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Development of Quality Attributes in Strawberry Fruit: A Review

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Abstract

Strawberry fruit quality has many components including appearance, firmness, size, color, uniformity, freedom from defects, taste, aroma, texture and nutritional value. Each of these, in turn, consists of additional components that contribute to overall quality. People have attempted to improve fruit quality for hundreds of years through breeding, cultural practices and postharvest handling. Yet, because of competing priorities within the industry and lack of agreement among consumers about what constitutes a quality strawberry, progress has been uneven. This review explores the development of quality attributes as the strawberry ripens including appearance, firmness, sweetness, acidity, polyphenol content and organic volatiles and how management practices affect each of these. By applying best management practices, growers and shippers can enhance quality attributes in their portfolio of cultivars.

From the ancient gardens of Mapuche communities in Chile to the modern labs of universities and private companies throughout the world, people have sought to improve the strawberry. Increases in size, firmness, shipping ability and seasonality are most apparent; less so are advancements in other quality attributes such as flavor and aroma (Harbut et al., 2016). The quest for a better strawberry is hampered by the different priorities of producers, shippers and consumers. For example, a strawberry shipped to a distant market must have acceptable firmness, so to achieve this they may be harvested before the flavor fully develops. In addition, consumer perception of quality can vary depending on age, ethnicity, gender, location and education level (Colquhoun et al. 2012). Therefore, generalizations about what constitutes an ideal strawberry are difficult to make, but appearance, firmness, taste, size, color, aroma, and nutritional value are each regarded as important for all constituencies. A quality strawberry has desirable levels of each of these criteria, and is not deficient in any. Understanding how to influence these attributes could lead to improvements in strawberry fruit quality and perhaps an increase in consumption. The growth in consumption of strawberries since 2000 underscores the importance of maintaining high fruit quality, although per capita consumption appears to have plateaued in the last few years (Shahbandeh, 2019) and quality remains inconsistent (Azodanlou et al. 2003).

Strawberry fruit development

The edible portion of a strawberry is a swollen receptacle; the true fruits are the achenes on the receptacle's surface. However, this edible accessory tissue will be referred to as the fruit for the purpose of this review. Strawberry fruits progress through several stages as they ripen: small green, large green, white, pink, and red. Fruits are considered ripe at the red stage (Huber, 1984; Hancock, 1999). On average, fruits reach the red stage approximately thirty days after anthesis. Growth through cell division of the receptacle occurs prior to anthesis, and roughly 80% of the fruit growth is due to cell enlargement after anthesis (Handley and

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Hancock, 1998). Cell enlargement, in turn, is driven by an increase in the vacuole count within the fruit cells (Cruz-Rus et al., 2011). Vacuoles can serve as storage compartments for wastes, enzymes, or nutrients. In strawberry fruit, water and soluble solutes such as sugars, ions, and phenolic compounds are stored in the vacuoles. Sugars and ions enter vacuoles after import from the phloem and through the cell walls into the organelles, whereas phenolic compounds are suspected to be synthesized *in situ* (Coombe, 1976). It is during cell enlargement and transition from green stages to white, pink, and red that sugars, volatile aromatic compounds, and phenolic compounds are produced within the fruit, primarily by enzymatic action. At the same time, acid concentration decreases. As enzymatic action shifts from starch degradation towards synthesis of sugars, phenolics, and volatiles, enzyme content overall declines. Souleyre et al. (2004) observed a five-fold decrease in overall protein concentration as strawberry fruit progressed from green to red stages of ripening. However, enzymes responsible for flavonoid and anthocyanin synthesis rose in abundance at advanced stages of ripening, a complex metabolic process that appears to be cultivar-dependent (Song et al., 2015).

