

# GRAPEVINE PHYSIOLOGY

How  
Does a  
Grapevine  
Make  
Sugar?



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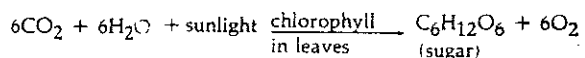
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# How Does a Grapevine Make Sugar?



All forms of viticultural produce (grapes, raisins, distilled wine alcohol) have their origins in the sugars produced within grapevine leaves by a process known as *photosynthesis*. When leaves photosynthesize they use energy from the sun to manufacture sugar from carbon dioxide ( $\text{CO}_2$ ), absorbed from the air and water drawn from the soil. Photosynthesis takes place in microscopic bodies called *chloroplasts* located within the cells of every green leaf. Chloroplasts contain the green pigments known as *chlorophyll*, which are responsible for trapping sunlight and converting that energy into carbohydrates. The photosynthesis process in its simplest form can be represented by the reaction:



This sugar, formed from the vine's foliage, represents atmospheric  $\text{CO}_2$  which has become fixed as carbohydrates, and is now available for root and vegetative growth and fruit production. Since a vine's total photosynthetic activity for the season determines to a large extent its yield, we are naturally interested in how various environmental factors, especially climate, limit photosynthesis. The climatic factors that will be discussed here are light, temperature, and soil moisture. Other environmental factors—such as oxygen and carbon dioxide—also affect the rate of photosynthesis. However, they will not be discussed here, since there is little a grower can do to change those factors under field conditions.

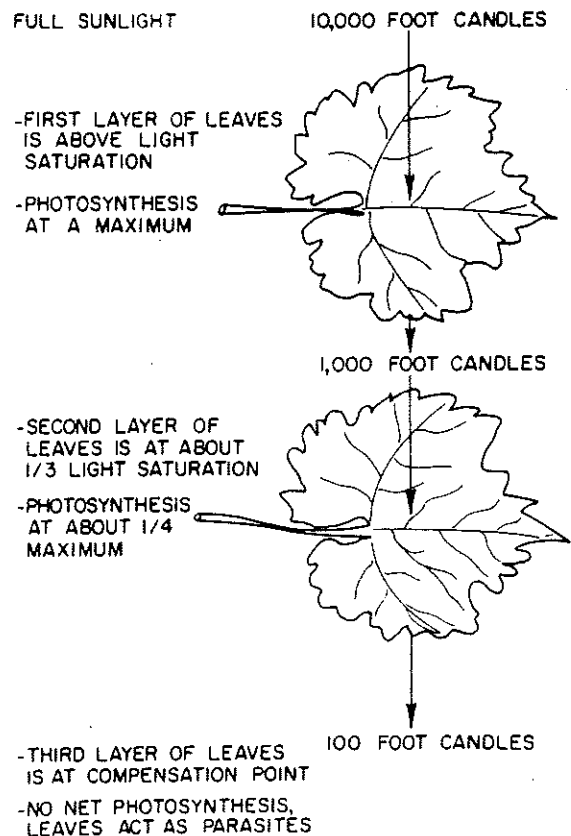
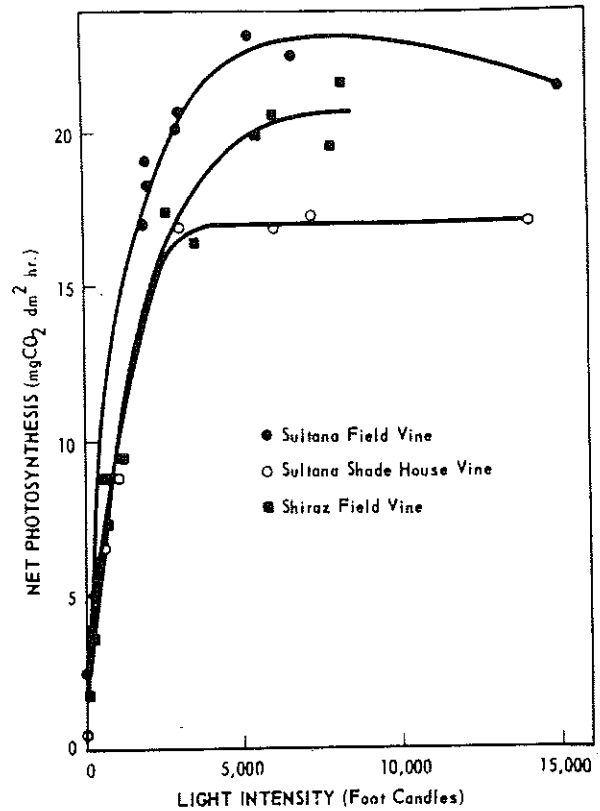
Fig. 1. Effect of light intensity on leaf photosynthesis of Sultana (Thompson Seedless) and Shiraz field vines. From Kriedemann and Smart (1971), *Photosynthetica* 5:6-15.

**Environmental factors.** *Sunlight* is the environmental factor that is most frequently not fully utilized by grape growers to maximize crop yields. By manipulating vine width and height through trellis-training systems, row direction, and vine and row spacing, a grower can greatly increase the total amount of light intercepted by foliage per unit area of vineyard and thereby increase photosynthetic capacity.

The light intensity required for maximum photosynthesis, where environmental conditions are optimal, ranges from 3000 to 5000 foot-candles, or 150 to 200 watts per meter square. To put this into terms more easily understood, it is equal to about one-third to one-half of full sunlight on a clear day around noon in California for a leaf held at a right angle to the sun's rays. (A typical light response curve is shown in fig. 1.) The light intensity where photosynthesis first reaches maximum is known as the *light saturation point* and is strongly influenced by the light environment under which leaves are grown, being lower for leaves grown under shaded conditions than for leaves grown in full sunlight.

