

Grapevine Structure and Function

Edward W. Hellman

This chapter presents an overview of grapevine structure and function to provide a basic understanding of how grapevines grow. Such understanding is the foundation of good vineyard management, and the practical application of this knowledge is emphasized throughout this book. The reader should consult the references cited in this chapter for more complete coverage of these topics. Much of the common viticultural terminology is introduced in this chapter.

Grapevine Structure

Cells and Tissues

The basic unit of plant structure and function is the *cell*. All cells have the same general organization, consisting of a cell wall, protoplasm (liquid-filled region containing living organelles), and the vacuole (region containing the cell sap). This basic cell structure is modified to create different cell types that are capable of specialized functions. Organized groups of specialized cells that perform specific functions are called *tissues*. For example, the outside protective “skin” of grape leaves, the *epidermis*, consists of one to several layers of specialized cells. A thorough discussion of the cell and tissue anatomy of grapevines has been prepared by Pratt (1974), or a general discussion of plant anatomy can be found in any introductory botany textbook.

Meristems

Certain plant cells, termed *meristematic cells*, perform the specialized function of growth by the creation of new cells through cell division. Groups of these cells are organized into *meristems* (or *growing points*), positioned at various locations on the vine. The *apical meristem* is a tiny growing point, hidden from view within the unfolding leaves at the tip of an expanding shoot. In addition to the apical meristem, the shoot produces many additional growing points at the base of each leaf, called buds; these are described in more detail below. Each root tip also contains a growing point. Two specialized meristems, the vascular cambium and the cork cambium, are responsible for the radial growth (diameter increase) of woody parts of the vine.

New xylem and phloem tissues (described below under Vascular System) are produced every year from a specialized meristem called the *vascular cambium* (or simply *cambium*). The location and arrangement of cambium, xylem, and phloem vary between plant parts (e.g., shoots and roots) and with the develop-

mental stage of the part. The cambium consists of a single layer of meristematic cells, which produce xylem cells to the inside and phloem cells outside (Figure 1). Thus, the annual increase in girth of woody tissues such as the trunk is a result of the addition of new xylem and phloem cells from the cambium. Xylem cells are larger and produced in much greater abundance than phloem cells, which form tissue only a few cell layers thick. This causes the cambium always to be positioned close to the outer surface of a woody stem. Older xylem can remain functional for up to seven years, but is mostly inactivated after two or three years. Some phloem cells continue to function for three to four years.

The exterior of woody parts of the vine is protected by *periderm*, which comprises *cork* cells and is covered by an outer *bark* consisting of dead tissues. Once a year, some of the cells within the outer, nonfunctional phloem become meristematic, creating the *cork cambium*. The cork cambium produces a layer of new cells that soon become impregnated with an impermeable substance, cutting off the water supply to the cork cells and older phloem that are external to the layer. These cells die and add to the layers of bark. Older bark cracks from the expansion growth of new bark beneath it, creating the peeling bark that is characteristic of older wood on grapevines.

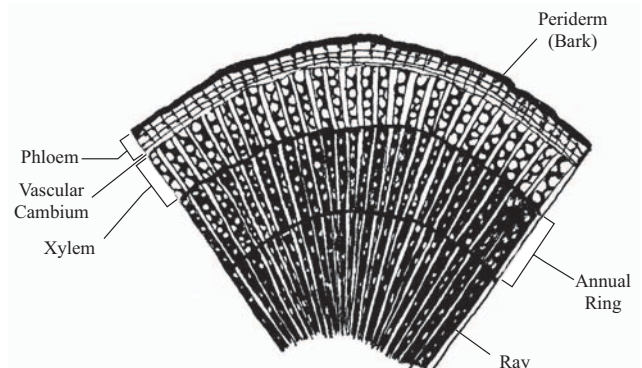


Figure 1. Cross section of 3-year-old grapevine arm. Redrawn from Esau (1948) by Scott Snyder.

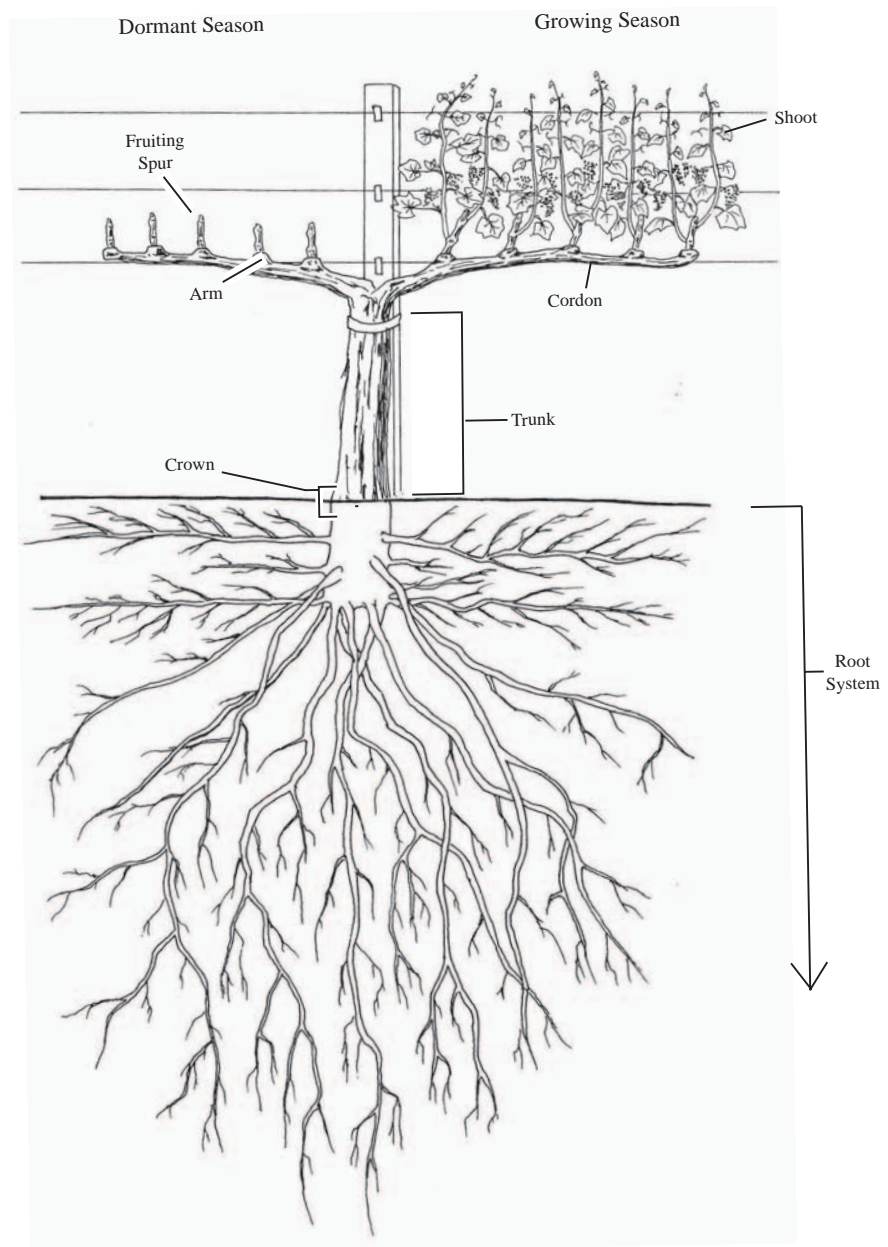


Figure 2. Grapevine structures and features: self-rooted vine. Drawing by Scott Snyder.

