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Effects of high temperature on the fruit development and sugar concentration in everbearing strawberry cultivars

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Abstract: In everbearing strawberry cultivars, understanding the effects of high temperature is crucial. Long-day everbearing cultivars are promoted for summer and autumn production whereas this is off-season for June-bearing varieties. This study investigated the effects of high temperature on the development and fruit quality of the everbearing cultivars Natsuakari and Dekoruju in a phytotron-simulating summer condition. Both cultivars showed a smaller number of flowering inflorescences at 30°C/25°C (day/night) compared to 20°C/15°C, indicating that flower bud development is sensitive to high temperatures. Fruit set rates were also negatively affected by the higher temperature. Fruit sugar composition of 'Natsuakari' fruits showed an increased sucrose concentration during the developmental stage from 75% colored fruit to 100% colored fruit. In the ripe fruit of 'Natsuakari,' the sugar content was measured higher due to greater amount of sucrose accumulation, whereas a remarkable decrease in the sucrose concentration was observed at 30°C/25°C temperature compared to 20°C/15°C. These results suggested that summer high temperatures negatively impacted flowering, fruit set, and sucrose content in everbearing cultivars, ultimately leading to reduced fruit production and quality. Additionally, the temperature effects varied between the two cultivars strawberry.

1. Introduction

Strawberries currently grown in Japan and many other countries are mainly June-bearing cultivars, whose flower buds differentiate under low temperatures and short days (Yano *et al.*, 2021; Janssens *et al.*, 2024). In the cultivation of June-bearing strawberries in Japan, fruits are produced from November to June of the following year by artificially controlling flowering and dormancy and performing forcing culture or semiforcing culture. The summer and fall seasons, from July to October, are the off-season of these cultivars, and strawberries are imported to meet the market demand. However, since imported fruits have problems with freshness and taste, there is a demand for domestically produced fruits

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(Nishiyama *et al*., 2020).

Methods for producing strawberries in summer and fall using June-bearing cultivars include retarding culture and short-day treatment. Retarding culture, which involves delaying plant development through long-term refrigeration which has several disadvantages, such as high refrigeration costs, plant weakening, and the increased risk of gray mold during refrigeration. As a result, this cultivation method is not widely practiced (Kobayashi and Yamamoto, 1994; Yamazaki, 2012). Similarly, June-bearing strawberry production through short-day treatment is also limited due to the high facility and labor requirements, as well as the instability of flowering, which can be affected by weather conditions (Hamano *et al*., 2012).

In addition to June-bearing cultivars, there are everbearing cultivars, which are quantitatively long-day plants. Everbearing cultivars can be differentiated from flower buds under high temperature and long-day conditions in summer (Durner *et al*., 1984; Smeets, 1980). Nishiyama *et al.* (1998, 1999) reported that these cultivars have critical day lengths for differentiating flower buds under summer conditions. Under high-temperature conditions simulating the summer season, the critical photoperiods of four everbearing cultivars were examined, and they varied among cultivars, ranging from 12 to 15 hours (Nishiyama *et al*., 2009). Due to their quantitatively long-day nature, everbearing strawberry cultivars are seen as a potential solution to the challenges of off-season fruit production faced by June-bearing cultivars.

In fruit vegetables, including strawberries, high temperatures in summer and fall often cause problems with fruit set, growth, and quality (Ito *et al*., 2022). Regarding the effects of high temperatures on strawberries, there are some findings in June-bearing cultivars. Regarding fruit set and fruit growth, it is reported that high temperatures during the flowering period reduce fruit achenes (Mori, 1998) and decrease fruit weight in fall and winter (Miura *et al*., 1994). In the former study, the effect of high temperature was examined by applying five temperature regimes ranging from a high of 32°C/27°C (day/night) to a low of 16°C/11°C (day/night), and in the latter study, the effect was investigated under constant temperatures of 19°C (high) and 15°C (low), respectively. Additionally, fruit sugar concentration tends to decrease under comparatively high temperature conditions, depending on the cultivar (Kumakura and Shishido, 1994; Ogiwara *et al*., 1999; Sato and Kitajima, 2007). High night temperatures have also been found to negatively affect fruit sugar content, as demonstrated by comparisons between night temperatures of 10°C and 20°C (Matsuzoe *et al*., 2006).

