Photoassimilate Distribution in Plants and Crops

Source-Sink Relationships

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Grape

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I. INTRODUCTION

Grape and wine production has played an important part in Western civilization. Today, grapevines are the number one fruit crop planted worldwide (Mullins et al. 1992). The species *Vitis vinifera L.* accounts for more than 90% of all cultivars planted. Grapes are used for wine, distilled liquors, juice, dried fruit (raisins), fresh consumption (table grapes), and concentrate. Climatic conditions, the end use of grapes, and the means used to harvest them dictate the production practices employed by those who grow grapevines. The ultimate goal of these practices is to produce grapes of high quality, although quality factors can very with type of grape being produced. For example, berry size and sugar/acid ratio are the primary quality factors used to determine harvest date of table grapes; flavor components and high sugar concentrations are quality factors used to harvest wine grapes. In many instances high yields and sugar concentrations are required when grapes are used for raisins or bulk wine production. The production practices used to maximize these quality attributes or yield can have significant effects on source-sink relationships of grapevines.

This chapter deals primarily with source-sink relationships of vines grown in the field, when possible. In addition, specific points are illustrated with various sets of unpublished data collected by the author. Much of what is presented provides quantitative data on vine growth. Thorough reviews of the basic biological characteristics of grapevines (Mullins et al. 1992) and the effects of environmental factors on vine physiological processes (Williams et al. 1994) have recently been published and can be used for further reference.

II. SOURCES OF CARBOHYDRATES

A. Photosynthesis

1. Contribution by Leaves

The C_3 pathway of photosynthesis occurs in gravevines. Therefore, the response of grapevine leaf photosynthesis to various environmental factors is similar to that of other C_3 plant species (Williams et al. 1994). Reported maximum individual leaf net CO_2 assimilation rates for *V. vinifera* and other *Vitis* species approach 20 μmol m^{-2} s^{-1} (During 1991; Gamon and Pearcy 1990; Kriedemann et al. 1970; Liu et al. 1978; Roper and Williams 1989). More commonly reported maximum rates fall in the range of 8

to 13 μmol CO_2 m^{-2} s^{-1} (Archer and Strauss 1990; Correia et al. 1990; Downton et al. 1987). Photorespiratory loss of CO_2 in unstressed grapevines ranges from 13% to 20% of the net CO_2 assimilation rate (During 1988, 1991).

The primary environmental factor limiting maximum rates of individual leaf photosynthesis of nonstressed vines on a diurnal basis is solar radiation (Kriedemann and Smart 1971). In addition to position within the canopy of an individual leaf, age determines its maximum rate of CO_2 assimilation (Kriedemann et al. 1970; Williams and Smith 1985). Schultz (1991) determined the influence of both leaf age and position in the canopy with regard to their CO_2 balance. There was a positive daily carbon balance of both immature and mature leaves irrespective of position in the canopy (Table 1). This study provided important data regarding the contribution of young leaves and shaded leaves to the carbon balance of the entire grapevine. In addition, Buttrose (1966) demonstrated that photosynthesis of shoots on grape cuttings was able to meet growth and respiration demands 17 days after bud break. At this time total leaf area of the shoot was approximately 50 cm^2.

Estimates of whole vine photosynthesis have been determined by modeling or measuring both light interception at the canopy surface and its attenuation within the canopy, the amount of leaf area exposed to those light levels, and the relationship between light intensity and leaf CO_2 assimilation. Smart (1974) concluded that a high proportion of whole vine CO_2 assimilation was due to the interception of direct light, though according to his calculations only 19% of the canopy was illuminated by direct solar radiation. Twelve estimates of canopy assimilation per projected ground area in that study averaged 0.084 mol CO_2 m^{-2} h^{-1} with a maximum value of 0.102 mol CO_2 m^{-2} h^{-1}. Assuming that the ground area subtended by foliage intercepting light in that study was approximately 4 m^2, the average and maximum values of whole vine photosynthesis would be 0.34 and 0.41 mol CO_2 h^{-1}, respectively. The greatest midday value of whole vine photosynthesis estimated by Downton and Grant (1992) for a spur-pruned cultivar was 0.41 mol CO_2 h^{-1}. Maximum photosynthetic capability by those vines was calculated to be 2.56 mol CO_2 $vine^{-1}$ day^{-1} at fruit harvest. Modeled estimates of maximum whole vine photosynthesis were approximately 1.7 mol CO_2 $vine^{-1}$ day^{-1} for vines grown in Switzerland (Wermelinger et al. 1991). The preceding results indicate the variability in whole vine carbon assimilation due to vine size and location where the vines are grown.

The diurnal assimilation of CO_2 by a hypothetical grapevine grown in the San Joaquin Valley, planted in east-west rows, is shown in Fig. 1. This estimate of CO_2 assimilation was based upon the response of grape leaf photosynthesis to light intensity and the amount of solar radiation intercepted by the top, north, and south curtains of the canopy in June (data taken from Figs. 4.2 and 6.2, respectively, in Mullins et al. 1992). The canopy was divided into sunlit and shaded leaf area by using the technique of Williams et al. (1993). Maximum CO_2 assimilation by the canopy at midday was approximately 0.5 mol $vine^{-1}$ h^{-1}, a value comparable to estimates of Smart (1974) and Downton and Grant (1992). The

Table 1 Daily, Estimated Carbon Balance of White Riesling Leaves on a Cloud-Free Day During Midseason[a]

	CO_2 Uptake, mmol day^{-1}		*CO_2 Respired, mmol $night^{-1}$*		*CO_2 Balance, mmol 24 h^{-1}*	
Leaf age[b]	*Sun*	*Shade*	*Sun*	*Shade*	*Sun*	*Shade*
Immature	*165*	*59*	*26*	*16*	*139*	*43*
Mature	*361*	*48*	*9*	*3*	*352*	*45*

[a]Carbon balances were calculated for leaves exposed to direct solar radiation and those growing in the shade.
[b]Immature leaves represent leaves of leaf plastochron indices from 0 to 4. Mature leaves represent leaves of LPIs 6 or greater. Values are expressed on a per square meter leaf area basis. LPI, leaf plastochron index.
Source: Adapted from Schultz 1991.

