Relationship Between Water Supply and Sugar and Capsaicinoids Contents in Fruit of Chili Pepper (*Capsicum annuum* L.)

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Environmental factors influence the contents of taste components, such as capsaicinoid compounds, in the fruit of chili pepper (*Capsicum annuum*). The present research was conducted to evaluate the effect of water supply and harvesting date after flowering on sugar and capsaicinoid contents in fruit of the Japanese chili pepper cultivars ‘Botankosho’, ‘Fushimiamanaga’, ‘Manganji’, and ‘Sapporo Oonaga Nanban’. The experiment was conducted in a greenhouse from April to October in 2016 and 2017. Three water supply treatments were applied: 260 mL (excess), 130 mL (standard), and 50 mL (drought) per application. Fruit were harvested at 20, 30, 40, and 50 days after flowering (DAF). Glucose, glutamic acid, and total sugar were measured using a portable spectrophotometer, and capsaicinoid content was measured by HPLC. Total sugar content and Brix tended to increase with later harvesting, whereas glucose content did not change significantly by DAF. Sugars in the fruit were dominated by fructose, and the ratio of fructose content to total sugar content increased as the fruit matured. Glutamic acid content in the fruit increased up to 40 DAF, and thereafter remained unchanged or decreased. The capsaicinoid content of the fruit increased with fruit maturation. Elevation in water supply induced an increase in the fruit glucose content and decrease in total sugar and glutamic acid contents. Previous studies of tomato (*Solanum lycopersicum* L.) found that total sugar and glucose contents decrease in response to increase in water supply. Therefore, it is suggested that sugar metabolism and accumulation differ in the fruits of tomato and chili pepper. The highest capsaicinoid content in chili pepper fruit was observed in response to the drought treatment.

Key Words: environmental factors, glutamic acid, harvesting dates, water stress.

Introduction

Chili pepper (*Capsicum annuum*) is a species in the genus *Capsicum* L., which is classified as Solanaceae. Chili pepper is widely grown for the fruit, which may be eaten as a fresh vegetable or used in the form of dried powder as a spice. Chili pepper originated in Mexico (Kraft et al., 2014) and was domesticated more than 6,000 years ago (Perry et al., 2007). Following the Columbian Exchange, many cultivars of chili pepper were disseminated around the world.

The pungency of chili peppers is derived from a group of heat-producing alkaloids, including capsaicin (8-methyl-N-vanillyl-6-nonenamide) and several related compounds, which are collectively termed capsaicinoids (Kosuge and Inagaki, 1962; Suzuki and Iwai, 1984). The greater the concentration of capsaicin, the greater the pungency of the fruit. Generally, capsaicin and dihydrocapsaicin are responsible for 90% of fruit pungency (Madhumathy et al., 2007). The amount of capsaicin in a chili pepper fruit also varies according to genetic and environmental factors. Capsaicinoid accumulation is associated with the age, size, and developmental stage of the fruit (Estrada et al., 1997; Zewdie and Bosland, 2000). Water-stressed chili pepper plants usually produce fruit with greater pungency. In water-
stressed plants of *C. chinense* Jacq., the capsaicin concentration increases in some parts of the fruit (Ruiz-Lau et al., 2011). However, in the case of *C. annuum*, a similarly detailed analysis was not conducted.

Water stress controls the physiological processes that determine the quality and quantity of growth (Kramer, 1969). According to Ullah et al. (1993, 1994), certain environmental stresses result in significant increases in the contents of glucose and fructose, and in some cases sucrose, ascorbic acid, and citric acid, in fruit of fava bean (*Vicia faba* L.) and tomato (*Solanum lycopersicum* L.). Moreover, water stress affects the sweetness of tomato fruit as a result of increases in the glucose and sucrose contents, and improves fruit quality via an increase in the concentrations of important acids. Environmental factors, such as temperature, solar radiation, water stress, and soil nutrient concentrations, influence sucrose and glutamic acid contents in tomato fruit (Ortiz et al., 2007). However, to the best of our knowledge, few investigations regarding the influence of environmental factors, especially water supply, on the pungency and contents of sugar and glutamic acid in chili pepper fruit were undertaken. Therefore, it is necessary to determine the relationship between water stress and contents of taste components (sugars, glutamic acid, and capsaicinoids) in chili pepper fruit to enable production of fruit with stable sweetness and pungency. The present study was conducted to determine the contents of sweetness components and capsaicinoids in response to three water supply treatments.

