Grape Anatomy and Physiology

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Contents

Abstract Grapes are vines that are cultivated in temperate climates around the world. There are an estimated 8000 grape varieties grown for consumption. The latest data showed table grape production of about 20 million tons. Vine growth and floral initiation result in the berry formation of the subsequent year. The growth and maturation of the grape berry and/or seeds affect changes in sugars, acids, and phenolic compounds. Pests and diseases are numerous as are the continuous searches for better chemical control. Natural resistance such as the grape plants'

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ability to escape infection through anatomical attributes and the production of phytoalexins such as resveratrol also play important roles in control of diseases. Grapes are a multiuse crop with nutritional and pharmaceutical applications.

1 Introduction

Grapes (Winkler et al. 1974; Creasy and Creasy 2009) are fleshy fruits produced from a single flower, containing one ovary (the definition of a berry), and produced by a woody vine in the genus *Vitis*. Grape berries are produced in clusters of varying numbers of individual berries. Grapes are usually found in temperate climates. *Vitis vinifera* is the major commercial species native to the Middle East but has been introduced all around the world. However, the largest number of species is found in North America (Weaver 1976). *Vitis labrusca* is one North American species; the varieties Concord and Niagara are mainly used to make grape juice. Other North American species, e.g., *V. riparia* and *V. rupestris*, have been crossed with each other and with *V. vinifera* and used as wine, table grapes, or as rootstocks to protect vinifera varieties from phylloxera, a root insect that almost destroyed the European grape industry in the nineteenth century. *Vitis rotundifolia* is a species native to the Southeastern USA. Varieties have been selected for juice and wine production.

2 Uses

Grapes can be eaten raw; canned; used to make wine, jam, juice, raisins, grape seed oil, and sugar for food additives (in foods or juices usually called "all natural" or "no sugar added"); extracted for pigments and fermented/distilled into grape neutral spirits; and sometimes utilized to make fortified wines.

3 Varieties

There are estimates of 8000 grape varieties differing in size, color, shape, flavor, and disease and insect resistance (Winkler et al. 1974). Europe is the region with the largest production of grapes, but China produces the greatest amount followed by Italy, the USA, Spain, and France (www.FAO.STAT3). The classic wine varieties are Cabernet Sauvignon, Chardonnay, Chenin blanc, Merlot, Pinot noir, Riesling, Sauvignon blanc, Semillon, and Syrah.

Major table grape varieties are Sultana (Thompson Seedless), Flame, Muscat, Almeria, and Emperor. World table grape production is about 20 million tons; China is the largest producer at 9 million tons; Turkey is second with almost 2 million tons. The USA produces about 1 million tons (USDA 2015).

4 Seedless Grapes

The modern table grape consumer prefers seedless grapes although some seeded cultivars remain popular, e.g., Red Globe. Black Corinth is the only truly seedless grape (a parthenocarpic fruit that grows without fertilization of the flower). It is occasionally sold as a table grape and has very small berries (frequently called the Champagne grape). The commercially available dried currant is actually a dried Black Corinth grape berry. Other "seedless" grapes abort their embryos soon after fertilization (Pratt 1971). The aborted seeds are called seed remnants and the size and hardness of the remnant are a quality factor in table grapes.

Most raisins are made from the Thompson Seedless variety. California and Turkey are the major raisin producers (www.FAS.USDA.gov/data/raisins-world-markets-and-trade, accessed on 25 Oct 2015).

5 Berry Anatomy

A berry consists of skin, flesh, and seeds or seed remnants. The skin is composed of the epidermis plus variety-dependent layers of thick-walled cells called the hypodermis. Grape epidermis contains fewer stomata than do leaves and therefore berry temperature is poorly regulated. The hypodermis contains most of the skin phenolic compounds. The flesh (mesocarp) is composed of large cells with large vacuoles. The seeds number 0–4 per berry and are made up of a seed coat, endosperm, and embryo. Seedless berries have a seed remnant, resulting from the abortion of the embryo early in the growing season.

