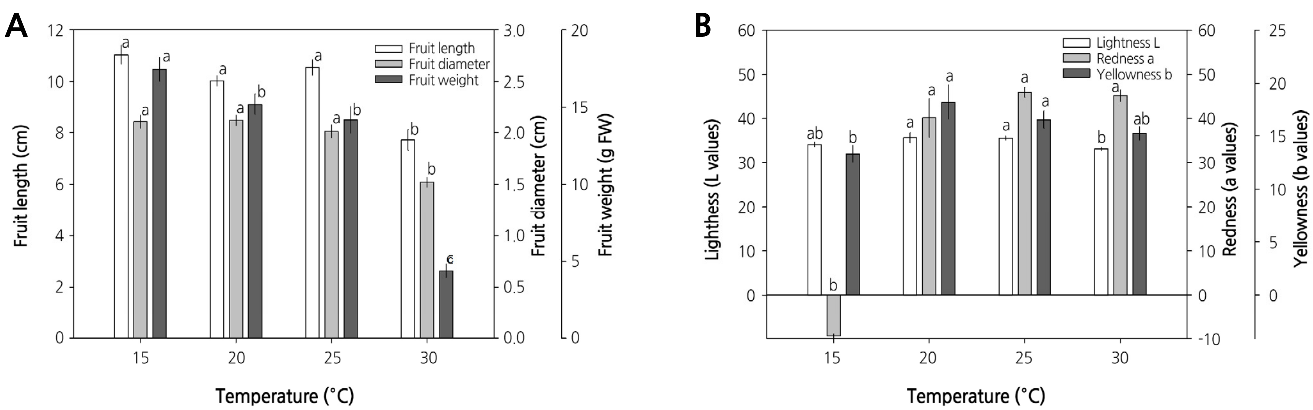

Fig. 1. Effect of temperature on morphological characteristics (A) and surface color characteristics (lightness, redness, and yellowness) (B) of fruits at the 5th/6th node of the main branch in hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju' grown for 80 days under different temperature regimes. Each value is expressed as the mean ± standard error of 10 independent measurements. The different letters in each bar indicate statistically significant differences among different temperature regimes ($p < 0.05$).

15 - 20°C.

The measured values for external appearance factors of the fruit, particularly the size, fresh weight, and color, were greater below 25°C (Fig. 1). The fruit length and diameter did not differ significantly among the temperature regimes in the range of 15 - 25°C, but decreased significantly at 30°C. The fresh weight of individual fruit decreased significantly as the temperature rose (Fig. 1A). The lightness (L) values of the fruit surface were about 35 at 15 - 25°C, with a significant decrease at 30°C. The redness (a) value was -10 at 15°C, and ≥40 above 20°C. The yellowness (b) value was high at 20 - 25°C, but low at 15°C (Fig. 1B).

Free Sugar and Capsaicinoid Contents of Fruit

The capsaicin, dihydrocapsaicin, and total capsaicinoid contents of red ripe fruit increased with increasing temperature in the range 15 - 30°C (Fig. 2). Particularly, the capsaicin and dihydrocapsaicin contents were remarkably high at 30°C (41 and 24 $\mu g \cdot g^{-1}$ dry weight, respectively) (Fig. 2A). The glucose and fructose contents also increased with increasing temperature. However, the sucrose content was low at 20 - 30°C, although it was high at 15°C. The total free sugar content of red-ripe fruit was significantly higher at 20 - 25°C (Fig. 2B).

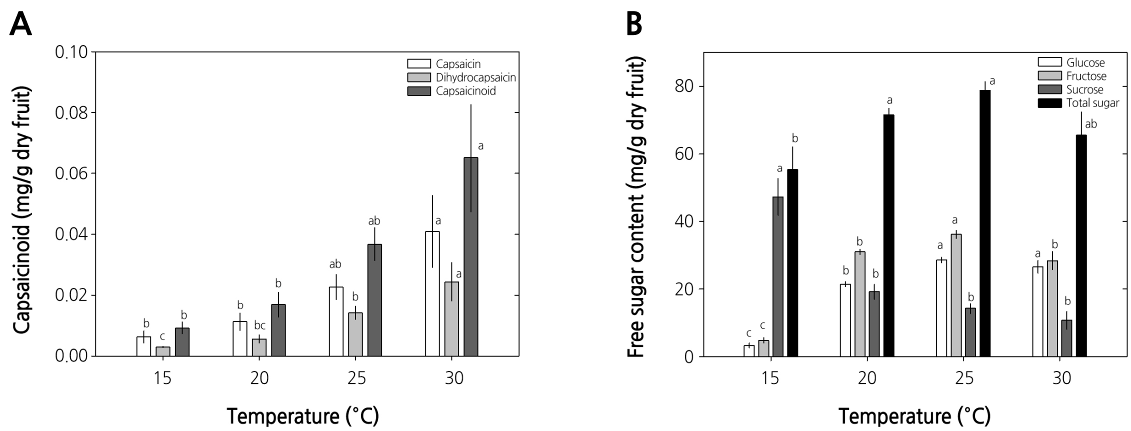

Fig. 2. Capsaicinoids (A) and free sugar contents (B) of fruits at the 5th/6th node of the main branch in hot pepper (*Capsicum annuum* L.) cultivar 'Muhanjilju' grown for 80 days under different temperature regimes. Each value is expressed as the mean ± standard error of 10 independent measurements. The different letters in each bar indicate statistically significant differences among different temperature regimes ($p < 0.05$).