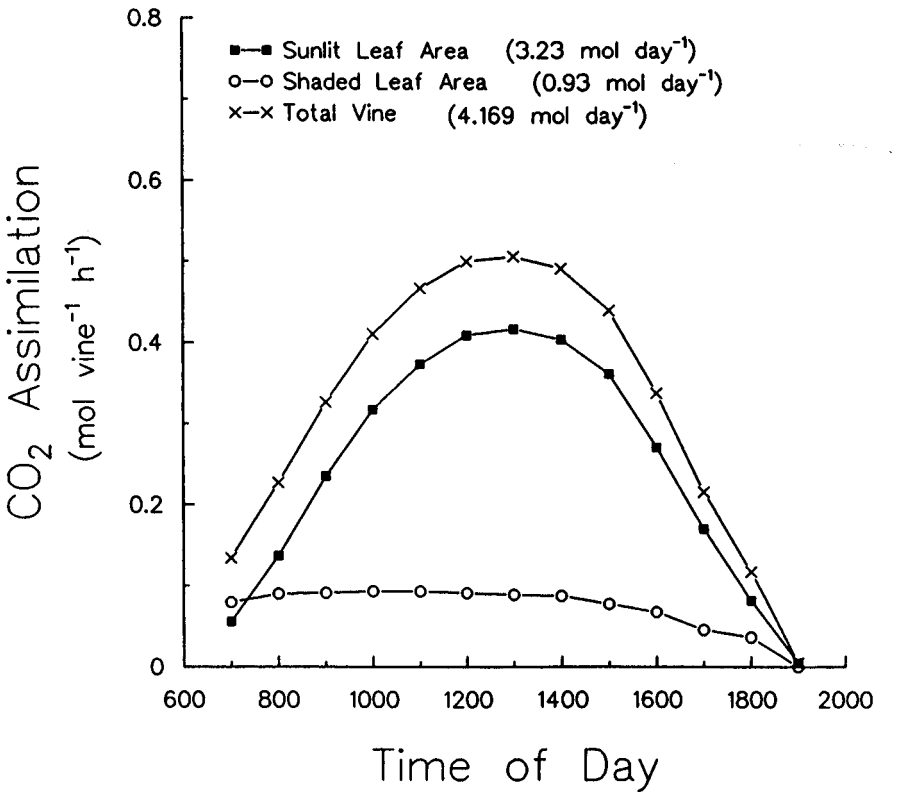

Figure 1 Estimated total vine CO_2 assimilation of a Thompson Seedless grapevine with a full canopy on a cloudless day in June. See text for further details.

daily, estimated amount of CO_2 assimilated by the vine (with 22.3 m^2 leaf area per vine) was 63% greater than that estimated by Downton and Grant (with 23.8 m^2 leaf area per vine). It is interesting to note that 22% of the daily assimilation of CO_2 was contributed by the interior leaves. Smart (1974) calculated that approximately 30% of a canopy's photosynthesis was contributed by leaf area intercepting diffuse light.

2. Contribution by Other Organs

Other aerial organs of the grapevine contain chlorophyll, indicating the possibility of photosynthetic activity. Photosynthesis was detected in both immature and mature stems (main axis of the shoot) of grapevines (Kriedemann and Buttrose 1971). Immature stems were able to reduce respiratory CO_2 efflux by 70% in diffuse light and 89% in diffuse + reflected solar radiation. Mature stems (i.e., with periderm) refixed 13% of the respiratory CO_2 efflux. Kriedemann and Buttrose concluded that immature stems are able to refix the bulk of respired CO_2, even if shaded by a leaf. They also hypothesized that after leaf fall, photosynthesis within the stem could compensate for approximately 10% of respiratory carbon loss at 25°C and even greater amounts at lower temperatures.

Organs of the grape cluster also contain chlorophyll and are covered with stomata (Blanke and Leyhe 1987, 1989). In addition to the C_3 pathway of photosynthesis, fruit possess a system which refixes respiratory CO_2 via phospho*enol*pyruvate carboxylase (E.C. 4.1.1.31) (Blanke and Lenz 1989). There is

a net uptake of CO_2 in the light by grape flowers 2 weeks before to anthesis; however, subsequent measurements before anthesis indicate that respiratory losses exceed uptake (Leyhe and Blanke 1989). Photosynthesis by grape berries after set is capable of refixing anywhere from 10% to 90% of the respiratory CO_2 loss in the light; the percentage is dependent upon growth stage (Frieden et al. 1987a; Geisler and Radler 1963; Koch and Alleweldt 1978; Kriedemann 1968). Reported rates of CO_2 assimilation vary from 600 μg CO_2 g^{-1} fresh weight (FW) h^{-1} shortly after anthesis to less than 10 μg CO_2 g^{-1} FW h^{-1} close to fruit maturity. Photosynthesis expressed on a per berry basis ranges from 10 to 120 μg CO_2 h^{-1}.

