RED COLOR DEVELOPMENT OF APPLE: A LITERATURE REVIEW

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This study was commissioned by C. M. Holtzinger Fruit Co. in memory of Jim Campbell of Tieton, Washington. Jim was a consummate grower and loved the challenge of coaxing fruit from his trees. In the words of his son, Craig Campbell, "growing up on the farm in Tieton, my father Jim Campbell was always trying something new in either tree fertilization or foliar application to enhance quality and color in apples. I think his Hort schooling at WSU enabled him to understand the scientific side of growing, which encouraged the desire for growing better apples."

Consumers buy on impulse; that is, when one goes to the market to buy fresh produce, he/she will generally buy that which "catches their eye" best. Producers of fresh fruits and vegetables are keenly aware of this fact and know that the best appearing produce has a competitive edge in the market place. Perhaps, nowhere is this better observed as with apples where the consumer has developed the long-held stereotype that the perfect apple is big and red. Good color is also important when grading the fruit (i.e., which apples will make U.S. Extra Fancy). For these reasons, apples which have the best color command the better prices. Even varieties which do not color very well (i.e., Gala and Fuji) are being bred to produce apples with deeper and deeper red. Therefore, as growers, it is extremely important that their fruit develop as much color as possibly.

So what can apple growers do to enhance the color of their produce and hence enhance their business? What causes the red color to develop in apples and what have researchers and growers around the world tried that works or doesn't work to increases apple color? Much has been researched and discovered about color development in apples. However, color development is a complicated process and there is much that still needs to be learned before techniques can be developed which will give the grower acceptable control over apple coloration.

The purpose of this report is to give a brief update on what is known about the factors (environmental and physiological) which influences color development of apples and discuss where new research might be needed to help growers "manage" the coloration of their crop in order to better meet the color criteria for the top grade and the demands of the impulse consumer. We have formatted this summary into discrete sections, removed as much "wordiness" as possible, and tried to succinctly list the "take home message" concerning each factor's effect on color development. Included with each section are citations relating to the original experiments and there is an extensive reference list at the end of this summary to assist the reader who wishes to investigate further.

BACKGROUND: THE PHYSIOLOGICAL AND BIOCHEMICAL BASIS FOR COLOR DEVELOPMENT.

The apple contains many compounds such as anthocyanins, chlorophyll, carotenoids, and flavonols which can blend together to produce its color. The most important of these compounds for the red coloration in apples are the anthocyanins, located in the skin, which can increase more than 5-fold during the ripening of some cultivars.

Figure 1 shows an outline of the biochemical pathways which lead to anthocyanin production. Some of the most important steps in this pathway discovered so far are the availability of sugars and the activity of the enzyme phenylalanine ammonia-lyase (PAL). Along the pathway are many steps which can each be individually influenced by different physiological and environmental factors and which when added up give rise to the final (or net) color we see. Each step leading to the production of anthocyanins must be optimized and the steps which divert anthocyanin precursors to other pathways or lead to the destruction of anthocyanins must be minimized in order to maximize color development. Thus, all of the physiological and environmental factors which have some effect on this pathway must be considered in relation to the others. For example, even though a fruit has good light exposure, the cultivar may be physiologically one that does not color well or the apple may be at a stage of development which is not genetically programmed to produce anthocyanins. This is why some treatments enhance color in some circumstances and not in others; under slightly different conditions other parts of the pathway may limit anthocyanin production.

(Lancaster et al., 1994; Lancaster, 1992; Saure, 1990; Faragher and Brohier, 1984; Chalmers et al., 1973; Creasy, 1968; Faust, 1965a).

ENVIRONMENTAL FACTORS

Light:

- Of the environmental factors which influence coloration of apples, light exposure is the most important.
- Although light is required for anthocyanin production, to what degree light stimulates apple coloration is highly dependent on the apple cultivar and the stage of development For example, late harvested 'Mclntosh' apples required longer exposures to light to induce a certain amount of color development than apples harvested earlier.
- Some researchers suggest that one of the ways that light increases anthocyanin production is by stimulating greater PAL activity in the apple.

