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Light Reflected from Red Mulch to Ripening Strawberries Affects Aroma, Sugar and Organic Acid Concentrations¶

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ABSTRACT

Strawberry (*Fragaria ananassa*) fruit size and flavor are important to both growers and consumers. Plastic mulches are frequently used in raised-bed culture to conserve water, control weeds with less herbicides, keep fruit clean and produce ripe berries earlier in the season. The most commonly used plastic mulch color is black. We hypothesized that changing mulch color to reflect more far-red (FR) and red light (R) and a higher FR/R photon ratio would keep those benefits and improve berry size and flavor by altering phytochrome-mediated regulation of pathways in ripening berries. Size and chemical composition of berries developed in sunlight over a specially formulated red plastic were compared with those that developed over standard black plastic mulch. Berries that ripened over red were about 20% larger, had higher sugar to organic acid ratios and emitted higher concentrations of favorable aroma compounds. We conclude that FR and the FR/R ratio in light reflected from the red mulch on the soil surface acted through the natural phytochrome system within the growing plants to modify gene expression enough to result in increased fruit size and improved concentrations of phytonutrient, flavor and aroma compounds.

INTRODUCTION

Yield and quality of plant products are influenced by the light conditions that exist during plant growth and development. Responses to photosynthetic photon flux, red (R)†, far-red (FR) and blue (B) light have been studied extensively under controlled environments. These wavebands can be influenced in the field because of competitive absorption by and reflection from nearby growing plants (1–6). Source–sink relationships in sungrown plants also respond to quantity and spectral distribution of light reflected from the soil surface (7,8) and from mulches on the soil surface (9).

Plastic mulches over trickle irrigation systems are widely used in raised-bed culture of strawberry (*Fragaria ananassa* Duch) and other food crops to conserve water, control weeds with less herbicides and keep low-growing fruit and leaves clean. Black is the most widely used color of plastic mulch (10). Recently developed colored mulch technology combines the benefits of black plastic mulch with additional growth regulatory benefits of reflected morphogenic light to improve yield and quality of field-grown plant products (9). It allows plants growing in natural sunlight to receive reflected light with different quantities of B, R and FR, with different R/B and FR/R photon ratios, which can function through the natural growth regulating system within a growing plant (2,3,5).

Based on earlier controlled environment experiments (2), it was predicted that a FR/R photon ratio higher than the ratio in incoming sunlight (at the same time and place) would favor shoot crops, and a FR/R ratio lower than the ratio in incoming light would favor below-ground crops. Plant responses were as predicted (9). The controlled environment experiments, combined with field studies of shoot crops grown over painted panels (with known reflection spectra), led to the development of a specially formulated red plastic mulch that increased the yield of tomato (*Lycopersicon esculentum* Mill.) relative to yield over standard black plastic mulch (11).

Because developing strawberry fruits are closer to the reflecting surface of colored mulch, it was hypothesized that strawberry yield advantage would be greater (in terms of percentage) than that of tomato grown over the red *versus* those grown over standard black plastic mulches. The hypothesis was proven correct in a 2 year, two-location experiment (12). Increased size per strawberry fruit contributed to greater yield when grown over the new red *versus* over standard black plastic mulch. Because strawberry is a high-value food crop that is consumed fresh or after processing it was important to determine whether the reflected light combination that resulted in increased yield would also affect flavor and/or phytonutrient content.

Some reports in the biochemical/botanical literature of the 1970s and 1980s are relevant to the present study of sugar and organic acid concentrations in strawberry fruit. For example, growing parts of seedlings that received FR (a high FR/R photon ratio) at the end of each day in controlled environments had higher concentrations of sugars and higher sugar to organic acid ratios than those of seedlings that re-

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†*Abbreviations:* B, blue light; FR, far-red light; GC, gas chromatography; R, red light; SPS, sucrose phosphate synthase.

