2 Grapevine Development and Basic Physiology

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The Goals of Viticulture

The common goal of viticulture is to make a profit but strategies that maximize vineyard profits can vary among growers, vineyards and regions and depend on:

- the cost and availability of resources including labour and water;
- vineyard environmental conditions (climate and soil) which affect vine performance and impacts of cultural practices, and cause periodic damage to vines such as frost and freeze damage;
- regional marketing forces and winery business goals which affect grape prices and payment incentives for quality;
- the value placed on environmental sustainability, and regulations related to environmental protection;
- the scale of the vineyard operation.

In most grape-growing regions, growing high-quality fruit has become the most profitable to growers, and thus modern viticultural techniques tend to focus on producing quality rather than high yields. However, as yield is an important determinant of revenue, yield is a goal to be balanced with fruit quality. Balance, in fact, underlies many viticultural principles because balancing the positive and negative effects of any resource input or viticultural practice is important for optimizing vineyard performance.

Basic Physiology

CO_2 + Sunshine + Heat + Water + Minerals =
Vine + Grapes

To understand the mechanisms underlying viticultural practices it is important to understand some basic vine physiological processes and how they can be manipulated. Grapevines, like all plants, make sugar which is used to supply energy for chemical processes, and as a substrate for the synthesis of all components of the vine and fruit. Sugar is also converted over the growing season into starch which is stored and invested in the protection of buds, roots and woody tissues over winter and used to support initial growth the following year. Sugar is made in the leaves through photosynthesis which is a multi-step chemical process that requires sunlight, CO_2 and water. For CO_2 to move into the leaves, the stomata (pores) on the leaf undersides must be open which allows for water vapour to be transpired. Nearly all of the water taken up by grapevines is transpired. The process of transpiration cools leaves and creates a stream that carries minerals and other chemicals from the root system via xylem in the trunk and woody branches (cordons and spurs) to shoots, leaves and fruit. The remaining small portion of water taken up is used in photosynthesis and other chemical processes, and as the solution solvent in cells and a medium for chemical reactions. Water, under pressure in cells, is also needed for expansive growth. Therefore water supplied to vines plays a critical role in sugar production, growth, the movement of minerals from roots to shoots, and as a major component of plant tissues. Respiration is the process that releases energy from the chemical bonds in sugars and compounds made from sugars. Malic acid is such a compound and is respired especially during the latter part of berry development. All live plant tissues respire, and the process requires oxygen. For roots, oxygen is provided from air in the soil pore space, thus waterlogged or highly compacted soils can be harmful or lethal to grapevines.

Nearly all chemical processes in plants, including the steps in photosynthesis and respiration, are catalyzed by special proteins called enzymes. Enzymes make up most of the protein in grapevines, and some of the most abundant enzymes are those involved in photosynthesis. A major mineral constituent of all proteins is nitrogen. As enzymes are important for all physiological processes in grapevines, nitrogen supply is of critical importance to grapevine growth and development. Other mineral nutrients are also essential as constituents of enzymes and other plant compounds. Examples are: sulfur which is another important enzyme component; magnesium which is a constituent of chlorophyll; phosphorus which is a constituent of the energy-transport compound adenosine triphosphate (ATP); and potassium which is used to balance osmotic pressures across membranes in cells. When these and other essential minerals are deficient, plant growth and development is hindered. Most or all of the vine's mineral nutrients are taken up from the soil by roots. Small amounts of mineral nutrients including nitrogen in specific forms (i.e. as urea, but not as N_2 gas) may be taken up by leaves.

Plant hormones are compounds produced in one part of the plant that trigger physiological changes or regulate physiological processes in another part. These signaling compounds are important in determining budbreak patterns, shoot growth, leaf function and many other processes in grapevines. Auxins are plant hormones that are produced in shoot tips and are transported away from this site where they have many effects, depending on their concentration, from stimulating elongation of shoots and roots to inhibiting bud development. Gibberellins are produced in several tissues and cause shoot elongation and are involved in breaking dormancy. Cytokinins are also produced in several tissues and stimulate cell division and prevent senescence. Ethylene is a gaseous hormone that is stimulated by auxin and may be involved in auxin-induced effects. Ethylene is produced in leaves where it triggers senescence, and in fruit where it may be required for fruit ripening. Abscisic acid (ABA) is involved in inducing dormancy, in the abscision of leaves, and in regulating stomatal conductance. Recently, abscisic acid was shown to influence important aspects of berry development including production of anthocyanins.

Vine Development

Grapevines are woody perennials. The shoots they produce each growing season turn woody in the fall, and if retained after pruning, serve as supporting structures in the following year. Three dormant buds (primary, secondary and tertiary) and a lateral bud form in every leaf axil during the growing season. Each dormant bud contains a compact shoot with up to three cluster primordia (undeveloped flower clusters). The primordia are initiated over a short period in the summer and the numbers that form in each bud is influenced by the light microclimate of the bud and subtending leaf and by the nutrient status of the vine at that time. Lateral buds develop into lateral shoots in the same season they form and may bear fruit in small clusters which are developmentally behind the clusters developing on shoots arising from dormant buds.