The Amount (Quantity) of Light Which Reaches an Apple is Critical for Anthocyanin Formation

- Shading fruit from the sun, such as within a tree canopy, can reduce anthocyanin formation and color development. For example, one researcher found that fruit colored best if they received more than 70% of full sunlight and did not color well if they received less than 40% of full sunlight.
- Apples require a minimum amount of light for anthocyanin production and this minimum changes with cultivar and stage of development.

The Wavelength (Quality) of Light Which Reaches an Apple is Critical for Anthocyanin Formation

- Blue-violet (BV) and ultraviolet (UV) light, especially UV-B, are the most effective at inducing color development. Increased UV light after rain or at higher elevations has been suggested to explain the greater development of apples color under such conditions.
- Red light has been found by some researchers to be weakly effective at inducing color development while others have found it to be more effective than the other visible wavelengths (i.e., not including UV light).

- Blue light was weakly effective at inducing color development.
- Far-red (FR) light was the least effective at inducing color development and could possibly even inhibit color development.
- Combining UV-B light with white or red light worked synergistically in inducing coloration while combining UV-B with blue light was only additive.
- Both phytochrome and the fruit's photosynthetic system appear to be important in triggering the fruit to produce anthocyanins.

(Dussi et al., 1995; Lancaster, 1992; Saure, 1990; Kubo, 1988; Kubo et al., 1988; Arakawa, 1988; Arakawa, et al., 1986; Arakawa et al., 1985; Mancinelli, 1985; Faragher, 1983; Jackson, 1980; Faragher and Chalmers, 1977; Bishop and Klein, 1975; Proctor et al., 1975; Proctor, 1974; Proctor, 1971; Proctor et al., 1971; Proctor and Creasy, 1971; Heinicke, 1966 not sure of yr.; Downs et al., 1965; Siegelman and Hendricks, 1958; Arthur, 1932; Streeter and Pearce 1931; Fletcher, 1929; Magness, 1928b).

Temperature:

- Again, temperature effects depend on the cultivar and stage of fruit development.
- Reddening of apple fruit is increased by low temperatures such as those encountered on cold nights. At temperatures below 70 ºF, researchers found that there was and inverse relationship between anthocyanin content and temperature.
- Researchers found that with 'Mclntosh' apples, low night temperatures were better correlated with good coloration than either average daily or daylight mean temperature. Practically no anthocyanin was produced when average night temperatures were above about 70 °F.
- 'Red Chief apples appeared to color better when night temperatures were about 52 °F than when night temperatures were about 72 °F.
- Low temperatures need not occur only during the night to induce color development but can enhance apple coloration if experienced during either the light or dark periods.
- The benefits of tow night temperatures can be completely negated by a subsequent exposure to even one hot (89 °F) day.
- It has been suggested that low temperatures may reduce the loss of sugars in the skin, by reducing respiration, which allows more sugar substrate for anthocyanin production.
- Some researchers suggest that one of the main ways that temperature influences anthocyanin production is by increasing (at low temperatures) or decreasing (at high temperatures) PAL activity. At high temperatures, the tissue may produce a PAL inactivator which reduces PAL activity while at low temperatures, this inactivator may not be as active.

(Lancaster, 1992; Saure, 1990; Blankenship, 1987; Faragher, 1983; Creasey, 1968; Creasy, 1966; Creasy, ~ 1966 New York State Horticultural Society; Uota, 1952; Arthur, 1932; Magness 1928b)

Nitrogen:

- In general, excess nitrogen (N), from either soil or foliar applications, is associated with reduced anthocyanin production and red coloration of apples.
- Although the percentage of well-colored fruit may be lower at the high N fertilization rates, the total yield of well-colored fruit may actually be higher.
- Excess N may also be used to inhibit anthocyanin production in green apple cultivars such as 'Granny Smith' where reddening is undesirable.
- Excess N inhibits coloration of apples most severely if present late in the growing season.
- Some researchers suggest that one of the ways N reduced red coloration is by increasing foliage and thereby reducing light penetration into the canopy.
- Several Washington State apple growers report better fruit coloration by reducing the total amount of N-fertilizer used and applying the bulk of it later in the season (late August) instead of in the spring. However, caution should be observed when applying very low rates of N because fruit size can be decreased and trees may go into alternate bearing.
- We didn't find any reports in the literature on the specific effect of the type of N fertilizer on apple color development.