ceived R (a low FR/R photon ratio) at the end of each day (13). The response to FR was photoreversible by R (and *vice versa*) suggesting that the natural phytochrome system within the growing plants was involved in biochemical events leading to the differences in sugar and organic acid concentrations in the plant tissues. Leaf morphology, chloroplast structure and sugar concentration in developing leaves were also affected by end-of-day FR/R photon ratios (14). Further, Jen *et al.* (15) determined that photoreversible phytochrome was present in developing tomatoes. The literature on penetration of light into fleshy leaves and cotyledons of growing plants has been reviewed by Vogelmann (16). Since tomato and strawberry yields were both higher over a red mulch (11,12), it is reasonable to expect that phytochrome was also present in our developing strawberry fruit. In the present study, it was hypothesized that sugar and organic acid concentrations in strawberry fruit developing in sunlight over a red mulch that reflected a FR/R photon ratio higher than the ratio in incoming sunlight would also have higher sugar concentrations and higher sugar/organic acid ratio than strawberries growing over standard black mulch, which reflected less than 5% across the visible and FR spectrum.

It is known that variations in the concentrations and specific types of aroma compounds produced by strawberry affect fruit quality (17–20). Accordingly, we extended our study to determine whether light reflected from the red and black mulches could modify concentrations of aroma compounds emitted by sungrown strawberries that developed and ripened over those colors.

Both yield and quality are important in production of high-value food crops. Higher yield of strawberries grown over the new red *versus* over the standard black plastic mulch has been documented (12). The objective of the present study was to determine whether light reflected from the red *versus* standard black plastic mulches could affect concentrations of sugars, organic acids and aroma compounds in strawberries that ripened in sunlight over the respective colors.

MATERIALS AND METHODS

Plant material and growth conditions. Strawberry (cv. 'Chandler') plants were grown in trickle-irrigated plots of Norfolk loamy sand (Typic Kandiudults) at the Coastal Plains Soil, Water and Plant Research Center near Florence, SC. The subplots were covered with standard black plastic mulch or with red plastic mulch (manufactured by Sonoco Products Co., Hartsville, SC, and marketed as Selective Reflective Mulch [SRM-Red] by Ken-Bar, Inc., Reading MA). Strawberries used for chemical analyses were subsampled from the second year of a 2 year study of yield over the black *versus* red plastic mulches (12).

The plots were fertilized according to recommendations of the Clemson University Extension Service. Black polyethylene mulch (1.5 m wide), trickle-irrigation tubing and bromomethane fumigation were all applied to the field plots in a single operation in mid-August. This operation also included raising the beds and covering the edges of the plastic with soil to keep it in place. The mulch-covered beds were 90 cm wide and 15 cm high. They remained undisturbed until early October when the red plastic was put in place, holes punched and strawberry transplanted. There were 10 replicated plots of black and red plastic mulch. The red mulched subplots were obtained by taping a layer of red plastic over the existing layer of black plastic just before the holes were punched. The within-row plant spacing was 30 cm and rows were 1.8 m apart. This spacing gave a high probability that strawberry fruit developing over the red mulch would receive R and FR reflected from the mulch surface. Soil temperatures 10 cm below the two colors of mulch were measured to the nearest 0.1°C.

Strawberries were harvested two or three times per week depending on ripening rate (12). Those used for sugar, organic acid and aroma compound analyses were subsampled from berries that ripened over the red *versus* those ripened over the black plastic mulches during several days of bright sunlight. Also, we used berries that ripened over red and those that ripened over black during several days of overcast weather as part of the sugar and organic acid component of our study. In all cases, the berries were weighed, sliced, placed in evacuated plastic bags and frozen at −65°C within an hour after removal from plants. Some of the frozen strawberries remained in the evacuated plastic bags in the freezer at −65°C until subsamples were weighed, crushed and analyzed for aroma compounds. Other samples were freeze-dried. Ten samples of freeze-dried strawberry fruit, weighing 1 g each, were prepared from each of the treatments. Each of the 1 g samples was kept in a separate air-tight plastic sample bag and transferred to the USDA-ARS Fruits Lab in Beltsville, MD, for sugar and organic acid analyses.