**Materials and Methods**

*Plant materials and experimental design*

The experiment was conducted from April to October 2016 in a greenhouse at the experimental farm (733 m a.s.l) of the Education and Research Center of Alpine Field Science, Faculty of Agriculture, Shinshu University in Minamiminowa, Nagano, Japan. The experiment was repeated in the same location from March to October 2017. In 2016, two Japanese cultivars of chili pepper, ‘Manganji’ and ‘Fushimiananaga’, were used in the experiment. Both cultivars are non-pungent vegetable cultivars that originated in Kyoto Prefecture. ‘Fushimiananagasa’ seeds were purchased from Takii & Co., Ltd. (Kyoto, Japan), and ‘Manganji’ seeds were purchased from Noguchi Seeds (Saitama, Japan). In addition, the local pungent ‘Botankosho’, which is used as a traditional vegetable in northern Nagano Prefecture, was used with seeds donated by the Madarao Botankosho Conservation Society (Nakano, Japan). In 2017, we included an additional pungent cultivar, ‘Sapporo Oonaga Nanban’ (Tsurushin, and (d) ‘Botankosho’ (Local).

Sumitomo Forestry Landscaping Co., Ltd, Tokyo, Japan). During the seedling rearing period, the greenhouse was heated using oil heaters at night until early April to keep the temperature above a 15°C minimum.

Seedlings approximately 150 mm in height were transplanted to plastic pots (diameter 18 cm, volume 1.8 L) filled with 1 kg of the same commercial potting medium on 6 June 2016 and 8 June 2017. In both years, the stress treatment was applied starting one week after the seedlings were transplanted. All flowers flowering before the stress treatment was applied were removed.

During the cultivation period a single application of slow-acting home gardening fertilizer (N:P:K, 10:10:10; Shizen Oyokagaku Co., Ltd, Nagoya, Japan) was applied (on 16 August 2016 and 5 August 2017). The plastic pots filled with 1 kg potting medium were filled to the brim with 130 mL water. Therefore, as treatments, we applied three volumes of water in individual applications to represent drought (D; 50 mL water per application), standard water supply (S; 130 mL water per application), and excess water supply (E; 260 mL water per application). In the excess water supply treatment, the excess water overflowing from the pot was retained in a dish placed under the pot to allow absorption through the pot base. The water supply treatments were applied considering the daily temperature and weather. On sunny days and/or when the day temperature exceeded 30°C, water was applied three times per day. On rainy or cloudy days and/or when the day temperature was less than 30°C, water was applied twice per day. During the period of the experiment the average temperature in the greenhouse was 27.8°C (Maximum 35.2°C, Minimum 20.5°C) in 2016 and 29.4°C (Maximum 35.6°C, Minimum 22.1°C) in 2017. Throughout the experiment, other management practices were applied equally to all plants in the same greenhouse.

During the stress treatment, each flower was tagged at the end of anthesis to ensure that fruit were harvested at 20, 30, 40, and 50 days after flowering (DAF). The harvested fruit were stored at −80°C until analysis.

Fruit harvested for each water supply treatment and at each harvesting date were used for analysis of glucose, total sugar (glucose and fructose), glutamic acid content, Brix percentage, and capsaicinoids content. Six
individuals of each cultivar were used for each treatment. Fruit from each individual were harvested at 20, 30, 40, and 50 days after flowering (DAF). Three samples each comprising 50 g of fruit (approximately 1–6 fruits) were chosen randomly for analysis of taste components. The sampling level reflected that the extract from 50 g of fruit tissue was required for spectrophotometric analysis. A randomized complete block design was used for the experiments.