6 Chemical Composition

Grape components are easily divided into two groups. Primary components are those associated with basic life processes, those common to all plants. These include water, proteins, amino acids, nucleic acids, cellulose, and many others. Of course the largest component of grapes is water, 75–85 % of their weight. Secondary components have roles in enhancing life processes or protecting the plant from damage. Presumably the biosynthetic pathways to produce these chemicals were mutations of primary metabolism. Some enabled plants to live upright out of water or to withstand dry conditions, avoid damage from light or UV radiation, and ward off attack by grazing animals, insects, or diseases. A mutation may have resulted in a survival advantage perpetuated in the genetics of the plant. There are so many secondary components that we might assume that not all of the challenges that resulted in a survival mechanism still exist. All plants are resistant to most microorganisms (probably billions) and disease is the exception. Grapes contain thousands of compounds that are classified as secondary components (Pezzuto 2008), and there are probably thousands more as yet unidentified.

7 Grape Berry Chemistry

7.1 Sugars

Grapes contain the highest concentration of sugars of any fresh fruit, 15–25 % of their weight. Accumulation of glucose and fructose in the vacuoles of berry flesh mesocarp cells occurs after veraison (start of ripening). Twenty days after the start of veraison, the hexose content of the berry is close to 1 M, with a glucose/fructose ratio of 1. Sucrose produced through photosynthesis in leaves is the main carbohydrate used for long-distance transport (Swanson and El-Shishiny 1958). Sucrose is loaded into the phloem by either a symplastic (via plasmodesmata) or apoplastic mechanism (Boss and Davies 2001). Because sucrose is the major translocated sugar in grapevine, the rapid accumulation of hexoses during berry ripening must involve the activity of invertases (Fillion et al. 1999). Invertases catalyze the hydrolysis of sucrose transported by the phloem into glucose and fructose. Hydrolysis of sucrose by cell wall invertase may promote unloading by preventing its retrieval by the phloem and by maintaining the sucrose concentration gradient. Both expression and activity of cell wall invertase increase around the onset of ripening and reach a high level in the late stage (Zhang et al. 2006).

7.2 Organic Acids

Rapid changes in the acid/sugar balance occur at the onset of berry ripening (veraison). Tartaric and malic acids generally account for 69–92 % of all organic acids in grape berries and leaves (Kliewer 1966). Minor amounts of citric, succinic, lactic, and acetic acids are also present in ripe grapes. The decrease of total organic acid content that begins at the onset of ripening is associated with a sudden induction of malate oxidation.

7.3 Simple Phenolics

Volatile phenolics, such as benzaldehyde, phenylacetaldehyde, benzyl alcohol, 2-phenylethanol, and vanillin, are found mainly in berry skin and are responsible for the primary aromas that develop during ripening (García et al. 2003). Benzoic acids with a simple C6–C structure (benzoic protocatechuic and gallic acid) are found in grapes, but they are present at low concentrations (Kennedy et al. 2006).

7.4 Phenylpropanoids

Cinnamic acids (C6–C3) are products of the phenylpropanoid synthesis pathway. Cinnamic acid is produced from phenylalanine by the enzyme phenylalanine ammonia lyase. This is the entry point into phenolic and lignin biosynthesis.

The hydroxycinnamates coutaric acid and caftaric acid are the third most abundant class of soluble phenolics in grape berries, after tannins and anthocyanins. They are present in hypodermal cells along with tannins and anthocyanins and in the mesocarp and placental cells of the pulp. On a per berry basis, total hydroxycinnamates in mesocarp tissues peak prior to veraison and then decline, leading to a constant amount (per berry) as the fruit ripens. Genetics is apparently more important than exposure or climate (Clifford 2000). Singleton et al. (1986) showed that the level of hydroxycinnamates in the juice of different vinifera varieties is highly variable, ranging from 16 to 430 mg/L.

Several reviews summarize the advances on the understanding of phenolic structures and diversity and enlighten the synthesis and distribution of these compounds in grape berry tissue types (Kennedy et al. 2006; Adams 2006).

7.5 Flavonoids

Flavonoids (C3–C6–C3) are formed by the condensation of 4-hydroxycinnamoyl-CoA with 3 malonyl-CoAs controlled by the enzyme chalcone synthase (Fig. 1) (Rupprich and Kindl 1978).

The berry skin contains tannins and pigments, the pulp contains juice but usually no pigments, and the seeds contain tannins (Fig. 2). From a biological perspective, the insoluble cutin of the epidermis and the insoluble lignin of the hard seed coat are phenolics, which are as important as the skin tannins and pigments and seed tannins.