Compared to June-bearing cultivars, the high temperature problem is even more severe in everbearing cultivars because their production is expected from summer to fall. However, there is little knowledge regarding the effect of high temperatures in everbearing cultivars. In addition, in previous reports using June-bearing cultivars, most of the experiments assumed the production period of June–bearing cultivars (Ono *et al*., 2023), and the experiments that assumed under high temperatures in summer like the present study, are lacking. In Japan, since the rise in temperature due to global warming is exceeding the world average, and the increase in annual average maximum temperature is higher in agricultural land as well as in urban areas (Murakami *et al*., 2011), it would be meaningful to investigate the impact of high summer temperature on fruit production. Furthermore, few reports have comprehensively investigated flowering, fruit growth, sugar concentration, and even sugar composition. Therefore, in this study, we controlled the temperature in a phytotron and investigated the effects of high summer temperature on various factors related to fruit production using two everbearing strawberry cultivars.

2. Materials and Methods

Plant materials

We used everbearing strawberries (*Fragaria × ananassa* Duch.) 'Natsuakari' and 'Dekoruju.' The cultivation method was the same followed by Nishiyama *et al*. (1998), in which runner seedlings were potted up, grown in an unheated greenhouse, and then moved to a phytotron and subjected to temperature treatments. The temperature treatments started in early November, with day (6:00 to 18:00)/night (18:00 to 6:00) temperatures set at 20°C/15°C or 30°C/25°C. Long-day treatment with a day length of 24 h was given to promote flowering, that is, sunlight from 9:00 to 17:00 and incandescent light bulb radiation (3.23 $W \cdot m^{-2}$) from 17:00 to 9:00. Because the critical photoperiod is influenced by cultivar and temperature (Smeets, 1980; Nishiyama *et al*., 2009), a 24-h day length was set as the maximum possible photoperiod to ensure stable flowering. Hand pollination was performed to ensure fruit set.

Measurement of flowers and fruits

The inflorescences were removed before starting the temperature treatment. The number of inflorescences with an open first flower (referred to as flowering inflorescence) was counted weekly during the temperature treatment. The number of flowers and fruits was also counted to calculate the fruit set rate. Fruit length and diameter of the first fruit in each inflorescence were measured using a vernier caliper every 2 to 3 days until ripening (100% coloration). Fruit length was measured as the maximum distance between the apical and peduncle ends of each fruit. The fruit diameter was measured as the maximum transverse diameter.

Determination of the fruit sugar concentration

Glucose, fructose, and sucrose concentrations were analyzed in white (W), 50%, 75%, and 100% colored fruit according to Sagor *et al*. (2015), Corvino *et al*. (2023), and Jia *et al*. (2011). Briefly, sugars were extracted with ethanol at 80°C, and maltose solution was added as an internal standard. After filtration using a Sep-pack C18 cartridge (Waters) and chloroform extraction, the sugars were measured using a sugar analyzer SU-300 (Toa DKK Co., Ltd., Tokyo, Japan).

Statistical analysis

Statistical analysis was performed using BellCurve for Excel (Social Survey Research Information Co., Ltd., Tokyo, Japan). Twelve plants were used in the temperature treatment at 20°C/15°C of 'Natsuakari' and at 20°C/15°C and 30°C/25°C of 'Dekoruju.' Ten plants were used in the temperature treatment at 30°C/25°C of 'Natsuakari' because two plants died during the experiment. The percentage data for the fruit set was subjected to arcsine transformation. Sugar concentration and fruit size changes were measured in three biological replicates.

3. Results

Effect of high temperature on flowering and fruit development

Figure 1 shows the changes in the number of flowering inflorescences during the temperature treatment, which changed similarly for both cultivars. During weeks 1-3, the number of flowering inflorescences was higher at 20°C/15°C than at 30°C/25°C in 'Natsuakari.' Similarly, during weeks 4-6, the number of flowering inflorescences was higher at 20°C/15°C than at 30°C/25°C in both cultivars. In weeks 7-9, the number of flowering inflorescences was similarly low under both temperature treatments. Temperature significantly affected the number of flowering inflorescences throughout the treatment period, but no cultivar differences or interactions were observed (Table 1). However, temperature difference and their interaction with cultivars was observed in case of fruit set rate although there were no cultivar differences (Table 1). The fruit set rate of 'Natsuakari' was reduced to one-third at 30°C/25°C compared to 20°C /15°C, whereas the reduction in 'Dekoruju' was moderate. The results suggest that 'Dekoruju' is more tolerable to high temperature in terms of fruit set rate.