In 2018, a third experiment was conducted to determine capsaicinoid production in the placenta. Capsaicinoids in the placenta of sampled fruit were quantified by high-performance liquid chromatography (HPLC). Only the drought (D; 50 mL water per application) and excess water supply (E; 260 mL water per application) treatments were applied, and all other experimental conditions were identical (except the climatic conditions) to those used in 2016 and 2017. This experiment was performed using the pungent cultivars ‘Sapporo’ and ‘Botankosho’ primarily to analyze capsaicinoids accumulation.

Solution preparation for analysis of sugar and glutamic acid contents

Extracts for sugar and glutamic acid analyses were prepared from a known amount of fruit tissue ground using a grinder (YMB-400; Yamazen Corporation, Osaka, Japan) and filtered with 125 mm filter paper (ADVANTEC®, Tokyo, Japan). Extracts were prepared for quantitative analysis of glucose, total sugar (glucose + fructose), and glutamic acid using a digital portable spectrophotometer (RQ flex plus 10; Merck, Darmstadt, Germany). According to Nonaka et al. (2012), glucose, total sugar, and glutamic acid contents in sweet pepper fruit detected using a RQ flex spectrophotometer and by capillary electrophoresis methods (Horie, 2009) yield similar results.

Solution preparation for analysis of Brix

Brix is primarily a measure of the sugar concentration in a solution. Extracts were prepared from fruit tissue ground using a grinder (YMB-400; Yamazen) followed by filtering through 125 mm filter paper (ADVANTEC®). Extracts were used directly to measure the Brix value with a digital portable refractometer (Pen-J, Atago Co., Ltd, Tokyo, Japan).

Capsaicinoids analysis

HPLC apparatus and analysis conditions

The HPLC analysis conditions were as follows: LC column (50 × 3.0 mm; Shimadzu Corporation, Kyoto, Japan), column temperature 40°C, mobile phase 70% methanol, flow rate 1 mL/min, and absorbance at 280 nm wavelength. To examine the effectiveness of the analysis conditions, capsaicin (Wako Pure Chemical Industries, Ltd., Osaka, Japan) was used as a standard. Standard capsaicin solutions of 62.5, 125, 250, and 500 μg/mL (Othman et al., 2011) were analyzed and a calibration curve was prepared. Sample solutions were prepared using 24 hours freeze dried chili pepper fruits, capsaicin was extracted after adding grinded chili pepper powder (2 mg) to methanol (20 mL) after being kept 1 hour under 40°C.

Results

Glucose content

Glucose content, expressed on a fresh weight (FW) basis, of chili pepper fruit showed a gradual, significant decrease up to 40 DAF in each cultivar, and thereafter increased slightly, but not significantly, at 50 DAF. In 2016, the glucose content of ‘Manganji’ differed significantly in fruit harvested at 30 and 40 DAF from drought-treated plants, and also differed significantly between drought and excess water supply treatment at 20 and 50 DAF (Fig. 2-M1). In 2017, the glucose content of ‘Manganji’ showed significant difference at 40 and 50 DAF in each of the three water supply treatments; in addition, fruit from drought treatment showed a lower glucose content and fruit from excess water supply treatment showed a higher glucose content (Fig. 2-M2). In ‘Manganji’ fruit at 20 DAF, a significant difference between drought and excess water supply treatments was observed in 2017. In ‘Fushimiamanaga’ fruit, glucose contents were significantly lower in drought treatment than excess water supply treatment at 40 and 50 DAF in 2016 (Fig. 2-F1) and fruit harvested in drought treatment at 20 and 30 DAF in 2017 (Fig. 2-F2). In 2017, ‘Fushimiamanaga’ fruit harvested at 50 DAF, showed a significant difference in glucose content between drought and excess water supply treatment. Fruit of ‘Botankosho’ showed similar trends, with significant differences in glucose content observed in drought-treated fruit harvested at 30, 40, and 50 DAF in 2016 (Fig. 2-B1) and at 40 and 50 DAF in 2017 (Fig. 2-B2). Also, in ‘Botankosho’ fruit harvested at 30 DAF in 2017 a significant difference in glucose content between drought and excess water supply treatment was observed. Fruit of ‘Sapporo’ showed a significantly lower glucose content under drought stress at 30, 40, and 50 DAF (Fig. 2-S2).