Sugar and organic acid analyses. Each 1 g sample of freeze-dried strawberry fruit tissue was extracted with 60 mL of 20 m*M* imidazol buffer (pH 7.0), then centrifuged at 5000 ***g*** for 10 min. The residue was reextracted and washed twice by centrifugation and resuspended in 20 m*M* imidazol buffer (20 mL each time). The supernatants were combined (the final total volume for each sample was 100 mL). Two milliliters of the extract were dried *in vacuo* in a derivatizing vial. Derivatization of sugars was carried out according to procedures described by Wang *et al.* (21). One microliter aliquots of the derivatized samples were injected for gas chromatographic (GC) separation and quantification. A Hewlett–Packard 5890 GC equipped with a flame ionization detector was used. A known amount of β-phenyl-D-glucopyranoside was included in all the samples as the internal standard. A 25 m crosslinked methyl silicon gum capillary column (0.2 mm i.d., 0.33 μm film thickness) was used. Chromatograph temperatures were as follows: injector, 250°C; detector, 275°C; and column, 100–250°C programmed at 10°C per min.

Twenty milliliters of imidazol buffer extract purified with a Baker-10 solid phase extraction system (Phillipsburg, NJ) was used for organic acid determination. Supernatants from the extracts were passed through quaternary amine columns, which were previously conditioned with hexane and methanol. The samples were then eluted from the columns with 0.1 *N* HC1. The eluates were concentrated to dryness *in vacuo* in derivatization vials. Procedures of derivatization and chromatography for organic acids were the same as those for sugars except that column temperatures were programmed from 180 to 250°C at 10°C per min. Separated sugars and organic acids were compared with the derivatized standards for qualitative and quantitative determinations. A Hewlett–Packard ChemStation was used to calibrate the peaks, record the data and calculate the results.

Aroma compounds. Collections were performed on a "push–pull" apparatus similar to that described in Loughrin *et al.* (22). It had six chambers for samples, each consisting of a 500 mL side-arm Erlenmeyer flask (18 cm tall) closed at the top with a no. 6 rubber stopper adapted for 0.635 cm o.d. (0.25 in.) copper tubing which served as an air-inlet line. Air was supplied to each inlet *via* a manifold connected to a 500 mL charcoal filter and continuous duty diaphragm air compressor. The copper tubing extended 4 cm into each flask and had an air diffuser (Reagent Pet Products, Moorpack, CA) attached to its end (total extension into flask 12 cm). On the side arm of each flask was attached, *via* Tygon tubing (Norton Performance Plastic Corp., Akron, OH), a 0.635 cm o.d. copper tube with Swage-lock fittings to accommodate 0.635 cm o.d. glass collection traps. Each trap contained 50 mg of Super Q absorbent (Supelco Inc., Bellefonte, PA) enclosed within glass wool plugs. Vacuum was applied to each chamber by another manifold constructed of 0.635 cm o.d. tubing and attached to a separate continuous duty diaphragm pump. The vacuum sent to each chamber was regulated by a separate flow controller; during collections air was pulled through each chamber at 150 mL/min. The pressure of the entire system was kept slightly above atmospheric pressure as measured by a separate flow controller connected to a vent attached to the head of the air-inlet manifold.

About 25 g of frozen berries were crushed into small pieces with a mallet and placed into each sampling chamber along with 10 μg each of cumene and hasmigone (2-[hex-2-enyl]-cyclopentanone) dissolved in 50 μL of CH_2Cl_2 as the internal standard. Collection traps were rinsed with 2 mL of high-purity hexane prior to attachment. Collections were of 4 h duration, and samples from berries grown over both red and black mulches were included in every collection.

Retained compounds were eluted from the traps with 320 μL of an 80:20 mixture of high-purity hexane:CH_2Cl_2. One microliter aliquots were injected onto a GC operated in splitless mode for 1 min; the GC was equipped with a 60 m × 0.32 mm Supelcowax 10 (Supelco Inc., Bellefonte, PA) column with 0.5 μm film thickness. GC operating conditions were as follows: injector 220°C, oven temperature 50°C for 1 min then programmed at 3°C per min to 180°C, flame ionization detector 240°C, helium carrier linear flow velocity 21 cm/s.

Collections were replicated seven times for samples grown over both red and black mulches for each of two harvest dates. Compounds were quantified against the internal standards. Mean values for the 14 replicates ± standard errors were calculated for each of the aroma compounds.