Vascular System

The interior of all the plant parts described below contains groups of specialized cells organized into a *vascular system* that conducts water and dissolved solids throughout the vine. There are two principal parts to the vascular system: *xylem* is the conducting system that transports water and dissolved nutrients absorbed by the roots to the rest of the vine, and *phloem* is the food-conducting system that transports the products of photosynthesis from leaves to other parts of the vine. The xylem and phloem tissues each consist of several different types of cells, some of which create a continuous conduit throughout the plant, and others provide support functions to the conducting cells, such as the storage of food products in xylem cells. A group of specialized cells are arranged in narrow bands of tissue called *rays*, which extend out

perpendicular from the center of a stem, through the xylem and phloem. Ray cells facilitate the radial transfer of water and dissolved substances between and among xylem and phloem cells and are a site for storage of food reserves. The vascular system constitutes the *wood* of older stems, and the thick cell walls of the xylem provide the principal structural support for all plant parts.

Parts of the Vine

The shape of a cultivated grapevine is created by pruning and training the vine into a specific arrangement of parts according to one of many *training systems*. Over the centuries, innumerable training systems have been developed and modified in efforts to facilitate vine management and provide a favorable growing environment for the production of grapes.

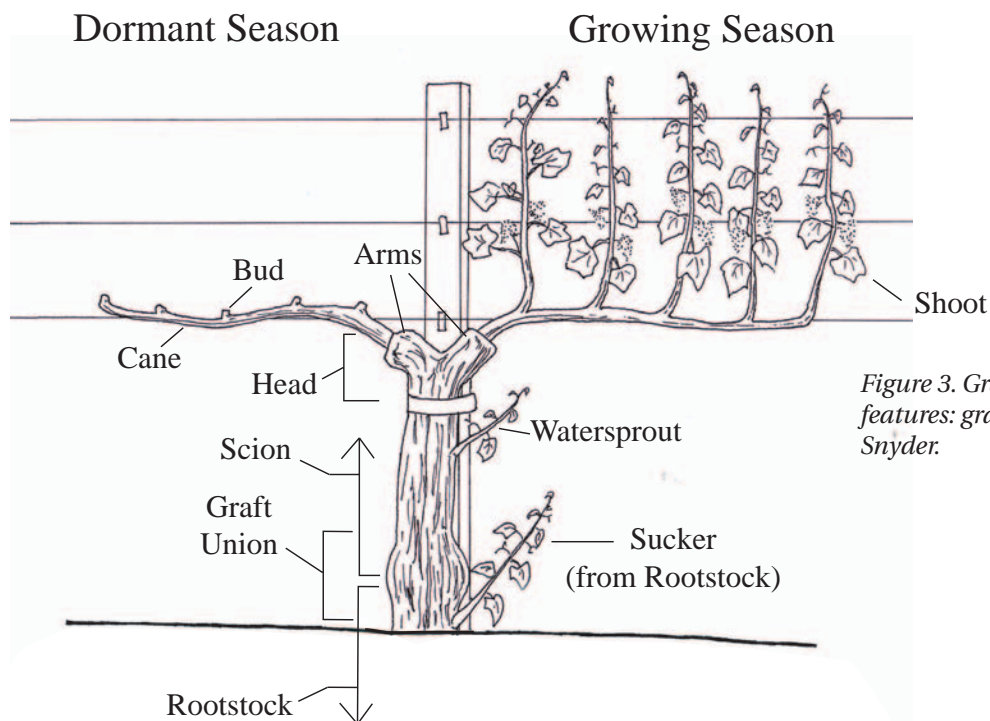


Figure 3. Grapevine structures and features: grafted vine. Drawing by Scott Snyder.

Figures 2 and 3 illustrate a mature grapevine as it might appear at two representative time periods, trained to two different systems. The parts of the vine are labeled with commonly used viticultural terms that often reflect how we manage the vine rather than describing distinct morphological structures as defined by botanists.

The Root System

In addition to anchoring the vine, roots absorb water and nutrients, store carbohydrates, other foods, and nutrients for the vine's future use, and produce hormones that control plant functions. The root system of a mature grapevine consists of a woody framework of older roots (Richards, 1983) from which permanent roots arise and grow either horizontally or vertically. These roots are typically multi-branching, producing lateral roots that can further branch into smaller lateral roots. Lateral roots produce many short, fine roots, which has the effect of increasing the area of soil exploited. Certain soil fungi, *mycorrhizae*, live in a natural, mutually beneficial association with grape roots. Mycorrhizae influence grapevine nutrition and growth and have been shown to increase the uptake of phosphorus.

The majority of the grapevine root system is usually reported to be within the top 3 feet of the soil, although individual roots can grow much deeper under favorable soil conditions. Distribution of roots is influenced by soil characteristics, the presence of hardpans or other impermeable layers, the rootstock variety (see below), and cultural practices such as the type of irrigation system.

Grapevines can be grown "naturally" on their own root system (*own-rooted* or *self-rooted vines*) or they may be grafted onto a rootstock. A *grafted vine* (Figure 3) consists of two general parts, the *scion* variety (e.g., Pinot noir), which produces the fruit, and the *rootstock* variety (often denoted by numbers, e.g., 101-14), which provides the root system and lower part of the trunk. The position on the trunk where the two varieties were joined by grafting and subsequently grew together is called the *graft union*. Successful healing of the graft union requires that the vascular cambiums of the stock and scion be in contact with each other, since these are the only tissues having the meristematic activity necessary for the production of new cells to complete the graft union. Healing of the graft union often results in the production of abundant *callus* (a wound healing tissue composed of large thin-walled cells that develop in response to injury) tissue, often making the area somewhat larger than adjacent parts of the trunk. Because rootstock and scion varieties may grow at different rates, trunk diameter can vary above and below the graft union.

Rootstock varieties were developed primarily to provide a root system for *Vitis vinifera* L. ("European" winegrape) varieties that is resistant or tolerant to *phylloxera*, a North American insect to which *V. vinifera* roots have no natural resistance. Most phylloxera-resistant rootstocks are either native North American species or hybrids of two or more of these species, including *V. riparia*, *V. berlandieri*, and *V. rupestris*. The rooting pattern and depth, as well as other root system characteristics, vary among the species and hybrid rootstocks, so the rootstock can

influence aspects of vine growth, including vigor, drought tolerance, nutrient uptake efficiency, and pest resistance. Rootstock variety selection is, therefore, an important factor in vineyard development.

The Trunk

The *trunk*, formerly an individual shoot, is permanent and supports the aboveground vegetative and reproductive structures of the vine. The height of the trunk varies among training systems, and the top of the trunk is referred to as the *head*. The height of the head is determined by pruning during the initial stages of training a young grapevine. The trunk of a mature vine has *arms*, short branches from which canes or spurs (defined below) originate; arms are located in different positions depending on the system. Some training systems utilize *cordons* (Figure 2), semi-permanent branches of the trunk, usually trained horizontally along a trellis wire, with arms spaced at regular intervals along their length. Other systems utilize *canes* (Figure 3), one-year-old wood arising from arms usually located near the head of the vine. The *crown* refers to the region of the trunk near the ground, from slightly below to slightly above ground level.

Shoots and Canes

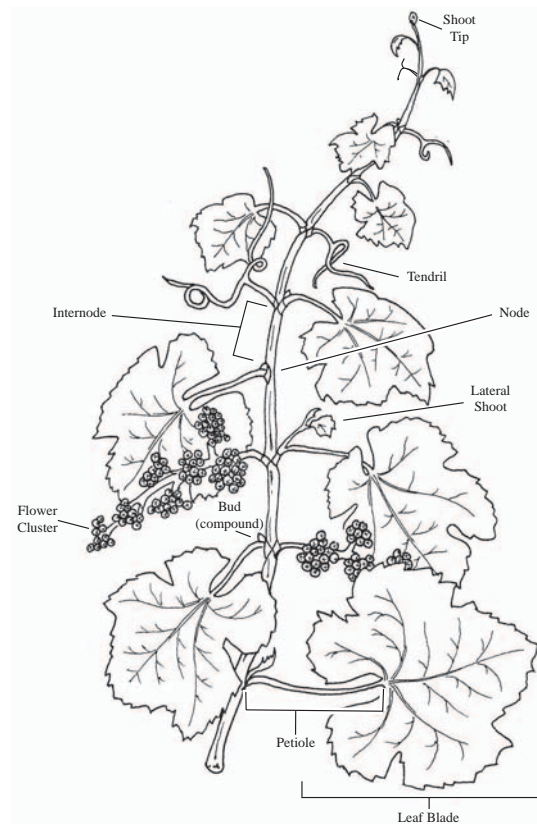


Figure 4. Principal features of a grapevine shoot prior to bloom. Drawing by Scott Snyder.

