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Grape Berry Growth and Development

NICK K. DOKOOZLIAN
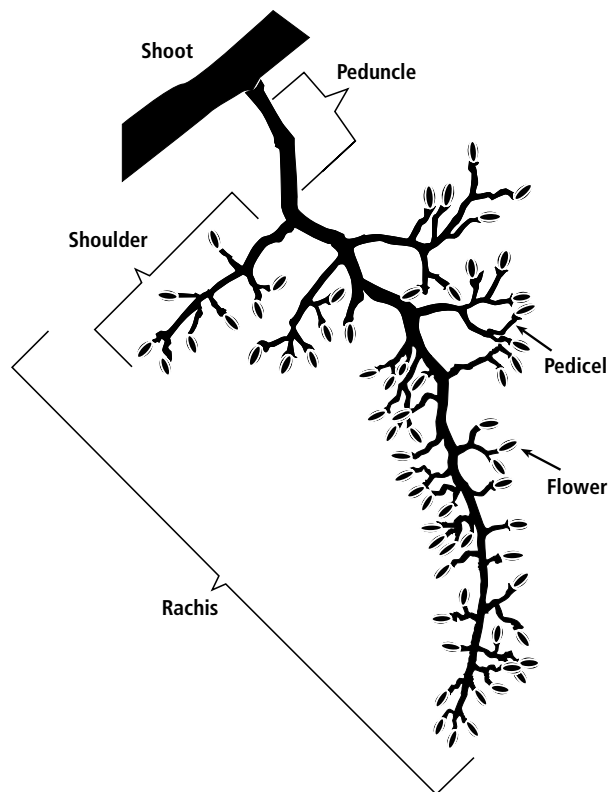

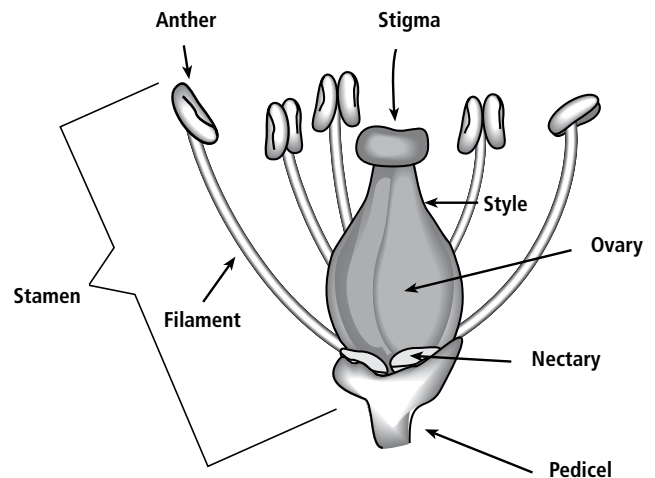**Figure 5.1** A typical 'Thompson Seedless' flower cluster prior to anthesis

Figure 5.2 A hermaphroditic (*perfect*) grape flower

Grape flowers are borne on an inflorescence or flower cluster (Figure 5.1). The main axis of the cluster is the rachis, and the individual flowers are attached to the rachis by the pedicel or capstem. Prominent branches arising from the rachis stem are referred to as shoulders. The peduncle attaches the cluster to the vine, extending from the shoot to the first branch of the rachis. At harvest, the rachis framework typically accounts for 2 to 5 percent of cluster fresh weight.

Nearly all commercially important *Vitis vinifera* grape varieties have hermaphroditic (*perfect*) flowers, containing functional male and female organs (Figure

5.2). Each of the five stamens, the male, pollen-bearing organs of the flower, consists of a pollen-producing anther and a filament or stalk. The female pistil consists of a stigma, a style, and an ovary. The stigma serves as the receiver of pollen. The style is a short, slender column of tissue arising from the ovary to the stigma. The ovary contains four ovules, and each ovule has one embryo sac containing a single egg. Located at the base of the flower are five odor glands commonly referred to as nectaries, although they produce no nectar. In many *Vitis* species these structures secrete odorous compounds that attract insects. In most *Vitis*

vinifera varieties, however, the substances produced by the odor glands seem to attract little attention from insects.