Total sugar content

Total sugar content, expressed on a FW basis, increased with progression of fruit maturation in all cultivars. The highest total sugar content was observed in drought treatment in fruit harvested at 50 DAF. The content of total sugar was increased in drought treatment compared with that observed in excess water supply treatment. Interestingly, this pattern showed the opposite trend to glucose content in the same cultivar. Fruit of ‘Manganji’ showed significantly higher total sugar content in drought-treated plants than in excess water supply treatment at 40 and 50 DAF in 2016 (Fig. 3-M1) and at all DAF in 2017 (Fig. 3-M2). The
total sugar content of ‘Fushimiamanaga’ fruit showed identical trends. The total sugar content of ‘Fushimiamanaga’ differed significantly between drought and excess water supply treatment at 30 and 50 DAF in 2016 (Fig. 3-F1) and at each DAF in 2017 (Fig. 3-F2). In 2016, fruit of ‘Botankosho’ harvested at 20, 40, and 50 DAF showed significant differences in total sugar contents between drought and excess water supply treatment (Fig. 3-B1). ‘Botankosho’ fruit showed no significant differences in total sugar content among water supply treatments except at 40 DAF in 2017 (Fig. 3-B2). The fruits of ‘Sapporo’ harvested at 30, 40, and 50 DAF in drought treatment showed significantly higher total sugar content than the other treatments (Fig. 3-S2).

Brix

The fruit Brix percentage of all four cultivars tended to increase with reductions in the amount of water applied and with later harvesting. The highest Brix percentage was observed in the drought treatment at an advanced stage of maturation (50 DAF).

Significant differences in Brix under excess water supply and drought stress was observed in ‘Manganji’ fruit at 20 DAF in 2016 (Fig. 4-M1) and at 30, 40, and 50 DAF in 2017 (Fig. 4-M2). Variation in Brix percentage was observed in the drought treatment at an advanced stage of maturation (50 DAF).

Fig. 2. Glucose content (mg/100 g fresh weight [FW]) at four stages of fruit maturation in chili pepper ‘Manganji’ (M), ‘Fushimiamanaga’ (F), ‘Botankosho’ (B), and ‘Sapporo Oonaga Nanban’ (S). Graph M1, F1, and B1 represent the year 2016 and M2, F2, B2, and S2 represent year 2017. Fruit were sampled at 20, 30, 40, and 50 days after flowering (DAF). Different lower-case letters a, b, and c above bars for the same treatment (drought, D; standard water supply, S; and excess water supply, E), indicate significant differences between treatments and between DAF, respectively (Tukey’s pairwise test, P < 0.05). Error bars indicate the standard error.
In the same year (2017), fruit harvested at 50 DAF in drought treatment showed significantly higher Brix compared with the other treatments (Fig. 4-F2). At 50 DAF in 2016 and 20 DAF in 2017, a significant difference in Brix was observed between the drought and excess water supply treatment in ‘Fushimiamanaga’ fruits. In ‘Botankosho’, fruit harvested at 20, 30, 40, and 50 days after flowering (DAF) showed significantly higher Brix in 2017. A significant difference was observed at 30 and 50 DAF in 2017 (Fig. 4-S2). Glutamic acid content showed no significant difference between drought and excess water supply treatment in 2016 and 20 DAF in 2017 (Fig. 4-B2). Fruit of ‘Sapporo’ showed similar variation in Brix to the other cultivars and significantly lower Brix was observed in excess water treatment at 40 DAF. In addition, a significant difference in the Brix of fruit from drought and excess water supply treatment was observed at 30 and 50 DAF in 2017 (Fig. 4-S2).