(Raese et al., 1997; Sanchez et al., 1995; Saure, 1990; Ruiz et al., 1986; Jones, 1980; Lüdders and Bünemann, 1969; Faust, 1965b; Kaether, 1965; Weeks et al., 1958; Beattie, 1954; Magness et al., 1940; Magness, 1928b; (Johnson and Johnson, p.289; Link p.286; Sharples, p.339 all in "Mineral Nutrition of Fruit Trees" by Atkinson, Jackson, Sharpies and Waller)).

Potassium:

- Potassium (K) fertilization appears to enhance anthocyanin accumulation and red coloration of apples.
- Potassium may be able to compensate for some of the negative effects of higher N on apple coloration.
- In other experiments, researchers suggest that high K may not significantly enhance coloration in itself, but rather it enhances the positive effects of low N and compensates for the negative effects of high N.
- K may enhance anthocyanin accumulation in apples of K-deficient trees by simply promoting normal fruit development.
- Using K to enhance anthocyanin accumulation of apples has to be weighed against possible increases in the incidence of bitter pit. One researcher found that increased bitter pit negated any benefits from increased apple coloration.

(Work of Bill Wolk in Canada cited by Guy Witney in “Fruit Grower,” May 1997; Saure 1990; Lüdders and Bünemann, 1974; Walter, 1967; Kaether, 1965; Bünemann, 1960; Weeks et al., 1958)

Boron:
Anthocyanin accumulation appears to be relatively insensitive to high boron concentration within the fruit.

(Peryea and Drake, 1991).

Phosphorous, Calcium and Other Nutrients:
Research on the effects of other nutrients are inconsistent and clear relationships cannot yet be established.

(Saure, 1990).

Soil pH:
Within soil pH values between 4.1 and 6.9, higher soil pHs were associated with increased fruit size and redder coloration of 'Red Delicious' apples.

(Raese, 1995).

Water Status:
There are conflicting reports concerning a direct effect of soil moisture on anthocyanin accumulation m apples. Water may promote coloration especially in dry areas or dry seasons when plants are under water stress. However, excess water may inhibit coloration.

(Saure, 1990; Walter, 1967).

Wounding:
Wounding stimulates anthocyanin production in the skin.

(Chalmers and Faragher, 1977a).

PHYSIOLOGICAL FACTORS

Cultivars:

- The effectiveness of light, temperature, and all other factors at inducing anthocyanin accumulation varies with cultivar.
- Each of the steps in the anthocyanin biochemical pathway is genetically "programmed" in each cultivar to respond differently to different conditions.

(Dussi et al., 1995; Saure, 1990; Arakawa, 1988b; Arakawa et al., 1986; Proctor 1974; Naumann, 1964)

Developmental Factors;

- Although environmental factors are critical for anthocyanin production at a particular stage of development, the capacity to produce anthocyanin is genetically controlled by the stage of development. Thus, the effectiveness of light, temperature, etc. at promoting anthocyanin accumulation will change as the fruit develops.
- There are generally two stages of fruit development characterized by large peaks in anthocyanin accumulation: 1) early in development during the phase of intense cell division, and 2) late m development around the time of fruit ripening.

- The fact that these peaks in anthocyanin accumulation occur under a wide range of environmental conditions demonstrates the overriding control that endogenous developmental "programs" have on anthocyanin accumulation.
- Even cultivars which typically do not color well, e.g., 'Golden Delicious' and 'Mutsu,' can have intense coloration during early fruit development.
- During the ripening of 'Cox's Orange Pippin' apples, anthocyanin and carotenoids increase while chlorophyll decrease.
- For some 'Delicious' strains of apples, a 10-day delay in harvest may increase color after long-term controlled atmosphere (CA) storage. However, such a benefit was not observed for 'Oregon Spur' apples.
- The age of the tree can also effect apple coloration. Older trees have more developed canopies which can shade the fruit.