<u>Appearance.</u> The size, shape, color intensity, glossiness of skin, protrusion of achenes and evenness of coloration contribute to the appearance of the strawberry. The modern strawberry, *Fragaria* x *ananassa* Duch., is a hybrid of two American strawberry species *F. virginiana* Duch. and *F. chiloensis* L. Hybrid strawberries are mostly self-fertile, but are known to produce more fruits of larger size when cross-pollinated (Handley and Hancock, 1998). During fruit development and ripening, the achenes release growth hormones, primarily auxins, in concentrations that promote the growth of the receptacle (Darrow, 1966), although swelling of the receptacle occurs when auxin release from the achenes begins to decrease (Given et al., 1988). Auxin is suspected to serve an inhibitory function in the ripening of non-climacteric fruits; it is the breakdown of auxin that allows the ripening process to proceed. Additional hormones found primarily in achenes during ripening include abscisic acid and indole-3-acetic acid (Symons et al., 2012). The role of ethylene in ripening of strawberry is currently unclear (Symons et al., 2012). Perkins-Veazie (1995) reported that ethylene application to immature fruit has little effect on softening and flavor development, but another study found that exposure to ethylene increases RNA and RNase levels within the fruit, raising questions about the function of these gene expression responses (Hancock, 1999).

Final fruit size is dependent on the number and distribution of the achenes on the receptacle as each achene only affects the growth of the localized section of the receptacle beneath it (Handley and Hancock, 1998). The location of the flower on the inflorescence will affect the number of achenes. The primary flower on an inflorescence contains the greatest number of pistils and, consequently, gives rise to the largest fruit. Pistil counts decrease from primary to secondary, tertiary, and quaternary flowers (Hancock, 1999). Marketable strawberries are usually in the range of 7 - 30 g/individual fruit.

Distribution of achenes can vary depending on cultivar and this gives rise to different strawberry shapes (Darrow, 1966). Some shapes are more desirable than others, and even within a given cultivar, the shapes can vary. This has led to the development of automated sorting of the nine basic shapes in strawberry (Ishikawa et al., 2018) to enhance uniformity of product.

<u>Firmness</u>. Firmness is a desirable trait for commercially-produced strawberries in order for fruits to withstand transportation and to provide an acceptable mouth-feel when eaten. Fruit that is either too soft or too firm is undesirable to consumers. Firmness is a combination of skin toughness and flesh firmness; a desirable range is a maximum puncture force between 2-3 N (Hietaranta

and Linna, 1999). Among ripe fruits of a given strawberry cultivar, larger fruits are usually less firm due to higher moisture content of the cells. Strawberry fruit firmness is highly influenced by temperature during measurement, and skin toughness of strawberry has been found to halve for every 12 °C increase in temperature (Darrow, 1966).

More study is still required to identify the driving factors behind fruit softening in *F.* x *ananassa*. Currently, it is known that enzymatic disassembly of the cell walls results in depolymerization of the glycan matrix as well as of cell wall pectins (Moya-León et al., 2019). The fruit of the cultivated strawberry's maternal parent, *F. chiloensis*, is known to soften at a faster rate than *F.* x *ananassa* (Moya-León et al., 2019). Figueroa et al. (2008) have identified polygalacturonases as one key enzyme class driving softening during ripening, in both *F.* x *ananassa* and *F. chiloensis*. This class of enzymes generates simple sugars during degradation of pectin starches. Further studies have identified that cellular regions most subject to structural change during ripening are those with high densities of HCl-soluble pectin (Figueroa et al. 2010; Moya-León et al., 2019). Depolymerization of starches via hydrolysis results in an increase of free water molecules and neutral sugars derived from pectin side chains (Brady, 2013). The gradual disassembly of cell walls is accompanied by swelling as well as an increase in porosity (Figueroa et al., 2008). This is followed by increased fluid and enzyme influx into the fruit cells themselves, and the distance between individual fruit cells increases (Moya-León et al., 2019).