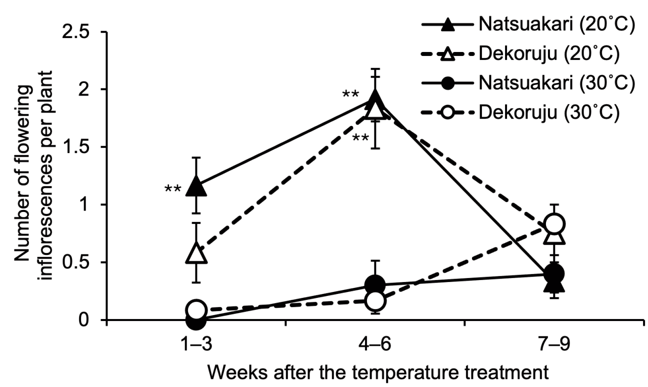

Fig. 1 - Changes in the number of flowering inflorescences per plant of 'Natsuakari' and 'Dekoruju' during the temperature treatment at 20°C/15°C (20°C on the graph) and 30°C/25°C (30°C on the graph). The number of flowering inflorescences is the sum of inflorescences in each 3-weeks shown on the horizontal axis. Values indicate means with SEs (n=10 for 'Natsuakari' at 30°C/25°C, n=12 for others). ** indicates significant differences at the 1% level between temperatures for each cultivar by t-test.

Fruit development during temperature treatment is shown in figure 2. The changes in fruit length were similar regardless of cultivars and temperatures, whereas fruit diameters tended to be larger at 30°C/25°C for both cultivars. Since the fruit length and diameter were measured until ripening, the timing of ripening can be seen on the graph. The result indicated that the fruit ripened earlier at 30°C/25°C than at 20°C/15°C. Higher temperatures

Table 1 - Effect of temperature on the number of flowering inflorescences and fruit set rate

Cultivar	Temperature day/night (°C)	Number of inflorescences [z]	Fruit set rate (%)
Natsuakari	20/15	3.42	91.4
	30/25	0.70	30.0
Dekoruju	20/15	3.17	71.4
	30/25	1.08	62.1
ANOVA [y]	Cultivar	NS [x]	NS
	Temperature	**	*
	Interaction	NS	*

[z] Number of flowering inflorescences per plant.
[y] Analysis of the variance.
[x] NS, **, and * indicate not significant and significant differences at P < 0.01 and P<0.05, respectively (two-way ANOVA).

