Influence of harvest date and light integral on the development of strawberry flavour compounds

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Abstract

Strawberries cv. Elsanta were grown in peat bags in a glasshouse and subjected to three shading levels (0%, 25%, 47%) for 2 weeks, commencing 1 week prior to first fruit ripening. Fruit was harvested at five intervals and analysed using Atmospheric Pressure Chemical Ionization (APCI) and direct liquid-mass spectrometry techniques. Thirteen volatiles implicated in strawberry flavour and three non-volatiles, sucrose, glucose and citric acid, were measured. Highly significant differences in volatile and non-volatile concentrations existed between harvest dates. Shading had a significant effect on hexanal, hexenal, ethyl methyl butyrate, and methyl butyrate concentrations at some harvests. In general, at each harvest the higher the level of shading the lower the level of the volatile in the fruit. Sucrose concentration showed a decrease throughout the harvest period, whereas glucose and citric acid showed less clear trends. Shading had a significant effect on glucose and sucrose concentrations. Some possible reasons for the variability in strawberry flavour are discussed.

Key words: Flavour volatiles, Fragaria x ananassa, harvest date, light integral, sugar accumulation.

Introduction

The characteristic flavour of fresh strawberry fruit is a complex interaction between a large number of volatile and non-volatile components. The non-volatile compounds, for example, sugars and acids, are responsible for the sweetness and tartness of the fruit; the volatile compounds, for example, esters and aldehydes, are central in producing the distinctive fruity flavour.

Gas chromatography studies by Tressl and co workers (Tressl et al., 1969) identified over 200 different volatiles from fresh fruit. Representatives from many different chemical families have been shown to make up strawberry aroma. These include esters, aldehydes, ketones, and furanones (Manning, 1993). There has been considerable debate as to which volatiles are the most important in producing the characteristic aroma of strawberry, although many authors include furaneol (2,5-dimethyl-4-hydroxy-3(2H)-furanone), ethyl hexanoate, ethyl and methyl butanoate, and cis-3-hexenal among their ‘character-impact’ compounds (Larsen et al., 1992; Larsen and Poll, 1992; Schieberle and Hofmann, 1997; Pérez et al., 1992). Strawberry cultivars also differ in the type and amount of volatiles they produce (Shamaila et al., 1992; Larsen et al., 1992).

Glucose, sucrose and fructose are the major soluble sugars found in strawberry fruit. Glucose and fructose are found in almost equal concentrations (Maas et al., 1996), sucrose levels are generally much lower (Forney and Breen, 1986). Citric acid forms the major organic acid found in strawberry fruit (Kim and Moon, 1993), representing 88% of the total organic acids in ripe fruit (Green, 1971). Malic acid is the second most prominent organic acid in the fruit (Green, 1971). Also present in the strawberry fruit are polyphenols or tannins, which are responsible for astringency (Ozawa et al., 1987).
Substantial fruit-to-fruit variation in flavour within a crop has previously been reported for strawberries and other fruit (Brauss et al., 1998; Gaillard et al., 1977). Several workers have demonstrated flavour differences between crops grown at different seasons (Proebsting and Mills, 1981; De Bruyn et al., 1971; Wrolstad and Schallenberger, 1981), at different locations (Rosenfeld et al., 1998; Wrolstad and Schallenberger, 1981) and from pick to pick within a single crop (R Watson, CJ Wright, T McBurney, unpublished results). Shaw (1990) determined that the soluble solid content of strawberry fruit was more dependent on environmental conditions during production than on the genetic make-up of the plant. Fruit from summer-planted strawberries had a higher soluble solid content and titratable acidity than winter planted fruit (Kader, 1991). From a fruit quality and marketability viewpoint, fruit-to-fruit variation in flavour is very important. Quality assurance tests are often based on the mean quality of a representative sample, whereas consumers judge the flavour quality of individual fruits. Therefore, within a highly variable crop which scores well in quality tests, there may be a significant number of strawberry fruit that are unacceptable to consumers. Pick-to-pick variation in flavour can compound this problem as consumers may associate disappointment with a specific cultivar, affecting ‘brand’ loyalty and repeat sales (Baldwin, 2002).