Flavonoids make up a significant portion of the phenolic material in grapes and include several classes, such as proanthocyanidins (tannins), anthocyanins, flavan-3-ol monomers, and flavonols. Flavonols and anthocyanins occur as glycosides in grape skins. Tannins or proanthocyanidins are polymers of flavan-3-ols and are the most abundant class of soluble polyphenolics in grape berries. Tannins confer astringency to fruits and are found in the hypodermal layers of the skin and the soft parenchyma of the seed between the cuticle and the hard seed coat. They are a

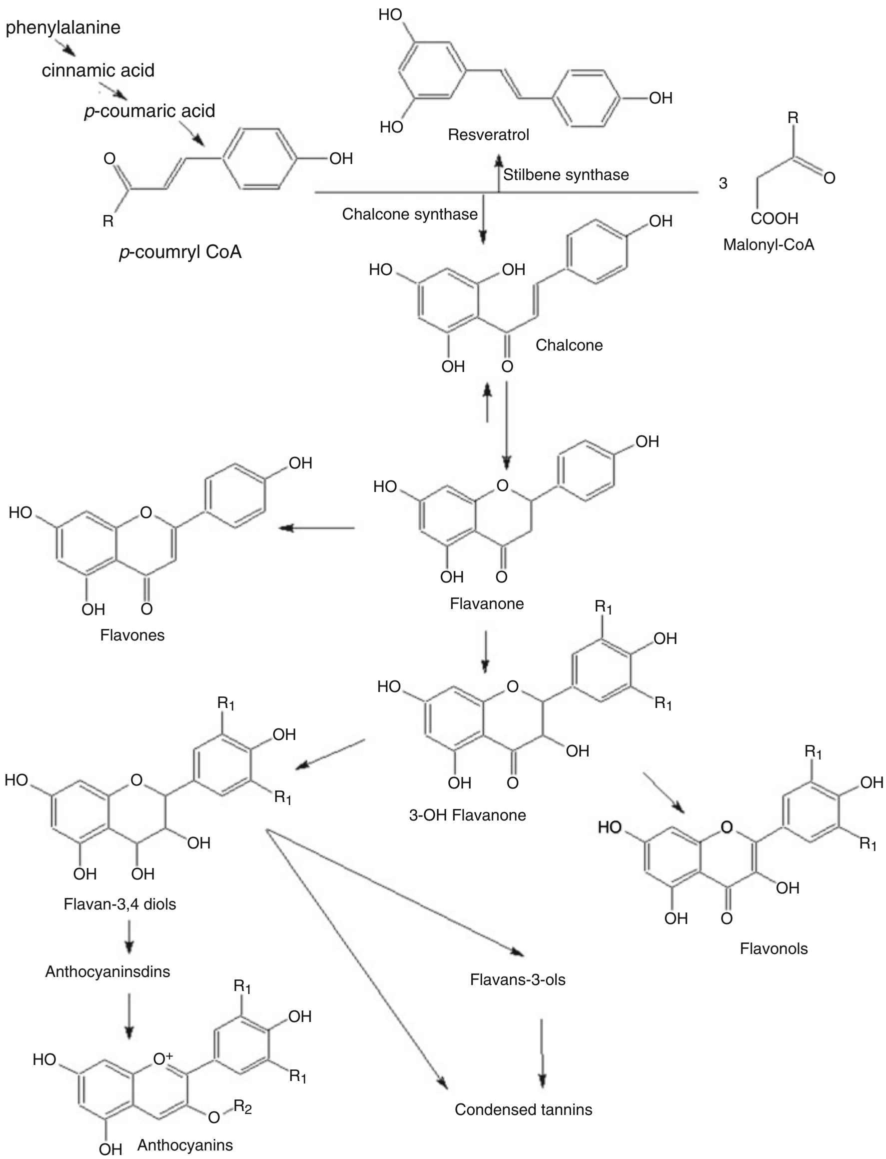


Fig. 1 Biosynthesis of grape resveratrol and flavonoids

very diverse set of biomolecules varying in size from dimers and trimers up to oligomers with more than 30 subunits (Kennedy et al. 2006; Adams 2006).