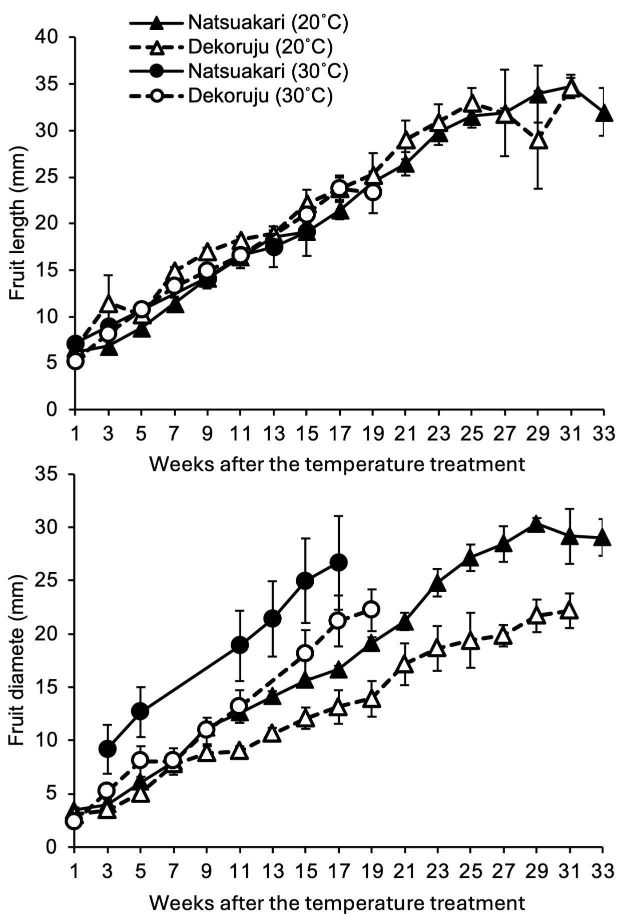

Fig. 2 - Changes in the length and diameter of 'Natsuakari' and 'Dekoruju' fruits during the temperature treatment at 20°C/15°C (represented as 20°C on the graph) and 30°C/25°C (represented as 30°C on the graph). The first fruit from each inflorescence was measured from flowering to ripening (100% coloration). Values represent means with SEs (n = 3). For 'Natsuakari,' there was considerable variation in fruit diameter at high temperatures and no significant difference between the temperature treatments. However, for 'Dekoruju,' a significant difference in fruit diameter was observed between the temperature treatments during the later stages of fruit development (P<0.05, t-test).

are considered to accelerate strawberry ripening primarily by enhancing the activity of enzymes involved in key ripening processes.

Fruit sugar accumulation and the effects of temperature on sugar concentration

To clarify the cultivar's characteristics of fruit sugar accumulation, sugar concentrations were measured at different ripening stages of 'Natsuakari' and 'Dekoruju' fruits at 20°C/15°C. Changes in glucose and fructose concentrations were similar in both cultivars with concentrations remaining at similar levels from white fruit to 75% colored fruit, then increasing from 75% to 100% colored fruit (Fig. 3). On the other hand, changes in sucrose concentrations differed between cultivars; that is, sucrose concentrations did not increase in 'Dekoruju,' whereas they increased in 'Natsuakari' from 75% to 100% colored fruit. The effects of temperature on the sugar concentrations in ripe fruits are shown in Table 2. There were no significant differences in the glucose and fructose concentrations in the cultivars at different temperatures, whereas significant differences in the sucrose concentrations were found between the cultivars at different temperatures.

4. Discussion and Conclusions

High temperature treatment at 30°C/25°C reduced the number of flowering inflorescences in both everbearing strawberry cultivars, indicating that such high temperatures affect fruit yield. The difference in the number of flowering inflorescences was greater during weeks 4-6 after the start of the treatment. However, the flower buds that opened

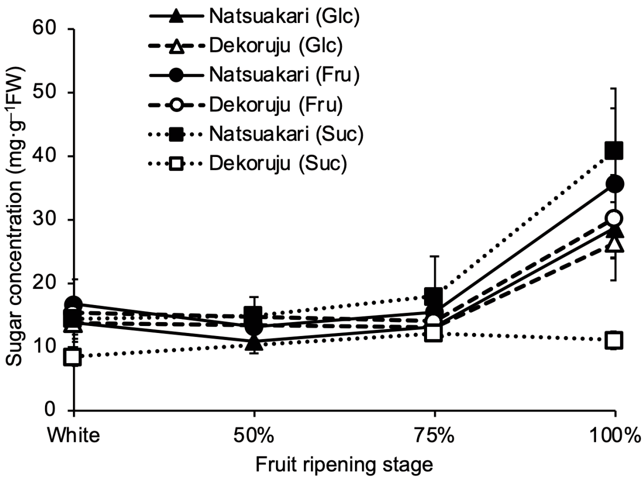

Fig. 3 - Changes in sugar concentration during the fruit ripening stages of 'Natsuakari' and 'Dekoruju.' The plants were grown at 20°C/15°C, and glucose (Glc), fructose (Fru), and sucrose (Suc) concentrations in white, 50%, 75%, and 100% colored fruit were measured. Values indicate means with SEs (n = 3). For 'Dekoruju,' data for 50% colored fruit is missing. Small error bars are hidden by the marker and cannot be seen.

fairly long period after flower bud differentiation. Until now, the effects of high temperatures have mainly been considered to be poor fruit set due to decreased fertility (Pipattanawong *et al*., 2009; Ledesma and Sugiyama, 2005). Therefore, a significant finding of this study is that flower bud development for several weeks after differentiation is inhibited, leading to a reduction in the number of flowering inflorescences under high temperatures. In the near future, it will be crucial to identify the stages of flower bud development that are sensitive to high temperatures and to develop efficient temperature control techniques based on the findings.