Thus, as the strawberry fruit ripens, the volume of internal liquid and the concentrations of soluble solids rise. Cultivar differences in firmness are attributed to differences in cell-to-cell adhesion at ripeness; on a cellular level, firmer cultivars are more cohesive, while the cells of softer cultivars are less connected within the pulp (Darrow, 1966). There is evidence that softer cultivars of strawberries have higher expression of β-galactosidases and α-arabinofuranosidases, enzymes which remove arabinose side chains from pectins and hemicelluloses (Rosli et al., 2009). Moya-León et al. (2019) speculate that this structural change increases the likelihood of further chemical degradation of the remaining polymer chain, in addition to reducing the integrity of the oligosaccharide matrix composing the fruit flesh.

<u>Sweetness.</u> In ripe strawberries, between 80-90% of the total soluble solids are sugars. The majority is sucrose, glucose, and fructose. The remaining soluble carbohydrates are mostly sorbitol, xylitol, and xylose (Perkins-Veazie, 1995, Souleyre et al., 2004). Sweetness tends to be more highly correlated with consumer preference than total volatiles (Azodanlou et al., 2003).

At different stages of ripening, sugars and starches are imported into the fruit (Batista-Silva et al., 2018). Approximately 3% of sugar content in ripe strawberries is synthesized *in situ*; these sugars originate from starches accumulated soon after anthesis (Souleyre et al., 2004). The remaining fraction of sugars in strawberry are imported from leaf tissue, and their synthetic pathways appear to be cultivar-dependent (Akšić et al., 2019). The wide genetic diversity of cultivated strawberry has allowed researchers to explore metabolic differences between high- and low-sugar cultivars. Lee et al. (2018) observed that high-sugar cultivars (with an average Brix of 13.6˚) had a high sucrose proportion in their sugar profile, whereas low-sugar cultivars (with an average Brix of 2.9˚) had a high fructose proportion. Recent developments suggest that sucrose may serve as a signaling molecule in strawberry ripening, regulating action of abscisic acid and auxin (Jia et al., 2013). Strawberries sprayed with exogenous sucrose had increased gene expression of ascorbic acid and anthocyanin biosynthesis (Luo et al., 2019).

The disaccharide sucrose possesses a natural, clean sweet taste and thus is used as the base for relative sweetness. Relative sweetness is an index which compares sugars and other sweet molecules in ratio against the relative sweetness of sucrose (100/100). The relative sweetness of glucose is 74/100. Glucose is the most abundantly utilized monosaccharide in plant metabolism and is imported into strawberry fruits for starch and acid synthesis, in addition to its role as a substrate for respiration. Fructose is the sweetest of all naturally occurring sugars; however, fructose is a reducing monosaccharide that possesses two measurements of relative sweetness. The five-membered ring form, α-D-fructose, has a sweetness index of 76, and the six-membered ring β-D-fructose is 180. The equilibrium of α-D-fructose to β-D-fructose tends to favor α-D-fructose at room temperature, and β-D-fructose at lower temperatures. Compared to sucrose, the sweetness of fructose is perceived earlier and diminishes faster on the tongue (Brady, 2013).

Acidity. The sensory contribution of sugars to consumer preference also depends on the acidity of fruit (Ikegaya et al., 2019). While the pH of the fruit remains around 3.5 throughout its development, the titratable acidity (TA) gradually decreases (Hancock, 1999). The sugar to acid ratio is most commonly expressed as the Brix:TA ratio. According to multiple studies on consumer preference, strawberries with high sweetness and moderate acidity are most desirable (Batista-Silva et al., 2018, Jouquand et al., 2008). Overall liking of strawberry taste was found to be strongly positively correlated with sweetness intensity, and weakly positively correlated with titratable acidity. Strawberry fruits with a low Brix:TA ratio are more likely to be perceived as unpalatably sour (Schwieterman et al., 2014). A desirable sugar:acid ratio in strawberry is identified as 16-17, with Brix ranging from 9-11° and acidity between 0.45 and 0.80 g/100 ml (Atago, 2020). Sweetness and acidity of ripe fruit are highly cultivar dependent (Hancock, 1999).