Compound identification. GC/mass spectroscopy was performed on a GC equipped with a 30 m × 0.25 mm HP-5 column (Hewlett–Packard, Palo Alto, CA) interfaced to a Hewlett–Packard GCD Plus mass selective detector. Injections were made onto the GC in the splitless mode for 1 min, and the mass ion detector used a scanning range of 40–450 amu. Operating conditions for the GC were: injector 220°C, column oven 40°C for 1 min then programmed at 3°C per min to 180°C. Compound identifications were performed by computer-assisted searches and coelution of authentic samples of compounds on the Supelcowax-10 column. Authentic samples of compounds were obtained from commercial sources.

Statistical analysis. Data were analyzed by analysis of variance as outlined by the SAS Institute (Cary, NC) (23).

RESULTS AND DISCUSSION

Strawberry size

The average size per berry was greater when grown over red than over black. For example, fresh weights of berries used in our study averaged about 22 g per berry that ripened over red and about 18 g per berry over black. These differences in size are consistent with those obtained in the 2 year, two-location study (12). In that study of fruit yield, the trend continued throughout the entire harvest season but the greatest size difference occurred during the first weeks of harvest, which coincided with the highest demand for fresh strawberries.

Because soil temperature affects production of horticultural crops (10) that component of the growth environment was minimized by taping the layer of red plastic over a layer of black plastic. The soil was less than 0.5°C warmer under the black plastic than under the red surfaced plastic mulch (12). In addition to minimal differences in soil temperature below the red *versus* black mulches, both surface colors reflected only about 5% of the incoming blue light. Therefore, differences in berry size (and chemistry) observed in our study are attributed to differences in R, FR and the FR/R photon ratio reflected from the mulch surfaces, as they contributed to spectral differences in the total light environment of the developing strawberries.

Flavor

Taste tests of coded samples by more than 50 volunteers during the harvest seasons of 1996 and 1997 indicated a preference for berries grown over the red *versus* those grown over black mulches. Flavor of berries that ripened over red mulch during sunny weather was typically described as being "sweeter," while those that developed in black-mulched plots were described as being more "tart." According to the same taste testers berries that ripened over the red mulches tasted "about the same" as those ripened over black plastic mulches if they ripened during an overcast period. Therefore, we did chemical analyses for sugars and organic acids in strawberries that ripened over red or black mulches during sunny weather and during overcast weather. These analyses were performed with freeze-dried samples in the USDA Fruit Lab at Beltsville, MD.

Table 1. Sugar and organic acid concentrations (mg/g dry wt) in strawberries that ripened outdoors over red *versus* black mulches during a period of sunny weather (values are means for 10 replications ± SEM)

Compound	Mulch color: Red	Mulch color: Black	Significance	Difference (%)
A. Sugars				
Fructose	356.5 ± 13.8	314.7 ± 8.6	*	13.3
Glucose	349.7 ± 8.5	283.4 ± 9.3	*	23.4
Sucrose	167.8 ± 8.6	141.2 ± 8.5	*	18.8
Total	874.0 ± 16.3	739.3 ± 16.4	*	18.2
B. Organic acids				
Malic	16.1 ± 2.1	16.6 ± 2.0	NS	−3.0
Citric	43.4 ± 3.2	43.4 ± 3.6	NS	0.0
Total	59.5 ± 3.6	60.0 ± 4.6	NS	−0.8
C. Sugars/organic acids (w/w ratio)				
	14.7	12.3	—	19.5

*Indicates values in the same line differ significantly at $P = 0.05$. NS indicates values in the same line are not significantly different at $P = 0.05$.

Sugars and organic acids

Concentrations of sugars and organic acids in strawberries that ripened over the red or black mulches during a period of sunny weather are summarized in Table 1. Higher concentrations of fructose, glucose and sucrose were evident in berries that developed over the red mulch. Also, the ratio of total sugars relative to total organic acids was greater over the red mulch. Strawberries from another sampling date that followed a period of predominantly sunny weather also had a higher sugar to organic acid ratio when grown over red *versus* over black surfaces. However, strawberries that developed during a period of overcast weather had about the same sugar to organic acid ratio over the red and black mulches (data not shown).