B. Reserves

The permanent structures of the grapevine are the primary sources of reserve carbohydrate for this perennial crop in the absence of shoots. The relative and absolute amounts of nonstructural carbohydrates have been determined for grapevine, with the results demonstrating seasonal variations in both (Mullins et al. 1992; Winkler and Williams 1945). The absolute amount of nonstructural carbohydrates in vines differs according to cultivar, vine size, age, crop load, environmental conditions, cultural practices, and presence of viral diseases. For example, total nonstructural carbohydrate in the roots, trunk, and cordons of 10-year-old Chenin blanc vines at budbreak was 798 g $vine^{-1}$ compared to 1913 g $vine^{-1}$ for 25-year-old Chenin blanc vines grown at a different location (Mullins et al. 1992; see tables 4.2 and 6.6 in that reference). Thompson Seedless grapevines of different ages grown at the same location using similar cultural practices had 173 and 447 g of nonstructural carbohydrates $vine^{-1}$ in the roots and trunk for vines aged 5 and 20 years, respectively, when harvested on the same date (unpublished data). Root + trunk dry biomass of the 20-year-old vines (3706 g dry wt $vine^{-1}$) was 2.38 times greater than that of the 5-year-old vines. A recent study investigated the influence of pruning method and virus inoculation on the accumulation of carbohydrate reserves in the permanent structures of Cabernet franc grapevines (Ruhl and Clingeleffer 1993). They found that total nonstructural carbohydrates in the permanent structures during dormancy varied from 1680 to 2216 g $vine^{-1}$, depending upon the pruning method. Inoculation of vines in that study with virus reduced total vine carbohydrate amounts in the permanent structures approximately 15% compared to those of the control. The reduction in carbohydrate amount of virus-inoculated vines was due mainly to a reduction in biomass production and not to differences in carbohydrate concentrations.

A data set collected on Thompson Seedless grapevines grown in the San Joaquin Valley of California provides an estimate of the seasonal dynamics of reserve carbohydrates in the permanent structures of the vine (Figs. 2 and 3). From the first of the calendar year until close to fruit harvest the concentration of soluble sugars decreased in both the trunk and the root system (Fig. 2). The starch concentration decreased in the trunk from budbreak until harvest and subsequently increased. The starch concentration in the root system generally increased from budbreak until harvest and then decreased. The seasonal patterns of sugar and starch concentrations in the trunk found here resemble data collected by Winkler and Williams (1945). However, the root data of these Thompson Seedless vines differ greatly from their data. It should be pointed out that a second year's data set collected on vines in the same Thompson Seedless vineyard resembled data found during the first year (Fig. 2). Both the root system and the trunk of these 5-year-old vines contained similar amounts of nonstructural carbohydrate reserves in January (Fig. 3). They both lost approximately 175 g $vine^{-1}$ between January and anthesis. The amount of carbohydrates in the two organs differed considerably after anthesis. These data illustrated that carbohydrate reserves were lower at anthesis than at any other time of the season followed by an increase. The Chenin blanc data (Mullins et al. 1992) also indicted that there was little increase in carbohydrate reserves in the permanent structures until after anthesis.

The current season's vegetative organs may also serve as a source of nonstructural carbohydrates in