Table 1 shows the content of major phenolics in seeded and seedless grape berry skins, flesh, and seeds or seed remnants. Skin resveratrol is not constant in grapes so the values are transitory. In seeds and remnants, resveratrol is possibly correlated

Fig. 2 Mature grape berry

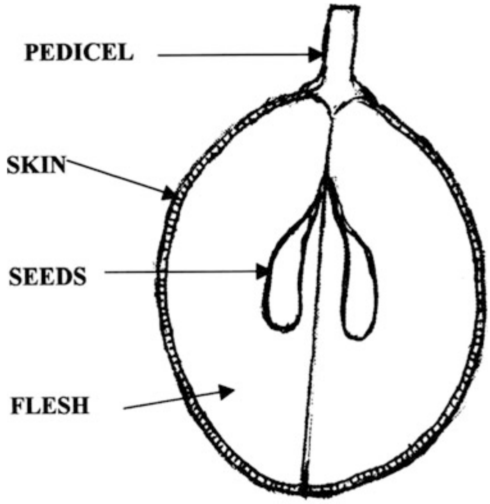


Table 1 Phenolic components of grape berries

	% of berry weight	Resveratrol (μmol/kg)	Flavans (μmol/g)	Total phenol (mg/g)
Globe = 9.5 g/bry				
Skin	7.6	0.16	22	1.6
Seeds	1.4	3.4	238	8.4
Flesh	90.9	0	0	0.2
Flame = 5.0 g/bry				
Skin	15.9	1.25	19	1.6
Remnants	5.2	0.79	11	1.2
Flesh	78.8	0	0	1.1

Resveratrol analyzed by HPLC, flavans by vanillin reaction, and total phenols by Folin reaction

with the degree of woodiness of the seed coat like the constitutive concentration in grape wood. No resveratrol was found in the grape flesh samples. Flavans are principally flavan-3-ols (catechins) and flavan-3,4-diols (leucoanthocyanidins). They are major components of seeds and not in remnants. The total phenols are largely hydroxycinnamic acids plus flavans and occur in all three parts of the berry including seed remnants. Remnants are chemically not seeds but not flesh either.

Grape anthocyanins and flavonols are found mainly in the skin as assorted glycosides; major ones are shown in Fig. 3. Many others occur in small amounts.

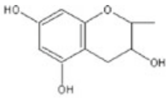
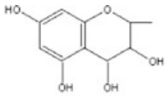
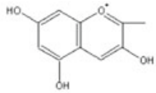
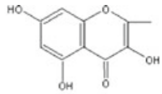
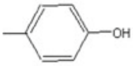
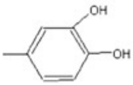
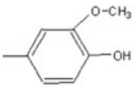
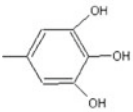
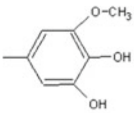
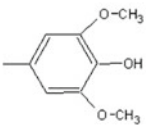
A ring and heterocyclic ring > B ring ∨	 Flavan-3-ols	 Flavan-3,4-diols	 Anthocyanins	 Flavonols
				Kaempferol-3-glucoside
	Catechin, Epicatechin	Leucocyanidin (as dimers and polymers terminated with a catechin)	Cyanidin-3-glucoside	Quercetin –3-glucoside
			Peonidin-3-glucoside	Isorhamnetin –3-glucoside
	Gallocatechin, Epigallocatechin		Delphinidin-3-glucoside	Myricetin-3-glucoside
			Petunidin-3-glucoside	
			Malvidin-3-glucoside	

Fig. 3 Names of major grape flavonoids

8 Flower Formation

Grape flowers are formed the year before bloom in the axils of leaves. By winter, the buds contain all of next year's flower parts in the axils of next year's shoots. Cool weather and hormonal restrictions assure that the buds will remain dormant until the next growing season. Growth begins with favorable weather and the enlarging shoots produce clusters of flowers. The flowers are self-fertile and not showy. The fruit starts growth immediately after fertilization (Pratt 1971).

9 Berry Growth

Berry growth follows a double sigmoid curve. Following flower fertilization, there is a stage of rapid cell division and the increase in berry size is largely due to an increase in cell number. This is followed by a period of slow berry growth and finally a third stage initiating rapid berry growth due to cell enlargement accompanied by ripening (veraison) (Pratt 1971).

10 Phytoalexins

Most grape component concentrations are controlled by variety, growth stage, or weather with modest variation provided by light exposure (Price et al. 1995) or cultural practices.