These relationships between sugar and organic acid concentrations in strawberries that ripened over red *versus* over black during sunny weather are consistent with the descriptions of "sweeter" berries over red mulch by participants in the preference test. The higher sugar concentration and sugar to organic acid ratio over red (see Table 1) are also consistent with the controlled environment responses of plant parts to high FR/R photon ratios (13,14). The red mulch used in the present study reflected more R and FR and a higher FR/R photon ratio than was reflected by the standard black mulch, which reflected less than 5% of any color.

It is apparent that the reflected R and FR (very likely acting through the natural phytochrome system within the

Table 2. Aroma compounds (ng/g fresh wt) identified in emissions from strawberries that ripened outdoors over red *versus* black mulches during sunny weather (values are means ± SEM)

Compound	Mulch color		Significance (P = 0.05)
	Red	Black	
A. Aliphatic esters			
2-Methylbutyl acetate	361 ± 57	307 ± 67	NS
Methyl butyrate	83 ± 11	42 ± 5	*
Ethyl butyrate	113 ± 12	62 ± 9	*
Methyl hexanoate	442 ± 26	197 ± 34	*
Butyl butyrate	22 ± 2	21 ± 2	NS
Ethyl hexanoate	181 ± 25	73 ± 17	*
Hexyl acetate	65 ± 3	48 ± 2	*
(*Z*)-3-Hexenyl acetate	20 ± 1	17 ± 1	*
(*E*)-2-Hexenyl acetate	123 ± 4	91 ± 5	*
Hexyl butyrate	11 ± 1	7 ± 1	*
Methyl octanoate	6 ± 1	7 ± 1	NS
Octyl acetate	10 ± 1	5 ± 1	*
B. Terpeniods			
2-Carene	7 ± 1	10 ± 1	NS
Linalool	49 ± 5	110 ± 33	*
Nerolidol	6 ± 1	8 ± 1	NS
C. Unesterified Compounds			
Hexanal	407 ± 20	296 ± 25	*
(*E*)-2-Hexenal	954 ± 84	828 ± 85	NS
(*Z*)-3-Hexenol	6 ± 1	5 ± 1	NS
Mesifurane	11 ± 3	3 ± 2	*

*Indicates values in the same line differ significantly at P = 0.05. NS indicates values in the same line are not significantly different at P = 0.05.

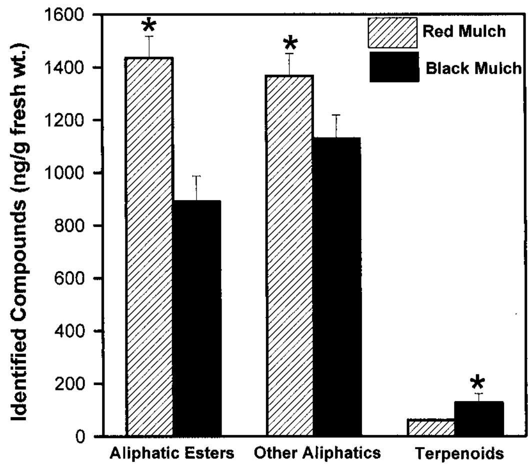

Figure 1. Concentrations of aliphatic esters, other aliphatics and terpenoids emitted by strawberries that ripened in sunlight over red *versus* black plastic mulches (values are mean ± SEM for 14 replicates and an * indicates that values differed at P = 0.05 over red *versus* black mulch).

developing strawberries) were involved in modifying chemical pathways leading to the observed differences in sugar and organic acid concentrations that contributed to differences in sweetness of berries that ripened over red *versus* over black surfaces. Elucidation of photoactivation of enzyme systems involved in the pathways leading to sweeter strawberries over the red surfaces was beyond the scope of our study. It is known, however, that sugar accumulation (sweetening) in many horticultural fruits, including strawberry, is controlled, at least in part, by activity of the enzyme sucrose phosphate synthase (SPS) within the developing fruit, especially during the later stages of ripening (24,25). Perhaps the higher FR/R photon ratio reflected from the red surfaces acted through the phytochrome system within the ripening strawberries to enhance activity of SPS leading to higher sugar concentrations and sweeter berries in our study.