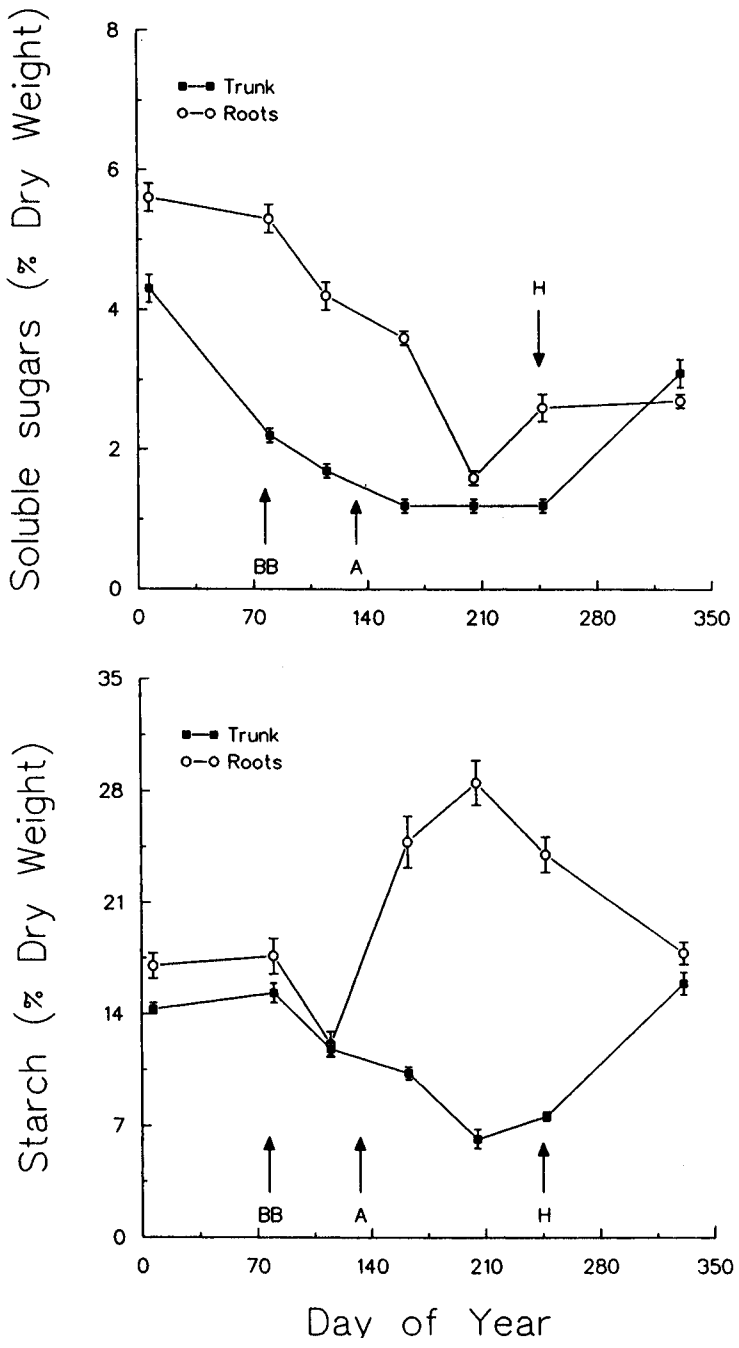

Figure 2 The seasonal change in starch and soluble sugar concentrations of the trunk and root system of Thompson Seedless grapevines. Each data point is the mean of at least six individual vine replicates with bars representing ± one standard error. Glucose, fructose and sucrose comprise the soluble sugars. BB, A, and H represent the dates of 50% budbreak, anthesis, and fruit maturity, respectively.

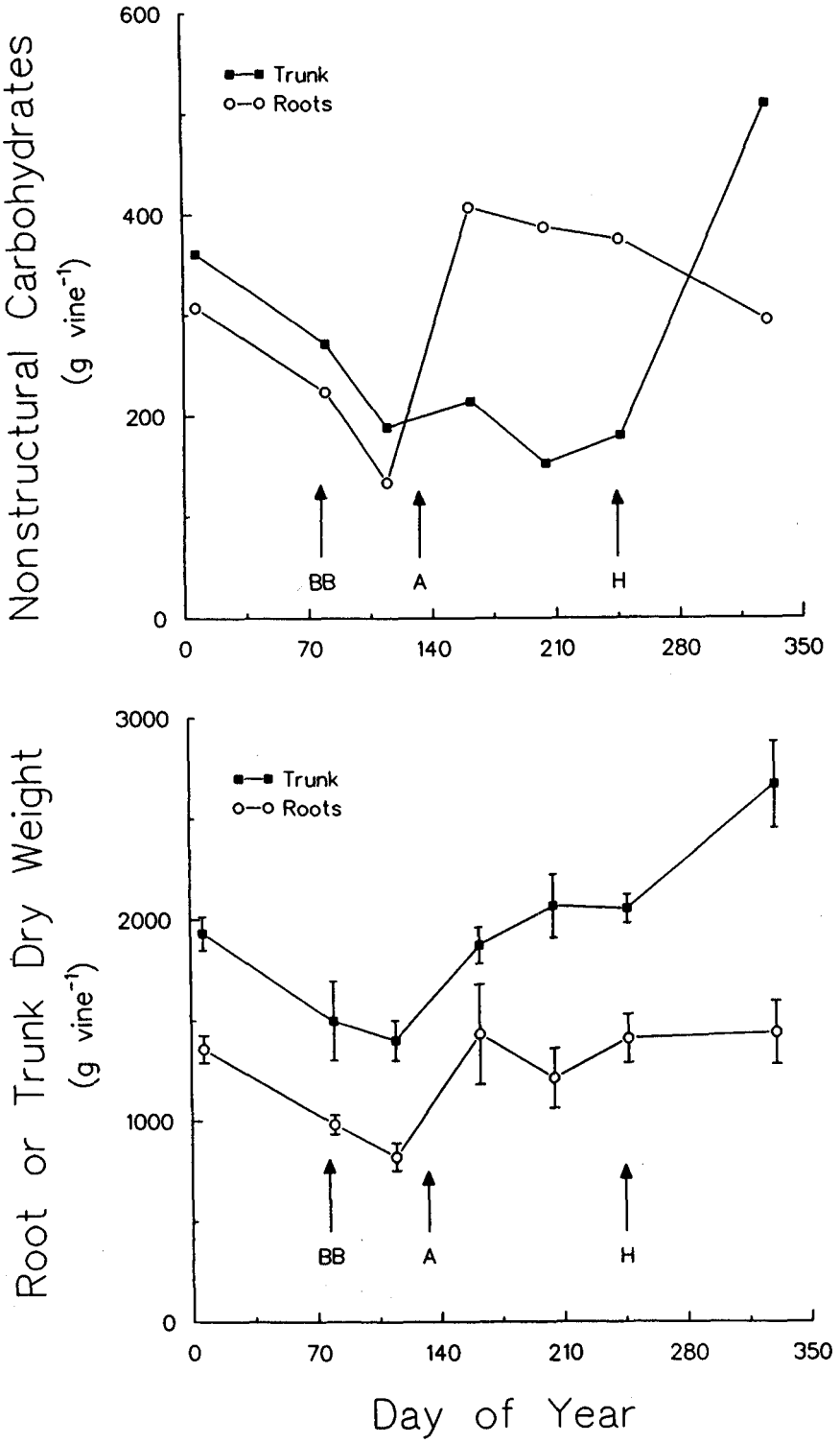

Figure 3 The seasonal change in root and trunk dry weight and total nonstructural carbohydrates of Thompson Seedless grapevines. Other information as in Fig. 2

