Journal of the American Pomological Society 75(3): 134-140 2021

Sugar Concentration in Strawberry Is Influenced by Temperature During Fruit Development

Anya Osatuke and Marvin Pritts[1]

Additional index words: *Fragaria* x *ananassa,* respiration, ripening, soluble solids

Abstract

Day neutral strawberries (*Fragaria* x *ananassa* Duch.) produce fruit over several months, even in climates with cold winters. Air temperatures during these long fruiting periods can range from near freezing to close to 40 ˚C. We divided fruit development into four developmental stages and divided the typical air temperature range during the growing season into four non-overlapping intervals from 7 to 32 ˚C. We sampled fruit from a day neutral strawberry planting approximately once a week from July to Nov., calculated the number of hours that individual fruits were exposed to a particular temperature interval during each of the four developmental stages, then correlated this number with the soluble solids concentration (SSC) of the harvested fruit. We found that warm air temperature exposure (16 - 23 ˚C) early in fruit development was positively correlated with final SSC at harvest, but SSC increased further when fruits were exposed to cooler air temperatures (7 - 15 ˚C) for the 15 days prior to harvest. Exposure to air temperatures above 24 ˚C at any developmental stage resulted in fruit with lower SSC. Our data provide field validation that strawberry sweetness is highest under moderately cool temperatures, and sugar concentration is reduced when developing fruits are exposed to hot (>24 ˚C) temperatures as fruit approach ripening. It may be possible for growers to minimize the amount of time air temperatures exceed 24 ˚C by using evaporative cooling, reflective low tunnel coverings or shade cloth to enhance the sugar concentration of fruit.

The sweet taste of a strawberry fruit is produced by the accumulation of sucrose, glucose, and fructose, with the amount of accumulated sugars affected by time of harvest, genotype, and environmental exposure during fruit development (Perkins-Veazie, 1995). Within a given cultivar, soluble solids concentration (SSC) can change from year-to-year (Jouquand et al., 2008; Mackenzie et al., 2011). Gündüz and Ozdemir (2014) estimated that 35% of variation in sugar concentration could be attributed to growing conditions. Day neutral strawberries and short day cultivars in certain locations fruit over many months and experience a range of environmental conditions within a single season, so the sugar concentration of fruit may vary temporally (Mackenzie and Chandler, 2009).

Intense sunlight and high temperatures can cause ripening fruit to heat to as much as 8 ˚C above the ambient air temperature (Wang et al., 2002). Such heating can induce cellular and molecular damage resulting in sunscald; at lesser intensities, high light and heat cause an increased transpiration flux in the fruit (Taghavi et al., 2019), resulting in increased metabolism of internal sugars and a reduction in sweetness (Montanaro et al., 2012). Gündüz and Ozdemir (2014) postulated that hot days and warm nights speed maturation of strawberry fruit, reducing the duration of sugar import and thus causing a reduction in sweetness and flavor. Lower temperatures have been found to induce higher concentrations of sucrose as well as ascorbic acid (Josuttis et al, 2011; Wang and Camp, 2000).

Growing sites with long photoperiods and cool night temperatures tend to produce

[1] Horticulture Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853.
The authors thank Richard Gaisser for managing the strawberry planting during the course of the experiment, the New York State Berry Growers Association/New York Agriculture and Markets, and the National Institute of Food and Agriculture, U.S. Dept. of Agric., Hatch grant 1017299 for providing funding for this study.
Corresponding author. E-mail address: mpp3@cornell.edu

strawberries with good flavor and sugar concentration (Hancock, 1999; Palemieri et al., 2017; Taghavi et al., 2019). Wang and Camp (2000) compared the influence of several temperature ranges on strawberry chemical composition and identified a low temperature range, with 18 ˚C day and 12 ˚C night temperatures as optimal for SSC and titratable acidity (TA) accumulation in 'Kent' and 'Earliglow.' In the same experiment, plants exposed to 30 ˚C days and 22 ˚C nights yielded fruits with the lowest SSC and TA concentration. However, none of these studies documented the specific stage of development when sugar concentration is most influenced by temperature. In a survey of 22 farms over three years across New York State, warm days and cool nights between first flower and pink fruit were found to be associated with increased TA and SSC at harvest in 'Jewel' (Osatuke and Pritts, 2021).