Seven to nine weeks after the start of the temperature treatment, the number of flower inflorescences at 20°C/15°C decreased to the same level as that at 30°C/25°C. In everbearing cultivars, in the case of strong promotion of flowering, most buds differentiate into flower buds instead of vegetative buds, leading to the loss of meristems and growth inhibition (Yoshida, 2009; Nishiyama *et al*., 2020).

Table 2 - Effect of temperature on the sugar concentration in ripe fruit

Cultivar	Temperature day/night (°C)	Sugar concentration (mg g^{-1} FW)		
		Glucose (z)	Fructose	Sucrose
Natsuakari	20/15	28.7	35.6	40.9
	30/25	23.8	28.1	22.9
Dekoruju	20/15	26.4	30.2	11.0
	30/25	12.8	15.1	5.6
ANOVA (y)	Cultivar	NS (x)	NS	**
	Temperature	NS	NS	*
	Interaction	NS	NS	NS

(z) Glucose, fructose, and sucrose concentration were determined.
(y) Analysis of the variance.
(x) NS, **, and * indicate not significant and significant differences at $P < 0.01$ and $P < 0.05$, respectively (two-way ANOVA).

during this period likely already differentiated, based on the time required for flower bud differentiation to flowering (Morishita, 2014). These results suggest that the development of flower buds after differentiation is inhibited by high temperatures such as 30°C/25°C, and this high temperature sensitivity is common to both cultivars. Furthermore, the number of flowering inflorescences was lower at 30°C/25°C during weeks 1-3 and weeks 4-6, in at least one of the two cultivars indicating that the development of flower buds is sensitive to high temperature during a

Besides, excessive fruit set in strawberries is known to weaken plant growth. Our results suggest that under optimal temperature and long-day conditions, it is necessary to regulate the number of flowering inflorescences. To solve this problem, light quality control and intermittent lighting techniques are promising (Nishiyama *et al*., 2020; Yamazaki *et al*., 2009).

Changes in fruit length and diameter from flowering to ripening are shown in figure 2. The change in fruit length was similar between 20°C/15°C and 30°C /25°C until ripening. At 30°C/25°C, fruit diameter was larger due to the occurrence of malformed fruit. Fruit ripened faster at 30°C/25°C, with a similar growth rate based on fruit length between the two temperature treatments, which may have resulted in a smaller fruit size at ripening. Therefore, early ripening under high temperatures is likely to influence yield, together with reductions in flower number and fruit set rate. Early ripening is also reported in June-bearing cultivars, where fruit harvested in April when temperatures are relatively high, ripens in fewer days (Ogiwara *et al*., 1999). Additionally, fruit ripens faster at higher temperatures within an average daily temperature range of 15°C to 25°C (Kumakura and Shishido, 1994). These previous reports and our results suggest that early ripening under high temperatures is common to everbearing and June-bearing cultivars. However, in this study, we investigated the effects of high temperatures simulating summer conditions, indicating that summer temperatures have a significant impact on everbearing strawberries. Regarding fruit growth curves, a previous report on June-bearing cultivars (Ogiwara *et al*., 1999), showed that fruits harvested in April rose faster than those harvested in January, which differs from our results. Therefore, the response of growth curves to temperature may differ depending on the temperature combinations or cultivars being compared.

Strawberries set fruit and develop fruit receptacles through the fertilization of many pistils on the flower receptacle. As a result, even if some pistils remain unfertilized, the fruit does not necessarily drop. A decrease in fertility at daytime temperatures of 30°C to 32°C has been reported in June-bearing cultivars (Pipattanawong *et al*., 2009; Ledesma and Sugiyama, 2005). In this study, the fruit set rate decreased under high temperatures, whereas there were cultivar-specific differences in fruit set inhibition caused by high temperatures. Additionally, the morphology of floral organs, such as filament length and sepal size, appeared to be affected in the 30°C 25°C area. Therefore, the effects of high summer temperatures should be examined from multiple perspectives, including fertility and morphology.