the grapevine. The concentration of reducing and nonreducing sugars and starch in leaves varies slightly during the day (Roper and Williams 1989) and throughout the season (Kliewer and Nassar 1966; Winkler and Williams 1945). The greatest amount of nonstructural carbohydrates in leaves reported in the literature varied from 45 to 91 g $vine^{-1}$, depending upon time of year (Mullins et al. 1992; Roper and Williams 1989). While the amount of nonstructural carbohydrates found within the current season's growth of the stems will vary with canopy size and time of year, reported values range from 38 to 194 g $vine^{-1}$ (Ruhl and Clingeleffer 1993; Mullins et al. 1992; Roper and Williams 1989).

III. PARTITIONING OF CARBOHYDRATES WITHIN THE LEAF

The metabolism and transport of carbohydrates within the grape leaf are probably similar to those described for other C_3 plant species (Hawker et al. 1991). Leaf age and time during the growing season influence the concentrations of reducing and nonreducing sugars and starch in grape leaves. Kliewer (1966) found that the concentration of glucose and fructose in the leaves of field-grown grapevines increased from unfolding until the individual leaf had expanded to one third of its final leaf area, after which their concentrations leveled off. The glucose/fructose ratio of leaves generally is greater than 1 and sometimes approaches values greater than 2. The concentration of sucrose usually is less than that of either glucose or fructose. The concentration of sucrose in leaf tissue also increases as the leaf ages (Kliewer and Nassar 1966; Sepulveda and Kliewer 1986). In the latter study the concentration of leaf sucrose increased as growth temperature increased. However, it has been shown that increasing growth temperatures decreases the concentration of starch in grape leaves (Buttrose and Hale 1971). The decrease in starch concentration is offset to some extent by an increase in total lipid concentration. Nonstructural carbohydrates in grape leaves increase as a result of CO_2 enrichment when compared to those of vines grown under ambient CO_2 pressures (Johnson et al. 1982). The concentration of starch found in the leaves of grapevines grown in warm environments ranges from 14 to 73 mg g^{-1} dry wt when measured on individual leaves (Roper and Williams 1989; Fig. 4) and from 0 to 93 mg g^{-1} dry weight when all leaves on a vine are sampled (Mullins et al. 1992; Roper and Williams 1989). Values can be considerably higher when vines are girdled to increase berry size (Roper and Williams 1989).

The accumulation of starch in the chloroplasts during photosynthesis is assumed to be an important reserve of carbohydrate for the plant. Starch accumulation in the leaf during the light and its degradation the ensuing evening have been demonstrated by using annual plants grown in environmentally controlled growth chambers (Allen et al. 1988; Potter and Breen 1980) and outdoors (Millhollen and Williams 1986). There appears to be only a slight increase during the day in either sugar or starch concentrations in sunlit leaves of girdled and nongirdled grapevines grown in the field (Fig. 4). The amount of CO_2 assimilated by the sunlit leaves of the control and girdled vines between 800 and 1600 h that day was 0.54 and 0.36 mol m^{-2}, respectively (unpublished data; see also study by Roper and Williams 1989, demonstrating the diurnal pattern of grape leaf photosynthesis in response to girdling). This is equivalent to 0.36 and 0.24 g carbohydrate produced g^{-1} dry wt for the control and girdled vines, respectively. The weight per unit leaf area used to calculate these relationships was assumed to be 45 g m^{-2} (Williams 1987a). The relative constancy of nonstructural carbohydrates during daylight may be due to the fact that an individual leaf, even on the exterior of the canopy, is exposed to direct light only during a small portion of the day. This may be due to mutual shading, leaf angle, row direction, and diurnal course of solar radiation. Another possible explanation is that in woody perennial crops, with significant carbohydrate reserves in the permanent structures, the leaves are not important in supplying carbohydrates to the plant during the evening. The preceding data also indicate that the photosynthate produced in the leaves of these vines was rapidly transported out of the leaf under the conditions of the experiment.