Considerable evidence exists for the effects of shading on the fruit flavour quality of orchard crops, largely from studies of canopy pruning and fruit thinning strategies (Gariz et al., 1998; Palmer et al., 1997; Marini et al., 1991) as well as improvements in trellis (Vanden Heuvel et al., 2000) and orchard design (Wagenmakers and Callesen, 1995; Pattern and Proebsting, 1986). However, there is little information on the effect of shading on strawberry flavour compounds. Mapping the response of strawberry flavour to changes in environmental conditions, including light, is an important step in understanding possible reasons for the variability in the flavour of the crop. Such an understanding may give growers the potential to manipulate fruit flavour quality by managing the growth environment, with the aim of producing fruit of a more consistent flavour and quality throughout a single crop and from season to season.

Analysis of strawberry volatile compounds is problematic because of the high metabolic rate of the fruit (Perkins-Veazie, 1995; Abeles and Takeda, 1990). Flavour changes can occur rapidly after picking so there is a need to carry out volatile flavour analysis quickly. Several workers have shown that, although soluble solid and titratable acid content remained relatively constant, freezing significantly changed volatile components (Larsen and Poll, 1995; Deng and Ueda, 1993). Deng et al. (1996) also reported the production of hydrogen sulphide from freeze-thawed berries. Thus freezing strawberry fruit for later analysis is not a valid technique if volatile content is to be measured. Atmospheric Pressure Chemical Ionization (APCI) is ideal for flavour studies as it allows all the volatiles present in a sample to be measured simultaneously within a couple of minutes (Brauss et al., 1998).

It is common for growers to measure the soluble solid content of fruit using refractometry, as it represents a quick and portable method for the determination of total sugar content under field conditions. However, there are problems associated with the use of the refractometer as the method is only accurate for pure sucrose solutions, requires temperature calibration and uses a non-linear scale which is difficult to work with (Southgate, 1976). Insoluble solids are known to interfere with the determination of refractive index (Joslyn, 1970). Refractometer readings are further affected by the number, mass and chemical structure of the dissolved particles (Chadha et al., 2001). These problems can be avoided, and a clearer picture as to the relationship between individual components making up the sweetness or tartness of a fruit can be achieved by using mass spectrometry.

The aims of this study were, firstly, to use APCI and direct liquid-MS techniques to measure volatile and non-volatile flavour compounds in strawberry cv. Elsanta. Secondly, to estimate the harvest-to-harvest variation in cv. Elsanta flavour compounds and, lastly, to test the hypothesis that a reduction of the carbohydrate source through shading would adversely affect fruit quality.

Materials and methods

Plant growth conditions

Strawberry plants (Fragaria ×ananassa L.) cv. Elsanta (Darby Brothers Farms Ltd, Norfolk, UK on behalf of Nuclear Stock Association Limited) were planted in 0.5 m peat bags (Westland Horticulture, Dungannon, County Tyrone) in an experimental glasshouse at the University of Nottingham, Sutton Bonnington Campus on 2 April 2001. Five plants were established in each bag with 16 bags for each level of shading. The plants were arranged as a randomized block design with four replicates of each treatment. The glasshouse was set to heat at 8°C and vent at 12°C. The plants were grown in natural light with no supplementary lighting. All flowers were pollinated manually twice weekly with a small, soft paintbrush. Plants were kept well-watered throughout the experiment via a drip irrigation system (Field Irrigation and Polysystems, Kent, UK) with one dripper spike per bag. Plants were fed at every watering with Polyfeed (18:18:18 N:P:K +2 Mg) (Hi-Chem (UK) Ltd). Chemical treatment for botrytis and powdery mildew were applied as necessary (Rovral at 7.5 g per 10 l (Aventis CropScience UK Ltd, Essex, UK) and Nimrod at 14 ml per 10 l (Syngenta Crop Protection UK Ltd, Cambridge, UK).