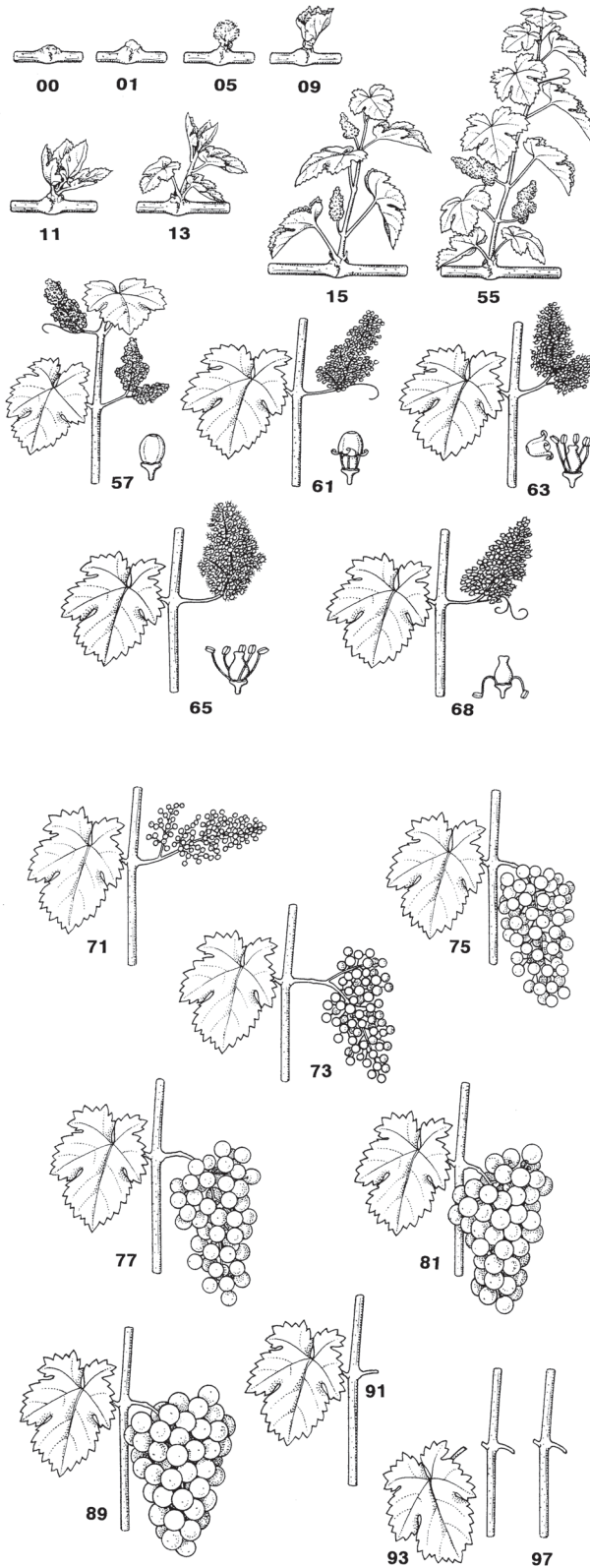
The *shoot* is the primary unit of vine growth and the principal focus of many viticultural practices. Shoots are the stemlike green growth arising from a bud. *Primary shoots* arise from primary buds (described below) and are normally the fruit-producing shoots on the vine. The components of the shoot are illustrated in Figure 4, and the stages of grapevine growth and flower and fruit development are shown in Figure 5. The main axis of the shoot consists of structural support tissues and conducting tissues to transport water, nutrients, and the products of photosynthesis. Arranged along the shoot in regular patterns are leaves, tendrils, flower or fruit clusters, and buds. General areas of the shoot are described as *basal* (closest to its point of origin), *mid-shoot*, and *apex* (tip). The term *canopy* is used to denote the collective arrangement of the vine's shoots, leaves and fruit; some viticulturists also consider the trunk, cordons, and canes to be parts of the canopy.

Shoot Tip. The shoot has many points of growth, but the extension growth of the shoot occurs from the *shoot tip* (growing tip). New leaves and tendrils unfold from the tip as the shoot grows. Growth rate of the shoot varies during the season. Grapevine shoots do not stop expanding by forming a terminal bud as some plants do; they may continue to grow if there is sufficient heat, soil moisture, and nutrients.

Leaves. Leaves are produced at the apical meristem. The shoot produces two or more closely spaced *bracts* (small scalelike leaves) at its base before it produces the first true foliage leaf. Leaves are attached at the slightly enlarged area on the shoot referred to as a *node*. The area between nodes is called the *internode*. The distance between nodes is an indicator of the rate of shoot growth, so internode length varies along the cane corresponding to varying growth rates during the season.

Leaves consist of the *blade*, the broad, flat part of the leaf designed to absorb sunlight and CO_2 in the food manufacturing process of photosynthesis (see below), and the *petiole*, the stemlike structure that connects the leaf to the shoot. The lower surface of leaf blades contains thousands of microscopic pores called *stomata* (s., *stomate*), through which diffusion of CO_2 , O_2 , and water vapor occurs. Stomata are open in the light and closed in the dark. The petiole conducts water and food material to and from the leaf blade and maintains the orientation of the leaf blade to perform its functions.

Flowers and Fruit. A *fruitful shoot* usually produces from one to three *flower clusters* (inflorescences) depending on variety, but typically two under Oregon conditions. Flower clusters develop opposite the leaves, typically at the third to sixth nodes from the base of the shoot, depending on the variety. If three



Principal growth stage 0: Sprouting/Bud development

- 00 Dormancy: buds pointed to round, light or dark brown according to variety; bud scales more or less closed according to variety
- 01 Beginning of bud swelling: buds begin to expand inside the bud scales
- 03 End of bud swelling: buds swollen, but not green
- 05 "Wool Stage": brown wool clearly visible
- 07 Beginning of bud burst: green shoot tips just visible
- 08 Bud burst: green shoot tips clearly visible

Principal growth stage 1: Leaf development

- 11 First leaf unfolded and spread away from shoot
- 12 2nd leaves unfolded
- 13 3rd leaves unfolded
- 14 Stages continuous until...
- 19 9 or more leaves unfolded

Principal growth stage 5: Inflorescence emerge

- 53 Inflorescences clearly visible
- 55 Inflorescences swelling, flowers closely pressed together
- 57 Inflorescences fully developed; flowers separating

Principal growth stage 6: Flowering

- 60 First caps detached from the receptacle
- 61 Beginning of flowering: 10% of caps fallen
- 62 20% of caps fallen
- 63 Early flowering: 30% of caps fallen
- 64 40% of caps fallen
- 65 Full flowering: 50% of caps fallen
- 66 60% of caps fallen
- 67 70% of caps fallen
- 68 80% of caps fallen
- 69 End of flowering

Principal growth stage 7: Development of fruits

- 71 Fruit set: young fruits begin to swell, remains of flowers lost
- 73 Berries swelling, clusters begin to hang
- 75 Berries pea-sized, clusters hang
- 77 Berries beginning to touch
- 79 Majority of berries touching