The major exception is the phytoalexin resveratrol. By definition, a phytoalexin is a small-molecular-weight antimicrobial substance not normally accumulated by a plant but induced by an interaction with a microorganism. Resveratrol is a phytoalexin of grape leaves (Langcake and Pryce 1976) and berries (Creasy and Coffee 1988). Resveratrol is also a major component of grape woody tissues (700 μg/g, about 3000 μmol/kg) where it may function to suppress disease as a constitutive component (Langcake and Pryce 1976).

11 Grape Disease Resistance

There are numerous and inevitable challenges in the production of a marketable product in large-scale cultivation of grapes. Even in an established vineyard with proven crop yield potential, control of pests is an ongoing process. Since the 1800s, grape diseases have historically resulted in economical losses for the industry (Pearson and Goheen 1988). The control measures used were toxic compounds such as copper, lime, and sulfur which also served as protectants and by changing cultivars to ones with natural resistance. Since that time, attention has focused to understanding of the etiology of the disease organism and the mechanisms of the plants' own defenses.

Studying the biology of the disease organisms, notably fungi, resulted in improved cultural practices for the plants (Pearson and Goheen 1988). Grapes, being vines, are amenable to manipulations for regulating size and shape. Training systems include the ornamental arbors to the refined systems to accommodate production requirements. Support structures such as posts and wires can train the vines to maximize sun exposure, allow air circulation within the canopy, and facilitate mechanization of cultural and harvesting procedures. Grafting to a disease-resistant rootstock is common practice to avoid injury and infection or to promote growth and fruiting. Understanding the growth, development, and reproductive parameters of the pathogens facilitated the development of a multitude of fungicides that meet the Environmental Protection Agency (EPA) registry parameters. Low mammalian toxicity, environmental friendliness, and target organism specificity have gained importance in the consideration of new pesticide introduction. Except for physical protectants such as clay coating of the plant tissue, chemical control has faced increasing challenges. Over the past decade, more weed, insect, and microorganisms have developed resistance to pesticides, thus limiting the application of existing pesticides, resulting in a vigorous and continuous search for new chemistries and formulations for control. Recommendations for pesticide applications change rapidly as the race of chemical control against the pest's abilities to escape injury surges on.

11.1 Pests and Diseases of Grapes

The development of pest-resistant cultivars through plant improvement and enhancing the plant's own defense mechanisms became more relevant and critical as a solution to disease suppression or avoidance. There are many economically significant pests in grape culture such as the root aphid phylloxera, sharpshooter aphids transmitting Pierce's disease, mealybugs transmitting leaf roll virus, and the bacterium *Agrobacterium tumefaciens* producing crown gall, but fungal pathogens receive more attention due to the availability of chemical control. Rating of commercial grape cultivars for their resistance to various fungal diseases (Weigle and Muza 2015) can be one of the tools in helping the grower with planting choices.

Several fungi causing diseases in grape production are economically significant, especially in humid climates. Of those, two pathogens require special attention since they affect berry development and can possibly result in total crop failure, thus requiring stringent vigilance and control throughout the production cycle. Managing air circulation within the canopy through training systems and removing leaves to allow sun exposure are some of the cultural means to combat the infections.

Powdery mildew is caused by the fungus *Uncinula necator*. The fungus attacks green, living tissue and establishes on the epidermis of the plant. The white spores give the affected tissue a powdery appearance. The spores are disseminated by rain, wind, or mechanical means. Severe infections reduce photosynthesis and debilitate the plant and its subsequent ability to produce fruit. When fruit is infected, it is discolored and distorted and has a bitter taste, which is not desirable for processing or the fresh market. Botrytis bunch rot, caused by the organism *Botrytis cinerea*, is a major disease of grape berries before and after harvest. This organism attacks many plant species and is present in living as well as dead tissue. The conidia (spores) can be disseminated by wind, water, as well as mechanical means, and the plant tissue attacking hyphae can grow under humid conditions in a wide range of temperatures.