Shade treatments

The plants were subjected to three shade treatments (0%, 25% and 47% shade) using shade netting (Tildenet Ltd, Bristol, UK) suspended above the experimental plots. Total irradiance under the shade netting was measured using a light meter (Skye Instruments, Powys, UK). The treatments were imposed 1 week prior to first ripe fruit for 2 weeks (5–19 June 2001).
Plant environment measurements

Total irradiance at canopy level, air and bag temperature, and humidity were recorded daily at 10 min intervals via a datalogger (Campbell Scientific, Leicestershire, UK). Volumetric moisture content in the peat bags was measured twice weekly using a Theta probe and meter (models ML2x and HH1, Delta-T devices, Cambridge, UK) and kept between 30-40% throughout the experiment.

Flavour analysis

Ripe berries were harvested five times during the fruiting period (8 June 2001, 11 June 2001, 13 June 2001, 17 June 2001, and 20 June 2001; or 0, 3, 5, 9, and 12 d after first harvest, respectively) and analysed for sucrose, glucose/fructose, citric acid content, and 13 volatile compounds. Eight berries from each treatment (i.e. two from every block) were used in each analysis. All berries were of a similar size and maturity (as assessed by reference to standard colour charts), and were picked and analysed on the same day. Efforts were made to choose berries of the same developmental status (ie position on the cyme).

Volatiles were analysed using Atmospheric Pressure Chemical Ionization–Gas Phase Analysis (APCI-GPA). This technique relies on a quadrupole mass spectrometer (Platform II, Micromass, Manchester, UK) operating in the API positive ion mode, equipped with a custom-built air-sampling interface (Linthorft and Taylor, Manchester, UK) and kept between 30-40% throughout the experiment.

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Results

Volatile profile: The relative proportions of the volatiles (Fig. 1) agreed well with previous studies of the headspace of cv. Elsanta (Linthorft et al., 1998). Methyl acetate had the highest mean peak height of the selected volatiles, followed by acetic acid and then acetaldehyde. Ethyl acetate, hexenal, methyl butyrate, and ethyl methyl butyrate all had similar headspace peak heights. Lower peak heights were found for hexenal, heptanone, ethyl butyrate, furanone, ethyl hexanoate, and ethyl methyl hexanoate.

Pick-to-pick variation: All of the volatile compounds tested in this study (Fig. 1) showed some highly significant differences with harvest date (P <0.01), although no consistent trend was seen across the harvest period. Data for hexanal, hexenal, ethyl methyl butyrate and methylbutyrate are shown in Figs 2 and 3.

Effect of shading: Hexanal, hexenal, ethyl methyl butyrate, and methyl butyrate showed some significant differences between control and 47% shading treatments (P <0.01) (Figs 2, 3). Generally it was the later harvests that showed differences. For instance, at 12 d after the first harvest, the volatile compounds in the 47% shade-treated fruit were reduced by between 1.5–2-fold that of the

Statistical analysis

Statistical analysis was carried out using Genstat 5 release 4.1 (Lawes Agricultural Trust, IACR, Rothamsted). Analyses of variance were carried out on the data. Variation between samples at any one harvest was expressed as percentage coefficient of variation (%CV; (standard deviation×100)/mean). Standard errors of differences of means (sed) were used to express variation between shading treatments.

Fig. 1. Mean headspace peak height of selected cv. Elsanta volatiles from control (unshaded) treatment. Data are the mean of 40 measurements taken from five harvests ±se.
control. In general, increasing the amount of shading decreased the amount of volatile present in the headspace.

Non-volatiles

Pick-to-pick variation: Sucrose, glucose and citric acid showed some significant differences with date of harvest ($P < 0.01$). Sucrose concentration decreased over the harvest period whereas glucose and citric acid showed less clear trends (Fig. 4).

Fruit-to-fruit variation: As observed with the volatile compounds, there is considerable fruit-to-fruit variation at every harvest in the non-volatile compounds tested (Table 1). For sucrose, the fruit-to-fruit variation in the 47% shade treatment was higher than that observed in the control treatment at every harvest. In general, for glucose, the fruit-to-fruit variation increased from harvest to harvest.