Anthesis

The calyptra (flower cap), which consists of five fused petals, covers and protects the flower organs before the flower opens in the spring (Figure 5.3). Flower opening, commonly referred to as anthesis or bloom, occurs when the calyptra detaches from the flower base and is shed, exposing the stamens and pistil. Anthesis normally occurs 6 to 8 weeks after the commencement of shoot growth, depending upon climatic conditions. In the central San Joaquin Valley, for example, flowers of 'Thompson Seedless' normally begin anthesis in early to mid-May. Anthesis proceeds rapidly when temperatures range between 85° and 95°F (29° and 35°C), with a typical 'Thompson Seedless' vineyard taking 6 to 7 days after the start of flower opening to reach full bloom (100 percent of calyptras detached). Anthesis may last as long as two weeks under cool conditions, and few flowers will open so long as temperatures are below 65°F (18.3°C).

Pollination and Fertilization

Immediately after the flowers open, the anthers split open and release their pollen grains. Some of the pollen grains adhere to substances secreted on the stigma, at the tip of the pistil. The stigmatic secretion consists primarily of sugars, proteins, and mineral nutrients essential for the subsequent development of the pollen tube. Grape varieties with hermaphroditic flowers are considered self-pollinating, and the activity of insects or the presence of wind is believed to be unnecessary for pollination. Pollination is complete once the pollen has reached the stigma. If environmental conditions are favorable, the pollen grains germinate and form pollen tubes (Figure 5.4). The pollen tube is a long, slender structure that grows through the tissues of the stigma and style, ultimately penetrating the ovule. The male gametes (sperm) travel through the pollen tube to the ovary. Fertilization occurs when sperm reaches and impregnates the eggs within the embryo sacs. Under normal field conditions, fertilization typically occurs two to three days after pollination. Temperature is an important factor controlling germination and pollen tube growth. Optimum temperatures for both germination and pollen tube growth range between 80° and 90°F (26.7° and 32.2°C), and both processes are greatly reduced or even inhibited when temperatures fall below 60° or rise above 100°F (below 15.6° or above 37.8°C).
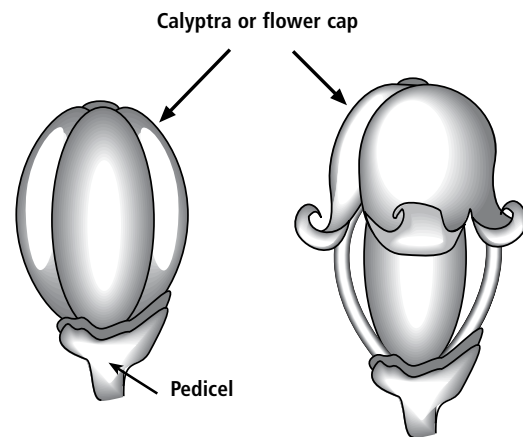

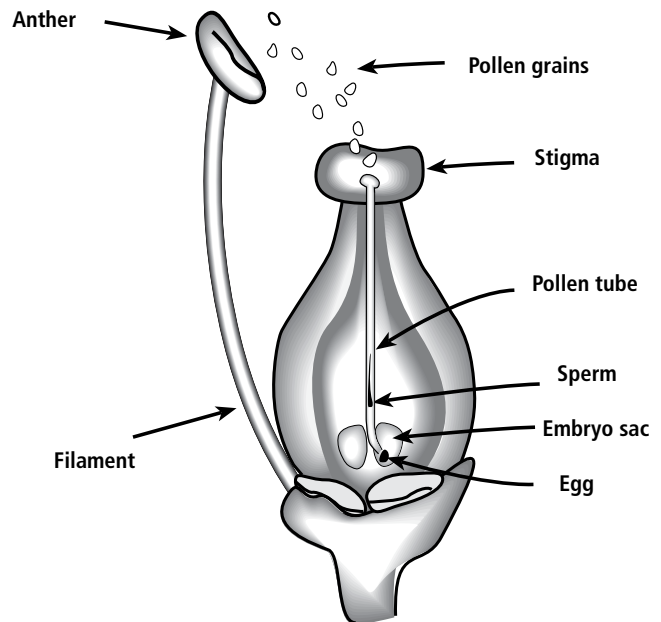**Figure 5.3** A grape flower shedding its *calyptra* (flower cap) during anthesis

Figure 5.4 An idealized view of pollination and fertilization of the grape flower

Fruit Set

In grapes, fruit set is defined as the stage when the berry diameter is between $1/16$ and $1/8$ inch (1.6 and 3.2 mm). In seeded varieties such as 'Muscat of Alexandria,' fruit set occurs after successful pollination and fertilization and the initiation of seed development. Each berry may contain as many as four seeds, though usually fewer.