Principal growth stage 8: Ripening of berries

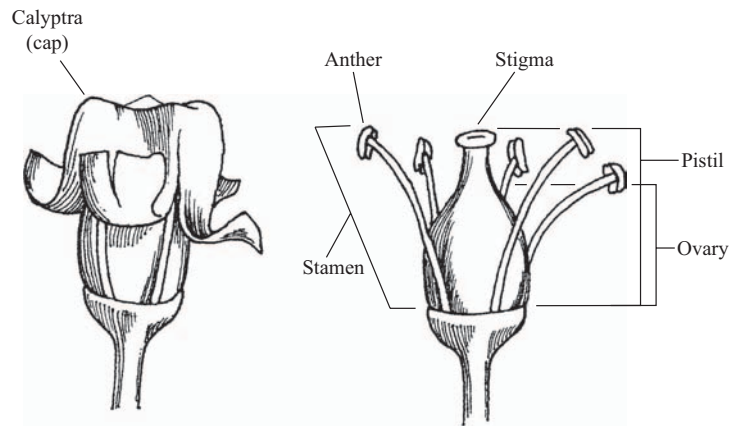
- 81 Beginning of ripening: berries begin to develop variety-specific color
- 83 Berries developing color
- 85 Softening of berries
- 89 Berries ripe for harvest

Principal growth stage 9: Senescence

- 91 After harvest; end of wood maturation
- 92 Beginning of leaf discoloration
- 93 Beginning of leaf-fall
- 95 50% of leaves fallen
- 97 End of leaf-fall
- 99 Harvested product

Figure 5. Stages of grapevine growth. Adapted with permission from Meier (2001).

Figure 6. Grape flower at two stages of bloom. Left, early bloom with cap separating from flower base. Right, flower in full bloom. Drawing by Scott Snyder.



flower clusters develop, two develop on adjacent nodes, the next node has none, and the following node has the third flower cluster. The number of flower clusters on a shoot is dependent upon the grape variety and the conditions of the previous season under which the dormant bud (that produced the primary shoot) developed. A cluster may contain several to many hundreds of individual flowers, depending on variety.

The grape flower does not have conspicuous petals (Figure 6); instead, the petals are fused into a green structure termed the *calyptra* but commonly referred to as the *cap*. The cap encloses the reproductive organs and other tissues within the flower. A flower consists of a single *pistil* (female organ) and five *stamens*, each tipped with an *anther* (male organ). The pistil is roughly conical in shape, with the base disproportionately larger than the top and the tip (the *stigma*) slightly flared. The broad base of the pistil is the *ovary*, which consists of two internal compartments, each having two ovules containing an embryo sac with a single egg. The anthers produce many yellow *pollen* grains, which contain the sperm.

The time during which flowers are open (the calyptra has fallen) is called *bloom* (also flowering or anthesis) and can last from one to three weeks depending on weather. Viticulturists variously refer to *full bloom* as the stage at which either roughly one-half or two-thirds of the caps have loosened or fallen from the flowers. Bloom typically occurs between 50 and 80 days after budburst in Oregon.

The stages of bloom (60-69) are illustrated in Figure 5. When the flower opens, the cap separates from the base of the flower, becomes dislodged, and usually falls off, exposing the pistil and anthers. The anthers may release their pollen either before or after capfall. Pollen grains randomly land upon the stigma of the pistil. This event is termed *pollination*. Multiple pollen grains can germinate, each growing a pollen tube down the pistil to the ovary and entering an ovule, where a sperm unites with an egg to form an embryo.

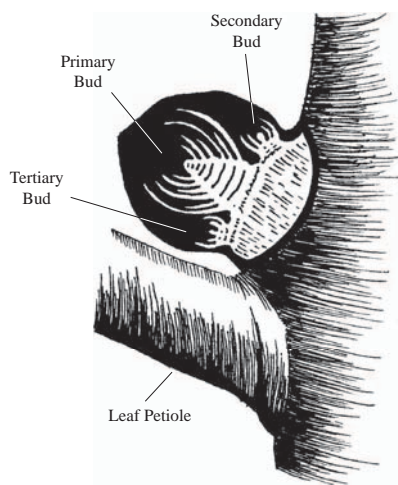
The successful union is termed *fertilization*, and the subsequent growth of berries is called *fruit set*. The berry develops from the tissues of the pistil, primarily the ovary. The ovule together with its enclosed embryo develops into the seed.

Because there are four ovules per flower, there is a maximum potential of four seeds per berry. Unfavorable environmental conditions during bloom, such as cool, rainy weather, can reduce both fruit set (number of berries) and berry size. Berry size is related to the number of seeds within the berry but can also be influenced by growing conditions and practices, particularly water management. Some immature berries may be retained by a cluster without completing their normal growth and development, a phenomenon known as *millerandage* or “*hens and chicks*.” See Pratt (1971) for a more complete botanical description of grapevine reproductive anatomy and process.

Tendrils. The shoot also produces *tendrils*—slender structures that coil around smaller objects (e.g., trellis wires, small stakes, and other shoots) to provide support for growing shoots. Tendrils grow opposite a leaf in the absence of a flower cluster, except the first two or three leaves and thereafter skipping every third leaf. Flower clusters and tendrils have a common developmental origin (Mullins et al., 1992), so occasionally a few flowers develop on the end of a tendril.

Buds. A *bud* is a growing point that develops in the leaf axil, the area just above the point of connection between the petiole and shoot. The single bud that develops in this area is described in botanical terms as an *axillary bud*. It is important to understand that on grapevines a bud develops in every leaf axil, including the inconspicuous basal bracts (scalelike leaves). In viticultural terminology, we describe two buds associated with a leaf—the *lateral bud*, and the *dormant bud* (or latent bud). The lateral bud is the true axillary bud of the foliage leaf, and the dormant bud forms in the bract axil of the lateral bud. Because of

Figure 7. Cross section of dormant grape bud in leaf axil, showing primary, secondary, and tertiary buds. Lateral bud not shown. Drawing by Scott Snyder.



their developmental association, the two buds are situated side-by-side in the main leaf axil.

Although the dormant bud (sometimes called an *eye*) looks like a simple structure, it is actually a compound bud consisting of three growing points, sometimes referred to as the *primary, secondary, and tertiary buds*. The distinction between secondary and tertiary buds is sometimes difficult to make and often of little importance, so it is common to refer to both of the smaller buds as secondary buds. The collection of buds is packaged together within a group of external protective bud scales (Figure 7). Continuing the bud development pattern, the primary growing point is the axillary bud of the lateral bud; the secondary and tertiary growing points are the axillary buds of the first two bracts of the primary growing point.

The dormant bud is of major concern at pruning, since it contains cluster primordia (the fruit-producing potential for the next season). It is referred to as dormant to reflect the fact that it does not normally grow out in the same season in which it develops.

The dormant bud undergoes considerable development during the growing season. The three growing points each produce a rudimentary shoot that ultimately will contain *primordia* (organs in their earliest stages of development) of the same basic components of the current season's fully grown shoot: leaves, tendrils, and in some cases flower clusters. The primary bud develops first, so it is the largest and most fully developed. If it is produced under favorable environmental and growing conditions, it will contain flower cluster primordia before the end of the growing season. The flower cluster primordia thus represent the fruiting potential of the bud in the following season. Reflecting the sequence of development, the secondary and tertiary buds are progressively smaller and less developed. They are generally less fruitful (have fewer and smaller clusters) than the primary bud. *Bud fruitfulness* (potential to produce fruit) is a

function of the variety, environmental conditions, and growing practices. Dormant buds that develop under unfavorable conditions produce fewer flower cluster primordia.

In most cases, only the primary bud grows, producing the primary shoot. The secondary bud can be thought of as a "backup system" for the vine; normally, it grows only when the primary bud or young shoot has been damaged, often from freeze or frost. However, under some conditions such as severe pruning, destruction of part of the vine, or boron deficiency, it is possible for two or all three of the buds to produce shoots (Winkler et al., 1974). Tertiary buds provide additional backup if both the primary and secondary buds are damaged, but they usually have no flower clusters. If only the primary shoot grows, the secondary and tertiary buds remain alive, but dormant, at the base of the shoot.