Short day cultivars produce fruit for only about 3 weeks in cold temperate climates and are not exposed to the air temperature extremes that day neutral plants experience over a much longer fruiting season. The air temperature range during fruit development across this extended season can range from near freezing to 40 ˚C. This fruiting pattern offers the opportunity to examine how wide temperature ranges affect sugar accumulation in developing fruit, and identify specific stages of fruit development when temperatures have an impact. Knowing this information would allow growers to predict the quality of fruit during a future harvest and perhaps modify the temperature environment to enhance sweetness.

Materials and Methods

Dormant 'Albion' strawberries were planted in raised white plastic mulched beds on 14 May 2020. The beds were established on a field of Arkport fine sandy loam (mesic Lamellic Hapludalf) at the Cornell University Agricultural Experiment Station (42.441582, -76.472487). Beds were 1.5 m on center with plants set in double rows 0.3 m apart. Plants were fertilized weekly at a N rate of 7 $kg \cdot ha^{-1}$ in the form of urea through a drip irrigation system. Soil moisture was maintained at an adequate level throughout the study. Standard management practices were followed (Orde et al., 2018).

Fruits were collected on 13 sampling dates between 11 July through 12 Nov. from 60 plants equally distributed across 4 plots that were 4.5 m long. Average fruit weight per plot was calculated and a subsample of the harvest was set aside for SSC and TA evaluation. For each sample, 3-4 red, ripe fruits were hand-harvested and stored in a 4˚C refrigerator for 20 - 24 h. Samples were brought to room temperature for 2 h before evaluation. SSC and TA data were collected using ATAGO 7104 PAL-BX/ACID4 Pocket Titrimeter-Refractometer for Strawberry (ATAGO USA, Bellevue, WA). The device calculated SSC through refractometry, and TA through a built-in ion-sensitive field-effect transistor probe. For SSC measurement, juice was hand-squeezed from one berry and deposited onto the refractometer. SSC values per harvest date were computed as the average of a three-berry subsample. SSC is expressed in % w/w and is often used as a proxy for fruit ripeness and sweetness. This metric is preferred to more direct methods of sugar quantification for its ease and speed of measurement, especially as new technological advances allow for non-destructive SSC readings.

Hourly weather data were collected from Ithaca Cornell Orchards from 14 May through 12 Nov 2020, located less than 1 km from the study site, using the Northeast Environment and Weather Application on-line database. In addition to air temperature, soil temperature, rainfall, soil moisture, humidity, and solar radiation data were measured.

Four distinct temporal stages of fruit development were defined based on visual cues (Table 1). The number of hours that fruit were exposed to four non-overlapping and approximately equal air temperature ranges between 7 and 32 ˚C was calculated for each of the four stages. This number was corre-

Table 1. Developmental and temporal start and end points for four stages of flower and fruit development in 'Albion' strawberry.

Stage	Duration (days)	Start point	End point
1: Month before anthesis	30	Harvest minus 60 days	Harvest minus 30 days
2: Anthesis to green fruit	15	Harvest minus 30 days	Harvest minus 15 days
3: Green fruit to pink fruit	10	Harvest minus 15 days	Harvest minus 5 days
4: Pink fruit to red fruit	5	Harvest minus 5 days	Harvest

lated with SSC and TA at harvest for each developmental stage. Other weather variables also were correlated with SSC and TA.

R- software was used for all statistical analyses, (1.1.456, © 2009-2018 RStudio, Inc., Boston, MA). Linear models were fitted to determine the relationship between hours within a particular temperature range during each of the four stages of fruit development and SSC.