There are two other fruit set mechanisms, howev-

er, that allow seedless or seemingly seedless berries to form. The first mechanism, *parthenocarpy,* is the only method by which truly seedless berries are produced. With this mechanism, only the stimulus of pollination (the presence of pollen on the stigma) is necessary for berry set. Parthenocarpic berries exhibit no ovule, and so no seed can develop after anthesis. The lack of normal ovule development is the result of defective embryo sac formation. An example of a parthenocarpic variety is 'Black Corinth,' the grape used to produce 'Zante Currant' raisins. The second mechanism, *stenospermo-carpy,* results in the formation of berries that appear to be seedless but are not. In this case, pollination and fertilization occur as normal, but the embryo aborts two to four weeks after fertilization. The ovary wall (pericarp), which is the berry flesh, continues to grow, but seed development ceases. The result is that partially developed seeds or seed traces can be found within the berry. Despite the presence of these seed traces, stenospermocarpic berries are generally considered seedless for commercial purposes. Almost all commercially important seedless raisin grape varieties, including 'Thompson Seedless,' 'Fiesta,' 'Black Monukka,' and 'DOVine,' set their fruit in this way.

The detectability of seed traces varies significantly between stenospermocarpic varieties. For example, 'Thompson Seedless' contains small, soft seed traces that normally go unnoticed in the fresh or dried fruit. In contrast, 'Black Monukka' contains large, hard seed traces that are easily detected in both fresh or dried fruit. Seed trace development can also be variable within varieties; for example, in 'Flame Seedless' they are detectable in some years' crops but not in others. Many factors influence the detectability of seed traces in stenospermocarpic varieties, including the size of the traces, their degree of development, the timing of embryo abortion, and the number of fertilized ovules. Embryo abortion generally occurs during the early stages of fruit growth in varieties with small seed traces, while the process may occur later in varieties with large seed traces. 'Thompson Seedless' berries, for example, developed prominent seed traces during one season when temperatures during bloom and the early stages of fruit growth were significantly below normal. Unusually cool temperatures during the early stages of fruit growth are thought to delay embryo abortion and may increase the number of noticeable seed traces.

Several other factors influence seed trace development, including the vine's rootstock and year. The influence of these factors on seed trace development in 'Fiesta' are presented in Table 5.1. In 1978 in Fowler, 'Fiesta' grafted to 'Harmony' or 'Freedom' rootstock produced fewer but larger (on a dry weight basis) seed traces per berry than did 'Fiesta' grafted to 'Thomp-

Table 5.1   Effect of rootstock and season conditions on seed trace development in 'Fiesta' raisins

Vineyard location	Rootstock	Mean number of seed traces per berry		Mean dry weight per seed trace (mg)	
		1978	1979	1978	1979
Fowler	own	1.67 ab*	1.55 a	1.96 b	4.61 b
	'Thompson'	1.95 b	2.20 a	1.16 a	1.35 a
	'Harmony'	1.32 a	2.00 a	2.90 b	3.08 b
	'Freedom'	1.51 a	1.77 a	2.46 b	3.58 b
Rolinda	own	1.86 bc	1.45 a	2.21 a	2.50 a
	'Thompson'	1.51 a	1.47 a	2.38 a	1.86 a
	'Harmony'	1.57 ab	1.72 a	3.10 b	3.47 b
	'Freedom'	1.98 c	1.79 a	3.04 b	3.68 b

*Numbers followed by the same letter within columns for a single location are not significantly different at the 5 percent level (Duncan's Multiple Range Test).
Source: Christensen et al. 1983. Am. J. Enol. Viticul. 34:257–59.

son Seedless.' That same season in Rolinda, 'Fiesta' on 'Harmony' rootstock produced fewer seed traces than did 'Fiesta' on 'Freedom,' and both rootstocks produced larger seed traces than either 'Fiesta' grafted on 'Thompson Seedless' or own-rooted 'Fiesta' vines. In contrast, rootstocks had no effect on the number of seed traces per berry at either location in 1979, while their effects on seed trace size were similar to those observed in 1978. Vine age may also play a role, as mature vines (older than 8 years) reportedly produce berries with fewer seed traces than young vines.

In most cases, only 20 to 30 percent of the flowers on a cluster develop into berries. For example, a 'Thompson Seedless' cluster may contain as many as 1,000 flowers at bloom, but seldom more than 300 berries at harvest. Most flowers shrivel and fall from the cluster during the initial stages of berry growth. A significant number of flowers drop approximately 8 to 12 days after full bloom, at a stage commonly known as berry shatter. Fruit set is achieved once the berry shatter period is complete.