Strawberries are classified into cultivar groups based on their sugar composition, including the fructose/glucose accumulating type, the sucrose accumulating type, and the intermediate type (Ogiwara *et al*., 1998). Although the cultivars used in this study were not included in the same report, they were considered to be intermediate types. However, the sucrose content at 20°C/15°C was higher at approximately 40% in ‘Natsuakari’ and low at around 15% in ‘Dekoruju’ showing characteristics more aligned with the sucrose accumulating type and the fructose/glucose accumulating type, respectively. The sucrose concentration in ‘Natsuakari’ fruit increased from 75% to 100% ripeness, whereas no enhancement was observed in ‘Dekoruju,’ suggesting that sucrose accumulation in the late stages of fruit development is a characteristic of the sucrose accumulating type. In tomatoes and pears, invertase and sucrose synthase play key role in determining the sucrose ratio (Kanayama, 2017), and recent genome editing of the invertase inhibitor-related factor has been recently reported (Kawaguchi *et al*., 2021). Therefore, it is expected that the development of this research will lead to the elucidation of the determining mechanism of fruit sugar composition and the improvement of fruit quality through its control.

In this study, the sum of the three sugar concentrations decreased by approximately 30% in ‘Natsuakari’ and by approximately 50% in ‘Dekoruju’ at 30°C/25°C compared to 20°C/15°C. One likely reason for this decrease is the reduction in sucrose concentration, which significantly differed between the two temperature treatments. A previous report on June–bearing cultivars suggested that low fruit sugar concentrations in April, from winter to spring, may be related to high fruit load or early fruit coloration (Ogiwara *et al*., 1999). In this study, the number of fruits was smaller at 30°C/25°C, and ripening was determined by fruit color; thus, early ripening likely contributed to the lower total sugar and sucrose concentrations. In particular, ‘Natsuakari’ may have been more strongly affected by early ripening, as sucrose accumulates during the later stage of fruit development, as described in this study. In tomatoes, sucrose synthase has been reported to play a role in reducing fruit sucrose concentration under high temperature conditions (Rosales *et al*., 2007). Therefore, understanding the relationship between sugar composition and sucrose-related enzymes in everbearing strawberries is essential to elucidate the mechanism behind quality decline during summer.

We conducted a temperature treatment assuming high temperatures in summer, which are important in the production of everbearing strawberries, using a phytotron and revealed its effects on the number of flowering inflorescences, sucrose concentration, and fruit set. The differences between cultivars in these traits under different temperatures described in this study can be useful for breeding and cultivation. There are divergent phenotypes for the flowering response to temperature, as described by the comparison of many everbearing cultivars in warm and cold regions (Hikawa-Endo *et al*., 2019). Although the sugar composition was not investigated by Hikawa-Endo *et al*. (2019), it is expected that there will be diversity in the high temperature sensitivity and sugar accumulation. The controlled environment experimental system in this study will contribute to the selection of high temperature resistance genes and biomarkers from such a variety of everbearing cultivars to maintain fruit production and quality in everbearing strawberries grown under high temperature conditions.

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References

CORVINO A., ROMANIELLO R., PALUMBO M., RICCI I., CEFOLA M., PELOSI S., PACE B., 2023 - *Image analysis to predict the maturity index of strawberries*. - Adv. Hort. Sci., 37(1): 83-87.

DURNER E.F., BARDEN J.A., HIMELRICK D.G., POLING E.B., 1984 - *Photoperiod and temperature effects on flower and runner development in day-neutral, June-bearing, and everbearing strawberries.* - J. Am. Soc. Hortic. Sci., 109: 396-400.

HAMANO M., YAMAZAKI H., YANO T., HONJO M., MORISHITA M., 2012 - *Effect of long-day treatments before planting on flower initiation and autumn yield of first-year runner plant of everbearing strawberry 'Natsuakari.'* - Hort. Res. (Japan), 11: 467-475. In Japanese with English abstract.

HIKAWA-ENDO M., HONJO M., SONE K., MORISHITA M., YUI S., 2019 - *Evaluation of flowering and runnering characteristics of everbearing strawberry, and selection of its suitable cultivar in warm-region cultivation from winter to spring in Japan.* - Hort. Res. (Japan) 18: 215-226. In Japanese with English abstract.