Results

The mean number of hours per day within specific air temperature ranges was found to be a significant predictor of SSC at harvest, but the relationship between temperature and SSC varied depending on developmental stage. For example, hours of exposure to temperatures from 16 to 24 ˚C prior to anthesis (Stage 1) was positively correlated with SSC at harvest. As the fruit began to ripen (Stages 3 and 4), length of exposure to this same temperature range was negatively correlated with SSC (Fig. 1). Within both stages 3 and 4, length of exposure to lower temperatures (between 7 and 15 ˚C) 15 days before harvest was positively correlated with SSC at harvest, while exposure to higher tempera-

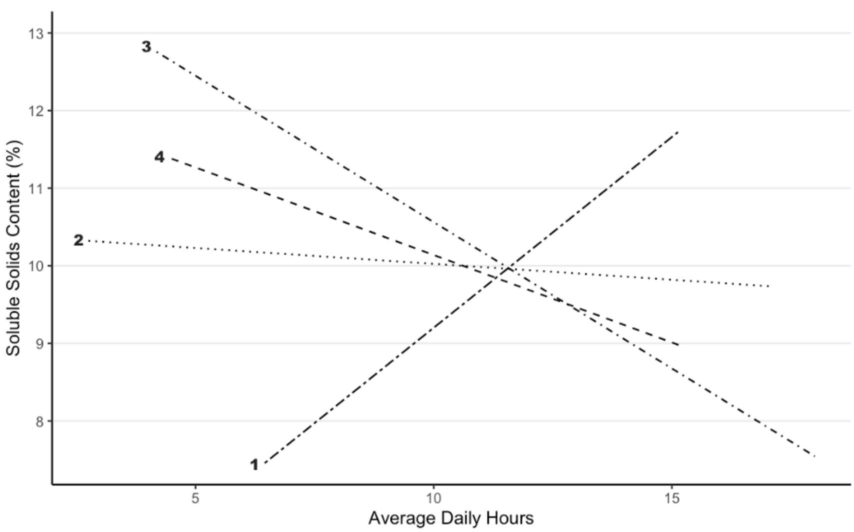

Figure 1. Soluble Solids Concentration of 'Albion' fruit and average number of hours per day that plants were exposed to warm temperatures (16 - 23˚C) during fruit development. Regression parameters, where m is the slope parameter for a linear equation: Line 1 = Harvest minus 60 days through harvest minus 30 days. $m = 0.49$, $r = 0.55$, $P= 0.05$, $n = 13$; Line 2 = Harvest minus 30 days to harvest minus 15 days. $m = -0.04$, $r = -0.08$, $P= 0.79$, $n = 13$; Line 3 = Harvest minus 15 days to harvest minus 5 days. $m = -0.38$, $r = -0.55$, $P= 0.003$, $n = 13$; Line 4 = Harvest minus 5 days to harvest. $m = -0.23$, $r = -.046$, $P= 0.12$, $n = 13$.