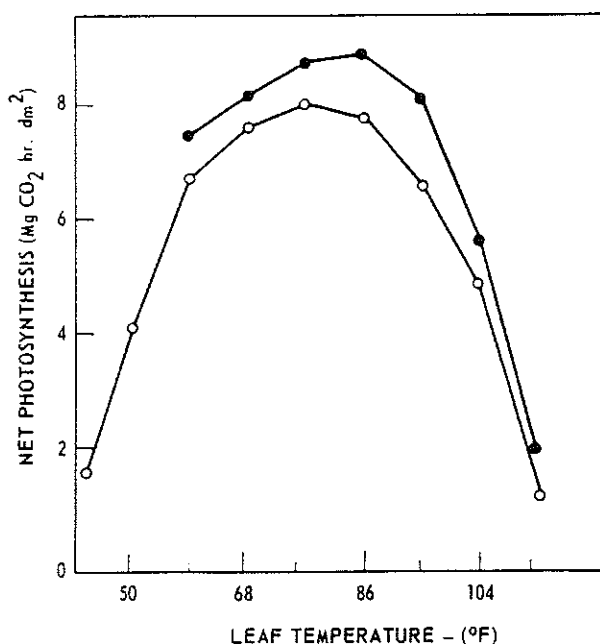
Seemingly, bright sunlight is not used very effectively by the grapevine. A typical vine canopy represents many layers of leaves and usually only relatively few of the leaves are directly exposed to full sunlight during the entire day. A single vinifera grape leaf of average thickness will absorb 90 to 95 percent of the solar radiation at wavelengths effective for photosynthesis (400 to 700 nm); but the level of light intensity reaching leaves beneath the first outer layer of the vine's canopy is less than that required for maximum photosynthesis (fig. 2). In fact, if light must pass through two layers of leaves the intensity of light reaching the third layer of leaves would theoretically be at about the *light compensation point* (100 to 125 ft-c or 2 to 5  $\text{wm}^{-2}$ ), or the light intensity where the rate of photosynthesis just equals the rate of respiration and a vine would neither gain nor lose weight.

Fig. 2. Diagrammatic representation of the relative amount of sunlight absorbed of different layers of grape leaves within a dense vine canopy. Light intensity of sun assumed to be 10,000 foot-candles.



Fortunately, two other phenomena help alleviate the low light conditions that normally prevail in interior parts of a vine's canopy. One is the presence of diffuse light. Diffuse light is light reflected from clouds, soil surface, impurities in the air or any other object. Most light reaching interior leaves within a canopy is diffuse light. A second factor that helps offset the detrimental effect of low light inside canopies is sunflecks of light that shine through gaps in the canopy caused by movement of leaves by wind. Experiments have shown that grapevines have a very efficient mechanism for utilizing these flecks of light hitting portions of leaves and only 1 percent of the area of a leaf needs to be illuminated to offset respiratory losses. However, even with diffuse light and sunflecks there may be leaves in interior parts of the vines with dense canopies that are below the light compensating point. Such leaves usually become yellow and eventually fall off the vine—nature's way of eliminating the unproductive and preventing those leaves from becoming parasitic. The condition can largely be eliminated by using a wide double-curtain type trellis system that enables most of a vine's leaf area to receive direct solar radiation.

Temperature determines the form of the light response curve, since photosynthesis involves both biochemical and photochemical reactions.



The photosynthetic temperature response curve can be divided into three temperature categories: suboptimal, optimal, and excessive. The rate of photosynthesis at temperatures below 20° C (68° F) is less than that at 25 to 30° C, due to both lower activity of carboxylating enzymes and photochemical activity. The optimum temperature for photosynthesis by grape leaves is 25 to 30° C or 77 to 86° F (fig. 3). That temperature, however, is not necessarily the optimum temperature for growth and development of all parts of the vine, since translocation of carbohydrates and subsequent metabolism in roots, shoots, and fruits might operate best at different temperatures. For example, it is well known that synthesis of red anthocyanin pigments in grape skins is greater at 15 to 20° C (60 to 70° F) than at 25 to 30° C (75 to 85° F).

Photosynthesis declines rapidly above 30° C (86° F) and falls to nearly zero at 45° C (113° F). High temperatures reduce photosynthesis through thermal instability of enzymes, tissue desiccation, and closure of stomata pores. Respiration increases at a faster rate than photosynthesis at temperatures above 30° C. Temperatures of leaves directly exposed to solar radiation at right angles during mid-day can exceed air temperature by as much as 10° C (18° F) but generally temperatures of sun-exposed leaves during the day are 0.5 to 5° C (1 to 10° F) above air temperature. Moisture deficit will also contribute to increasing temperature of leaves above ambient temperature.

Water is of considerable importance in photosynthesis not only as a major reaction constituent, but also through its control of stomatal opening and its effect on wilting of leaves. The water that combines biochemically with CO<sub>2</sub> from the atmosphere represents less than 1 percent of the water absorbed by vine roots; the remaining 99+ percent is lost in transpiration. If evaporative demand causes leaf transpiration to exceed water supply, a moisture stress develops within the

Fig. 3. Effect of leaf temperature of Thompson Seedless vines on net photosynthesis. Light intensity was constant at about 4,000 foot-candles. Absolute magnitude of net photosynthesis values can change according to seasonal influences. Solid circles are for vines grown under full sunlight and open circles are for vines grown in the greenhouse. From Kriedemann (1968), *Vitis* 7:213-220.

foliage. If the stress, which is usually expressed as leaf water potential, exceeds -13 atmosphere, the stomates close and photosynthesis stops (fig. 4). If sufficient water becomes available, leaf water supply generally recovers, particularly at night when evaporative demand is low. If water supply remains inadequate the vine eventually wilts. In this event, stomatal function is temporarily impaired because stomata then fail to re-open despite restoration of adequate moisture within the leaf. Nearly a week can elapse before stomatal function and photosynthesis are fully restored (fig. 5). The delay in recovery of photosynthetic performance has been shown to involve abscisic acid, an inhibitory hormone that occurs naturally in plants. When moisture stress builds up in a grapevine, levels of abscisic acid correspondingly increase. Abscisic acid is known to induce stomatal closure so that a massive accumulation of the hormone in leaves could very well prolong the effects of moisture stress on stomatal function and thus account for the slow recovery of photosynthesis.