The most commonly-occurring acids in strawberries are citric and malic acid (Kallio et al., 2000; Ikegaya et al., 2019). These non-volatile organic acids are synthesized from glucose via glycolysis, or from byproducts of fatty or amino acid metabolism (Zhang et al., 2011). Additional acids present in strawberry include phosphoric, succinic, and quinic acid. Relative acid concentration is highest in immature fruit due to the gradual increase in soluble sugars, amino acids, and secondary metabolites. Even as the percentage of sugar to acid in ripening fruit is inversely correlated, citric and malic acid contents increase as fruits ripen (Batista-Silva et al., 2018; Zhang et al., 2011).

Several acids in strawberries do more than contribute to the acidity of the fruit; they serve as antioxidants and are the subjects of health studies, often with promising results. Strawberries are a well-known source of Vitamin C or ascorbic acid (Perkins-Veazie, 1995). Ascorbic acid content can vary significantly depending on cultivar (Taghavi et al., 2019). Ascorbic acid possesses antioxidant and metabolic functions in the human diet and is present throughout the strawberry plant tissues. The primary mode of ascorbic acid synthesis in strawberry fruits is the Smirnoff-Wheeler pathway using L-galactose as the initial substrate (Wheeler et al., 1998). A byproduct of pectin breakdown, D-galacturonic acid, has also been named as a minor source of ascorbic acid in strawberry (Gallie, 2013).

The metabolic pathways that synthesize tart acids generate phenolic compounds as well: products of the pentose phosphate pathway and glycolysis can be further modified in the shikimate pathway, which generates volatile aromatic compounds as well as phenolic acids (Zhang et al., 2011). Products of the shikimate pathway can then be converted to flavonoids in the phenylpropanoid pathway (Lin et al., 2016). Two groups of polyphenolic antioxidant acids are gallic and ellagic acids. Strawberries contain relatively high levels of these acids; both have been studied for their impacts on cancer cells (Brady, 2013; Ceci et al., 2018). There are multiple molecular forms of gallic and ellagic acids. Both free forms and forms esterified to glucose have been measured in strawberry pulp (Hannum, 2010). Compared to the pulp, the achenes of ripe strawberries contain nearly one-thousand times more of the β-glucogallin form of gallic acid, while gallic and ellagic acid concentrations were half that of β-glucogallin (Schulenburg et al., 2016). Gallic acid contains one phenol group, while ellagic acid contains several. Hydrolyzable tannins in strawberry are synthesized from gallic acid, while ellagic acid is released from hydrolyzable tannins during hydrolysis (Brady, 2013). However, the end stages of fruit ripening correlate with a decrease in both gallic and ellagic acids (Schulenburg et al., 2016). Ellagic acid, in particular, has been reported to have health-enhancing properties (Anttonen et al., 2006, Brady, 2013 and Hannum, 2010**)**.

Polyphenols. There are many polyphenolic compounds synthesized in strawberry fruits, including tannins, and flavonoids, a group which encompasses pigments. Tannins in strawberry are hydrolyzable, a class that is less astringent and bitter than the tannins found in wine. Tannin concentration decreases sharply during the final stages of ripening. Pigments in strawberry are anthocyanins, a class of molecules that reflect red, blue, or purple color depending on the molecular structure and the pH of their surrounding medium (Brady, 2013). Anthocyanin content increases nearly 400-fold during ripening and can increase further in post-harvest storage (Hannum, 2010). The primary anthocyanin found in strawberry is pelargonidin. Pelargonidin is most abundant in ripe fruit and forms a complex with the sugars glucose, rutinose, or arabinose (Pinto et al., 2007). Three other flavonoids that have received attention for their medicinal properties include cachethin, quercetin, and kaempferol (Brady, 2013). The phenolic content of 1 cup, or 150g, of strawberry fruit is approximately 300 mg. These concentrations are suspected to be high enough to offer some protection against lung cancer when strawberries are regularly consumed (Hannum, 2010).