ITO H., KANAYAMA Y., SHIBUYA T., MOHAMMED S.A., NISHIYAMA M., KATO K., 2022 - *Effect of short-term temperature stress on fruit set and the expression of an auxin reporter gene and auxin synthesis genes in tomato.* - Sci. Hortic., 300: 111039.

JANSSENS P., BOONEN M., BYLEMANS D., MELIS P., VAN DELM T., VENDEL I., HERTOG M., ELSEN A., VANDENDRIESSCHE H., 2024 - *Limited irrigation of field-grown strawberry (*Fragaria × ananassa *cv. 'Elsanta') in a temperate climate: Effects on yield and quality*. - Eur. J. Hortic. Sci., 89(1).

JIA H., CHAI Y., LI C., LU D., LUO J., QIN L., SHEN Y., 2011 - *Abscisic acid plays an important role in the regulation of strawberry fruit ripening*. - Plant Physiol., 157: 188-199.

KANAYAMA Y., 2017 - *Sugar metabolism and fruit development in the tomato*. - Hort. J., 86: 417-425.

KAWAGUCHI K., TAKEI-HOSHI R., YOSHIKAWA I., NISHIDA K., KOBAYASHI M., KUSANO M., LU Y., ARIIZUMI T., EZURA H., OTAGAKI S., MATSUMOTO S., SHIRATAKE K., 2021 - *Functional disruption of cell wall invertase inhibitor by genome editing increases sugar content of tomato fruit without decrease fruit weight*. - Sci. Rep., 11: 21534.

KOBAYASHI T., YAMAMOTO Y., 1994 - *Investigative studies on the present condition of the retarding in strawberry in Hyogo prefecture and handling methods of cold-stored seedlings.* - Bull. Hyogo Pre. Agri. Inst. (Agriculture), 42: 33-36. In Japanese.

KUMAKURA H., SHISHIDO Y., 1994 - *The effect of daytime, nighttime, and mean diurnal temperatures on the growth of 'Morioka-16' strawberry fruit and plants*. - J. Japan. Soc. Hort. Sci., 62: 827-832. In Japanese with English abstract.

LEDESMA N., SUGIYAMA N., 2005 - *Pollen quality and performance in strawberry plants exposed to high-temperature stress.* - J. Am. Soc. Hortic. Sci., 130: 341-347.

MATSUZOE N., KAWANOBU S., MATSUMOTO S., KIMURA H., ZUSHI, K., 2006 - *Effect of night temperature on sugar, amino acid, ascorbic acid, anthocyanin and ellagic acid in strawberry (*Fragaria × ananassa *Duch.) fruit.* - J. Sci. High Tech. Agric., 18: 115-122.

MIURA H., YOSHIDA M., YAMASAKI A., 1994 - *Effect of temperature on the size of strawberry fruit.* - J. Japan. Soc. Hort. Sci., 62: 769-774.

MORI T., 1998 - *Effect of temperature during flower bud formation on achene number and fresh weight of strawberries*. - J. Japan. Soc. Hort. Sci., 67: 396-399. In Japanese with English abstract.

MORISHITA S., 2014 - *Basic knowledge of strawberries:*

ecology and cultivation techniques. -Seibundo Shinkosha, Japan. In Japanese.

MURAKAMI M., KUWAGATA T., ISHIGOOKA Y., NISHIMORI M., 2011 - *A selection of monitoring AMeDAS stations over the agricultural land and its regional characteristics of the tendencies of temperature change.* - Climate Biosphere, 11: 41-50. In Japanese with English abstract.

NISHIYAMA M., EBIHARA Y., KANAHAMA K., 2009 - *Differences in critical photoperiod for flower bud initiation among everbearing strawberry cultivars*. - Hort. Res. (Japan), 8: 35-39. In Japanese with English abstract.

NISHIYAMA M., OHKAWA W., KANAHAMA K., 1998 - *Induction of reproductive growth of everbearing strawberry plants in dormant condition by controlled temperature and photoperiod*. - J. Japan. Soc. Hort. Sci., 67: 228-235. In Japanese with English abstract.