Dormant buds require exposure to cold and then warm temperatures (as in winter followed by spring) to break and develop into full shoots. In the spring, after the temperature requirements for budbreak have been met, the primary bud at each node will develop into a shoot if there are sufficient carbohydrate reserves in the bud and nearby vine wood to support the bud's development, and if the bud is not suppressed by chemical signals from other nearby developing buds or shoots. Often, if the vine has abundant reserves, the secondary and sometimes tertiary buds will develop into shoots. If the primary bud has been damaged over winter, the secondary bud will often be undamaged and will develop into a shoot. However secondary buds most often bear fewer clusters than do primary buds.

Initially, shoot growth is supported by stored reserves of carbohydrate and mineral nutrients, but soon after the shoot elongates and its leaves become fully functional, its growth begins to be supported by sugars produced by its own leaves and by minerals newly taken up by the roots. Sugars move through the shoot and woody parts of the vine via phloem. The direction of flow in phloem is dependent on demand, known as sink strength, exerted by developing tissues. Tissues and organs with strong sink strengths include growing shoot tips and developing clusters. When clusters are undergoing a high rate of sugar accumulation, their sink strength is particularly strong and will suppress growth of shoots.

The nutritional status of the shoot and the light microclimate surrounding its developing buds determines not only the number of primordia in dormant buds but the size of cluster primordia. In the following year, primordium size is correlated with the size and number of flowers borne by the clusters that develop. Thus the yield components cluster number and flowers per cluster are influenced significantly by conditions in the previous year. During the year the clusters develop, the stage most vulnerable to environmental conditions is the fruit-set period. Low temperatures during bloom can greatly reduce the number of berries that set.

Berry growth follows a double-sigmoidal pattern common to other fruit crops. In the first rapid phase of growth, cell division and expansion both contribute to the growth of the skin (exocarp), flesh (mesocarp) and seeds. Further development and maturation of seeds dominate in the lag (slow-growth) phase that follows. In the final, rapid growth phase commencing with veraison, growth is mainly due to cell expansion in skin and flesh tissues. A high rate of dry matter accumulation is typical in the final growth phase while sugars are accumulating.

Heat drives all growth and developmental processes in grapevines, and thus growing season temperatures can substantially influence the timing of fruit maturation. The basal temperature for growth and development of grapevines is considered to be 10^{o}C which is commonly used in the calculation of growing degree days for predicting phenological dates and fruit maturation. However, from our work conducted in the Okanagan Valley on Merlot vines, it appears that the basal temperature for vegetative growth is near 0^{o}C, and for cluster development is near 10^{o}C, and thus cool temperatures would favour vegetative growth. Grapevine varieties differ in phenological timing, and this is likely due to differences in temperature response including basal and maximum temperatures for growth and development.

In addition to the strong influence of temperature, the supply of water and mineral nutrients also affects the progress of vine development. Low availability of water and nutrients hinders growth and physiological processes and leads to delays in the development and maturation of fruit, and in poor fruit quality. However, excess supplies of water and nutrients, especially nitrogen, can lead to a combination of excess vigour, shady canopies, large berries, high yields, delayed fruit maturation and poor quality fruit. Thus there are optimum levels at which resources should be supplied to prevent excesses in water and nutrient stress, vine vigour and berry growth.

The concept of vine balance refers to the achievement of a balance between vegetative growth and crop level that results in full maturation of the crop by the end of the growing season and in fruit of a particular quality goal. Vine balance is achieved mainly through a combination of vine training and pruning, shoot and/or cluster thinning, and the supply of optimum levels of water and nutrients. Appropriate vine spacing during vineyard establishment can also contribute to the achievement of a balanced vineyard. A commonly accepted way to measure vine balance is to determine the weight ratio of crop to prunings (C/P). Depending on viticultural goals, C/P of a balanced vineyard can range from 4 to 11. For example, optimum C/P for a white variety growing in a warm region might be 10, whereas for a red variety growing in a cool climate it might be 4. Vines out of balance produce fruit of inferior quality. If C/P is too low, vines can develop excess vigour and shady canopies that are detrimental to fruit quality and result in reduced bud fruitfulness (number of cluster primordia in dormant buds). If C/P is too high, vines are overcropped and fruit may not mature, and if the canopy is sparse excess fruit exposure can result in sunburn damage. Supply of water and nutrient resources can influence fruit quality at a specific C/P level. Providing more abundant supplies of water and nutrients can increase both vegetative vigor and yield without affecting C/P, but fruit quality will likely be different. In either case (low or high resource supply), fruit quality can be affected further by canopy management. Further information on canopy management methods and effects can be found in Pruning and Canopy Management Sections.