Climatic factors have a significant effect on fruit set. Due to inhibition of pollen tube growth and ovule fertilization, fruit set is greatly reduced when temperatures fall below 65°F (18.3°C) or exceed 100°F (37.8°C) during set. Cold temperatures are often associated with incomplete detachment of the calyptras, while both cold and hot temperatures may reduce fruit set by preventing the growth of pollen tubes and ovule development. Rainfall or high humidity may reduce fruit set, hindering pollination by impeding the complete detachment of the calyptras. Rain can also dilute the stigmatic fluid and thus interfere with the germination of pollen grains.

GRAPE BERRY GROWTH

Following fruit set, the grape flower ovary develops into a fleshy berry (Figure 5.5). The grape berry is a simple fruit, consisting of two seed cavities (locules) surrounded by a ovary wall (pericarp). In seeded varieties there may be as many as four seeds. In the case of stenospermocarpic varieties, the locules contain seed traces resulting from the abortion of the ovules early in their development. The stylar remnant or scar is present at the berry apex, opposite the pedicel or capstem. The cuticle, a thin wax-coated secretion of lipids, covers the berry surface. The fleshy pericarp consists of an exocarp (skin) 6 to 8 cells wide, and a mesocarp (the pulp) 25 to 30 cells deep. In most seedless varieties, the mesocarp accounts for 85 to 90 percent of the berry's fresh weight. The vascular system of the berry includes dorsal (peripheral), ventral (central), and ovular vascular bundles. The vascular bundles contain the xylem and phloem tissues through which water, sugars, and other substances are supplied to the berry.

Increases in berry weight, volume, or diameter during development are typically characterized by a double-sigmoid curve resulting from two consecutive stages of growth separated by a phase of slow or no growth (Figure 5.6). Grape berries advance through three distinct stages of development during their growth:

Stage I: the first phase of rapid berry growth. A period of rapid berry growth comes immediately after bloom. During this time, berries grow both through cell division and cell enlargement. Berry texture is firm, while its color is green due to the presence of chlorophyll. The sugar content of the berry remains low, while organic acids accumulate. This stage lasts between 3 and 4 weeks for most raisin grape varieties grown in the central San Joaquin Valley.

Stage II: the lag phase of berry growth. Berry growth slows markedly during the second period while the berries' organic acid concentration reaches its highest level. Berries remain firm, but begin to lose chlorophyll. The lag stage normally lasts between 2 and 3 weeks in the central San Joaquin Valley, depending upon the climatic conditions and grapevine variety.

Stage III: the second phase of rapid berry growth and fruit ripening. The resumption of rapid berry growth and initiation of ripening commences with the beginning of this stage. The term *berry softening* (in French, *veraison*), which characterizes the initial stages of color development, is commonly used to describe the striking changes in fruit characteristics that mark the beginning of stage III. Berries soften and lose chlorophyll, while in colored varieties red pigments begin to accumulate in the skin. Sugar also begins to accumulate, and the concentration of organic acids declines (Figure 5.7). Aroma and flavor components accumulate in the fruit. Berry growth during this stage is limited to cell enlargement, and normally lasts between 6 and 8 weeks.

The potential size or fresh weight of the berry is controlled by three principle factors: number of cells, cell volume, and organic solute (sugar) content. The number of cells in a grape berry is established during the first three weeks after anthesis. No further cell division occurs after this period (Figure 5.8). In fact, the number of times cells divide before anthesis is the primary determinant of the number of cells per berry. A field-grown 'Thompson Seedless' berry contains approximately 200,000 cells prior to anthesis and 600,000 cells at harvest. In this example, the total number of cells per berry doubled 17 times prior to anthesis, but less than twice thereafter.
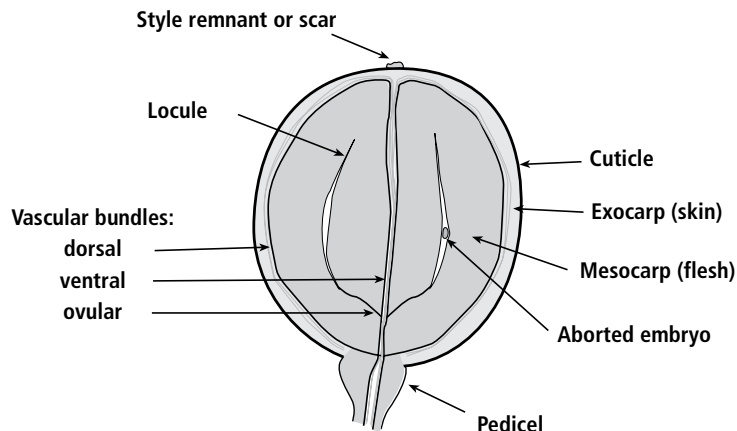