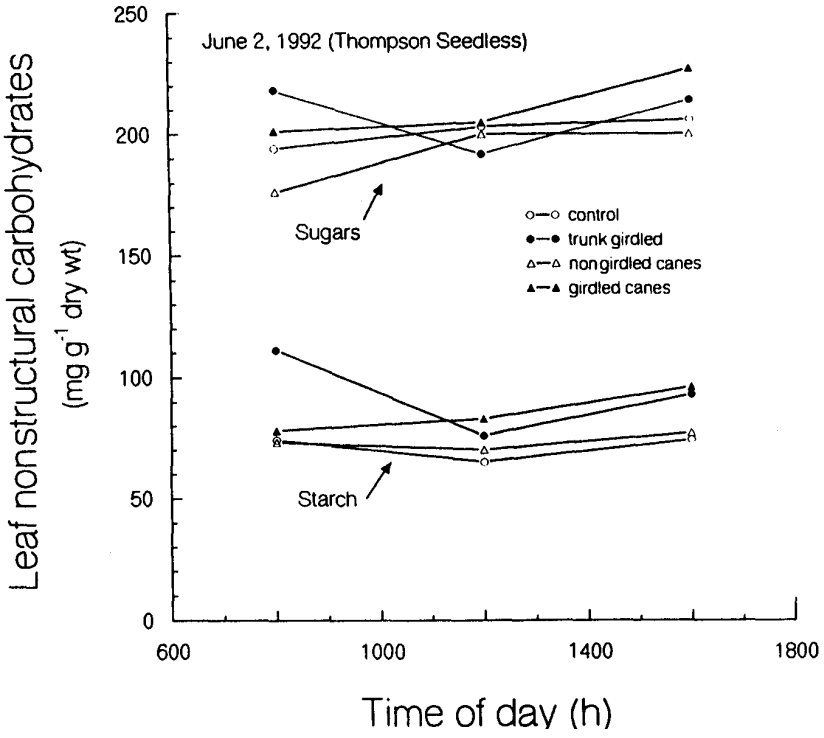

Figure 4 The diurnal change in leaf nonstructural carbohydrates of Thompson Seedless grapevines. Treatments include a control, vines that were trunk-girdled, and vines in which one-half of the fruiting canes were girdled and the other half were not girdled. The upper set of data points are the soluble sugars and the lower set starch. Each value is the mean of six individual leaf replicates. Leaves were killed in liquid nitrogen and then lyophilized. Carbohydrates were determined as described by Roper and Williams (1989).

IV. WHOLE VINE CARBON PARTITIONING

A. Cycle of Vine Growth

1. Seasonal Aerial Vegetative Growth

Shoot growth of grape is initiated in the spring from compound buds, which consist of one primary and two secondary buds. The primary bud usually contains 10 to 12 leaf primordia along with 1 to 2 cluster primordia, located opposite leaf primordia at node positions three to six from the base. Shoot growth generally is initiated from the primary bud and occasionally one of the secondary buds also grows. Secondary bud growth is initiated in the event that the primary bud dies or the primary shoot dies, as occurs after a spring freeze. A low amount of chilling may be needed in breaking dormancy of *V. vinifera* (Antcliff and May 1961). Budbreak generally occurs when the daily mean temperature exceeds 10°C. Subsequent growth of the shoot is dependent upon environmental factors, management practices, and disease or pest problems. The base temperature for vegetative growth has been observed to range from 5°C to 8°C (Moncur et al. 1989). Degree day summations (base temperature >10°C) have also been used successfully to predict the time between various phenological events (Williams et al. 1985b; Williams 1987b). The total number of shoots that develop on a vine is primarily determined by the pruning pattern.

The rate of shoot elongation is greatest early in the growing season and then steadily decreases thereafter (van Zyl 1984). The increase in stem length is sigmoidal when expressed as a function of either calendar days (De La Harpe and Visser 1985) or degree day summations (Williams 1987a). The increase in dry mass of shoots is almost linear until fruit set occurs, with subsequent shoot growth diminishing or leveling off (Gutierrez et al. 1985). Weight per unit stem length, however, continues to increase (Williams 1987a). The amount of biomass partitioned to stems of the same cultivar differs among vineyards (Williams et al. 1985a). In addition, pruning method determines the amount of biomass found in the current growing season's stems. The amount of biomass partitioned to the stems declines as the number of shoots per vine increases (Clingeleffer and Krake 1992). Shoot orientation also influences the partitioning of biomass to the main stem (Kliewer et al. 1989). Shoots positioned downward had less stem biomass than those positioned vertically or horizontally in that study. Finally, the indeterminate growth habit of *Vitis* species, the use of different trellis systems, and the need to drive equipment down the rows in the vineyard may necessitate summer pruning or hedging of the canopy. The loss of shoot dry matter due to summer pruning in modeling grape growth is set at 10% to 25%; the percentage depends upon when hedging takes place (Wermelinger et al. 1991; Williams et al. 1985a).

A similar type of pattern to that described for shoot (stem) growth can also be observed for the increase of leaf weight and area per vine for mature vines (Wermelinger and Koblet 1990; Williams 1987a). Weight per unit leaf area increased linearly as the season progressed in both of the studies mentioned. The increase in weight per unit leaf area is not associated with an increase in nonstructural carbohydrate concentration (unpublished data). Seasonal increments in leaf biomass and leaf area per vine are dependent upon vine age and pruning pattern. Araujo and Williams (1988) found that leaf biomass and area increased throughout the growing season for 2-year-old vines (as the vines were trained up the stake). Leaf biomass and area were shown to increase throughout the season for nonirrigated Cabernet Sauvignon vines grown in the Napa Valley of California (Williams and Biscay 1991). Leaf area development increased more rapidly for minimally pruned vines than for those that were spur-pruned (Downton and Grant 1992). Leaf area per vine 1 month after budbreak was five times greater for the minimally pruned than for the spur-pruned vines. Thus, the concept of a typical pattern of leaf area development of vines under all conditions and situations may not be valid.

The development of the canopy and its size is dependent upon the rate of leaf area expansion, shoot growth, and cultural practices that influence the growth of lateral shoots. The production of leaves appears to be a function of temperature, cultural practices, and shoot length. A leaf appearance model of grape, which assumed that appearance rate was dependent upon temperature and that it declined for each subsequent leaf formed, predicted leaf appearance of three of four cultivars grown in the Chianti region of Italy (Miglietta et al. 1992). Leaf initiation rate differed on shoots of Cabernet Sauvignon grapevines when the shoots were oriented in various directions (Kliewer et al. 1989). The growth rate of expanding leaves (younger than 250 degree days [dd]) was shown to be 4.3 mg dd^{-1} followed by a rate of 0.6 mg dd^{-1}(Wermelinger and Koblet 1990). Thompson Seedless leaves were shown to grow at a rate of 2.74 mg dd^{-1} until they were fully expanded (Williams et al. 1985a). Canopy leaf area development was shown to be linearly related to degree days from budbreak until fruit growth rapidly increases (Williams 1987a).