The lateral bud grows in the current season, but growth may either cease soon after formation of the basal bract or continue, producing a *lateral shoot* (summer lateral) of highly variable length. Regardless of the extent of lateral bud development, a compound bud develops in the basal bract, forming the dormant bud. Long lateral shoots sometimes produce flower clusters and fruit, which is known as *second crop*. But because they develop later in the season than fruit on the primary shoot, second crop fruit does not mature fully in Oregon. If a lateral bud does not grow in the current season, it will die.

Suckers and Watersprouts. Shoots may also arise from bud locations on older wood such as cordons and trunks. *Suckers* are shoots that grow from the crown area of the trunk. *Watersprout* is a term sometimes used to refer to a shoot arising from the upper regions of the trunk or from cordons. Buds growing from older wood are not newly initiated buds; rather, they developed on green shoots as axillary buds that never grew out. These buds are known as *latent buds*, because they can remain dormant indefinitely until an extreme event such as injury to the vine or severe pruning stimulates renewed development and shoot growth.

Suckers often arise from latent buds at underground node positions on the trunk. In routine vine management, suckers are removed early in the season before axillary buds can mature in basal bracts of the sucker shoots. Similarly, aboveground suckers are typically stripped off the trunk manually so that a pruning stub does not remain to harbor additional latent buds that could produce more suckers in the following year.

Latent buds come into use when trunk, cordon, or spur renewal is necessary. Generally, numerous latent buds exist at the "renewal positions" (a pruning term)

on the trunk or cordons. Dormant secondary and tertiary buds exist in the stubs that remain after canes or spurs have been removed by pruning.

Canes. The shoot begins a transitional phase about midseason, when it begins to mature, or *ripen*. Shoot maturation begins as periderm develops, starting at the shoot base, appearing initially as a yellow, smooth “skin.” Periderm continues to extend development toward the shoot tip through summer and fall. As periderm develops, it changes from yellow to brown and becomes a dry, hard, smooth layer of bark. During shoot maturation, the cell walls of ray tissues thicken and there is an accumulation of starch (storage carbohydrates) in all living cells of the wood and bark. Once the leaves fall off at the beginning of the dormant season, the mature shoot is considered a *cane*.

The cane is the principal structure of concern in the dormant season, when the practice of pruning is employed to manage vine size and shape and to control the quantity of potential crop in the coming season. Because a cane is simply a mature shoot, the same terms are used to describe its parts. Pruning severity is often described in terms of the number of buds retained per vine, or *bud count*. This refers to the dormant buds, containing three growing points, described above. The “crown” of buds observed at the base of a cane includes the secondary and tertiary growing points of the compound bud that gave rise to the primary shoot, as well as the axillary buds of the shoot’s basal bracts (Pratt, 1974). These basal buds are generally not fruitful and do not grow out, so they are not included in bud counts and may be referred to as *noncount buds*.

Canes can be pruned to varying lengths, and when they consist of only one to four buds they are referred to as *spurs*, or often as *fruiting spurs* since fruitful shoots arise from spur buds. Grapevine spurs should not be confused with true spurs produced by apple, cherry, and other fruit trees, which are the natural fruit-bearing structures of these trees. On grapevines, spurs are created by short-pruning of canes. Figure 2 illustrates a vine that is cordon-trained, spur-pruned. Training systems that use cane-pruning (Figure 3) sometimes also use spurs for the purpose of growing shoots to be trained for *fruiting canes* in the following season. These spurs are known as *renewal spurs*, indicating their role in replacing the old fruiting cane.

Major Physiological Processes

Photosynthesis

Grapevines, like other green plants, have the capacity to manufacture their own food by capturing the energy within sunlight and converting it to chemical energy (food). This multi-stage process is called *photo-*

synthesis. In simple terms, sunlight energy is used to split water molecules (H_2O), releasing molecular oxygen (O_2) as a byproduct. The hydrogen (H) atoms donate electrons to a series of chemical reactions that ultimately provide the energy to convert carbon dioxide (CO_2) into carbohydrates (CH_2O). Details of this complex process are beyond the scope of this chapter and have been summarized elsewhere (Mullins et al., 1992).

Photosynthesis occurs in chloroplasts, highly specialized organelles containing molecules called *chlorophyll*, which are abundant in leaf cells. The structure of a leaf is well adapted to carry out its function as the primary site of photosynthesis. Leaves provide a large sunlight receptor surface, an abundance of specialized cells containing many chloroplasts, numerous stomata to enable uptake of atmospheric carbon dioxide, and a vascular system to transport water and nutrients into the leaf and export food out.

The products of photosynthesis are generally referred to as *photosynthates* (or assimilates), which include sugar (mostly sucrose) and other carbohydrates. Sucrose is easily transported throughout the plant and can be used directly as an energy source or converted into other carbohydrates, proteins, fats, and other compounds. The synthesis of other compounds often requires the combination of carbon (C) based products with mineral nutrients such as nitrogen, phosphorus, sulfur, iron, and others that are taken up by the roots. Starch, a carbohydrate, is the principal form of food energy that the vine stores in reserve for later use. The carbohydrates cellulose and hemicellulose are the principal structural materials used to build plant cells. Organic acids (malic, tartaric, citric) are another early product of photosynthesis and are used directly or converted into amino acids by the addition of nitrogen. Amino acids can be stored or combined to form proteins.

Photosynthates are the food energy used to fuel plant growth and maintain plant function. The allocation of photosynthates to different parts of the vine is described in terms of “sources” and “sinks.” Leaves are the *source* of photosynthates, and any plant part—such as shoots, fruit, or roots—or metabolic process that utilizes photosynthates is considered a *sink*. The amounts of food materials moved to different points of need (sinks) varies through the season, depending upon photosynthate production and demand from the various plant parts (Williams, 1996). Thus, the majority of foods and food materials are first sent to actively growing areas such as shoot tips, developing fruit, and root tips. Later, when growth has slowed and a full canopy is producing more photosynthates than are demanded by growing points,

increasing quantities of food are directed to the roots, trunk, and other woody tissues for storage as reserves. However, during the ripening phase of fruit development, the fruit cluster is the main sink for photosynthates, and only surpluses go to reserves. After harvest, all woody tissues, especially roots, are the principal sinks. Food reserves in the roots and woody parts of the vine provide the energy for initial shoot growth in the spring, before new leaves are capable of producing more food than they consume.

Sunlight. The process of photosynthesis is obviously dependent upon sunlight, and it is generally assumed that between one-third and two-thirds full sunlight is needed to maximize the rate of photosynthesis. The optimization of sunlight captured by the vine is an important component of canopy management that not only affects the rate of photosynthesis but also directly influences fruit quality. Sunlight exposure on a vine is highly dependent upon the training system and the shoot density and can be influenced by the orientation of the rows and row spacing. The term *canopy management* encompasses many vineyard practices designed to optimize the sunlight exposure of the grapevine.

Other Environmental Influences. The rate of photosynthesis in grapevines is also influenced by leaf temperature; the apparently broad optimum range of 25–35°C (77–95°F) may be attributable to differences in grape variety, growing conditions, or seasonal variation (Williams et al., 1994). Leaf temperature can be highly dependent upon vine water status but otherwise cannot be influenced to the same extent as sunlight exposure in the canopy, so it is of less concern to vineyard management.

Water status of grapevines can have a strong impact on photosynthetic rate through its control over the closing of leaf stomata, the sites of gas exchange critical for photosynthesis. A *water deficit* exists when the plant loses more water (via transpiration, described below) than it takes up from the soil. One consequence of water deficits is the closure of stomata, which reduces water loss but also reduces the uptake of CO₂ necessary for photosynthesis. The extent of stomatal closure, and therefore the impact on photosynthetic rate, is related to the severity of water deficit. Vines are considered to be under *water stress* when the deficit is extreme enough to reduce plant functions significantly. The major impact of water deficits on vine photosynthesis is the reduction of leaf area (Williams, 1996).

Inadequate supply of certain nutrients (nitrogen and phosphorus) may also limit photosynthesis directly, or indirectly by reduced availability of elements (iron and magnesium) for the synthesis of chlorophyll.