*Internal factors* influence photosynthesis. Leaves have a finite capacity for CO<sub>2</sub> assimilation. That capacity is determined by the genetic makeup of the plant, and is set by diffusive resistances in the leaf in combination with enzyme activity at carboxylation sites within chloroplasts. Either component may become rate limiting and both are subject to internal control.

Under favorable conditions leaves generally have the capacity to photosynthesize faster as the demand for their products increases within the genetic limitations of the plant. The principle of photosynthetic response to demand is generally found throughout the plant kingdom and is generally referred to by plant physiologists as the *source-sink* relationship; where leaves are usually considered the source of assimilates, and the sink is any part of the plant that attracts the products of photosynthesis. Rapidly growing fruits, shoot, and root tips would then be considered sinks in this context.

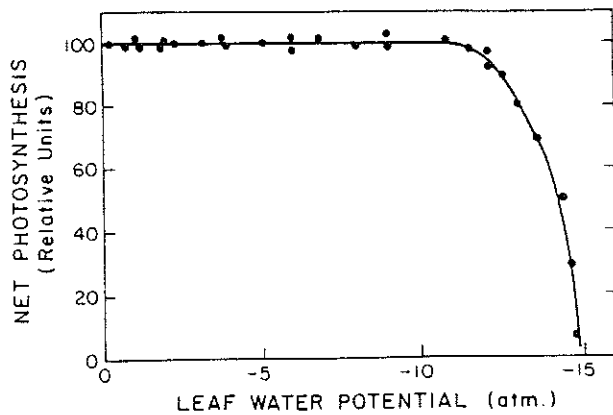


Fig. 4. Changes in rate of photosynthesis of Shiraz leaves with increase in water stress. Net photosynthesis expressed in relative units where 100 = 17.5 mg CO<sub>2</sub>dm<sup>-2</sup> hr.<sup>-1</sup>. Data from Kriedemann and Smart, *Photosynthetica* 5:6-15 (1971).

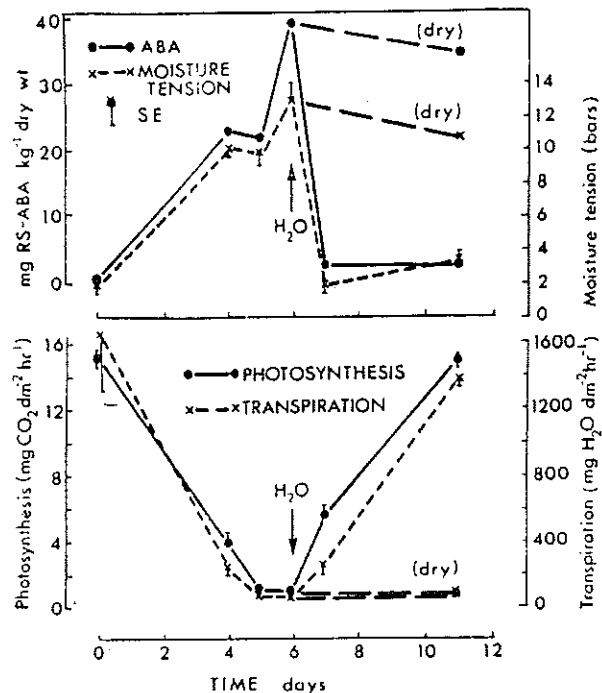


Fig. 5. Thompson Seedless potted vines deprived of irrigation over a 6-day period show a progressive increase in moisture tension with an associated increase in abscisic acid-like inhibitors (ABA level rises by a factor of 44). Peak values coincide with stomatal closure. Once vines are irrigated leaf water potential is restored almost immediately and ABA level falls precipitously, but stomatal function remains impaired for several days. (From Kriedemann and Loveys, *Physiol. Plant.* 28:476-79, 1972).

TABLE 1. Variation of Photosynthesis in *Vitis vinifera* L. cv. Cabernet Sauvignon According to Crop Load and Leaf-Number

Treatment*	Photosynthesis† ng (CO <sub>2</sub> )cm <sup>-2</sup> s <sup>-1</sup>	Stomatal resistance (s cm <sup>-1</sup> )	Internal resistance	Absciscic acid (μg kg <sup>-1</sup> )	Phaseic acid
Fruit present					
6 leaves	52.8	2.6	7.3	74	79
3 leaves	65.8	2.0	5.9	43	37
Fruit removed					
6 leaves	38.3	2.5	11.9	62	81
3 leaves	58.3	1.8	7.8	33	35

\*Potted vines were trimmed to 3 or 6 leaves (± bunch) before transfer from a greenhouse to controlled environment cabinets.

†Leaf gas exchange rates (lab. measurements) adjusted to new conditions and treatments, within 5 days.

SOURCE: Kriedemann, et al., Aus. J. Plant Physiol. 2:553-567, 1975.

*Crop load in relation to leaf number.* The effect of reducing the size of the sink (in our example, fruit) as well as reducing the source (leaves), on the rate of photosynthesis is shown by the data in Table 1. When fruit was removed from small potted Cabernet Sauvignon vines, the rate of photosynthesis immediately decreased by 11 to 27 percent. Also, when half the leaves were removed from vines with or without fruit the rate of photosynthesis was increased by 24 to 34 percent. The increase in photosynthesis following leaf removal was attributed to reduced stomatal resistance (stomates open wider), increase in enzyme activity, and freer movement of assimilates in the phloem to growth sites.

Although grapevines retain some capacity to respond to demands of developing fruit, in the majority of field situations bud fruitfulness (i.e. the number of clusters per shoot) and fruit-set are the primary limitations of yield in grapevines. Here the key factor is better light exposure, about which more will be said later.