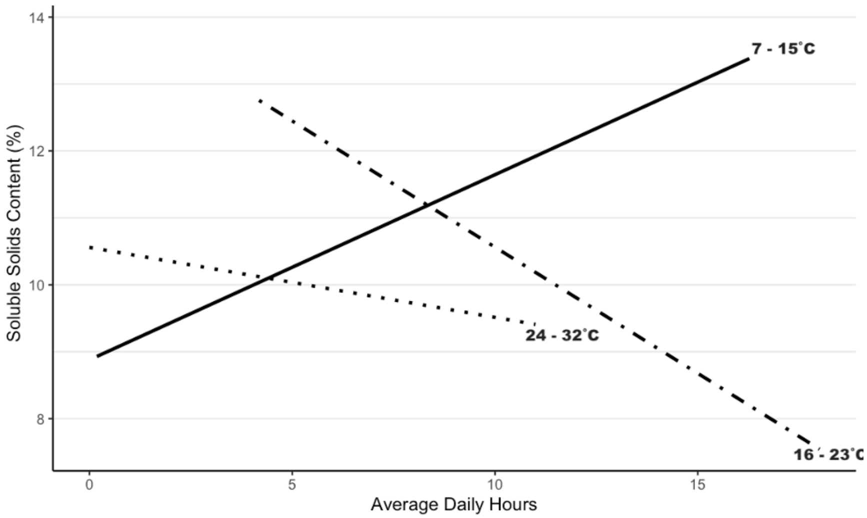

Figure 2. Soluble Solids Concentration of ‘Albion’ fruit and average number of hours per day that plants were exposed to low (7-15 ˚C), moderate (16-23 ˚C), or high (24 - 32 ˚C) temperatures during fruit ripening between green fruit and pink fruit (Stage 3) (10 days). Regression parameters, where m is the slope parameter for a linear equation: Low: m= 0.28, r = 0.71, P = 0.006, n = 13; Moderate: m= -0.38, r = -0.55, P = 0.003, n = 13; High: m= -0.1, r = -0.24, P = 0.43, n = 11.

tures (> 16 ˚C) was associated with reduced SSC (Figs. 2 and 3). The number of hours that developing fruit were exposed to the highest temperature range (24 - 32 ˚C) was not significantly linearly related to SSC, but SSC was consistently low when plants experienced these high temperatures (Figs. 2 and 3). Across all development stages, the number of hours at temperatures greater than 24 ˚C tended to be negatively associated with SSC (Fig. 4), although these correlations were not statistically significant. The seasonal temperature pattern tracked in the opposite direction of SSC, but the seasonal pattern of SSC was not related to crop load (Fig. 5).

Other variables, such as total rainfall, average relative humidity, average soil temperature, and solar radiation were not significantly correlated with SCC or TA during any developmental stage over the course of the July - Nov. harvest season.

Discussion

Temperature plays an important role in plant development and sugar accumulation in strawberry. Warm (16 to 24 ˚C), but not hot (>24 ˚C) temperatures may speed vegetative growth and development of the strawberry plant, setting it up for potentially high SSC in subsequent fruit (Wang and Camp, 2000; Gündüz and Ozdemir, 2014). However, as the fruit ripens, our data suggest that those same warm temperatures become negatively correlated with SSC about 15 days prior to harvest (Fig. 1). Since cellular respiration increases with temperature, it is likely that sugar content of fruit is reduced as temperatures increase near harvest. For an individual fruit in our study, the highest SSC occurred when temperatures were between 16 to 24 ˚C for the first 15 days after fruit set when cell division occurs (Havis, 1943), but then fell to 7 to 15 ˚C for the last 15 days during cell expansion (Figs. 2 and 3).

Since day neutral strawberries ripen continuously, there is no ideal temperature pattern that optimizes SSC across a range of developing fruit. While higher temperatures up to 24 ˚C enhance the potential for high SSC in early-developing fruit, lower temperatures

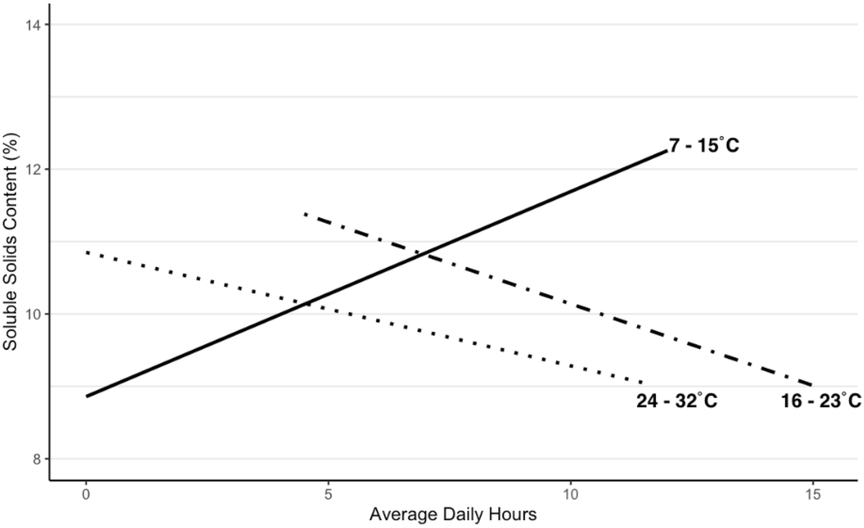

Figure 3. Soluble Solids Concentration of 'Albion' fruit and average number of hours per day that plants were exposed to low (7-15 ˚C), moderate (16-23 ˚C), or high (24 - 32 ˚C) temperatures during the fruit ripening stage between pink fruit and red fruit (Stage 4). Regression parameters, where *m* is the slope parameter for a linear equation: Low: $m = 0.28$, $r = 0.62$, $P = 0.025$, $n = 11$; Moderate: $m = 0.23$, $r = -0.46$, $P = 0.12$, $n = 13$; High: $m = -0.16$, $r = -0.35$, $P = 0.24$, $n = 12$.