Glutamic acid content
Glutamic acid content, expressed on a FW basis, increased in each cultivar with delay in harvesting up to 40 DAF. However, in the majority of cases glutamic acid content showed no significant difference between fruit harvested at 40 and 50 DAF, except for ‘Fushimiamanaga’ fruit in 2017 (Fig. 5-F2). In addition, all cultivars showed higher contents of glutamic acid in drought treatment compared with the other water supply treatments. In ‘Manganji’ a significant difference in glutamic acid content was observed between drought
and excess water supply treatment at all DAF in 2016 (Fig. 5-M1) and at 40 and 50 DAF in 2017 (Fig. 5-M2). In 2016, significantly lower glutamic acid content was observed in excess water treatment compared with drought treatment in ‘Fushimiamanaga’ except for fruit harvested at 20 DAF. Interestingly, in ‘Fushimiamanaga’, glutamic acid content was significantly higher in fruit of drought-treated plants at 30, 40, and 50 DAF compared with the other water supply treatments in 2017 (Fig. 5-F2). In the same year, significantly lower glutamic acid content was observed in fruits from excess water-treated plants than other water supply treatments at 20 DAF. In ‘Botankosho’ fruit, glutamic acid content was significantly higher in drought treatment at 20, 40, and 50 DAF in 2016 (Fig. 5-B1), and at 20, 30, and 40 DAF in 2017 (Fig. 5-B2), compared with the other water supply treatments. A significant difference in glutamic acid content between drought and excess water supply treatment was observed in ‘Botankosho’ fruit at 50 DAF in 2017. The glutamic acid content in ‘Sapporo’ fruit was significantly lower in excess water supply treatment at 40 DAF. In addition, significant differences between drought and excess water supply treatment were observed in ‘Sapporo’ fruit at 30 and 50 DAF (Fig. 5-S2).

Capsaicinoid content

Capsaicinoids were detected only in ‘Botankosho’ and ‘Sapporo’ fruit. Patterns of capsaicinoid content tended to be similar to those of total sugar content. Capsaicinoid content increased with later harvesting of the fruit and with reductions in water supply from excess to...
The size of chili pepper fruits increased with development and growth ceased at < 30 DAF. The color of the pericarp changed from green to red coincident with fruit maturation at around 40 DAF. However, the color of the pericarp of ‘Sapporo’ changed at < 40 DAF. This sequence was common to all cultivars and treatments in the present study (Fig. 8). According to Minami et al. (1998), the fruits of C. annuum ‘Takanotsume’ plants, grown in the same experimental field of Shinshu University as that used in the current research, stopped growing by < 20 DAF and turned red from 50 to 60 DAF. Comparing the present results with those of this previous study, fruit enlargement was slower and the change in pericarp color to red was earlier in the present investigation. The difference in timing of fruit growth cessation is considered to be because ‘Takanotsume’...
fruit are smaller than those of the cultivars used in the present study. The difference in the timing of fruit color change is possibly because the plants were grown in a greenhouse in the present study but in cool, outdoor fields in the study by Minami et al. (1998).

Total sugar content and Brix of the fruit tended to increase with later harvesting, but the glucose content showed only limited changes with increases in DAF. Given that the highest total sugar content recorded among all treatments, cultivars, and DAF sampling points was about 8,000 mg, compared with the highest glucose content of about 1,600 mg, the present results showed that the ratio of glucose content to total sugar content was small. In addition, the sucrose content is extremely low in fruit of sweet and pungent peppers (Ministry of Education, Culture, Sports, Science and Technology <https://fooddb.mext.go.jp/index.pl>, March 15, 2020); therefore it is predicted that the ratio of sucrose content to total sugar content is also extremely low. These results indicated that the majority of the sugars contained in chili pepper fruits were fructose, and the ratio of fructose content to total sugar content likely increased as the fruit matured.