*Leaf age.* Young expanding grape leaves show a sigmoidal growth curve and maximum photosynthetic activity is attained as the leaf reaches full size—30 to 40 days after unfolding from the shoot apex (fig. 6). The photosynthetic rate of the newly fully-expanded leaves generally remains maximal for 2 to 3 weeks but then gradually declines until the leaf becomes senescent. The increase in photosynthetic activity during leaf expansion is due to greater level of chlorophyll per unit leaf area, increase in carboxylating enzyme activity and reduced stomatal resistance.

The export of photosynthate from expanding leaves follows roughly the same pattern as the increase in photosynthesis. When a grape leaf reaches one-third to one-half full size, more food

is exported from the leaf than imported and a net contribution in growth occurs.

The time during the season when a leaf is formed also apparently has a large effect on photosynthetic capacity. Recent research has shown that a recently fully-expanded leaf formed in the spring had over twice the photosynthetic capacity of a leaf of the same age formed during mid-summer. Whether this is due to changes in source-sink relationships or environmental factors is not known.

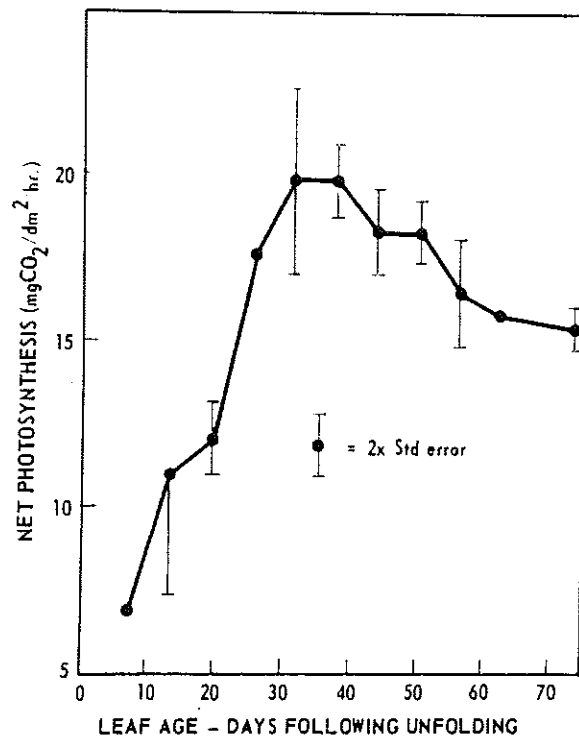


Fig. 6. Relationship between leaf age and net photosynthesis of Thompson Seedless vines. (From Kriedemann, Kliewer, and Harris, 1970, *Vitis* 9:97-104, 1969).

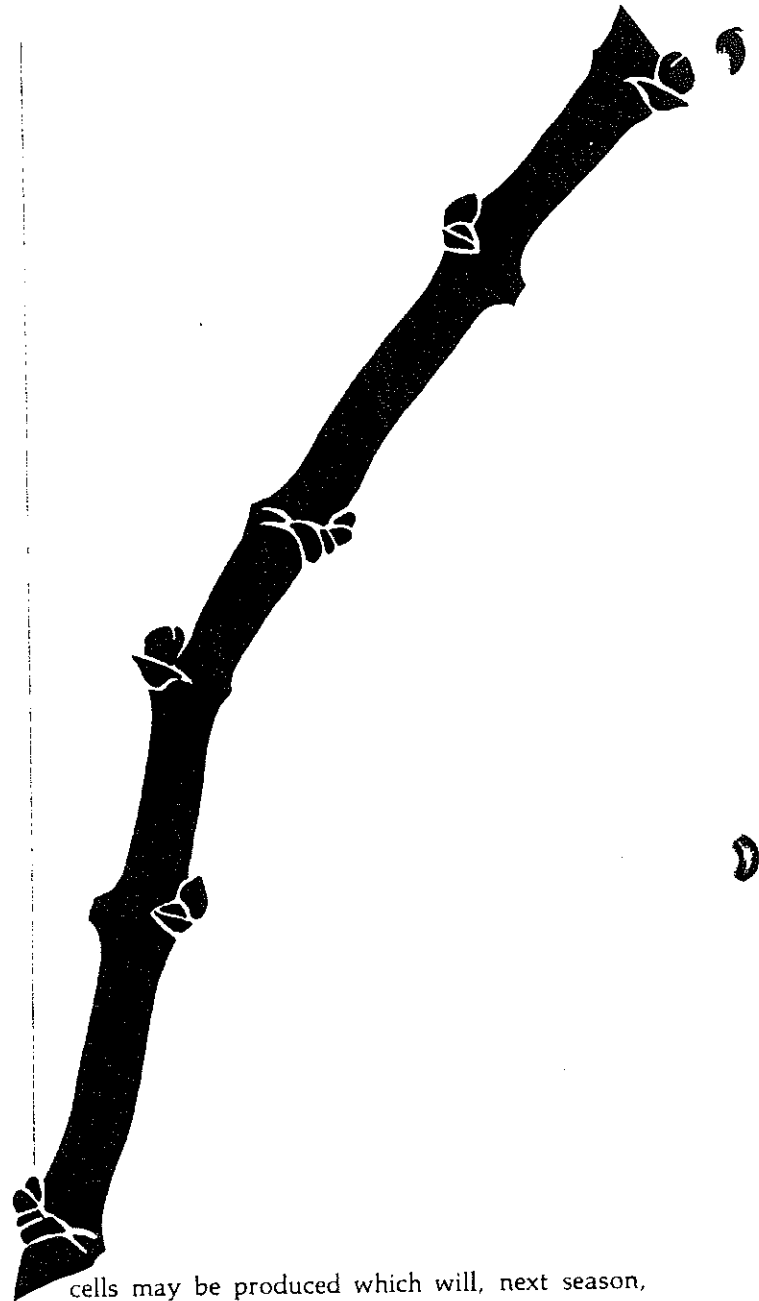
## Fruit Bud Formation

It is well known that varieties differ considerably in their bud fruitfulness. For example most wine varieties have fruitful basal buds, whereas some of our table grape varieties such as Thompson Seedless and Emperor tend to have unfruitful basal buds. Some varieties are much more erratic in both the number and the form of the clusters that are produced than others. The physiology of fruit-bud differentiation is not understood sufficiently to explain all the differences in fruitfulness between varieties. Considerable work has been done to determine when fruit-bud initiation occurs in grapevines and how climatic and cultural factors affect differentiation and formation of fruit primordia in buds.