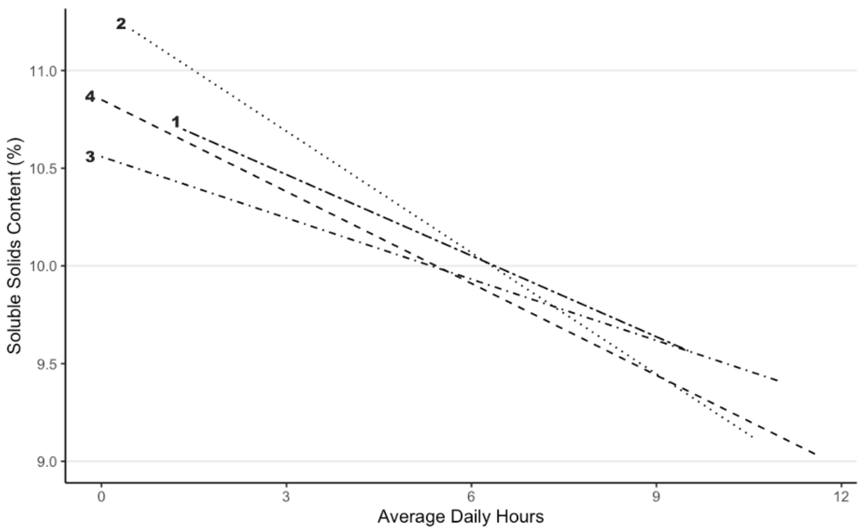

Figure 4. Soluble Solids Concentration of 'Albion' fruit and average number of hours per day that plants were exposed to high temperatures (24 - 32 ˚C) during fruit development. Regression parameters, where *m* is the slope parameter for a linear equation: Line 1 = Harvest minus 60 days through harvest minus 30 days. $m = -0.14$, $r = -0.19$, $P = 0.523$, $n = 13$; Line 2 = Harvest minus 30 days to harvest minus 15 days. $m = -0.1$, $r = -0.39$, $P = 0.19$, $n = 13$; Line 3 = Harvest minus 15 days to harvest minus 5 days. $m = -0.1$, $r = -0.24$, $P = 0.43$, $n = 11$; Line 4 = Harvest minus 5 days to harvest. $m = -0.16$, $r = -0.35$, $P = 0.24$, $n = 12$.

(<16 ˚C) close to ripening also are associated with higher SSC. Our data suggest that this sensitivity to high temperatures occurs about 15 days prior to harvest when fruit just begin to color. Fruit experiencing lower temperatures between anthesis and 15 days before harvest, followed by higher temperatures during the last 15 days of ripening, are likely to have low SSC at harvest. Fruit exposed to temperatures greater than 24 ˚C for several hours per day are also likely to have low SSC. Although correlations were not statistically significant for length of exposure to hot temperatures and SSC, trends across all four stages were consistently negative (Fig. 4).

Our data provide an explanation for the observation that day neutral flavor is best under consistent and moderately cool temperatures (Hancock, 1999; Palemieri et al., 2017; Taghavi et al., 2019). MacKenzie et al. (2011) also found that SSC was related to temperature prior to harvest. Fruits harvested from plants in a growth chamber at 15 °C for 3 weeks after flowering had higher SSC than fruit from plants grown at 22 °C. Furthermore, they found a negative correlation between SSC and mean temperature over the 8-day period before harvest across a 6-year span.