(Drake and Eisele, 1994; Lancaster, 1992; Saure, 1990; Hunter and Proctor, 1986; Faragher and Brohier, 1984; Faragher, 1983; Diener and Naumann, 1981; Chalmers and Faragher, 1977a; Gorski and Creasey, 1977; Chalmers et al., 1973; Knee, 1972; Naumann, 1964; Bömeke 1959a; Arthur, 1932; Fletcher, 1929)

Attached vs. Detached Fruit:

- Care needs to be taken when relating research conducted using detached apples to attached apples because they often respond to treatments differently.
- Harvested apples often begin to blush much more rapidly when exposed to light than fruit still attached to the tree.
- Exposing immature apples to sunlight induces coloration in detached fruit but not in attached fruit.
- Higher temperatures inhibit anthocyanin accumulation more in attached 'Mclntosh' apples than in detached ones.
- The enhanced coloration of detached fruit is possibly a result of accelerated ripening.

(Saure, 1990; Watanabe and Arakawa, 1983; Uota, 1952; Hoffman, 1937)

Roots:

- Dwarfing and semi-dwarfing rootstocks and possibly growth-reducing interstocks tend to increase anthocyanin accumulation in apple fruit because of less canopy shading.
- Rootstocks may also have a more direct effect on coloration; fruit grown on dwarfing rootstocks colored better than fruit grown on vigorous rootstocks even when they were exposed to the same amount of light.

(Saure, 1990; Drake et al., 1988; Proctor, et al., 1975; Walter, 1967; Jackson, 1967)

Leaves:

- The number of leaves per fruit appears to enhance anthocyanin accumulation up to a point.
- This may be a result of more photosynthate being available per fruit and thus more sugar available for anthocyanin production.
- Researchers found that 'Jonagold' apples colored better as the number of leaves were increased up to 45 leaves per fruit.
- 'Delicious' apples have progressively better fruit color development as the number of leaves increases to 75 or more per fruit.

(Saure, 1990; Wertheim, 1987; Heinecke, 1966; Fletcher, 1929; Magness, 1928)

Planting Density and Training System:

Not much research has been conducted relating these factors to color development. The effects may primarily be a result of enhancing or diminishing light penetration into the canopy.

(Wertheim, et al., 1986)

Pruning:

- Shoot pruning can cause a number of different responses in anthocyanin accumulation. Coloration may be enhanced because of better light penetration, or reduced because of stimulated shoot growth and shading of the fruit.
- Root pruning can increase anthocyanin accumulation but may also reduce total yield.

(Saure, 1990; Schupp and Ferree, 1988; Schumacher et al.; 1986; Saure, 1981; Brunner and Droba, 1980)

Thinning:

Fruit thinning can increase apple coloration possibly by increasing the relative number of leaves per fruit. However, the degree of thinning required for optimum color development is not well established.

(Saure, 1990)

METHODS USED TO INCREASE APPLE COLOR DEVELOPMENT

Chemical Applications:

- Warmer nights prior to application may enhance the effectiveness of color-promoting chemicals.
- Thiocyanate sprays can enhance apple coloration but have been shown to damage the foliage and can give inconsistent results.
- Alar (daminozide or SADH) treatments retard growth and promotes anthocyanin biosynthesis. However, Alar can produce inconsistent results and is no longer used commercially in the U.S. because of public health concerns.
- CPPU (N-(2-chloro-4-pyridyl)-N'-phenylurea; also known as fenclopyr, KT-30, 4-PU, and CN-11-3183) was found to enhance color of spur 'Delicious' apples.

- Paclobutrazol (PP333, Cultar) is a growth retardant which appears to have inconsistent effects on anthocyanin accumulation.
- Ethephon (CEPA) is a compound that slowly releases ethylene which in turn can stimulate anthocyanin accumulation in apples. Ethylene accelerates the ripening process. Researchers have been looking for ways to eliminate ethephon's effect on hastening ripening by also spraying growth retardants (like daminozide) or by using compounds which release ethylene more quickly and thus shorten the time that fruit are exposed to the ethylene. Another way ethylene may stimulate anthocyanin accumulation is by stimulating PAL activity in the apple skin. Treatments with ethylene may increase abscission and early fruit drop.