**The bud system.** In grapevines, buds are formed only in the axil of each leaf. They are compound buds and normally consist of three partially developed rudimentary shoots enclosed inside common scales. This group of buds is called an "eye." Often only the middle or primary growing point of the three rudimentary shoots grows when the vine leafs out in the spring, but occasionally two or all three of the growing points burst and develop into shoots. In addition to the compound bud which develops in the axil of each leaf there is a lateral bud which always grows in the same season it is formed. It may cease growth early and grow only a few millimeters or it may develop into a long lateral shoot. Recent studies have shown that the compound bud actually originates at the lowermost node on the lateral shoot, but early establishes direct vascular connections with the main shoot. Grape buds may be either leaf buds or fruit buds. A leaf bud is a rudimentary sterile shoot that forms only leaves and tendrils and does not bear fruit. A fruit bud contains rudimentary leaves, flower clusters, and tendrils. It is impossible to tell a leaf bud from a fruit bud by their outer appearance; this can only be done by microscopic examination.

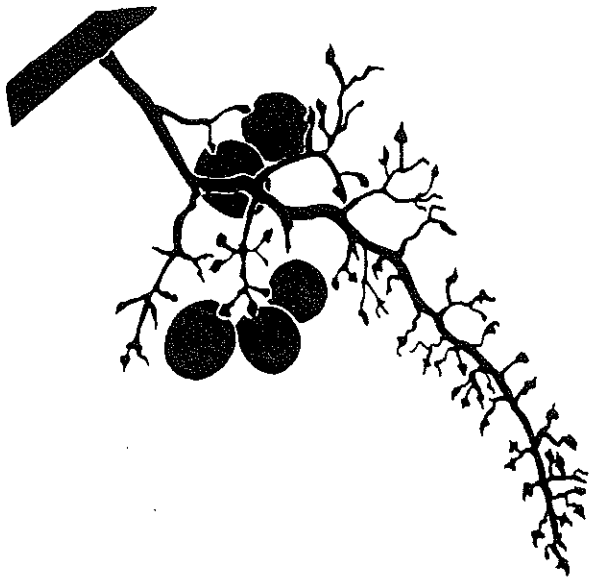
**Fruit bud formation in buds.** The rudiments or primordia of the grape flower cluster are formed during the season preceding the year in which the flowers bloom. For example, whether a shoot in 1981 has a cluster is determined already in 1980.

At some stage during the period when rudimentary leaves are being formed in the developing bud during spring time, one or more groups of



cells may be produced which will, next season, grow into either a flower cluster (inflorescence) or tendril. Whether these groups of cells or primordia develop into an inflorescence or a tendril is determined quite early during the growth of the bud. Indications are that induction of cells into cluster primordia occurs the first few weeks after a node separates from the shoot apex. However, the actual initial existence of a cluster primordia in a basal bud, detectable through a microscope, is not usually apparent until around bloom time (end of May to early June). Recent Australian work has shown that a tendril can be made to differentiate into a flower cluster by application of cytokinin to the tips of the tendril.





The cluster primordia continue to develop in size and complexity for 8 to 12 weeks, until August or September. At this stage the total number of potential flowers for next season's crop has already been decided, but the actual differentiation of the cluster primordia into individual flower parts (stamens, pistils, and so on) does not occur until the following spring. Therefore the maximum possible size of a crop in 1981 has already been determined by September 1980. However, the actual size of the 1981 crop will depend not only on the fruitfulness of individual buds, but also on the percentage of buds that break and develop into shoots, the amount of flowers that set fruit, the size of individual berries, and, finally, the amount of sugar that accumulates in the berries.

For any given grape cultivar the number of fruit clusters per bud can vary considerably from

year to year. The seasonal variation in bud fruitfulness may be due to climatic factors, cultural practices, or diseases. Among the climatic factors that have been most studied are light, temperature, water stress, and daylength. Cultural practices that have the greatest influence on bud fruitfulness include pruning, training-trellis system, fertilization (especially nitrogen), irrigation, and growth regulators.

**Climatic factors on fruit bud formation.** Exposure of leaves and buds to *light* is the single most important factor that influences bud fertility in most grape growing areas of California. Viticulturists have long known that "sun canes" (shoots that grow most of the season in full sunlight) are superior to shade canes (shoots that grow in the interior part of the vine canopy) for pruning wood. Not only are the buds on sun canes more fruitful, but a greater number of buds on such canes burst and develop into shoots. In addition, clusters on sun canes are almost invariably larger than clusters on shade canes. The data presented in Table 2 for Thompson Seedless collected at Davis and Pinot noir collected at Oakville support those conclusions. It does not matter whether the canes originate from latent buds on older wood in the head of the vine, i.e., sucker canes, or from two-year-old wood (spurs or last-year canes) as long as the canes grew fully exposed to sunlight. The message here is clear: when pruning, determine whether the cane was exposed to sun during most of the growing season. Some characteristics of sun canes are their round shape and relatively short internodes as opposed to flat canes with long internodes for shade canes.