High soluble solids concentration has been ranked as the most important taste attribute for strawberry quality (Azodanlou et al., 2003), and a trained sensory panel can detect a change in sweet taste with a Δ1% in SSC (Harker et al., 2002). From our findings, an additional 4 hours per day at the 7 - 15 ˚C temperature range during Stage 3 will produce this detectable rise in SSC, while a daily increase in 5 hours of warmer air temperatures (>16 ˚C) during Stage 3 could result in a perceptible decrease in sweet taste.

It is theoretically possible that SSC is influenced by crop load as well as temperature (Cervantes et al., 2020). However, in our study as in MacKenzie et al. (2011), crop load and SSC appear to be independent from each other. SSC and temperature moved in opposite directions as explained by our analysis (Fig. 5). It is possible that various cultivars respond differently to temperature as we examined only one genotype.

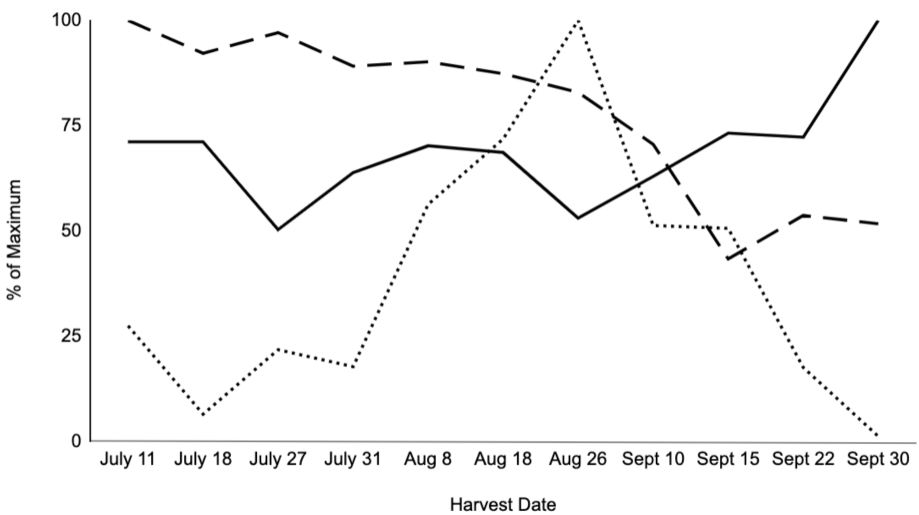

Figure 5. Relative measurements of soluble solids concentration, air temperature, and yield for 'Albion' during the 2020 harvest season based on the maximum observed value. Values were divided by the maximum observed value, then multiplied by 100% to calculate percent of maximum. Solid line: Soluble Solids Concentration (%). Dashed line: Average weekly temperature (˚C). Dotted line: weekly yield (g/plant).

Growers may be able to minimize the amount of time air temperatures exceed 24 ˚C by using evaporative cooling, reflective low tunnel coverings or shade cloth. Some growers have used evaporative cooling techniques to prevent white shoulders in short-day strawberries, a side effect of early ripening in response to high temperatures (Hokanson and Finn, 2000). Preliminary data at our location show that a reflective cover can reduce the number of hours that plants are exposed to temperatures over 32 ˚C by more than 60%. Implementing cooling technologies in the field is expensive and may not be worth the investment for sweeter fruit. Regardless, knowing how fruit responds to temperature may aid in site selection and the choice of how to market fruit.

Literature cited

Azodanlou, R., C. Darbellay, J. L. Luisier, J. C. Villettaz, and R. Amadò. 2003. Quality assessment of strawberries (*Fragaria* species). J Agric. Food Chem. 51(3):715-721. Doi: 10.1021/jf0200467

Cervantes, L., M. T. Ariza, L. Miranda, D. Lozano, J. J. Medina, C. Soria, and E. M. Ferri. 2020. Stability of fruit quality traits of different strawberry varieties under variable environmental conditions. Agron. J. 10: 1242 doi: 10.3390/agronomy10091242

Gündüz, K. and E. Ozdemir. 2014. The effects of genotype and growing conditions on antioxidant capacity, phenolic compounds, organic acid and individual sugars of strawberry. Food Chem. 155: 298-303. doi: 10.1016/j.foodchem.2014.01.064

Hancock, J. F. 1999. Strawberries. CABI: New York, NY.