Organic volatiles. As strawberries ripen, a diversity of aromatic, volatile metabolites are produced that result in the characteristic aroma of specific varieties. Furanones terpenoids, esters, and lactones form the key elements of strawberry aroma. Secondary metabolites such as aldehydes, alcohols, carboxylic acids, sulfur-containing compounds, and volatile benzenoids can also contribute to the scent of fresh strawberries (Aharoni et al. 2004; Urrutia et al., 2017). The metabolic precursors of furanones, lactones and terpenoids are carbohydrates. Carboxylic acids can be converted to aldehydes and alcohols, while esters arise when alcohols react with carboxylic acids (Beekwilder et al., 2004). Amino acids are considered to be the precursors of benzenoids. The metabolic precursors of sulfur-containing compounds are currently unknown (Hancock, 1999; Yan et al., 2018).

Although the individual molecular composition of a strawberry's aroma is highly cultivar-dependent, several molecules of each class occur frequently in the volatile analysis of *F.* x *ananassa* cultivars. Some common esters include ethyl butanoate, ethyl hexanoate, methyl butanoate and methyl hexanoate. The most common lactone is 2,5-dimethyl-4-hydroxy-3(2H)-furanone (also known as strawberry furanone) and the most impactful furanone is 4-methoxy-2,5-dimethyl-3(2H)-furanone (also known as strawberry furanone methyl ether). Two prominent terpenoids in strawberry are linalool and neridiol (Yan et al., 2018). The volatile profile of woodland strawberry, *Fragaria vesca*, contains similar esters to cultivated strawberry, but a vastly different terpene profile (Urrutia et al., 2017). Unlike the floral linalool and nerolidol in cultivated strawberry aroma, the terpene profile of woodland strawberries is more diverse and muskier. Woodland strawberries synthesize olefinic monoterpenes, many of which were named after their discovery in tree oleoresins (Martin et al., 2002). Examples include α-pinene and β- myrcene.

Methanethiol is a putrid-smelling sulfur-containing compound that is a plant metabolite; levels of methanethiol in strawberry fruit remain constant throughout ripening. Other sulfur-containing compounds, many of which contribute savory and pungent aromas, double in concentration between ripe and over-ripe stages of fruit maturation. Several volatile compounds can increase sweetness perception even if the sugar concentration of the fruits remains constant, independent of sugar profile constituents: four are esters (amyl butyrate, hexyl butyrate, capryl acetate, isopropyl butanoate), one lactone (γ-dodecalactone), and one alcohol (ethyl vinyl ketone) (Schwieterman et al., 2014).

Isobutyl methyl ketone decreases sweetness perception independent of sugar content. Ethyl octanoate and prenyl acetate also can decrease sweetness perception independently of glucose and sucrose concentrations, but within the context of a complete sugar profile, their influence on sweetness perception is small (Jouquand et al., 2008; Schwieterman et al., 2014). These compounds differ from ethanol, acetaldehyde, and ethyl acetate that are responsible for off-flavors in strawberry during post-harvest storage. These three develop under low O_2, high CO_2, or extended periods of storage (Hancock, 1999).

Aroma is assessed by the volatile profile as sensed by the human nose. Given the large number of odor receptors in the nose, and the existence of odor blindness, it is likely that different people prefer different flavor profiles (Spence, 2015). This makes identifying optimal volatile profiles difficult.