Respiration

The process by which the stored energy within food is released for the plant's use is called *respiration*. In simple terms, the end result can be considered to be the reverse chemical reaction of the photosynthetic process, although the multiple reactions and sites of activity are completely different. Respiration involves the reaction of oxygen with the carbon and hydrogen of organic compounds, such as carbohydrates, to form water and CO₂ and release energy. Many forms of carbohydrates, including sugars and starch, can be oxidized (broken down) by respiration, as can fats, amino acids, organic acids, and other substances. The decrease of malic acid, and to a lesser extent tartaric acid, in ripening fruit is largely attributed to respiration.

The respiration process has been reviewed by Mullins et al. (1992), and this summary is primarily based upon their review. Respiration can be considered to perform two functions: supplying energy for growth, and supplying energy for organ maintenance. It is probable that a large portion of the daily photosynthate produced by a grapevine is consumed in maintenance respiration. The food energy demands of maintenance respiration are considerable even during times of little vine growth, and it is significant that respiration, unlike photosynthesis, occurs continuously. The energy derived from maintenance respiration is used to meet the demands of many physiological processes, including carbohydrate translocation, protein turnover, nitrogen assimilation, and nutrient uptake in the roots. The synthesis of substances integral to vine maintenance and growth, including proteins, enzymes, colors, aromas, flavors, acids, and tannins, is fueled by respiration.

The rate of maintenance respiration is dependant upon grapevine size, whereas growth respiration rates vary with the level of growth activity. Temperature is the most influential environmental factor affecting the rate of respiration. Increasing temperatures cause a progressive increase in respiration rate up to a point where tissue damage occurs. At 50°F (10°C), respiration of a mature grape leaf is close to zero, but respiration rate approximately doubles with every 18°F (10°C) increase in temperature.

Translocation

The long-distance movement of water, mineral nutrients, food, and other materials through the vascular system is called *translocation*. Water and dissolved mineral nutrients absorbed by the roots are moved upward in the xylem to all parts of the grapevine. The phloem is the conduit primarily for food materials and their derivatives to be moved throughout the plant.

Movement of photosynthates in the phloem throughout the growing season has been described by Kliewer (1981) and Williams (1996) and is summarized here. Beginning at budburst and continuing for about two to three weeks, carbohydrates and nitrogenous compounds are moved upward from their storage locations in roots and woody parts of the vine to support the new shoot growth. When the shoot and leaves develop to the point that some leaves (those greater than 50% of their final size) produce more photosynthates than they consume, food materials begin to move in both directions in the phloem. Mature leaves from the apical portion of the shoot supply the growing shoot tip, and the remaining leaves export photosynthates out of the shoot to the parent vine: canes, arms, trunk, and roots. This pattern continues until about bloom, when growth from the shoot tip generally begins to slow down. From fruit set until the beginning of fruit ripening, photosynthates move primarily to three sinks: shoot tip, fruit cluster, and the parent vine. The fruit cluster is the primary sink from the start of ripening until harvest; the parent vine and growing tips of primary and lateral shoots are weaker sinks. After harvest most of the photosynthates moves out of the shoot into the storage reserve parts of the vine: roots and woody tissues. Generally there is a period of root growth after harvest, so the growing root tips would further favor carbohydrate movement to the roots.

In grapevines, sucrose is the main carbohydrate translocated, so starch and other carbohydrates must first be broken down to release sucrose for transport. Plant hormones, which have a role in controlling plant functions, are also moved through the xylem and phloem. Some cross-movement (radial translocation) of water and materials between the xylem and phloem occurs through vascular rays, which also function as storage sites for food reserves.

Mineral nutrients absorbed by the roots (see discussion below) are moved into the xylem of the root, and from there they are translocated upward to the shoot and distributed in the plant to the areas of use. Nutrient reserves are stored in the roots and woody parts of the vine and are remobilized and translocated in the phloem when uptake from soil is inadequate to meet the current need. Remobilization from storage reserves is an important source of nutrients, especially nitrogen, during the early stages of shoot growth in the spring, before roots have begun active growth.

Transpiration

Transpiration is the loss of water, in the form of vapor, through open stomata. Stomatal pores open into the empty spaces between mesophyll (interior cells) cells

of the leaf. This creates an uninterrupted path between the outside environment and the inner environment of the leaf. The outside environment almost always has a lower relative humidity than the protected interior of the leaf, which is assumed to be 100%. Thus a vapor pressure gradient exists, causing water vapor to move out of the leaf from the area of high vapor pressure (high water content) to the area of lower vapor pressure. When the thin-walled mesophyll cells lose water from transpiration, their absorptive power is increased due to concentration of the dissolved solids in the cell sap and partial drying of solid and semisolid materials of the cell. The partially dried cells then have a greater potential to absorb water, which they obtain from the xylem. Thus, the absorptive force, called *transpirational pull*, is applied to the continuous column of water (*transpiration stream*) in the xylem that extends from the leaves to the roots.

The rate of transpiration is dependent upon the extent to which stomata are open, which is primarily related to light levels and secondarily influenced by external environmental conditions: humidity, temperature, and wind. Stomata can, however, be partially or completely closed in response to varying degrees of water deficit, overriding the influence of light and other environmental conditions. Transpiration also has an evaporative cooling effect on the leaf because water molecules absorb heat energy during the conversion of water from the liquid phase to the gas phase within the leaf.

Absorption of Water and Nutrients

Water. The suction force of transpirational water loss is transmitted throughout the unbroken column of water in the xylem all the way to the roots, providing the major mechanism by which water is taken up from the soil and moved throughout the vine. Water is pulled into the root from the soil. Young roots absorb the majority of water, primarily through root hairs and other epidermal (outer layer) cells. But older suberized (“woody”) roots uptake water at a lower, but constant, rate. Water then moves through the cells of the inner tissues of the root and into the xylem ducts, where it continues its movement upward, reaching all parts of the vine, and is eventually lost via the stomata.

The effect of transpiration on the rate and quantity of water uptake is obvious, but new root growth is also necessary because roots eventually deplete the available water in their immediate area and soil water movement is slow at best. Therefore, conditions that influence root growth affect the rate of water uptake.

Nutrients. Mineral nutrients must be dissolved in water for uptake by roots. Nutrient uptake often occurs against a concentration gradient; that is, the concentration of a mineral nutrient in the soil solution is

usually much lower than its concentration in root cells. Thus an active process, consuming energy, is required to move nutrients against the concentration gradient. Active transport is a selective method of nutrient uptake, and some nutrients can be taken up in much greater quantity than others. Nitrates and potassium are absorbed several times as rapidly as calcium, magnesium, or sulfate. There are also interactions between nutrient ions that influence their absorption. For example, potassium uptake is affected by the presence of calcium and magnesium. In rapidly transpiring vines, nutrient uptake also occurs by mass flow (a passive process) with water from the soil solution (Mullins et al., 1992).

Major Developmental Processes

Shoot Growth

Shoot growth begins with *budburst* (or *budbreak*), when previously dormant buds begin to grow after they have received adequate heat in the spring. This usually occurs when average daily temperature reaches about 50°F. Representative stages in the growth and fruiting of a grapevine are illustrated in Figure 5. At budburst, the primary growing point usually contains 10–12 leaf primordia and one or two cluster primordia, located opposite leaf primordia at node positions three to six. Development of these structures continues as the shoot grows out from the bud. Early shoot growth is relatively slow, but soon it enters a phase of rapid growth called the *grand period of growth*, which typically continues until just after fruit set. Even when the shoot is only a few inches long, developing flower clusters can be seen opposite the young leaves.

As each new leaf unfolds, the lateral bud and dormant bud begin to develop in its axil. Some lateral buds in the leaf axils grow into lateral shoots, but many produce only one or a few small leaves, then stop growing. Other laterals grow out to varying lengths. Under some circumstances, such as excessive vine vigor, or in response to summer pruning (tipping or hedging) of primary shoots, the lateral shoot grows out with substantial vigor.