(Curry and Greene, 1993; Saure, 1990; Drake et al., 1989; Murphey and Dilley, 1988; Westerlaken and Scholtens, 1987; Tymoszuk and Mika, 1986; Lever, 1986; Graf, 1986a; Graf, 1986b; Schumacher et al., 1986; Arakawa et al., 1985; Lee and Kim, 1985; Faragher and Brohier, 1984; Williams, 1984; Castro et al., 1984a, b; Jones, 1979; Chalmers and Faragher, 1977b; Grauslund, 1976; Blanpied et al., 1975; Jenkins et al., 1973; Looney, 1971; Edgerton et al., 1967; Smock, 1966; Edgerton and Hoffman, 1966; Edgerton and Hoffman, 1965; Bömeke, 1959b; Dustman and Duncan, 1940)

Evaporative Cooling:

Evaporative cooling of apples by overhead sprinkling can enhance anthocyanin accumulation by reducing the negative effects of hot day temperatures. However, evaporative cooling requires large amounts of water, can promote fungal disease, and can leave deposits on the fruit if the water quality is poor.

(Warner, 1991; Saure, 1990; Unrath, 1975; Anderson et al., 1973)

Baggings:

- Apple bags generally have two layers: an outer layer that eliminates practically all light and a red or blue waxed liner.
- Preventing light from reaching the fruit inhibits chlorophyll production and gives the fruit an ivory color instead of a green one.
- The choice of a specific color for the inner liner is arbitrary because research has not shown that one color works better than the other at enhancing anthocyanin production.
- After removal of the bags, apples show enhanced anthocyanin production.
- After removing the apple bags, some anthocyanin production can even be stimulated in some non-red cultivars.

(Kikuchi et al., 1997; Saure, 1990; Kikuchi, 1964)

Artificial Lighting:

Artificial lighting can induce anthocyanin accumulation in both attached and harvested apples.

(Saks et al., 1990; Saure, 1990; Hoffman, 1937)

Reflective Material:

Reflective material placed between the rows of apple trees can reflect sunlight up into the canopy and thus increase apple coloration.

(Andris and Crisosto, 1996)

POSSIBLE AREAS FOR FUTURE RESEARCH

- By default, areas listed above which have little or conflicting results are good candidates for future research.
- More research should be conducted investigating the use of reflective materials. The little research we found in this area looks promising.
- We did not find any research investigating specifically the effects of organic fanning practices on the color development of apples. Some effects of organic farming on apple color development can be inferred from the above information (e.g., light penetration, nitrogen content, etc.). Future work should focus on how organic growing practices affect soil fertility, tree growth and microclimate (light, temperature, etc.).
- More basic research is needed to understand how each of the steps in anthocyanin production is regulated. There are many physiological steps leading to the production of anthocyanins, each with its own unique response to different environmental factors. For example, the activity of the enzyme PAL has its own important contribution to anthocyanin biosynthesis and is affected by different environmental and developmental factors. Although much has been learned about the process of anthocyanin production, there is much that is still unknown. For example, the key regulating enzyme(s) between cinnamic acid and the formation of anthocyanin is not well understood. Thus, if we better understand how all of the steps leading to anthocyanin production respond to different environmental and developmental/genetic factors, we can better predict how a given set of environmental factors will affect color development and how the process can be optimized. Using this information, breeding and molecular techniques may also be used to enhance anthocyanin development of future cultivars.
- Since the anthocyanin content in apples is a function of the rate of its production and destruction, then understanding and controlling the rate of anthocyanin breakdown could greatly increase the net anthocyanin content. There is very little known about the breakdown of anthocyanins and research in this area could provide some effective tools to manage color development.

REFERENCES:

Due to length, the complete list of references is in its own document: http://postharvest.tfrec.wsu.edu/REP2007A-ref.pdf

Anthocyanin Biosynthetic Pathway

Figure 1