Aroma compounds

After determining that reflection from the red mulch surface influenced the sugar and organic acid concentrations, we compared concentrations of aroma compounds emitted from strawberries that ripened over the red *versus* over the black mulches during sunny weather to further determine effects of reflected R and FR on components of flavor. Nineteen aroma compounds were quantified. They consisted of aliphatic esters, terpenoids, unesterified aliphatic compounds and the sugar-derived compound mesifurane (Table 2). A number of other compounds (phenylpropanoids such as phenethyl acetate, terpenoids such as linalool oxide and α-pinene and some additional aliphatic esters) occurred in relatively minor amounts, and were not quantified.

In general, higher concentrations of individual aroma compounds were obtained from berries grown over red plastic than from those grown over black plastic. These differences were most pronounced in the case of the aliphatic esters (Fig. 1), and concentrations of individual esters were significantly higher for every compound with the exception of 2-methylbutyl acetate and the relatively minor compounds methyl octanoate and butyl butyrate (see Table 2). Total amounts of unesterified aliphatic compounds were also higher from berries grown over red than from those grown over black plastic mulch (see Fig. 1 and Table 2).

We obtained relatively higher concentrations of hexanal and (*E*)-2-hexenal than have previous researchers (18,20). High levels of these volatile compounds, which have a 'green-leaf' character and are formed by the hydroperoxidation of unsaturated fatty acids by lipoygenase and subsequent cleavage by hydroperoxide lyase (26,27), are generally more characteristic of fresh than frozen berries (20). It is probable that freezing and storing the berries at −65°C rather than at the higher temperatures, more typical of those found in commercial storage, helped preserve enzymatic activity in our samples. While these compounds occurred in greater amounts in berries grown over the red plastic than from those grown over black, the difference was most pronounced for hexanal. Only small amounts of the more reduced forms of (*E*)-2-hexenal, (*Z*)-3-hexenol and (*E*)-2-hexenol, were detected. However, relatively high amounts of (*E*)-2-hexenyl acetate were evident. Given that the levels of aliphatic esters were enhanced from berries grown over the red plastic, the data suggest that esterase activity was enhanced in berries grown over red relative to those grown over black plastic.

In contrast to aliphatic compounds, higher concentrations of terpenoids were obtained from berries grown over black than from those grown over red plastic (see Fig. 1). This difference was most pronounced in the case of the monoterpene alcohol linalool (see Table 2).

Strawberry fruits have complex aroma profiles, and various researchers have implicated different compounds as being the most important components of desirable aroma. Some investigators consider mesifurane (2,5-dimethyl-4-methoxy-3(2*H*)-furanone) and furaneol (2,5-dimethyl-4-hydroxy-3-(2*H*)furanone) to be characteristic of aroma compounds of strawberries (19,20). The estimation of furaneol is difficult by GC (28), and we did not detect this compound in our samples. Mesifurane, however, occurred in significantly higher levels in berries grown over the red mulch. Lambert *et al.* (29), in contrast, considered furaneol and nerolidol to be the most desirable aroma constituents of strawberries, while Hirvi (18) considered ethyl hexanoate, ethyl butyrate, (*E*)-2-hexenal, linalool and furaneol to be most characteristic. We found that growing the berries over red plastic mulch resulted in increased concentrations of most of the measured aroma compounds and would likely improve perceived fruit quality.

In summary, it is well known that growth and development of a plant are regulated by a combination of its genetics and the total environment in which it grows. Both photosynthetic and photomorphogenic light are important components of the growth environment. For example, in nature phytochrome in a growing plant senses FR reflected from nearby plants as an indicator of competition for space and as a signal to prioritize shoot growth (which increases the probability of keeping some leaves in photosynthetic light above the competing plants) (4,6). Our work utilizes this FR-sensing mechanism to modify yield and quality of food crop plants by reflecting a preselected FR/R ratio from plastic mulch (over trickle-irrigation tubes) on the soil surface to the developing parts of sungrown plants (11,12). In effect, this allows photosynthesis in full sunlight, while the photomorphogenic light reflected to the developing parts influences how the photosynthate is allocated and used within the growing plant parts, including strawberry fruits. Our data indicate that the FR/R ratio reflected from the red mulch surface allowed us to modify expression of existing genes in the growing plants to increase berry size and the concentrations of phytonutrient, flavor and aroma compounds in sungrown strawberry without significantly altering other field production procedures.

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