Figure 5.5 A typical berry of a stenospermocarpic variety, such as 'Thompson Seedless,' near harvest
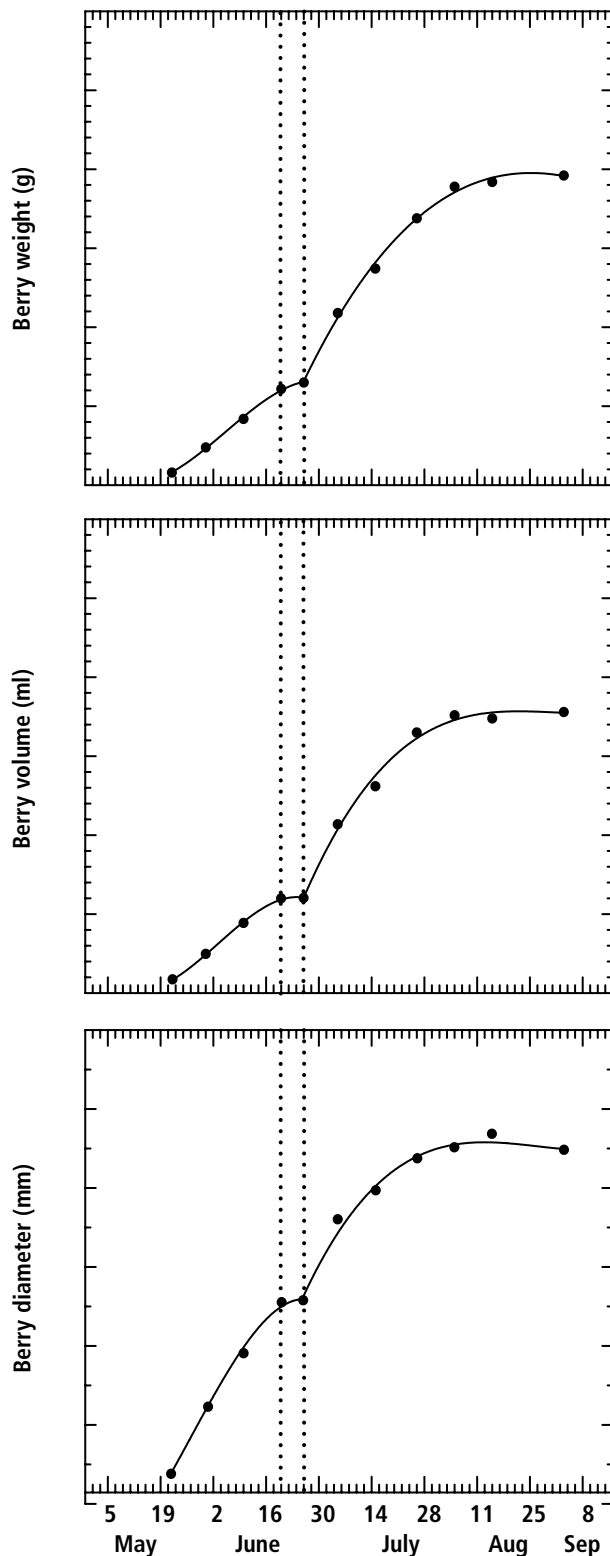
Figure 5.6 Changes in berry weight (*upper graph*), volume (*middle graph*), and diameter (*lower graph*) of 'Thompson Seedless' during the 1996 growing season. Each of the three parameters of berry growth exhibits a double-sigmoid curve, with three distinct stages (I, II, and III) of berry development. Source: Christensen and Moriyama (unpublished data).

Cell volume increases significantly during stage I, remains relatively constant during stage II, and resumes rapid expansion in stage III. The concentration of organic solutes (primarily sugars) per unit of cell volume also increases sharply during stage III. Cell volume increases about 300-fold between anthesis and harvest, and the content of organic solutes per unit of cell volume increases fourfold during the same period.