The morphology of the epidermal tissue of the leaves and berries is the first line of defense against hyphal intrusion. The epicuticular waxy layer and/or the presence of trichomes can prevent the accumulation of water and the adhesion of the conidia, rendering the conditions not conducive for fungal growth. However, breaks in the epidermis of the plant will allow the establishment of the spores and result in hyphal penetration of the skin. Fungal colonization of the berries liquefies the cells and renders the fruit useless for processing or for the fresh market, and postharvest fungicidal treatment for fresh market grapes has regulatory mandates. The resiliency of the berry skin against cracking and the amount of room on the rachis to allow for berry expansion can prevent cracks in the berry skin. Therefore, berry anatomy and cluster architecture are also characteristics to consider in disease resistance. Control of animal and insect feeding is essential for preventing damage to the berries. New production health standards such as Good Agricultural Practices (GAPs) certification regulate human and animal contact to produce sold for human consumption. Postharvest handling practices have strived to minimize physical injury to the skins and prevent infection during storage and transit.

11.2 Resveratrol

Antifungal compounds, notably phytoalexins, are produced by the grape plants to counteract the establishment of fungal colonies on and inside the plant tissues (Langcake and Pryce 1976).

Resveratrol, a stilbene, was reported in medicinal plants as early as the 1930s (Takaoka 1940). In the compendium of traditional Chinese herbs and their uses *A Barefoot Doctor's Manual* (The Revolutionary Health Committee of Hunan Province 1977), poultices of the leaves and roots of *Polygonum cuspidatum* were used to treat inflammation and to improve blood flow. Later studies of this plant showed it to be a rich source of resveratrol. Biochemists in Japan and Korea isolated and studied the structure of resveratrol and its mode of action (Kimura et al. 1983). Resveratrol in wood was extensively studied by Hillis and his group (Hart and Hillis 1974) as benefiting the lumber industry. Until the onset of DNA fingerprinting, stilbenes, including resveratrol, were used for chemotaxonomy of plant species and cultivars (Hathaway 1962).

In 1976, Langcake and Pryce (1976) found a major antifungal component of grape woody tissue and described it to be a phytoalexin in leaves, the structure of which is identical to the resveratrol studied in the 1930s by Takaoka (1940). Resveratrol was utilized in leaves as a marker for identifying resistance potential of grape cultivars.

Resveratrol was found to be rapidly produced in berry skins by Creasy and Coffee (1988). This discovery was not only important in the postharvest quality of the fruit but also resulted in a new look at disease resistance of detached fruit tissue. In 1992, this study of resveratrol in berries led to the discovery of berry skin resveratrol in wines (Siemann and Creasy 1992) and links to the medicinal results of Asian studies (Arichi et al. 1982). This was eventually followed by biological investigations (Jang et al. 1997) resulting in a cascade of research efforts and a supercharged wine industry and made resveratrol a household name (Better Homes and Gardens 1992).

Interest in the presence of resveratrol in all fruits flourished. Value-added grape products, raisins, and grape juices were also analyzed (Creasy and Creasy 1998). Although resveratrol was found to be unstable in light (*cis–trans*), it is resistant to heat evidenced by its presence in heat-processed grape products. Raisin analysis revealed the affect of drying method on resveratrol content; sunlight isomerization is a factor. Extensive analysis of the production of Concord grape juice showed that resveratrol content was unchanged after heat extraction of the berries (Creasy, unpublished). Grape seed extracts have been used for human consumption and pomace from the pressing of wine grapes as animal feeds. Analyses of these products reflect that the original content of resveratrol and the handling and processing procedures affect the concentration of resveratrol in the products.

Field studies of resveratrol production showed that this phytoalexin can be induced in berries by fungal attack as well as by fungicide sprays.

Resveratrol synthesis does not continue after the disease event. Excess resveratrol is subject to turn over, thus protecting the cell from toxic concentrations (Langcake and Pryce 1976).

Other defense mechanisms by plant tissues exist, but none sparked the interest or has been as studied as completely as resveratrol (Park and Pezzuto 2015).

11.3 Transgenic Crops

New studies in genomics may assist in the revelation of the mechanisms of the plant cell vs. diseases interactions. Insertion of the patented gene for resveratrol synthesis into non-grape plant cultivars has already taken place (Hain et al. 1992). Genetically modified field crops have changed the productivity and profitability for the commodities crop as well as the pharmaceutical/pesticide industry. Incidents of resistance of weeds and insects to pesticides have become more prevalent, resulting in the need for new cultural and chemical strategies for production. However, fruit and vegetables will face more stringent government scrutiny and consumer resistance. In the USA thus far, only sweet corn and squash have received approval and are sold commercially. Transgenic tomatoes and potatoes made only a fleeting appearance on the market (Dias and Ortiz 2012). The endgame between genetically modified organism (GMO) labeling and successful promotion for consumer acceptance of transgenic produce may not be in the near horizon as evidenced by the upsurge of consumer products touting no GMOs. Growers of perennial crops such as grapes with several years of lag time between planting and harvesting of a marketable crop may need to wait to invest until the game plays out.