Effect of shading: Fruit sucrose concentrations showed a significant difference between control and 47% shading treatments ($P < 0.01$) at all harvest dates (Fig. 4). For example, at 12 d after the first harvest, the sucrose concentration of 47% shaded berries was 0.1% compared with 0.7% in the control fruit. Glucose/fructose showed similar differences between shaded and unshaded treatment, but these differences were only significant at some harvests. In general, the sucrose and glucose concentration was inversely proportional to the level of shading. The shade treatments had no significant effect on the fruit citric acid concentration. A sugar/acid ratio was calculated for the fruit from each harvest. As total sugar and acid concentrations were not measured in this experiment, the ratio consisted of sucrose and glucose/fructose concentrations combined divided by the concentration of citric acid. At each harvest the sugar/acid ratio of the control fruit was higher than that of the fruit from the 47% shade treatment. At harvests two and four (day 3 and day 9) the sugar acid ratio of the control fruit was 2.5 times that of the 47% shaded fruit.

Discussion

APCI and direct liquid–MS techniques are ideally suited to measuring volatile and non-volatile flavour compounds in strawberry fruit, allowing rapid analysis of a large number of experimental samples. Furthermore, since there
is no extraction step, the generation of artefacts is avoided. As the techniques separate compounds by mass alone they cannot distinguish between stereoisomers. This is not greatly problematic as the proportion of each isomer represented can be resolved by analysis with GC–MS.

The data presented in this paper suggest that light integral has effects on strawberry flavour compounds. 47% shading of the strawberry plants caused a significant reduction in the concentration of hexenal, hexanal, ethyl methyl butyrate, and methyl butyrate in the headspace of the fruit compared with the control at some harvest dates (Figs 2, 3). Furthermore, this shade treatment resulted in a significant reduction of sucrose and glucose/fructose compared with the unshaded treatment (Fig. 4).

Importantly, it can be seen from this experiment that a relatively short period of low light had a significant effect on the flavour quality of strawberry. This has implications for growers in that a brief duration of overcast weather during fruit ripening may have a significant influence on the marketability of their crop. The apparent sensitivity of strawberry flavour to light environment could explain the poor taste sometimes associated with autumn-grown crops (R Watson, CJ Wright, T McBurney, unpublished results).

Production methods will also affect the amount of light to which a crop is exposed. Solar radiation experienced by crops grown in a polythene tunnel with new plastic may be 10% less than an outdoor crop (P Keutenius, personal communication). A glasshouse could reduce light levels by 30% or more compared to that of an outdoor crop (Cockshull et al., 1992).

Other workers have shown that the timing and duration of a shading period can play an important part in influencing flavour quality of other fruit crops (Pattern and Proebsting, 1986; Garriz et al., 1998; Marini et al., 1991).

This experiment showed that there is a large amount of variation in flavour quality between fruits at any pick (Table 1) and also variation from harvest to harvest (Figs 2, 3, 4). Fruit-to-fruit variation may be due to there being fruit at different stages of maturity and ripeness within any pick. It is also probable that a sample of strawberries from a pick will be made up of a mixture of several cohorts, for example, secondary, tertiary and quaternary fruit that differ in their flavour make-up. In this experiment efforts were made to minimize such variation within individual harvests, but they were probably an important factor in the harvest-to-harvest differences observed. Variation from harvest to harvest is, however, probably more complex than simply the effect of berry class. It has been shown in this paper that light influences strawberry flavour compounds. The light environment experienced by the crop is likely to vary widely from harvest to harvest. This was the case in this experiment (data not shown). Previous data from tomatoes (Winsor and Adams, 1976) showed a high correlation between juice sugar content and solar radiation across a season. The results show the difficulty in interpreting data where there is a variable light integral as well as differences in fruit developmental stages at the time of shading. However, this will always be the case in commercial cropping systems and the results illustrate that, even under such variable conditions, effects of shading on fruit flavour can be seen. More data linking growth environment, especially light integral under more controlled conditions, to strawberry flavour components is required.