Important to achieving vine balance in most vineyards is shoot and/or cluster thinning. The timing of these practices can influence canopy microclimate and the partitioning of vine resources among shoots and clusters at critical developmental stages that ultimately affect bud fruitfulness and fruit quality. To achieve timely increases in light and vine resources provided to shoots and clusters, shoot thinning should be done early in the growing season when shoots are small and can be easily removed.

Similarly, to increase vine resources and light (when clusters are stacked) received by developing clusters, cluster thinning should also be done early, in the early stages of berry development. The practice of "bleeding off" an overabundance of vine resources (i.e. carbohydrate, water and nitrogen) that leads to rank growth and large berries by retaining excess numbers of shoots and/or clusters until late in the season achieves little benefit to fruit quality other than the late cluster thinning to cull immature or diseased clusters. Late removal of sound clusters of the same quality as those retained does little other than reduce yield.

Fruit compositional development is influence by many environmental and viticultural factors. There is abundant literature indicating that fruit microenvironment including ambient temperature and light, can affect the colour, aroma, tannin profile and other fruit compositional components that influence winemaking quality. Thus canopy management practices that influence fruit microenvironment are essential for attaining desirable fruit quality. Sunlight exposure and ambient temperature both influence berry temperature which affects the rate of berry development and relative rates of metabolic processes involved in the degradation of acid and synthesis of phenolics and aroma compounds.

Another important contributor to berry quality is berry size which is influenced heavily by vine water status and by the supply of other vine resources. Berry size affects the relative amount of skin, flesh and seed tissues in berries, and each contributes different compositional components to must. Much of the benefit of deficit irrigation to must and wine quality is likely due to small berry size and the higher amounts of berry skin and seeds relative to flesh. However, there is good reason to believe that water stress affects berry quality characteristics other than size and relative tissue amounts. ABA produced in roots in response to moisture deficits is translocated to leaves where is causes partial closure of stomates which conserves water. Recent research findings indicate that ABA directly enhances the production of berry anthocyanins.

We have shown that reduced irrigation in the Okanagan Valley can affect fruit quality by advancing fruit maturation. Moisture deficits resulting from drip irrigation as compared with sprinkler irrigation were found to increase vineyard temperatures by reducing cover crop growth, vine canopy size and transpiration rates. Despite having substantially lower leaf areas and photosynthesis rates, vines under drip irrigation produced fruit that matured earlier. This effect could be beneficial in vineyards where fruit does not always reach full maturity. However, fruit that matures too early in the growing season under warm temperatures tends to be lower in acidity and may lack some of the aroma and other quality components that develop in fruit ripening over a longer cooler period late in the season.

Effects of Vine Injury

Grapevines can be injured or killed by a number of agents including pests, diseases, frost and cold. A vine's ability to withstand or recover from injury depends on which organs or tissues have been damaged, and the health and physiological state of the vine at the time of injury.

As most vines have more leaf area than needed to produce sufficient sugar to ripen a moderate crop yield, perceptible amounts of insect damage to leaves can usually be tolerated and will have no effect on production or quality. However, if total leaf area is low relative to the crop level (C/P is high), vines are under stress from lack of water or nutrients, or leaf function has been impaired due to disease, then small amounts of insect damage can impact fruit development and the carbohydrate available to be stored as reserves. Other causes of leaf injury including frost and foliar diseases often damage a large portion of total leaf area which can significantly impact fruit development. Growers should consider the extent of leaf damage and potential impact to the crop and stored reserves when deciding on controls to prevent leaf damage. When a large portion of leaf area has been damaged before the crop is mature, the crop should be thinned or removed to ensure there will be sufficient carbohydrate stored in reserves over winter to support early growth in the following spring.

Damage to vine buds, especially primary buds, can significantly impact the current year's crop by reducing the number of shoots and/or clusters. Cold temperatures in winter, or cutworm grazing in spring, can kill a significant number of primary buds. Often secondary buds will develop and produce clusters when primary buds have been killed, but secondary shoots usually bear fewer clusters and these may mature later due to their delayed development. Despite these possible impacts to the crop, the development of secondary shoots can be important in maintaining the carbohydrate status of the vine. If winter temperatures reach below -22°C, substantial numbers of buds may be killed, including secondary and tertiary buds. Bud hardiness, which is the ability of buds to withstand cold temperatures, increases as vines are exposed to subzero temperatures that become progressively colder over a number of days or weeks. Such well-acclimated buds can withstand temperatures as low as -23°C without perceptible damage. Vines that have been exposed to warm temperatures near or above 0°C for a period can be inflicted with lethal damage to buds and vine tissues if exposed suddenly to temperatures near -15°C. Vine death can result from prolonged exposure to temperatures below - 25°C. Susceptibility to cold injury depends on the level of acclimation, the variety, length of exposure, and health of the vine.