One characteristic of phytoalexins is that they are synthesized very rapidly following interaction with microorganisms only at the site of stimulation (Dercks

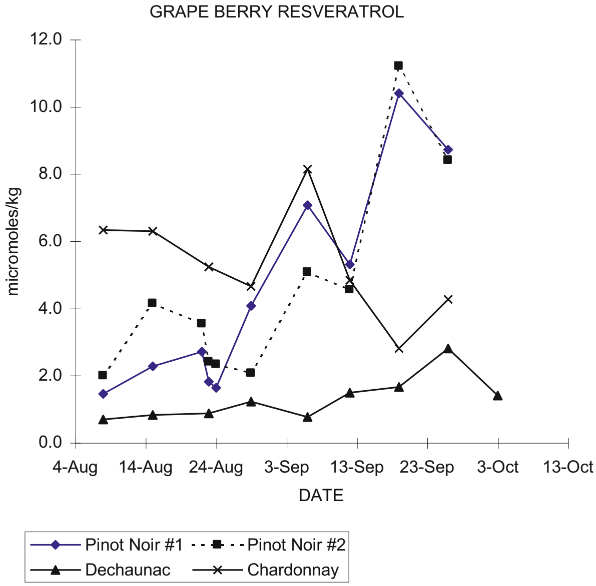


Fig. 4 Whole berry resveratrol content in the vineyard

and Creasy 1989). Resveratrol is toxic to grape cells at the localized concentration and breaks down rapidly. Therefore, the amount of resveratrol in a grape berry at any time is ephemeral. Grape analyses through a season in the vineyard show peaks of production but nothing constant (Fig. 4).

The time of harvest is the major factor in harvested grape resveratrol concentration. Since there is a reasonably frequent challenge of berries by microorganisms, there are always some berries with appreciable concentrations.

12 Stimulation of Resveratrol Production in Berries

There have been attempts to stimulate resveratrol production in berries. Stimulation must occur close to harvest. UV irradiation is the most common since it induces many cells at a time. Microorganisms or their extracts also work but have practical limitations. Experiments irradiating grapes in the vineyard with UV stimulated resveratrol production but only for a limited number of irradiation cycles (Creasy, unpublished). Pesticides have been applied near harvest with occasional success. The superior oil used for powdery mildew control showed promise although the stimulated concentrations in resveratrol only followed rain events (Fig. 5) (Creasy and Creasy, unpublished). Rain fell Sept. 3–4, Sept. 8–9, Sept. 11–12, Sept. 14–15, and Sept. 21–24. The rain dates correlated with increases in berry resveratrol. Oil sprays are legal in many states up to the day of harvest, but in subsequent years of experiments with no rain, there was no stimulation in resveratrol concentration. We

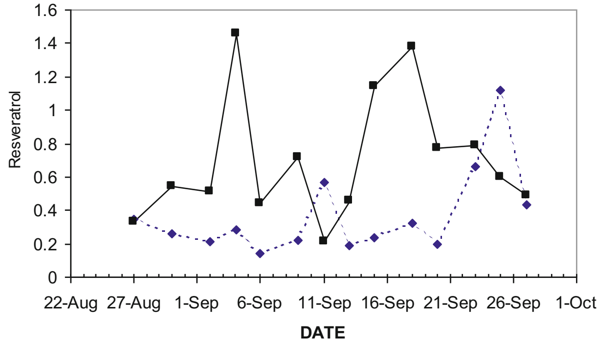


Fig. 5 Berry resveratrol content in the vineyard. *Dotted line* is control (sprayed with water on the 27th of August); *solid line* was sprayed with 1.5 % superior horticultural oil (JMS Stylet Oil) on the same day

did not detect the reported reduction in sugar accumulation due to the oil sprays (Baudoin et al. 2006).

13 Conclusions

Grapes are a multiuse horticultural crop with challenging requirements in disease control. The unique chemical composition of the fruits provides many avenues of potential use in nutritional and pharmaceutical applications.

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