TABLE 2. Influence of Cane Exposure to Sunlight on Budbreak, Bud Fruitfulness, Cluster Weight, and Crop Yields of Thompson Seedless and Pinot Noir Vines

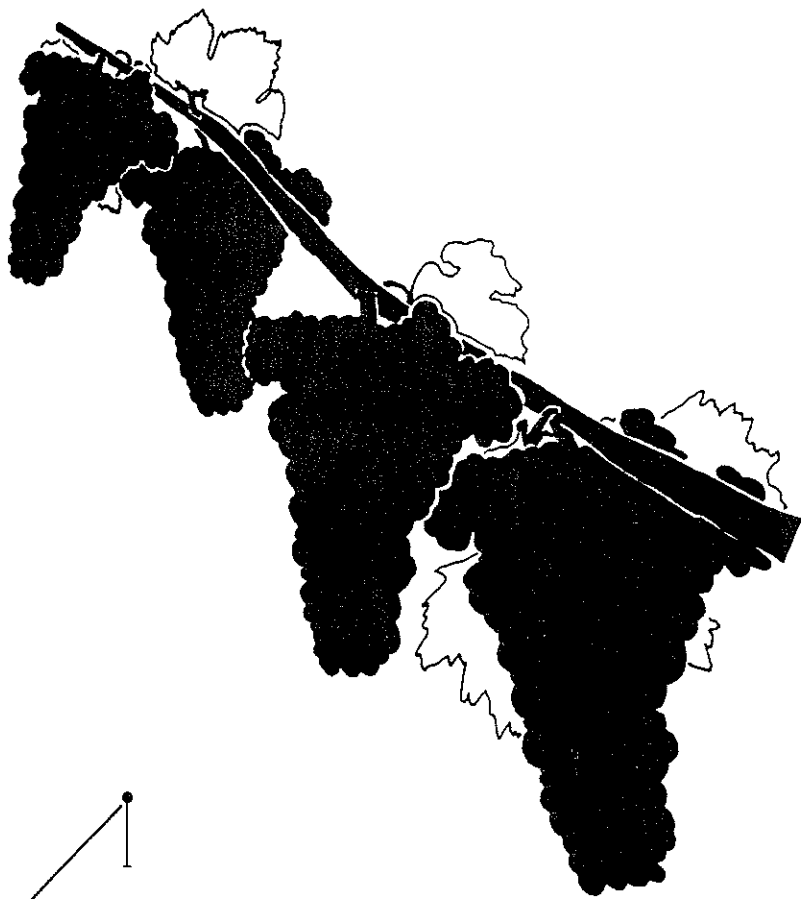
Variety	Cane exposure*	Percent budbreak	No. of clusters per node	No. of clusters per cane	Cluster wt (lb)	Yield per node (lb)	Yield per cane (lb)	Brix of fruit
Thompson Seedless	"sun cane"	85 <sup>‡</sup>	1.22	25.1	0.89	1.11	22.3	20.6
Thompson Seedless	"shade cane"	80	0.98	19.9	0.78	0.76	15.2	21.2
Pinot noir†	"sun cane"	84	2.01	24.7	0.165	0.33	4.06	25.6
Pinot noir	"shade cane"	72	1.32	15.9	0.160	0.21	2.54	25.1

\*Sun and shade canes were chosen at pruning time by judging whether they were primarily grown in the sun or shade during the previous growing season.

†Thompson Seedless vines were grown at Davis and Pinot noir at Oakville.

‡Data are the average of 24 canes from 6 vines of each variety.

SOURCE: Kliewer and Lider, unpublished information.



**PRIMORDIA PER BUD**

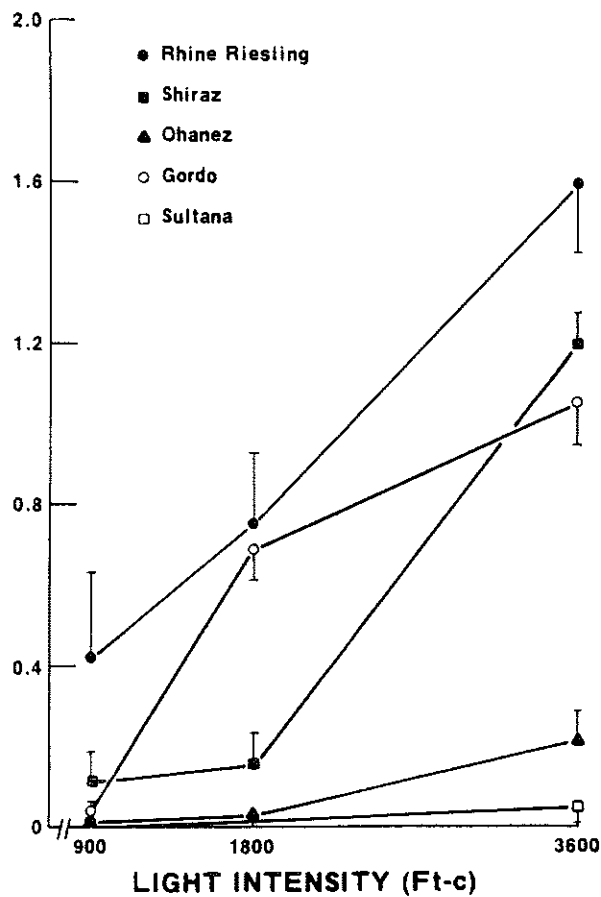


Fig. 7. Effect of light intensity on the mean number of bunch primordia per bud for the basal 12 buds on shoots of five grape varieties grown in controlled growth cabinets. Temperature was 25° C (77° F) for 16-hour days. Vertical bars equal 1 X standard error of the mean. (Data from Buttrose, *Vitis* 9:121-25, 1970).

Experiments done with potted vines using environmental control growth cabinets verify the importance of light intensity on bud fruitfulness. The data in figure 7 show that the number of bunch primordia per bud increased with increasing light intensity over the range of 900 to 3600 foot-candles. Differences in variety response to light are also apparent. White Riesling formed some fruitful buds at 900 foot-candles, whereas Muscat of Alexandria, Thompson Seedless, and Ohanez (Almeria) remained barren (no clusters formed).