What is the reason for the reduction in strawberry flavour compounds in plants exposed to shading? Information on the biosynthesis of strawberry volatile compounds has only recently come to light. Several alcohols, aldehydes and esters may be secondary lipid metabolites derived from linolenic and linoleic acids by the action of lipoxygenase and hydroperoxide lyase (Gardner, 1991). These enzymes produce volatile aldehydes from which alcohols and esters can be formed via NAD- and NADP-dependent alcohol dehydrogenase and alcohol acyltransferase enzymes (Manning, 1998; Mitchell

Table 1. Fruit-to-fruit variation: the minimum and maximum percentage coefficient of variation (%CV) for flavour compounds from 0% and 47% shade-treated cv. Elsanta plants

<table>
<thead>
<tr>
<th>Compound</th>
<th>0% shade (%CV)</th>
<th>47% shade (%CV)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>Hexenal</td>
<td>19</td>
<td>28</td>
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<tr>
<td>Hexanal</td>
<td>15</td>
<td>32</td>
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<tr>
<td>Methyl butyrate</td>
<td>27</td>
<td>37</td>
</tr>
<tr>
<td>Ethyl methyl butyrate</td>
<td>28</td>
<td>49</td>
</tr>
<tr>
<td>Sucrose</td>
<td>30</td>
<td>51</td>
</tr>
<tr>
<td>Glucose/fructose</td>
<td>14</td>
<td>55</td>
</tr>
<tr>
<td>Citric acid</td>
<td>4</td>
<td>76</td>
</tr>
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and Jelenkovic, 1995; Pérez et al., 1993, 1996). In work on tomato, Gardner (1995) and Baldwin and colleagues (2000) determined that lipoxygenase, hydroperoxide lyase and alcohol dehydrogenase enzymes are important in the synthesis of volatile compounds which contribute to ‘green or grassy’ and ‘fresh’ notes in ripe fruits. Indeed, enzyme activity during ripening has been observed for lipoxygenase (Riley et al., 1996), hydroperoxide lyase (Riley et al., 1996) and alcohol dehydrogenase (Chase et al., 1982).

Whatever the pathways involved, the starting point for volatiles begins with carbon dioxide and photosynthesis, leading to the production of primary metabolic products (Herbert, 1989). Therefore, it might follow that a reduction in photosynthesis through shading will reduce the amount of primary metabolic products produced by the plant and, in turn, will mean less raw materials for volatile synthesis. Another explanation could be a direct result of shading of fruit. Shading is known shown to affect colour formation in fruits. Light influences anthocyanin synthesis in fruit skin (Erez and Flore, 1986) and thus fruit colour (Marini et al., 1991). Génard and Bruchou (1992) found that reducing sugars and pH increased with light exposure in ‘Suncrest’/GF 677 peaches. These authors observed that fruit effectively exposed to sun in the afternoon had low concentrations of sucrose and malate and high concentrations of citric acid. Such relationships between carbohydrates, organic acids and light exposure may be due to the effect of light on the synthesis of some plant hormones (Letham et al., 1978) or because of effects on the temperature of the fruit. Austin et al. (1960) showed that in strawberry fruit temperatures can exceed air temperatures by as much as 8 °C on sunny days of 26.5 °C. Research in grapes demonstrated that fruit temperature of berries exposed to high levels of incident light exhibited temperatures of 15.9 °C above ambient air temperature (Tarara et al., 2000). High fruit temperatures could inhibit enzymes, such as sucrose synthetase, which acts on sucrose production (Moriguchi et al., 1990). Increased fruit temperatures may also induce a higher transpirational flux within the fruit. This would stimulate the translocation of nutrients and hormones to the fruit sink, and increase sink strength (Lasko, 1994).

The question as to whether the reduction of volatiles by shading is related to a decrease in carbon fixed or due to the direct effect of light on the fruit is an important one. Although growers would not have much control over light environment in outdoor or tunnel-grown crops, if light acted directly on the fruit, an easy management tool available to them would be to use wires to hold back the leaves to prevent self-shading of the fruit and increase the amount of light incident on them. Clearly, further experimentation is required to determine the mode of action of light on flavour compounds.