Discussion

Variations in growth, fruit productivity, and fruit quality in hot pepper are affected by environmental factors, such as climate, temperature, soil fertility, and irrigation, and by culture systems. High temperatures usually favor the vegetative growth of young plants, but adversely affect fruit development and quality. In some cultivars, the percentages of unmarketable fruit increase due to fruit cracking and fruit-tip end rot under high temperatures (Olle and Bender, 2009; Song et al., 2014). The rate of fruit development can also be low due to the high abscission rates of flowers and young fruit at high temperatures (Erickson and Markhart, 2002; Ghai et al., 2016). Furthermore, the capsaicinoid content of chili cultivars is known to decrease at high temperatures (Gurung et al., 2011). So, we have investigated the effects of temperature on vegetative growth, fruit development, and fruit characteristics as well as the free sugar and capsaicinoid contents to develop a cropping system of red pepper cultivar 'Muhanjilju' for producing high-quality fruit.

The vegetative growth characteristics of hot pepper, such as plant height, number of branch nodes, number of fruit, leaf dry weight, and stem dry weight, were significantly greater at 30°C compared with the temperature range of 15 - 25°C. However, root dry weight and fruit dry weight were low at 30°C (Table 3). Furthermore, the temperature of 30°C not only reduced the number of fruit, but also caused the formation of short fruit (Fig. 1A). This was due to a low photosynthetic rate at 30°C leading to low sucrose loading at source leaves (Table 2). These results indicate that the temperature of 30°C is favorable for vegetative growth, but undesirable for fruit productivity and quality. This result is very similar to that observed by Heo et al. (2013), in which exposure of hot pepper to high temperature during early growth increased the growth rate, but significantly reduced yield.

Photosynthetic characteristics per unit leaf area, such as the A, g_s, E, WUE, and CE, decreased with rising temperature, but R_d did not show significant differences among the temperature regimes (Table 2). Moreover, leaf color changed from dark green to light green with rising temperature (data not shown). These results demonstrate that high temperature markedly decreased the photosynthetic activity by decreasing the photosynthetic pigments in leaf chloroplasts. Subsequently, leaf length, width, and thickness also decreased with rising temperature (Table 1). These changes may be related to the leaf adaptability to temperature. As shown in Table 1, the leaves of plants were small and thin at 30°C relative to the other temperatures (Heo et al., 2013), indicating that a temperature above 30°C reduced the leaf volume as well as the leaf photosynthetic capacity, and subsequently reduced fruit size and productivity (Table 3 and Fig. 1A). However, at temperatures of 20 - 30°C, the developmental period of fruit from flowering to deep-red fruit was shortened by 9 - 22 days and the surface color redness was high, compared with that at 15°C (Table 4 and Fig. 1B). This indicates that the time to harvest of fully-colored ripe fruit could be advanced by 10 days or more at 20 - 30°C and the harvest of mature green fruit could be advanced by 5 - 9 days at 20 - 25°C. Fruit growth and maturation involve changes in morphological and physiological attributes, including fruit fresh weight, pericarp color, photosynthetic and respiration rates, and chemical composition. Our findings indicate that all of these characteristics were affected by elevated temperatures. As shown in Table 4 and Fig. 1B, higher temperatures caused a more rapid change in fruit color. Furthermore, at temperatures of 20 - 25°C, the fruit length and diameter did not differ from those at 15°C, although fruit weight was reduced slightly.

Not only the morphological characteristics, including photosynthetic attributes, described above, but also the chemical composition of fruit should be considered when evaluating fruit quality. The pungency and sweetness of hot pepper fruits are very important for industrial purposes, since these attributes are required to produce fruits applicable as ingredients in food. Capsaicinoids are especially important because of their use in food (as a main ingredient of hot sauces), for defensive measures (as a repellent against herbivorous insects and animals), and for the pharmaceutical industry (as an additive to pads for relieving muscular pain). In these studies, the capsaicinoid and sugar contents of mature hot peppers seemed to depend on the temperature. The capsaicin, dihydrocapsaicin, and total capsaicinoid contents of red ripe fruit increased with increasing temperature in the range of 15 - 30°C. However, the glucose, fructose, and total free sugar contents of hot pepper fruit increased significantly, while the sucrose content decreased, in the temperature range of 20 - 25°C (Fig. 2B), as shown in previous studies (Navarro et al., 2006; Serrano et al., 2010). This suggests that for the production of high-quality fruit it is desirable to culture hot pepper cultivar 'Muhanjilju' in the temperature range of 20 - 25°C.

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