<u>Consumer preference</u>. Web-based customer surveys suggest that sweetness and complex flavor are the most desirable attributes of strawberry fruit, while perceived health benefits have little impact on consumer preference (Colquhoun et al., 2012). Sensory evaluations have found that strawberry sweetness and texture are slightly more significant in predicting consumer preference than aroma intensity, while fruits ranked as sour are least likely to be preferred (Yan et al., 2018). In addition to cultivar, the local climate, soil, growing practices and time of harvest have been the subject of studies exploring strawberry quality (Given, 1985; Kader, 1999; Kays, 1999; Prange and DeEll, 1995). Goals in producing strawberries may differ between a grower with a U-pick operation and one intending to sell their harvest in grocery stores, particularly when considering trade-offs between shipping quality and eating quality.

Consumers regard the strawberry as a highly nutritious fruit. Under most growing conditions, strawberries have very high levels of Vitamin C (60 mg/100 g), and modest levels of K (153 mg/100 g), P (24 mg/100 g) and fiber (2 g/100 g) (USDA FoodData Central, 2019).

Influence of genetics on fruit quality

Breeding for fruit quality in strawberry is challenging. Not only do many traits contribute to quality, but most of these traits are likely quantitatively inherited (Zorrilla-Fontanesi et al., 2011). In addition, cultivated strawberry plants are octoploid and many alleles are involved in fruit development and ripening. More than 10% of the genome is associated with these processes in *Arabidopsis* (He et al. 2001). Unlike strawberry, this plant does not rely on the production of aroma volatiles to encourage fruit consumption and dispersal so the percentage of the strawberry genome involved in ripening could be higher.

The octoploid strawberry genome has been found to consist of several subgenomes, with one dominant genome having significantly greater gene content and gene expression abundance (Edgar et al., 2019). Pathway analyses in the same study found the dominant subgenome to largely control metabolic pathways involved with strawberry sweetness, color, and aroma. Gündüz and Ozdemir (2014) reported that approximately 70% of variation in fruit anthocyanin content was attributed to the genome, but 50% of variation in phenolic content was associated with growing conditions. Hundreds of volatile chemicals are released during ripening, so identifying those that are important for flavor and which are under genetic control are arduous tasks. Combining qualitative trait loci identification with candidate gene mapping has proven successful in identifying clustered traits, including those involved in volatile synthesis (Zorrilla-Fontanesi et al., 2011). However, some of these volatiles are attractive to humans and other frugivores so are important determinants of flavor, but others may have different functions that are yet to be discovered such as disease suppression (Archbold et al., 1997).

The perception of flavor includes not just the volatile profile, but also the sugar, acid, nutrient and phenolic content of the fruit. The relationships among the strawberry genome, the environment, cultural practices and components of fruit quality are extremely complex, with significant genotype X environment interactions involving quality attributes (Palmieri et al., 2019). An exhaustive review of the genetics, breeding and inheritance of quality traits is beyond the scope of this paper.

Influence of the environment and management practices on fruit quality

Harvesting fruits when they are fully ripe and consuming them immediately provides the best eating experience. However, this is not possible when strawberries are not in season and have to be shipped from distant production areas. Strawberry cultivars themselves also differ markedly in quality attributes and fruits of the same cultivar may display a high degree of variability from year to year. One study showed two-fold increases in total fruit sugars in the same plots from one year to the next (Souleyre et al., 2004). Sensory evaluations of strawberry fruits often yield ambiguous results which some researchers attribute to the uneven distribution of sugars and acids within the strawberry fruit itself (Ikegaya et al., 2019).

Light. Several causes of year-to-year variation have been described for strawberries. Higher light levels are associated with greater soluble solids, lower acid levels and higher antioxidant content, but the response is cultivar dependent (Cervantes et al., 2019). The positive relationship between photoperiod and soluble solids concentration is well established (Darrow, 1966; Perkins-Veazie, 1995). Short photoperiod is associated with a decrease in final fruit size most likely associated with a reduction in net photosynthates available to developing fruits. Reduced carbohydrate availability from short photoperiods also is correlated with reduced vitamin C content, and strawberries grown in low light conditions have reduced skin glossiness (Oke et al., 2013; Taghavi et al., 2019). Due to the carbohydrate-derived origins of terpenoids and furanones, reduced photoperiod has impacts on these constituents of the volatile profile. The impact of pre-harvest light exposure on strawberry fruit aroma has not been well-studied, but at least one study showed that decreasing light interval was associated with fewer aroma volatiles (Watson et al., 2002). Self-shading is known to affect firmness at the red stage (Darrow, 1966), perhaps due to the inadequate import of soluble carbohydrates from shaded plants that limits the establishment of a firm intercellular matrix in ripe fruits.