Other factors will also exert their effect on flavour. As discussed above, a reduction in light could be expected to reduce plant photosynthetic rates which would, in turn, lead to less sugar available for translocation to individual fruits. Fruit sink strength could also be expected to influence carbohydrate allocation. Fruit load will increase over time meaning that even at similar light levels the amount of assimilates available to individual fruits will change throughout the harvest period. The greatest demand for assimilates will occur during the development of secondary and tertiary fruits.

Fig. 4. Mean concentration of sucrose, glucose and citric acid with time after first harvest for control and shaded cv. Elsanta (closed circles, 0% shade; open circles, 25% shade; closed inverted triangles, 47% shade). Each data point represents the mean of eight berries. Error bars represent s.e.d.
It is important to consider what the shade-related changes in volatile and non-volatile compounds observed in this experiment actually mean in terms of human perception. Hexanal and hexenal are aldehydes derived from linoleic and linolenic acids, respectively. Hexanal is thought to give a rancid odour, whereas hexenal may be responsible for an herbaceous odour. Ethyl methyl butyrate and methyl butyrate are esters and they represent fruity notes in the strawberry aroma (Scheerens and Stetson, 1996). Hexenal, ethyl methyl butyrate and methyl butyrate are included by many authors among character-impact compounds (Schieberle and Hofmann, 1997) and so a decrease in these compounds may be detrimental to the flavour of the fruit. Sugar/acid ratios are often used as an index of consumer acceptability and quality in fruits. In this experiment, shading caused a marked decrease in the sugar/acid ratio of the fruit. Less sweet fruits may reduce palatability to consumers, although this is an over-simplification of the process of flavour perception. Studies have shown that often there is a synergy between compounds that affects flavour perception. For example, aroma and acid concentrations affect perception of sweetness in tomato (Malundo et al., 1995). Work by Davidson and co-workers (1999) showed that the perception of menthone in mint chewing gum was strongly influenced by the presence of sucrose. Unfortunately, a taste assessment was not carried out on the fruit from this experiment so the instrumentally-measured variation cannot be linked to the human perception of flavour quality. The measured changes in volatile and non-volatile flavour components with shade may be too small to affect the flavour of the fruit significantly, as perceived by consumers. This lack of data relating instrumental measurements and human sensory perception is a common one (Brennan et al., 1997) and the assessment of fruit by a panel of tasters should be included in future studies.

The data presented in this paper and results from other workers (Veit-Köhler et al., 1999; Awang et al., 1993; Ehret and Ho, 1986) shows the potential for growers to manipulate the flavour quality of their fruit crop through adjustments in the growing environment. Furthermore, relating detailed monitoring of growth conditions to flavour data may allow modelling of plant and fruit responses to their environment. This could provide a powerful tool to growers and retailers allowing the probability of a poor tasting crop to be determined.

Several authors have shown that genetic transformation of strawberry plants is possible (Woolley et al., 2001; Barcelo et al., 1998). Work by Griffiths et al. (1999) on transgenic tomatoes shows the value of gene technology in determining the relative importance of different enzymes or biochemical pathways in the expression of flavour compounds. However, the data from this study suggest that locating genes responsible for the production of specific flavour compounds and expressing these genes in transgenic plants may be futile in improving fruit flavour, because environmental conditions seem to have a major influence on flavour compound generation. This is in agreement with Shaw (1990) who determined that the soluble solid content of strawberry fruit was more dependent on environmental conditions during production than on the genetic make-up of the plant.

In summary, APCI and direct liquid–MS techniques allow rapid analysis of flavour compounds in strawberry fruit. The techniques were used here to demonstrate that there are large variations in volatile and non-volatile flavour compounds between fruit at any pick and also between harvests. Furthermore, several components of strawberry flavour were significantly reduced by plant shading treatments. The mechanisms by which low light levels incident on the crop reduce concentrations of flavour compounds in the fruit remain to be determined. What the observed variations in flavour compounds meant in terms of human perception were not elucidated in this study, but they could explain consumer disappointment with some crops.

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