NISHIYAMA M., OHKAWA W., KANAHAMA K., 1999 - *Interaction between temperature and photoperiod on inflorescence development on everbearing strawberry 'Summerberry' plant*. - J. Japan. Soc. Hort. Sci., 68: 192-194. In Japanese with English abstract.

NISHIYAMA M., YAMAZAKI H., KANAYAMA Y., 2020 - *Effect of light quality on flowering in everbearing strawberry cultivars.* - Hort. Res. (Japan), 19: 49-54. In Japanese with English abstract.

OGIWARA I., MIYAMOTO R., HABUTSU S., SUZUKI M., HAKODA N., SHIMURA I., 1998 - *Variation in sugar content in fruits of four strawberry cultivars grown in the field and under forced culture, harvest years, and maturation stage.* - J. Japan. Soc. Hort. Sci., 67: 400-405. In Japanese with English abstract.

OGIWARA I., SHIROISHI M., HAKODA N., SHIMURA I., 1999 - *Causes of low sugar levels in forced strawberry fruits.* - J. Japan. Soc. Hort. Sci., 68: 130-137. In Japanese with English abstract.

ONO S., YASUTAKE D., KIMURA K., KENGO I., TERUYA Y., HIDAKA K., YOKOYAMA G., HIROTA T., KITANO M., OKAYASU T., OZAKI Y., 2023 - *Effect of microclimate and photosynthesis on strawberry reproductive growth in a greenhouse: using cumulative leaf photosynthesis as an index to predict the time of harvest.* - J. Hortic. Sci. Biotech., 99: 223-232.

PIPATTANAWONG R., YAMANE K., FUJISHIGE N., BANG S., YAMAKI, Y., 2009 - *Effects of high temperature on pollen quality, ovule fertilization and development of embryo and achene in 'Tochiotome' strawberry*. - J. Japan. Soc. Hort. Sci., 78: 300-306.

ROSALES M.A., RUBIO-WILHELMI M.M., CASTELLANO R., CASTILLA N., RUIZ J.M., ROMERO L., 2007 - *Sucrolytic activities in cherry tomato fruits in relation to temperature and solar radiation.* - Sci. Hortic., 113: 244-249.

SAGOR G.H.M., BERBERICH T., TANAKA S., NISHIYAMA M., KANAYAMA Y., KOJIMA S., MURAMOTO K., KUSANO T., 2015 - *A novel strategy to produce sweeter tomato fruits with high sugar contents by fruit-specific expression of a single bZIP transcription factor gene.* - Plant Biotechnol. J., 14, 1116-1126.

SATO K., KITAJIMA N., 2007 - *Change in fruit quality during the harvesting season and the relationship between fruit quality and temperature during fruit maturing stage of the 'Amaou' strawberry cultivar.* - Bull. Fukuoka Agric. Res. Cent., 26: 45-49. In Japanese with English abstract.

SMEETS L., 1980 - *Effect of temperature and daylength on flower initiation and runner formation in two everbearing strawberry cultivars*. - Sci. Hortic., 12: 19-26.

YAMAZAKI A., 2012 - *Summer and autumn cultivation-June-bearing strawberry (in Japanese): Agro-technology System. - Vegetables Series 3. Strawberry*. - Rural Culture Association, Japan, pp. 169-175.

YAMAZAKI K., KUMAKURA H., HAMAMOTO H., YAMADA M., ISHIWATA M., 2009 - *Effects of overnight illumination with green or yellow lights on flowering and growth in some strawberry cultivars.* - J. Agric. Meteorol., 65: 261-272.

YANO T., KINOSHIT A.T., YAMAZAKI H., NAGASUGA K., YAMAZAKI H., INAMOTO K., HAMANO M., HONJO M., MORISHITA M., YOSHIDA Y., 2021 - *Effect of intermittent long-day treatment on flowering of branch crown and yield in everbearing strawberry cultivars*. - Hort Res. (Japan), 20: 171-177. In Japanese with English abstract.

YOSHIDA Y., 2009 - *Physiological disorder of strawberry (in Japanese): Agro-technology System. Soil Fertilization Series 4. Soil Diagnosis and Growth Diagnosis*. - Rural Culture Association, Japan, pp. 392.