Relatively little is known about the physiological or anatomical factors responsible for differences in berry size and growth potential among grape varieties.   It is likely that both the number of cells per berry and the size of those cells are closely related to the final fresh weight of the berry. Biophysical factors such as berry cell turgor and cell wall extensibility and plasticity also influence berry growth. For example, expansive stage III growth of some grape varieties often stops because it has caused splits or cracks in the berry skin. The causes of berry cracking are unknown, but they probably involve interactions between environmental conditions and the extensibility or integrity of the berry cell walls.

Temperature influences both cell division and enlargement. The optimum temperature for berry growth is between 68° and 77°F (20° and 25°C). Berry growth during stage I is quite sensitive to temperature: temperatures in excess of 95°F (35°C) reduce growth rate and size at harvest. Light is also important for optimum berry growth. Berries that are subject to heavy shade immediately after berry set are significantly smaller at maturity than berries that have been well exposed to light. This suggests that light stimulates cell division or cell expansion in grape berries during stage I.

Vines undergoing water stress during stage I normally produce smaller berries than non-stressed vines. Since the effects of water stress during stage I on berry growth cannot be reversed by subsequent watering, decreased growth probably indicates a reduced number of cells per berry or a permanent reduction in the size or volume of the cells. Water stress during phases II and III may also decrease berry weight, but in that case the reduction is related to reduced cell volume or diminished solutes (sugar) in the cells. Nutrient deficiencies and other disorders that reduce photosynthesis may also reduce berry growth or slow ripening by decreasing the supply of sugars to the fruit.

Grape Ripening

Many factors, including grape variety, climate, and crop level, influence fruit ripening and harvest date. The specific number of heat units (usually expressed as degree-days[DD]) required for berry maturation varies significantly among varieties. For example, an

early ripening variety such as 'Fiesta' requires fewer degree-days to mature its crop than the later-ripening 'Thompson Seedless.' When grown under similar conditions and crop levels, 'Thompson Seedless' fruit normally requires 7 to 10 additional days of ripening to reach the same maturity or sugar level as 'Fiesta.' Seasonal differences in degree-day accumulation also influence the rate of ripening. When temperatures are low and degree-day accumulation slow, ripening is delayed. When conditions are warm and degree-days accumulate rapidly, ripening is accelerated. Prolonged periods of excessively high temperatures following berry softening, however—for example, 3 to 4 consecutive days above 105°F (40.6°C)—may retard ripening. The effects of elevated temperatures on fruit ripening are temporary and, depending upon the degree of heat stress, sugar accumulation can proceed normally once temperatures return to a normal range.

Crop level also influences fruit maturation rate, with large crop loads taking more time to ripen than small crops. Most studies report that 'Thompson Seedless' vines require 1.6 to 2.2 square inches (10 to 14 cm²) of leaf area per gram of fruit weight, or approximately 18 leaves per cluster, for optimum fruit maturation. If the leaf-area to fruit-weight ratio or the number of leaves per cluster drops significantly below this level, fruit maturation is delayed. However, nearly all commercial raisin grape vineyards produce more than enough leaf area to effectively ripen their crops.

Grape Composition

Water. Grape berries require a significant amount of water for growth and development, and water typically contributes 70 to 80 percent of berry fresh weight at harvest. Although they lack functional stomata soon after fruit set, berries transpire significant amounts of water during their development. Prior to veraison, most of the water required by the fruit is supplied by the xylem. However, shortly after veraison the xylem vessels entering the berry are blocked. With water flow via the xylem disrupted, the phloem becomes the primary supplier of water to the berry. Sugar, mineral cations, and other compounds entering the fruit during ripening are also supplied by the phloem.

Sugars. The sugar (in the form of sucrose) necessary for fruit growth and ripening must be imported into the berry from the leaves. Sugar also provides the carbon skeleton or foundation for many compounds, such as organic and amino acids, synthesized and found in the fruit. Sugar must also be transported to other non-photosynthetic organs such as the trunk and roots for their growth and maintenance. From the initiation of ripening until harvest, however, fruit is the dominant
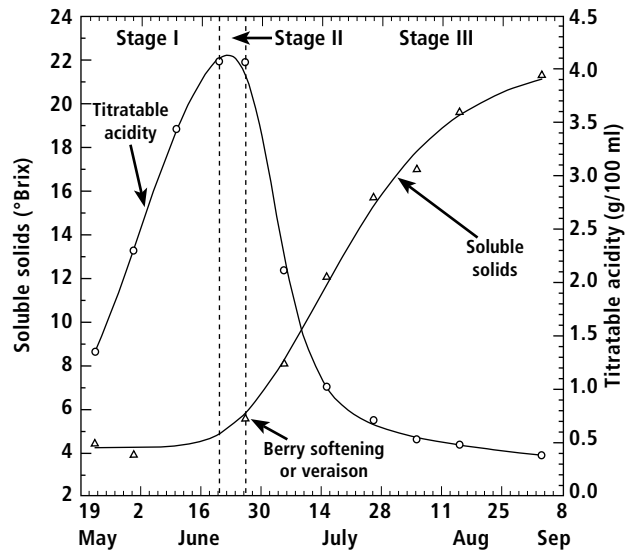