In addition to the beneficial effects of adequate light exposure on pre-harvest strawberry fruit quality, the wavelength of the light has impacts. Strawberries grown on red plastic mulch have more favorable aromas than those grown on black plastic mulch; these differences were explained as mulch effects on the ratio of red to far red light that influences gene expression (Anttonen et al., 2006). Later studies confirmed that exposure to light through a reddish-orange filter positively impacted fruit size, phytonutrient concentrations, sugar, acid, and aroma compounds. Conversely, strawberries grown under green-filtered light had the lowest values for these attributes (Kai et al., 2006). The results suggest that red and far-red light reflected from red mulch is absorbed by phytochromes, affecting gene expression (Taghavi et al., 2019) and, ultimately, fruit quality. Evidence also suggests that ultraviolet light may play a role in the development of flavonols. Palmieri et al. (2019) showed a reduction in several flavonols when UV-B radiation was blocked and an increase when exposed to blue light. Phenolics increase in strawberries when strawberries are grown at higher temperatures or when the carbon dioxide concentration is elevated (Wang and Zheng, 2001).

Temperature. Most strawberries have better flavor and sugar concentration when grown in regions with cooler summers or at high altitudes due to beneficial effects of exposure to longer photoperiods and lower night temperatures (Hancock, 1999; Palmieri et al., 2019; Wang and Camp, 2000). Both ascorbic acid and sucrose concentration rise in fruits grown at cooler temperatures (Josuttis et al, 2011; Wang and Camp, 2000). A small difference between day and night temperature can induce faster maturation in fruit, but lowers sugar concentration in the process (Gündüz and Ozdemir, 2014). Temperatures near freezing can negatively affect strawberry size and shape (Ariza et al., 2012), even in the absence of frost damage.

Soil. Human impacts on soil can be beneficial or deleterious, depending on the nature of the soil, the human activity, and the desired outcome from soil management. Reganold et al. (2010) compared the quality of organic strawberries to conventionally grown strawberries from fumigated fields and concluded that overall quality was better in organically-managed fields. Fernández et al. (2006) reported strawberries grown in soilless systems had less sugar, more malic acid and a lower Brix:TA ratio than field grown strawberries in the same location.

Nutrition. Supplemental fertilization with N, particularly in spring, reduces firmness of strawberry fruits (Shoemaker and Greve, 1930; Pritts, 1998) and overall content of flavonols and ellagic acid (Anttonen et al., 2006). Ojeda-Real et al. (2009) found that higher rates of N increased esters, soluble carbohydrates and amino acids in fruit, but also increased levels of hexanal, an undesirable volatile. The best flavor was obtained at a moderate level of N (3 mmol nitrate in solution). Taghavi et al. (2004) found a higher ammonium:nitrate ratio resulted in fruit that was less red and lower in acid. Organic sources of N frequently contribute additional nutrients to the soil, such as P and S. Amino acid status and metabolism may have an impact on volatile synthesis in strawberry, but plants receiving excessive N that develop poor color also tend to have poor flavor (Perkins-Veazie, 1995), suggesting that an overabundance of N may not result in desirable increases in amino-acid derived esters and benzenoids, relative to the undesirable effects observed.