Cherry tomato, the total sugar content increased with fruit maturation, but the glucose content also increased (Hayata et al., 1998). Consequently, we assume that sugar metabolism and accumulation differ in tomato fruit and chili pepper fruit. The glutamic acid content in the fruit increased up to 40 DAF, and thereafter remained unchanged or decreased. According to Nonaka et al. (2012), the glutamic acid content of red fruit (< 60 DAF) of ‘Botankosho’ is three times higher than in green fruit (< 50 DAF). The inconsistency of the present results with those of Nonaka et al. (2012) may

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**Fig. 6.** Capsaicinoid content (µg·g⁻¹ dry weight [DW]) at four stages of fruit maturation in chili pepper ‘Botankosho’ (B) and ‘Sapporo Oonaga Nanban’ (S). Graph B1 represent the year 2016 and B2 and S2 represent year 2017. Fruit were sampled at 20, 30, 40, and 50 days after flowering (DAF). Different lower-case letters a and b for the same DAF, and different lower-case letters w, x, y, and z for the same treatment (drought, D; standard water supply, S; and excess water supply, E), indicate significant differences between treatments and between DAF, respectively (Tukey’s pairwise test, P < 0.05). Error bars indicate the standard error.

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**Fig. 7.** Capsaicinoid content of placenta (µg·g⁻¹ dry weight [DW]) at four stages of fruit maturation in chili pepper ‘Botankosho’ (B) and ‘Sapporo Oonaga Nanban’ (S) in 2018. Fruit were sampled at 20, 30, 40, and 50 days after flowering (DAF). Different lower-case letters a and b for the same DAF indicate significant differences between treatments (Tukey’s pairwise test, P < 0.05). Error bars indicate the standard error.
be because the latter authors analyzed fruit from ‘Botankosho’ plants grown in open fields at high altitude. With regard to fruit color, the present results are consistent with those of Nonaka et al. (2012), because red fruit (equivalent to 40 DAF in the present study) showed significantly higher glutamic acid content than green fruit (equivalent to 30 DAF in the present study). However, in the current study the glutamic acid content of red fruit was not more than three times higher than in green fruit.

The capsaicinoid content increased with fruit development. A previous report showed that capsaicinoid content increases until just before the fruit turns red and then decreases after the pericarp has turned red (Minami et al., 1998). In the present study, capsaicinoid content did not decrease even after 40 DAF, when the fruit had turned red, and no significant difference was observed among the majority of treatments from 50 DAF. It is possible that the discordance in results between studies was due to the difference in cultivars used.

Changes in the glucose content and total sugar content with fruit growth showed opposing trends. A previous report showed that capsaicinoid content increases until just before the fruit turns red and then decreases after the pericarp has turned red (Minami et al., 1998). In the present study, capsaicinoid content did not decrease even after 40 DAF, when the fruit had turned red, and no significant difference was observed among the majority of treatments from 50 DAF. It is possible that the discordance in results between studies was due to the difference in cultivars used.

The relationship between glutamic acid content in the fruit and water supply was consistent with the relationships observed for total sugar content and Brix. According to the Umami Information Center (<https://www.umamiinfo.com/richfood/foodstuff/tomato.html>, March 11, 2020), tomato fruit contain high contents of the umami provider glutamic acid, especially as the fruit ripens. However, chili pepper tended to have the highest glutamic acid content at 40 DAF in the present study.

Capsaicinoid content also showed a similar response to water supply as total sugar content, Brix, and glutamic acid content. The highest capsaicinoid content was observed in the drought treatment. However, Bosland and Votava (2002) recorded high capsaicinoid content in fruit at a high rainfall site in New Mexico. The authors reported that the pungency of chili pepper fruit increased after water was applied by furrow irrigation. The present results are therefore incongruous. However, Estrada et al. (1999) reported similar results to the present findings in that capsaicinoid content was increased under drought stress. Sung et al. (2005) reported that pungency under drought stress is stronger than that of the control and thus drought stress provides a good criterion for evaluation of hot pepper cultivars with high capsaicinoid content. Ruiz-Lau et al. (2011) reported that capsaicin and dihydrocapsaicin contents caused an increase in glucose content and a decrease in total sugar content. These results imply that by increasing water availability, the fructose content was reduced, but the ratio of glucose content to total sugar content was small. In cherry tomato, increases in water supply decreased the total sugar content as well as the glucose content (Hayata et al., 1998). Thus, it is suggested that sugar metabolism and accumulation differ in tomato fruit and chili pepper fruit.