Harker, F. R., K. Marsh, H. Young, S. H. Murray, F. A. Gunson and S. B. Walker. 2002. Sensory interpretation of instrumental measurements 2: sweet and acid taste of apple fruit. Postharv. Biol. Technol. 24(3):241-250. doi:10.1016/S0925-5214(01)00157-0

Havis, A. L. 1943. A developmental analysis of the strawberry fruit. Am. J. Bot. 30(4): 311-314. doi: https://doi.org/10.2307/2437460

Hokanson, S. C., and C. E. Finn. 2000. Strawberry cultivar use in North America. HortTechnology 10(1): 94-106.

Josuttis, M., G. Dietrich, C. Patz and E. Krueger. 2011. Effects of air and soil temperatures on the chemical composition of fruit and agronomic performance on strawberry (*Fragaria x ananassa* duch.). J. Hort. Sci. Biotechnol. 86: 415-421. doi: 10.1080/14620316.2011.11512783.

Jouquand, C., C. Chandler, A. Plotto and K. Goodner. 2008. A sensory and chemical analysis of fresh strawberries over harvest dates and seasons reveals factors that affect eating quality. J. Amer. Soc. Hort. Sci. 133:859-867.

MacKenzie, S. J.; Chandler, C. K. 2009. The late season decline in fruit soluble solids content observed in Florida is caused by rising temperatures. Acta Hort. 842: 843-846. doi: 10.17660/ActaHortic.842.186

MacKenzie, S. J., C. K. Chandler, T. Hasing and V. M. Whitaker. 2011. The role of temperature in the late-season decline in soluble solids content of strawberry fruit in a subtropical production system. HortScience 46(11): 1562 - 1566. doi: https://doi.org/10.21273/HORTSCI.46.11.1562

Montanaro, G., B. Dichio, and C. Xiloyannis. 2012. Fruit transpiration: mechanisms and significance for fruit nutrition and growth. In: IntechOpen. Advances in selected plant physiology aspects. Ed. G. Montanaro. IntechOpen: Online. 10:233-250. doi: 10.5772/21411

Osatuke, A. and M. Pritts. 2021. Strawberry flavor is influenced by the air temperature differential during fruit development but not management practices. Agronomy 11: 606. https://doi.org/ 10.3390/agronomy11030606

Orde, K., B. Sideman, M. Pritts and K. Demchak. 2018. Low tunnel strawberry production guide. Univ. New Hampshire. Accessed 9 Feb. 2021. https://extension.unh.edu/resources/files/Resource007429_Rep10703.pdf

Palemieri, L., D. Maseuro, P. Martinatti, G. Baratto, S. Martens and U. Vrhovsek. 2017. Genotype-by-environment effect on bioactive compounds in strawberry (*Fragaria* x *ananassa* Duch.). J. Sci. Food Agric. 97:4180-4189. doi:10.1002/jsfa.8290

Perkins-Veazie, P. 1995. Growth and ripening of strawberry fruit. Wiley and Sons, Hoboken, New Jersey.

Taghavi, T. M., R. Siddiqui and L. K. Rutto. 2019. The effect of preharvest factors on fruit and nutritional quality in strawberry. In: IntechOpen. Strawberry: Pre- and post-harvest management techniques for higher fruit quality. Ed. T. Asao. IntechOpen: Online. 1:1-22. doi:10.5772/intechopen.73748

Wang, S. Y., W. Zhang, and G. J. Galletta. 2002. Cultural system affects fruit quality and antioxidant capacity in strawberries. J. Agric. Food Chem. 50(22):6534-6542. doi: https://doi.org/10.1021/jf020614i

Wang, S. Y. and M. J. Camp. 2000. Temperatures after bloom affect plant growth and fruit quality of strawberry. Scientia Hort. 85(3):183-199. doi: 10.1016/S0304-4238(99)00143-0.