Phosphorous is a relatively immobile nutrient with low water solubility. Supplemental fertilization with soluble P, particularly phosphoric acid, increased sugar concentration in strawberry fruits (Cao et al. 2015; Darrow, 1966; Zhang et al., 2017) and, along with B, may increase fruit size at certain soil pH levels (May and Pritts, 1993). Boron deficiency inhibits auxin activity and can result in poorly-shaped fruit (Hancock, 1999). Foliar application of K-based fertilizers also can increase fruit size and Brix (Valentinuzzi et al., 2018). The impacts of K on other quality traits of strawberry fruit are debated, with studies contradicting one another on the impact of K on fruit acidity (Etienne et al., 2013) and flavor (Perkins-Veazie, 1995). Due to the high K content of strawberry fruit, the likelihood of K deficiency increases with crop load.

Calcium plays an essential role in the polysaccharide matrix of strawberry flesh, providing an ionic bridge between the pectin chains (Brady, 2013). Ca is implicated in cell wall integrity, cell-to-cell adhesion and cellular turgor, a possible explanation for the phenomena of delayed ripening and senescence processes in strawberries receiving supplemental Ca (Taghavi et al., 2019). Calcium is typically applied to strawberries as a foliar spray or amended into the soil as lime. Foliar application of Ca 3-4 days before harvest increased firmness and preserved brightness of color and glossiness of skin (Hancock, 1999), but effects are not always reproducible (Taghavi et al., 2019). Ultimately, the role of Ca supplementation on enhancing strawberry fruit quality appears to depend on the cultivar as well as yet undefined growing conditions (Hancock, 1999; Taghavi et al., 2019).

Biotic factors. The number of fertile achenes and strawberry shape can be negatively affected by damage from insect feeding, poor pollination and virus infection. High levels of pollinator activity are known to improve size and shape in certain cultivars (Taghavi et al., 2019; Ariza et al., 2012). Ibanez et al. (2019) found that wounding strawberry leaves to mimic insect damage led to an increase in phenolic content as well as soluble sugars in the resulting fruits. Organically-grown strawberries produced higher fruit concentrations of the flavonol kaempferol (Hannum, 2010) and the author hypothesized that the increased levels were caused by the response to a pathogen attack. A review of the many pathogens and arthropods that cause physical damage to strawberry fruit is beyond the scope of this paper.

Storage conditions. Strawberry fruits increase in firmness upon exposure to high CO_2 such as occurs during shipping (Larsen and Watkins, 1995; Watkins et al., 1999). While strawberries can increase in color intensity after harvest and in storage, CO_2-treated fruits tend to be lighter in color and less intensely red than air-treated fruit (Watkins et al., 1999; Shin et al., 2008). Modified atmosphere packaging tends to reduce aroma volatile production, while higher CO_2 /lower O_2 levels increase the production of off-flavors (Yan et al., 2018). Ascorbic acid concentration increases in strawberries during ripening and can increase further during post-harvest storage when the fruits are treated with ozone (Cruz-Rus et al., 2011).

While much is known about factors that influence fruit quality, manipulating these factors for consistent quality continues to be challenging for the strawberry industry, particularly since some desirable attributes are in opposition. Yet, improvements in overall quality will likely be necessary if consumers are to be persuaded to eat more strawberries relative to other fruits.

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Dellon Marcus Dewey began providing nurserymen with books of “portraits colored from nature” in 1857. Inspired by nursery salesmen’s practice of carrying cut-out illustrations to help sell their stock, Dewey hired artists to create images of nurseries’ best-selling plant varieties: his1859 price list indicated 275 different plates for sale. By 1872 that number had increased to 1,322 and by 1881, it had nearly doubled to 2,400 different fruits, flowers, shrubs and trees, created by his 30 artist-employees. In addition to selling individual plates, Dewey also produced plate books, ready-made or with customized contents. In 1888, D. M. Dewey consolidated his “Fruit Plate and Nursery Supplies business” with the Rochester Lithographing and Printing Company, whose imprint is on this stencil.