There is some indication in the literature that light actually falling on the bud influences fruitfulness, rather than whole plant illumination and total photosynthesis. However, the requirement of a bud itself for light has only been demonstrated for a few varieties, specifically Thompson Seedless and Concord. The requirement for light hitting a bud was not absolute, but exclusion of all light from a bud by wrapping it with aluminum foil did greatly reduce bud fruitfulness of the above two varieties, with much less effect on most vinifera wine varieties.

The fruitfulness of grapevines is improved by relatively high temperatures (75 to 95° F). This has been determined by both statistical correlations with air temperature during different periods of bud development and by growing vines at controlled temperatures in growth rooms. Later studies have shown that fruitfulness of a bud is directly related to the temperature surrounding the bud during a period of about three weeks, during which time the node subtending it changes position, as a result of shoot growth, from the shoot apex to ten nodes back on the shoot. The effect of temperature on the fruitfulness of the buds back of the shoot apex fell proportionately, reaching zero for buds at node ten from the shoot tip. The number of fruit primordia per bud of five varieties increased linearly between 59° F to either 86 or 95° F (fig. 8). There was considerable difference among varieties with regard to temperature effects on bud fertility. Muscat of Alexandria, Thompson Seedless, and Almeria produced no fruitful buds when grown at 68° F (3600 ft-c of light, 16-hour daylength for 13 weeks), whereas White Riesling and Shiraz averaged slightly over one cluster for every two buds under the same

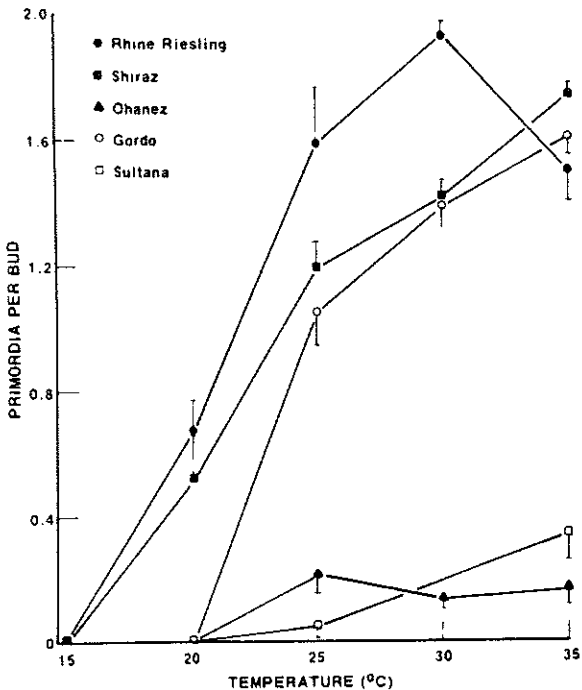


Fig. 8. Effect of temperature on the mean number of bunch primordia per bud for the basal 12 buds on shoots of five grape varieties grown in controlled environmental cabinets. Light intensity was 3600 foot-candles for 16-hour days. The vertical bars equal 1 X standard error of the mean. (Data from Buttrose, *Vitis* 9:121-25, 1970).

conditions of light and temperature. However none of the five cultivars produced fruit primordia at 60° F under the same light conditions and length of exposure.

In the same controlled climate studies it was found that bud fruitfulness was related to the maximum temperature experienced each day, rather than to heat summation (i.e., the number of degree-hours above 50° F), provided that the maximum temperature was maintained for at least a four-hour period during either the day or night.

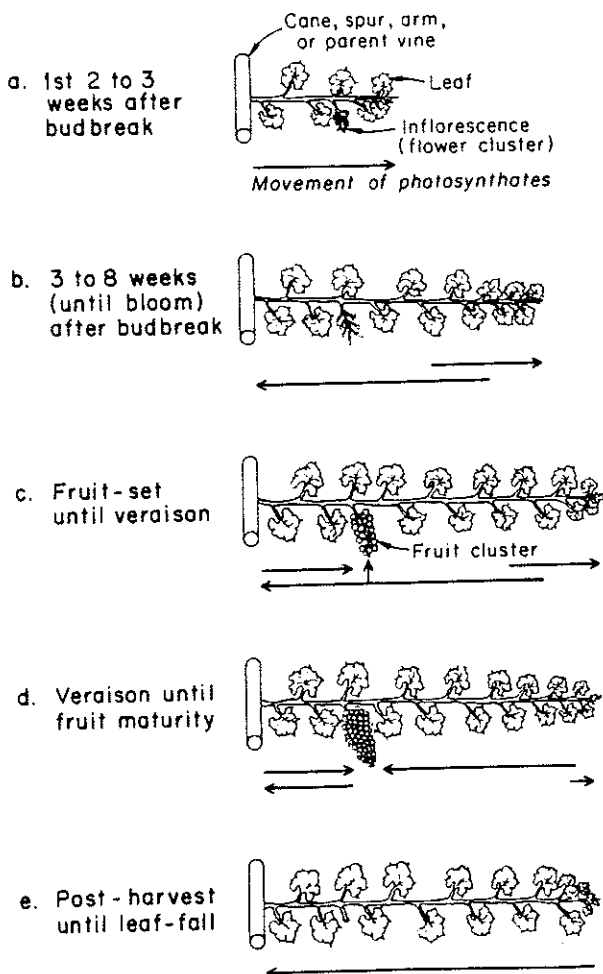
Fruit crops can be classified by *daylength* (short-day, long-day and day-neutral plants) with regard to floral induction. Floral induction in grapevines does not appear to be under photoperiodic control in that fruit primordia can be formed under short days or long days and are not improved by applying low intensity light throughout the night. However, bud fruitfulness is generally higher under long days than short days. In experiments with growth cabinets, Muscat of Alexandria bud fruitfulness increased with the total number of hours of high-intensity light given per day from 0.20 fruit primordia per bud at 8 hours of 3600 foot-candles/16 hours dark to 1.23 primordia/bud at 24 hours of high light per day.