At full canopy, 30% to 85% of the total leaf area can be found on the outside of the canopy depending upon trellis configuration and row spacing (Downton and Grant 1992; Mullins et al. 1992; Smart et al. 1985; Williams 1987a). The proportion of leaf area from lateral shoots that comprise total vine leaf area varies from a low of 6% to 9% to greater than 50% (Smart et al. 1985; Wermelinger and Koblet 1990). The low amount of lateral shoot leaf area in the former study was probably due to the lack of supplemental irrigations, whereas in the latter study primary shoots were summer-pruned several times during the season, thus releasing apical dominance. Canopy development proceeded much more rapidly for minimally pruned vines than for spur-pruned vines (Downton and Grant 1992). However,

canopy leaf area at the end of the season was approximately 40% greater for the spur-pruned than for the minimally pruned vines. Canopy surface area is greater for vines grown at closer row spacings even though leaf area per vine is less at the closer row spacing (Mullins et al. 1992). Finally, various measures of canopy size and density can vary considerably from one site to another for the same cultivar (Dokoozlian 1990).

2. Growth of the Permanent Aerial Structures

The permanent above-ground organs of grapevines consist of the trunk and cordons (horizontal extension of the trunk). The rate of the trunk's increase in diameter reaches a maximum at anthesis, decreasing afterward with a smaller peak after veraison (van Zyl 1984). Total trunk biomass decreases from the middle of dormancy until anthesis (Fig. 3). Subsequent to anthesis trunk biomass increases for the rest of the growing season. This pattern was observed over two growing seasons (Williams 1991). The initial decrease in trunk dry weight is associated with a decrease in nonstructural carbohydrate content (Fig. 3). Trunk biomass was shown to increase from budbreak until fruit harvest for Chenin blanc grapevines (Mullins et al. 1992). A study on 2-year-old vines showed that the trunk tripled in dry weight from budbreak until the first of September (Araujo and Williams 1988).

The seasonal increment in trunk biomass accumulation varies with growing conditions and genotype. Approximately 527 g dry matter vine^{-1} year^{-1} was partitioned to the trunk of Thompson Seedless grapevines from initial planting until the vines were 7 years of age (Fig. 5). Closer examination of the data points indicates large differences in the yearly accumulation of dry matter in the trunk (i.e., yearly accumulations were greater in 1986 and 1988 than in 1987). When averaged over the 18-year life of Cabernet Sauvignon grapevines grafted onto the rootstock 5C, approximately 240 g dry matter was partitioned to the trunk vine^{-1} year^{-1} (Williams and Biscay 1991).

The amount of biomass partitioned to the cordon depends upon the training system used (i.e., unilateral, bilateral, or quadrilateral cordon system). Most studies that have quantified the biomass of cordons used vines trained to bilateral cordons. Approximately 300 g dry biomass vine^{-1} year^{-1} was partitioned to the trunk and cordons of Chenin blanc vines grafted onto 101-14 Mgt rootstock when averaged over a 12-year period (Saayman and van Huyssteen 1980). Ten-year-old Chenin blanc grapevines grown in the San Joaquin Valley partitioned an average of 638 g dry matter vine^{-1} year^{-1} to the trunk and cordons (Mullins et al. 1992). A similar value (612 g dry matter partitioned to trunk and cordons vine^{-1} year^{-1}, calculated from fresh weight data and a dry/fresh weight ratio of 0.45) was obtained for 15-year-old spur-pruned Cabernet franc grapevines grown in the Murray River Valley of Australia (Clingeleffer and Krake 1992).

3. Growth of the Root System

Studies examining the growth of grapevine roots have quantified the periodicity of new root initiation and turnover (Freeman and Smart 1976; McKenry 1984; van Zyl 1984). Results from these studies demonstrate that a flush of root growth occurs shortly after shoot growth begins in the spring, peaking at anthesis. New root initiation decreases rapidly, with few new roots seen between fruit set and harvest. A second, major flush may begin after fruit harvest. Root biomass of Thompson Seedless grapevines decreases during the period from the middle of the dormant portion of the season until anthesis (Fig. 3). As with the trunk, some of the decrease in weight is due to a decrease in nonstructural carbohydrates (Fig. 3). The decrease may also be associated with root death and turnover. After anthesis there is a significant increase in root biomass. The increase in root biomass through the season in this study corresponds to some extent to the observed root flushes. It should be emphasized, however, that root biomass increased throughout the season for young Thompson Seedless grapevines (Araujo and Williams 1988), mature Cabernet Sauvignon grafted on 5C (Williams and Biscay 1991), and own-root