In tomato fruit, total sugar content and Brix increase in response to drought (Nahar and Gretzmacher, 2002). The soluble solid content (Brix) in tomato shows a strongly adverse relationship with yield under drought. Plants with low water supply are able to support only about 20% of the potential yield; thus, the highest Brix is observed under low water supply. This was considered to be due to the fact that if the number of developing fruit is low, the amount of sugars photosynthesized in the leaves that are distributed to individual fruit increases (Bakr et al., 2016). However the results of the present study supported these previous reports on tomato because there was a tendency towards a reduction in the number of leaves and fruit on plants in drought treatment compared with those in the other water supply treatments. We did not record yield in this experiment because we harvested many immature fruit in order to focus on taste component behavior with fruit growth. Therefore, it is necessary to investigate the relationship between yield, leaf number, photosynthetic ability, and sugar content in more detail in the future.
are increased in fruit of water-stressed plants of ‘Habanero’ pepper (Capsicum chinense) compared with those of control plants. Moreover, the contents are correlated with fruit age. These results are similar to those for capsaicinoid contents observed in the present experiment for Capsicum annuum cultivars. An additional possible reason for the increase in the capsaicinoid content of a whole fruit in response to drought stress is a decrease in the placenta to pericarp ratio as a result of the reduction in fruit size. However, the capsaicinoid content of the placenta in fruit of chili pepper plants subjected to drought stress was higher than that of plants grown under excess water supply in the 2018 data. However, how the placenta and pericarp ratio affected pungency of whole fruit was not clear because we did not measure the ratio in this study; the reason for the increase in capsaicinoid content in fruit due to drought stress was presumably that the capacity for capsaicinoid synthesis in the placenta was increased.

The present study clarifies the relationships among fruit growth, water supply, and the taste components (sugars, glutamic acid, and capsaicinoids) of chili pepper fruit. However, it is necessary to further investigate the relationship between fruit yield, fruit size, fruit water content, leaf number, photosynthesis ability, and the contents of taste components to resolve questions of how environmental factors affect the change in contents of taste components. In addition, it is necessary to elucidate the genetic mechanism by conducting expression analysis of the genes involved in the synthesis and accumulation of taste components.

**Literature Cited**

Bakr, J., H. G. Daood, Z. Pek, L. Helyes and K. Posta. 2016. Yield and quality of mycorrhized processing tomato under water scarcity. Appl. Ecol. Environ. Res. 15: 401–413.

Bosland, P. W. and E. J. Votava. 2002. Peppers: Vegetable and Spice CABI, New York.

Estrada, B., F. Pomar, J. Diaz, F. Merino and M. A. Bernal. 1997. Evolution of capsaicinoids in Capsicum annuum L. var. annuum cv. Padron fruit at different growth stages after flowering. Capsicum Eggplant News. 16: 60–63.

Estrada, B., F. Pomar, J. Diaz, F. Merino and M. A. Bernal. 1999. Pungency levels in fruit of the Padron pepper with different water supply. Sci. Hortic. 81: 385–396.

Hayata, Y., T. Tabe, S. Kondo and K. Inoue. 1998. The effects of water stress on the growth, sugar and nitrogen content of cherry tomato fruit. J. Japan. Soc. Hort. Sci. 67: 759–766 (In Japanese with English abstract).

Horie, H. 2009. Analysis for the taste components in various vegetables by capillary electrophoresis. Bunsei Kagaku 58: 1063–1066 (In Japanese).