There are conflicting reports with regard to the effects of *water stress* on bud fruitfulness of grapevines, some indicating improvement and others reduction. It is difficult to evaluate the effects of water stress on bud fertility under field conditions because close control is impossible and dry conditions are usually accompanied by high temperature and light.

It is well established that with increasing water stress there is a decrease in the rate of shoot growth. If water stress is properly timed to coincide with the period of fruit bud initiation, bud fertility could be enhanced by diverting assimilates from shoot growth to development of fruit primordia inside buds. On the other hand, if water stress is severe, stomates close, photosynthesis is depressed, and over-all carbohydrate production and accumulation is reduced.

Studies with potted Cabernet Sauvignon vines showed that bud fertility of vines watered when they reached 20 percent of field capacity was markedly less than in vines watered at 40 and 60 percent of field capacity. However, it should be emphasized that vines growing in pots are much different from vines growing under field conditions and it is difficult to convert the results to the vineyard situation.

Fig. 9. Main direction of movement of photosynthate at different physiological stages of shoot and cluster development.



## Carbohydrate Storage and Utilization

Relationship of stage of shoot and fruit development and photosynthate movement. Figure 9 shows diagrammatically the main direction of movement of assimilates in shoots at five different stages of development.

- The first two to three weeks after budbreak the movement of assimilates in shoots is essentially all toward the shoot tip. At this stage the shoots are mainly dependent on the parent vines for stored carbohydrates and nitrogenous compounds. New leaves do not begin to export photosynthate until they are one-third to one-half full size.
- From two to three weeks after budbreak until bloom (about eight weeks after budbreak), movement of assimilates is bi-directional. Leaves from apical part of the shoot supply photosynthate mainly to the shoot tip. Photosynthate from the remaining leaves moves basally out of the shoot to the parent vine (spur, canes, arm, trunk, and roots). The flower cluster attracts very little photosynthate.

- (c) From fruit set until veraison photosynthate moves mainly toward three sinks: shoot tip, fruit cluster, and parent vine. The arrows in the diagram indicate approximately which leaves on the shoot are mainly supplying each of these three sinks.
- (d) From veraison (color change and fruit softening) until fruit maturity (20 to 25° Brix) the main sink is the fruit cluster, with the parent vine and shoot and lateral tips constituting weaker sinks.
- (e) After harvest most of the photosynthate moves out of the shoot into the parent vine. All woody storage tissues constitute sinks at this time with the roots playing a primary role. Generally, there is a period of root growth following harvest which would further favor movement of assimilates to roots.

Utilization and storage of carbohydrates, and shoot and fruit growth and sugar accumulation in fruit. Storage and utilization of carbohydrates in grapevines depend on the status of shoot growth as well as the amount of crop. The rate of shoot growth, in turn, is largely a function of water status of soil, air temperature, amount of available nitrogen, and crop load.

The annual cyclic utilization and storage of carbohydrate in and from canes in relation to rate of shoot growth, berry growth and sugar accumulation in fruit is shown in figure 10. The normal period of carbohydrate utilization from canes,

arms, and spurs occurs from budbreak until about bloom, at which time the rate of shoot elongation usually begins to slacken markedly. The exact time that shoot growth begins to slow may vary greatly from vineyard to vineyard and depends on many factors, among the most important being soil moisture, climate (temperature, light, humidity, and so on), soil fertility (especially nitrogen), crop load, and variety. As long as shoot elongation continues at a rapid rate, accumulation of carbohydrate will be delayed. If shoot growth remains unchecked late into the fall without "hardening off" then there is the danger of frost killing the shoot.

About the time the rate of shoot growth begins to decline there is a short period when the amount of carbohydrates utilized from cane is about equal to that stored from current photosynthesis—a period termed the "period of self support." For the remaining part of the growing season following the period of self support there is net storage and accumulation of carbohydrates in woody tissues (canes, spur, arm, trunk, roots). Also, soon after shoot elongation has slowed down, carbohydrates begin to accumulate in the new shoots themselves. The accumulation starts in the mid-section of the new shoot and progresses downward and upward during the remainder of the season. The accumulation is slow at first but accelerates as fruits approach maturity. The accumulation in shoots and woody tissues is principally starch. The level of sugars remains relatively constant, except during mid-winter, when starch is hydrolyzed to sugar to protect the vine against low temperatures.

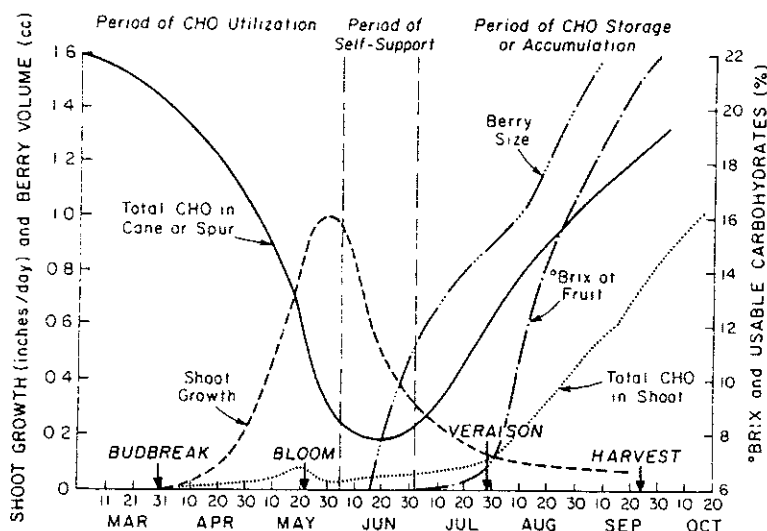


Fig. 10. Seasonal changes in shoot and berry growth in relation to changes in level of carbohydrate in cane, new shoots, and fruit.