After fruit set, shoot growth generally continues to slow, to a halt or nearly so, by about the time the fruit begins to ripen. Under circumstances of high vigor, however, shoot growth may continue at a steady rate throughout the season. This situation can arise from one or more of the following causes: abundant water, excessive nitrogen fertilization, severe pruning, or extreme undercropping. Smart and Robinson (1991) describe the “ideal” shoot to be 2–3 feet long with 10–15 full-sized leaves.

Flower Cluster Initiation

As the shoot grows, considerable development takes place within the dormant buds in the leaf axils. Of greatest interest is the development of flower cluster primordia, since they represent the fruiting potential of the vine for the following season. The period at which flower cluster primordia begin to form on the rudimentary shoot is called *flower cluster initiation*. The process occurs first in the midsection of the primary shoot at node positions four through eight, beginning soon after bloom of the current season's flower clusters (initiated in the previous season) and continuing for up to six weeks. The buds at basal nodes one to three undergo cluster initiation a little later, and initiation continues progressively in buds toward the growing tip. Usually, by the end of the season, fruitful buds exist along the cane to the extent to where it is fully ripened.

Grape flower initiation is described and illustrated in Mullins et al. (1992) and summarized below. Flower development in *V. vinifera* is described as a three-step process, occurring within the developing dormant buds. The first step is the formation of uncommitted primordia by the growing points of developing dormant buds (which are not dormant at this early developmental stage) in leaf axils of the current season's shoots. The primordia are described as uncommitted at this point because they can develop into either flower clusters or tendrils, depending on environmental and growing conditions experienced by the specific bud and the shoot in general. In the second stage the primordia become committed to becoming a flower cluster or a tendril. Mullins et al. report flower cluster initiation coinciding with the beginning of periderm development on the shoot, but others have found it to begin before bloom with some varieties (L. E. Williams, personal communication) or at about the time of bloom (Winkler et al., 1974). Cluster primordia develop during the current season, and the final step, formation of flowers from the cluster primordia, begins after budburst in the following spring. The later stages of flower development are completed as bloom time is approached.

Sunlight and temperature are the most influential environmental factors on grapevine flower cluster initiation, although opinions vary on which is the dominant factor. According to Williams et al. (1994), the development of uncommitted primordia into either flower clusters or tendrils is dependent upon the amount of sunlight striking the bud during development. The number and size of cluster primordia increase with increasing sunlight levels. Mullins et al. (1992) conclude that it is probable that a combination of exposure to high temperature and high light intensity is necessary for maximum

fruitfulness of dormant buds. They also report that sunlight and temperature requirements for initiation of flower cluster primordia are known to vary among varieties. From a vineyard management perspective, it appears that, for a grape variety with demonstrated adaptation to a region's temperatures, sunlight exposure of the developing buds is the most critical concern. Thus training systems and canopy management practices that facilitate good sunlight exposure promote better fruitfulness than those that create conditions of shade.

Dormancy, Acclimation, and Cold Hardiness

In autumn, the vine enters *dormancy*—the stage with no leaves or growth activity, which extends until budburst the following spring. Despite the apparent inactivity of this stage, it can be a critical time for grapevines when they may be exposed to potentially damaging low temperatures. The ability of a dormant grapevine to tolerate cold temperatures is referred to as its *cold hardiness*. Grapevine cold hardiness is a highly dynamic condition, influenced by environmental and growing conditions, and varying among grapevine varieties and tissues and over time. Therefore, cold hardiness *cannot* be viewed or described in absolute terms such as “Variety X is cold hardy to -8°F.”

There are three stages of the dormant season: *acclimation*, the period of transition from the non-hardy to the fully hardy condition; midwinter, the period of most severe cold and greatest cold hardiness; and *deacclimation*, the period of transition from fully hardy to the non-hardy condition and active growth.

Acclimation is a gradual process, beginning after shoot growth ceases and continuing through autumn and early winter. The combination of declining day length and decreasing temperatures in autumn are important factors influencing acclimation and cold hardiness. The process of acclimation in grapevines is not well understood, but it involves many simultaneous activities that collectively increase cold hardiness. Water content of some tissues decreases, while increases occur in cells' solute (dissolved solids) concentration, membrane permeability, and the thermal stability of several enzymes.

Howell (2000) has reviewed the mechanisms by which grapevines survive cold temperatures. The primordial tissues of dormant buds survive by avoiding the formation of ice crystals in the tissue by *supercooling*—a process by which a liquid remains fluid below its normal freezing temperature. Other tissues survive by increasing their capacity to tolerate both ice in the tissue and increased concentration of solutes in the cell. Increased solute concentration in the cell lowers its freezing point.

Because of the different mechanisms involved, tissues vary in tolerance to freezing temperatures. Woody tissues of the trunk, cordon, and canes generally have greater cold hardiness than dormant buds and roots. In comparisons of grapevine woody tissues, the vascular cambium is thought to be the last tissue to be damaged by cold temperatures, followed in sequence by younger xylem, older xylem, and phloem (Wample et al., 2000). Within dormant buds, primary buds are typically less cold hardy than secondary buds, and tertiary buds are the most hardy.

Species and varieties of grapes exhibit a broad range of potential cold hardiness based on their inherent genetic characteristics. This fundamental genetic potential for cold hardiness is influenced by both environmental conditions and the circumstances under which the vine grew in the previous season. Poor management practices or growing conditions can inhibit the acclimation process, resulting in reduced cold hardiness. Acclimation is promoted by exposure of shoots and leaves to sunlight and is associated with periderm development and low relative water content. Cold hardiness can vary considerably between and within vines. Reduced hardiness has been associated with large, dense (shaded) canopies, canes with either long internodes or large internode diameter, and canes with large persistent lateral canes. Additionally, heavy fruit loads or defoliation (early leaf fall due to stress, disease, or pest activity) inhibit acclimation, probably through reduced availability of photosynthates. Contrary to popular belief, neither nitrogen fertilization nor irrigation practices reduce grapevine cold hardiness, unless nonstandard practices are used that encourage continued late-season growth, which inhibits acclimation (Wample et al., 2000).

Cold hardiness of buds is fairly stable through the winter months, but sharp increases in temperature can cause buds to deacclimate and lose hardiness, and the extent of deacclimation can vary by variety or species. Bud hardiness has been correlated with air temperature of the preceding five-day period. Cold hardiness decreases as the grapevine rapidly deacclimates in response to warm temperatures in the spring. Deacclimation is much less gradual than cold acclimation in the fall, and the rate of deacclimation accelerates through the dormant season.

Fruit Growth

Berry development commences after successful pollination and fertilization of ovules within a flower. Flowers with unfertilized ovules soon shrivel and die, while those remaining begin growth into berries. Many of these tiny berries, *abscise* (drop off) within the first two to three weeks. Following this drop period (called

shatter), the retained berries generally continue to develop to maturity. Commonly, only 20–30% of flowers on a cluster develop into mature berries, but this is adequate to produce a full cluster of fruit.

The berry develops from the tissues of the pistil, primarily the ovary. Although pollination and fertilization initiate fruit growth, seed development seems to provide the greatest growth stimulus, as evidenced by the relationship of fruit size to the number of seeds within the berry. The maximum number of seeds is four, but lack of ovule fertilization or ovule abortion reduces the number of developing seeds, generally resulting in smaller berry size.

Berry growth occurs in three general stages—rapid initial growth, followed by a shorter period of slow growth, and finishing with another period of rapid growth. A graph of grape berry growth thus appears as a double sigmoid pattern. Berry growth during the first stage is due to a rapid increase in cell numbers during the first three to four weeks, followed by two to three weeks of rapid cell enlargement. During this stage the berries are firm, dark green in color, and rapidly accumulating acid. Seeds have attained their full size by the end of the first growth stage.