Figure 5.7 Changes in soluble solids (°Brix) and titratable acidity of 'Thompson Seedless' grape berries during fruit development in 1996. Soluble solids remained low during stage I of berry development, increased in a linear fashion as fruit entered stage III, and then leveled off near maturity. In contrast, titratable acidity increased rapidly during stage I, reaching its greatest concentration at the end of this period. Titratable acidity changed little during stage II and then declined rapidly with the initiation of berry ripening and stage III. The rapid decline in titratable acidity leveled off as the fruit reached maturity. Source: Christensen and Moriyama (unpublished data).
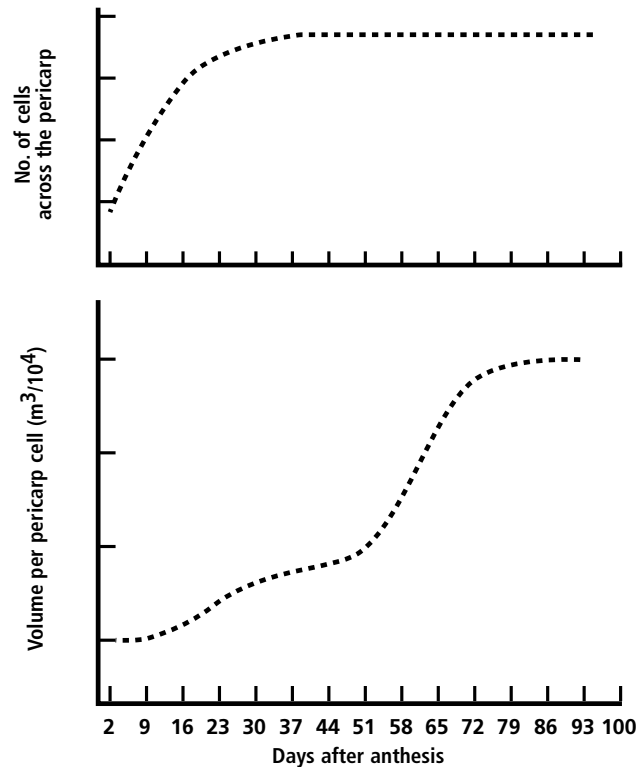

Figure 5.8 Changes in the number of cells per berry (*upper graph*) and berry cell volume (*lower graph*) in 'Thompson Seedless' during fruit development. Source: Harris et al., Vitis 7:106–9.

destination for sugar produced by the leaves. Grapes accumulate higher concentrations of sugar during ripening than do many other fruits. This characteristic makes grapes particularly well suited for dried fruit production, since raisin quality is highly correlated with sugar concentrations in the fresh fruit.

During the initial stages of fruit growth, the sugar concentration of the berry is quite low, usually around 2 percent of berry fresh weight. Beginning near the onset of veraison, sugar concentration increases rapidly, and may reach 25 percent or more of berry fresh weight by the time of harvest. Sucrose, the predominant sugar transported in the phloem, is made by joining one molecule of glucose with one molecule of fructose. Once sucrose reaches the berry it is converted back to glucose and fructose, and these sugars are found in the fruit. Glucose and fructose are present in approximately equal amounts in grape berries at harvest, each ranging from 8 to 12 percent of fruit fresh weight. Sucrose and several other sugars are also present in the berry in small amounts.

Organic acids. Tartaric and malic acids are the principal organic acids of the grape berry, making up approximately 90 percent of total fruit acidity. Both acids are produced in the berry, along with small amounts of citric acid and several other nonnitrogenous organic acids. Grape varieties vary in the relative amounts of tartaric and malic acids present in their fruit, with most raisin grape varieties containing relatively small amounts of malic acid at harvest.