Kraft, K. H., C. H. Brown, G. P. Nabhan, E. Luedeling, J. J. L. Ruiz, G. C. d’Eeckenbrugge, R. J. Hijmans and P. Gepts. 2014. Multiple lines of evidence for the origin of domesticated chili pepper Capsicum annuum in Mexico. Proc. Natl. Acad. Sci. USA 111: 6165–6170.

Kramer, P. J. 1969. Plant and water relationships. A modern synthesis. McGraw-hill, New York.

Kosuge, S. and Y. Inagaki. 1962. Studies on the pungent principles of red pepper. Part XI. Determination and contents of the two pungent principles. J. Agric. Chem. Soc. 36: 251–254 (In Japanese).

Madhumathy, A. P., A. A. Aivazi and V. A. Vijayan. 2007. Larvicidal efficacy of Capsicum annuum against Anopheles stephensi and Culex quinquefasciatus. J. Vet. Borne. Dis. 44: 223–226.

Minami, M., M. Toyoda, T. Inoue, K. Nemoto and A. Uijihara. 1998. Changes of capsaicinoid contents during maturing stage in chili pepper (Capsicum spp.). J. Fac. Agric. Shinshu Univ. 35: 45–49 (In Japanese with English abstract).

Nahar, K. and R. Gretzmacher. 2002. Effect of water stress on nutrient uptake, yield and quality of tomato under subtropical conditions. Die Bodenkultur. Res. 53: 45–51.

Nonaka, T., K. Matsushima, M. Minami, K. Nemoto and Y. Hamazu. 2012. Changes in antioxidant and taste compounds in ‘Botankoshou’ (Capsicum annuum L.) fruit, a local chili pepper variety from Nagano during stage. Hort. Res. (Japan) 11: 379–385 (In Japanese with English abstract).

Ortiz, R., J. Crossa, M. Vargas and J. Izquierdo. 2007. Studying the effect of environmental variables on the genotype × environment interaction of tomato. Euphytica 153: 119–134.

Othman, Z. A. A., Y. B. H. Ahmed, M. A. Habila and A. A. Ghalar. 2011. Determination of capsaicin and dihydrocapsaicin in Capsicum fruit samples using high performance liquid chromatography. Molecules 16: 8919–8929.

Perry, L., R. Dickau, S. Zarrillo, I. Holst, D. M. Pearsall, D. R. Piperno, M. J. Berman, R. G. Cooke, K. Rademaker, A. J. Ranere, J. S. Raymond, D. H. Sandweiss, F. Scaramelli, K. Tarble and J. A. Zeidler. 2007. Starch fossils and the domestication and dispersal of chili peppers (Capsicum spp. L.) in the America. Science 315: 986–988.

Ruiz-Lau, N., F. M. Lara, Y. M. Garcia, E. Z. Moreno, A. G. Antonio, I. E. Machado and M. M. Estevez. 2011. Water deficit affects the accumulation of capsaicinoids in fruits of Capsicum chinense Jacq. HortScience 46: 487–492.

Sung, Y., Y. Y. Chang and N. L. Ting. 2005. Capsaicin biosynthesis in water-stressed hot pepper fruits. Bot. Bull. Acad. Sin. 46: 35–42.

Suzuki, T. and K. Iwai. 1984. Constituents of red pepper species: Chemistry, biochemistry, pharmacology, and food science of the pungent principle of Capsicum species. The Alkaloids: Chemistry and Pharmacology 23: 227–299.

Ullah, S. M., M. H. Gerzabek and G. Soja. 1994. Effect of sea water and soil salinity on onion uptake, yield and quality of tomato (fruits). Die Bodenkultur 45: 227–237.

Ullah, S. M., G. Soja and M. H. Gerzabek. 1993. Ion uptake, osmoregulation and plant water relations in faba bean (Vicia faba L.) under salt stress. Die Bodenkultur 44: 291–301.

Zewdie, Y. and P. W. Bosland. 2000. Evaluation of genotype, environment, and genotype- environment interaction for capsaicinoids in Capsicum annuum L. Euphytica 111: 185–190.