The middle stage, called the *lag phase*, is a time of slow growth. The embryo is rapidly developing within each seed, and the seed coat becomes hardened. Berries reach their highest level of acid content and begin to accumulate sugar slowly. Toward the end of lag phase, berries undergo a reduction in chlorophyll content, causing their color to change to a lighter green.

The final stage of berry growth coincides with the beginning of fruit maturation (*ripening*). The beginning of ripening, referred to by the French term *veraison*, is discernable by the start of color development and softening of the berry. The color change is most easily visible on dark-colored varieties, but “white” varieties continue to become lighter green, and some varieties turn a yellowish or whitish-green color by harvest. Softening of the berry and rapid sugar accumulation occur abruptly and simultaneously. Berry growth, occurring by cell enlargement, becomes rapid again in this final stage of ripening. It is thought that most of the water entering the berry after *veraison* comes from phloem sap, since xylem at the junction of the berry and its *pedicel* (stem) appears to become blocked at this time (Coombe, 1992).

During ripening, acid content declines and sugar content increases. It is widely believed that flavors develop in the later stages of ripening. Berries begin to accumulate sugar rapidly at the start of the ripening period, and the rate tends to remain steady until accumulation slows as the end of the maturation period is approached. Sugar is translocated as sucrose

to the fruit, where it is quickly converted into glucose and fructose. Both sugars and acids primarily accumulate in cells constituting the *pulp* (flesh) of the berry, although a small amount of sugar accumulates in the skin.

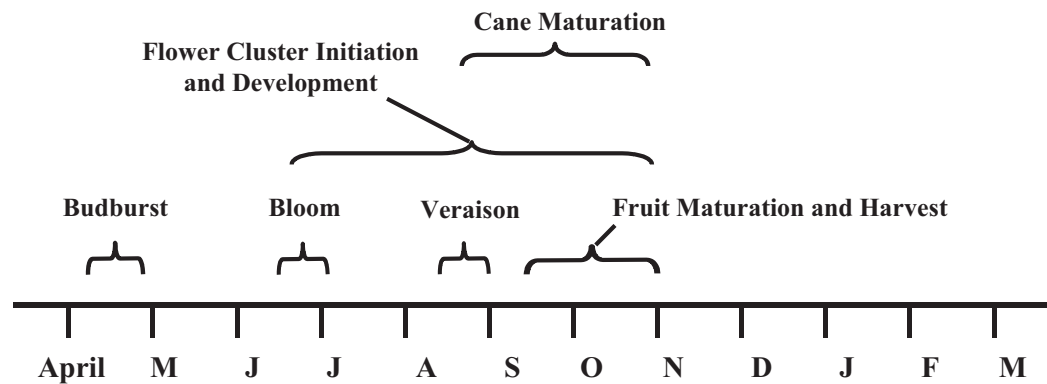
The skin (epidermis) and the thin tissue layer immediately below it contain most of the color, aroma and flavor constituents, and tannins contained in the berry. Thus, all things being equal, small berries have greater color, tannins, and flavor constituents than large berries because the skin constitutes a larger percentage of the total mass of small berries. Seeds also contain tannins that can contribute to the overall astringency of wine.

The chemical composition of grape berries is complex, consisting of hundreds of compounds, many in tiny quantities, which may contribute to fruit quality attributes. The single largest component is water, followed by the sugars fructose and glucose, then the acids tartaric and malic. Other important classes of chemical compounds within grape berries include amino acids, proteins, phenolics, anthocyanins, and flavonols. The reader is referred to a review of the biochemistry of grape ripening by Kanellis and Roubelakis-Angelakis (1993) for a thorough discussion of this topic.

Berries are considered to be fully *ripe* when they achieve the desired degree of development for their intended purpose, and they are generally harvested at this time. Ripeness factors of the fruit that are typically considered when scheduling harvest are sugar content, acid content, pH, color, and flavor. The combination of these factors determines the *fruit quality* of the harvest. Ripening processes in the fruit cease upon harvest, but while fruit is on the vine ripening is a continuous process. So there is usually a short time, influenced by weather, during which the fruit remains within the desired ripeness parameters. Berries can become *overripe* if harvest is delayed until the fruit has developed beyond the desired range of ripeness. Consider also that ripeness parameters can vary considerably depending on the intended use. For example, Pinot noir grapes for sparkling wine production are harvested much earlier, at lower sugar and higher acid content, than Pinot noir for non-sparkling red wine. Thus, the terms “fruit ripeness” and “fruit quality” do not have absolute values but are defined subjectively.

Fruit ripening can be delayed, and the attainment of desired ripeness parameters inhibited, by an excessive *crop load* (amount of fruit per vine). A vine that is allowed to produce more fruit than it can develop to the desired level of ripeness is considered to be *overcropped*. Severe overcropping can negatively impact vine health as well as fruit quality by precluding

Figure 8. Annual cycle of grapevine growth. Figure by Ed Hellman.



the vine from allocating adequate photosynthates to weaker sinks: shoots, roots, and storage reserves. Viticulturists generally seek to attain *vine balance*, the condition of having a canopy of adequate, but not excessive, leaf area to support the intended crop load to the desired level of fruit ripeness.

Climatic factors, particularly temperature, have long been recognized to have a major influence on the fruit quality of grapes and subsequent wine quality. The principal effect is on the rates of change in the constituents of the fruit during development and the composition at maturity. Hot climates favor higher sugar content and lower acidity; cool climates tend to slow sugar accumulation and retain more acidity. Grape varieties tend to ripen their fruit with a desirable combination of quality components most consistently in specific climates. Thus, some varieties, such as Pinot noir and Gewürztraminer, are considered to be “cool climate varieties,” whereas others such as Carignane and Souzão are considered to be “warm” or “hot climate varieties.” A few varieties, most notably Chardonnay, are capable of producing high-quality wines in different climates by adjusting the wine style for the varying expression of fruit characteristics in each climate. The relationship of climate, and in particular temperature, to fruit ripening and wine quality has been incorporated into methods of matching grape varieties to climate; Winkler’s heat summation (degree days) system for California (Winkler et al., 1974) is one such system, and there are other more elaborate methods (see, e.g., Jackson and Cherry, 1988; Gladstones, 1992). *Phenology* is the study of the relationship between climatic factors and the progression of plant growth stages and developmental events that recur seasonally.

Thus, the first step in the production of high-quality winegrapes is the selection of a site with appropriate climatic characteristics for fruit ripening of the varieties to be grown. Vineyard practices, including training systems and canopy management, are utilized to optimize the sunlight and temperature characteristics of the canopy for fruit ripening. In cool

climates, canopy management practices that provide good exposure of leaves and fruit to sunlight have generally improved grape and wine composition. Vines in which the canopy interiors are well exposed to sunlight usually produce fruit with higher rates of sugar accumulation, greater concentrations of anthocyanins and total phenols, lower pH, and decreased levels of malic acid and potassium compared to vines with little interior canopy exposure (Williams et al., 1994). Improved fruit quality under such circumstances may be due to higher temperatures in addition to better sunlight exposure, but it is extremely difficult to separate these factors.

The Annual Cycle of Growth

The annual growth cycle of the grapevine involves many processes and events that have been briefly introduced above. Figure 8 illustrates the sequence of major processes and events in a timeline. It should be recognized that the timing and duration of developmental events are subject to variations due to the grape variety, local climate, and seasonal weather, but the sequence of events remains constant. It is significant that many of these events overlap others for a period of time, requiring the vine to allocate its resources among competing activities. For example, during the time that the vine is developing and ripening the current season’s fruit, flower cluster initiation and development is underway in dormant buds and carbohydrates are being moved into storage reserves. Therefore, it is of critical importance for the long-term growth and productivity of grapevines that adequate photosynthates be produced to supply the complete needs of the vine. This goal can be achieved by supplying adequate water and nutrients to the vine, maintaining a healthy canopy, providing good sunlight exposure, and developing an appropriate balance between crop load and canopy size.

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