From anthesis until just before the initiation of fruit ripening, malic acid, tartaric acid, and total acidity progressively increase in the berry. These acids' concentrations reach their highest levels near veraison, and then decline through the ripening period. Once synthesized, tartaric acid is believed to be stable, since no enzyme capable of degrading it has been found in the berry. The decrease in the concentration of tartaric acid observed during ripening is attributed to a dilution effect, since berry volume increases while the amount of tartrate per berry remains constant. In contrast, several enzymes capable of metabolizing malate are present in the berry, and the acid is readily respired to form CO_2 and H_2O. Reductions in malic acid concentration after veraison result from respiration and enzyme degradation as well dilution. The amounts of free tartaric and malic acids in the berry decline during ripening due to the formation of acid-salts with potassium and other cations in the berry. The total acidity (tartaric and malic acids) of 'Thompson Seedless' raisin grapes typically ranges between 0.4 and 0.6 gram per 100 ml of fresh juice at harvest.

Temperature is a key factor controlling berry acid content. During the initial stages of fruit development, the optimum temperature for acid synthesis ranges between 68° and 77°F (20° and 25°C). It is also well established that fruit acidity at harvest is negatively correlated with temperature during the ripening period. In general, fruits ripened at low temperatures have greater total acidity (particularly of malic acid) than fruits ripened at high temperatures. Fruit acidity therefore varies among regions and years, with higher levels of acidity found in cooler regions or growing seasons.

Juice pH. The juice pH is a measure of the hydrogen ion concentration in the berry, and is generally related to juice acidity. Juice pH is relatively constant during the early stages of berry development, remaining near a value of 2.5, and then rises gradually during ripening as acid anions are formed and the amount of malic acid in the berry declines. The juice pH of 'Thompson Seedless' grapes at harvest usually ranges between 3.5 and 3.9.

Phenolic compounds. Phenolic compounds include tannins and flavonols, as well as anthocyanins, the pigments responsible for berry color. These compounds are synthesized in the berry and concentrated in the berry skin, and in seeds when present. The fruit of colored grape varieties contain much greater concentrations of phenolic compounds than white grapes, since the latter contain no anthocyanins. Phenolics are important constituents of the grape berry because they play a key role in determining fruit color and astringency. The oxidation of caftaric acid, the major phenolic compound in grape pulp and juice, is believed responsible for the formation of the characteristic brown pigment of naturally sun-dried raisins. The contributions of phenolic compounds to the nutritive value of grape products, and their potential health benefits as antioxidants, are currently active areas of investigation.

Nitrogen compounds. Although grape berries contain little nitrate (NO_3), nitrogen is present in the form of ammonium cations (NH_4^+) and organic nitrogen compounds such as amino acids and proteins. During the initial stages of berry growth, ammonium ions account for more than half of the total nitrogen in the fruit, and amino acids are relatively low. After veraison, amino acid synthesis in the berry increases sharply and the ammonium concentration declines as the ions are incorporated into amino acids. The amino acid concentration of the fruit may increase two- to fivefold during ripening, with wide variations depending upon variety and fruit maturity. Arginine and proline are the main amino acids in the fruit of most grape varieties at harvest. Arginine is the dominant amino acid in 'Thompson Seedless' juice at harvest, typically ranging between 0.30 and 0.80 mg per ml.

Inorganic minerals. Inorganic minerals in the soil are taken up by the roots and either transported directly to the fruit or remobilized from permanent organs (the trunk or roots) via the xylem (before veraison) or phloem. The principal minerals found in grape berries include the cations potassium, calcium, and sodium. The most common mineral anions are phosphate and chloride. The mineral cation concentration in the fruit increases two- to threefold during ripening, with potassium as the dominant mineral. The potassium concentration of 'Thompson Seedless' juice ranges between 1,200 and 2,000 mg per liter at harvest.

Aroma and flavor compounds. The type and concentration of aroma and flavor compounds found in grapes varies widely among varieties. Some raisin varieties such as 'Muscat of Alexandria' produce fruit with easily distinguished aromas and flavors, while others such as 'Thompson Seedless' produce fruit with a neutral aroma and flavor. The best-known and best-described flavor compounds of *Vitis vinifera* are monoterpenes, which are responsible for the floral characteristics normally associated with muscat varieties. These compounds accumulate during the latter stages of ripening and are present in trace amounts at harvest. The availability of information on other flavor and aroma compounds in fresh and dried grapes is likely to increase as more sensitive and accurate detection methods are developed.

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