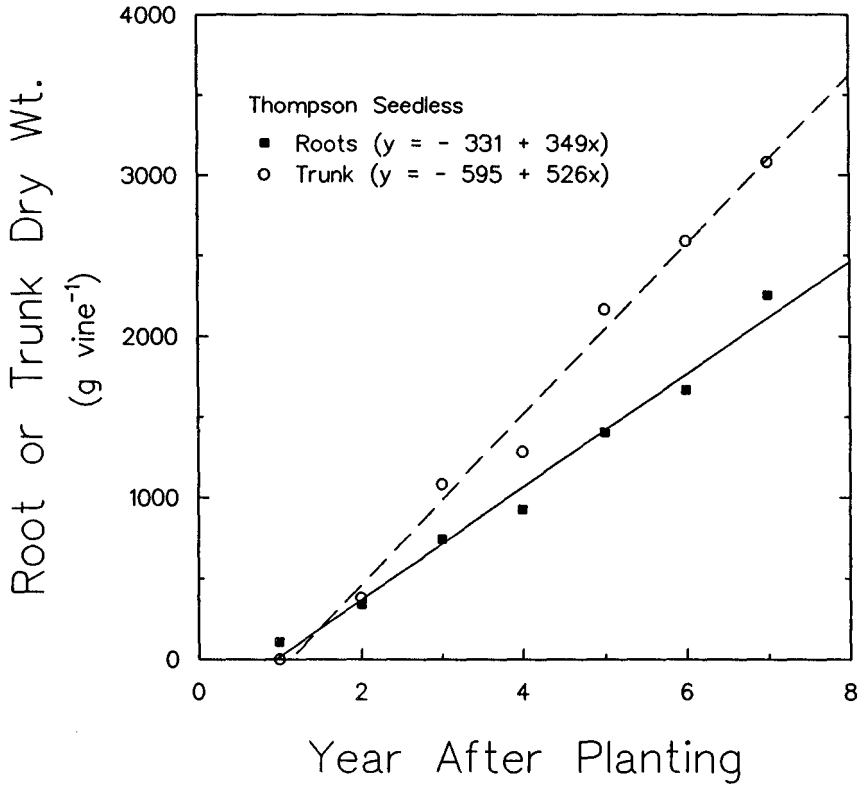

Figure 5 The accumulation of root or trunk biomass of Thompson Seedless grapevines from the time the cuttings were planted through seven growing seasons. Vine and row spacings were 2.44 and 3.66 m, respectively. Biomass was determined each year approximately the first week in September or at fruit maturity. Each value is the mean of six individual vine replicates.

Chenin blanc grapevines (Mullins et al. 1992). These studies would indicate that the seasonal dynamics of root biomass partitioning depend upon the age of the vine and perhaps the cultivar and may not reflect observed root flushes.

The partitioning of biomass to the roots of Thompson Seedless grapevines averaged approximately 350 g dry weight vine^{-1} year^{-1} from the time of planting until the vines were 7 years old (Fig. 5). Up to 20% of this biomass may be nonstructural carbohydrates. Approximately 360 g dry wt vine^{-1} year^{-1} (determined by dividing root biomass by vine age) is the average partitioned to the roots of the Chenin blanc-101-14 Mgt. scion-rootstock combination (Saayman and van Huyssteen 1980). A value of 262 and 130 g dry wt vine^{-1} year^{-t} is the average yearly increment in biomass partitioned to the roots of Chenin blanc-own roots and Cabernet Sauvignon-5C, respectively (Mullins et al 1992; Williams and Biscay 1991). Whole vine harvests of Thompson Seedless grapevines of various ages (from initial planting to vines more than 30 years old) at the University of California Kearney Agricultural Center indicate that the partitioning of biomass to the root system is 60% of that partitioned to the trunk (Fig. 6). Biomass partitioning to the root system of another cane-pruned cultivar was approximately 50% of that partitioned to the trunk when averaged across all harvest dates and rootstock combinations (Williams and Biscay 1991; Williams and Smith 1991). The partitioning of biomass to the root system of Chenin blanc was approximately 40% of that allocated to the trunk + cordons (Mullins et al. 1992); that

fraction was 33% for spur-pruned Cabernet franc (Clingeleffer and Krake 1992). The biomass partitioned to the root system in the Saayman and van Huyssteen study, however, was greater than that partitioned to the trunk + cordons.

4. Fruit Growth

Unlike many deciduous tree fruit crops, in which anthesis occurs at budbreak, anthesis in grape does not occur until there is an appreciable vine canopy (Pratt and Coombe 1978; Wermelinger and Koblet 1990; Williams 1987a). The growth of a grape berry does not proceed at a constant rate but rather with periods of ascending and descending growth rates delineated into various phases. Many have characterized berry growth as a double-sigmoid growth curve (Coombe 1976). This type of growth curve has been divided into three, four, and five arbitrarily assigned stages. When three stages are used to describe berry growth, the initial stage (I) consists of rapid growth due to both cell division and expansion. Stage II, a lag phase, is characterized by little berry enlargement; however, maturation of the seed proceeds. The last phase of berry growth (III) is due solely to cell expansion. This phase also is characterized by a massive accumulation of hexose sugars and a decrease in titratable acidity. The double-sigmoid growth curve is also observed for berries of seedless cultivars.

The growth of a berry also can be characterized as occurring in two phases (Staudt et al. 1986). A study reevaluating the double-sigmoid growth curve has concluded that fruit growth of peach *(Prunus persica* L. Batsch) can be divided into two growth stages, based upon relative growth rates (dry weight increment g^{-1} dry weight dd^{-1} or day^{-1}) (Deiong and Goudriaan 1989). Blanke (1992) also concluded that berry growth, based on relative growth rate, can be divided into two growth stages. The lag phase is characterized as a transition between two growth stages rather than a separate growth stage.

The final weight of the flesh of a ripe fruit is determined by cell number, volume, and density. The number and volume of cells at ripeness are influenced by the cell number and volume at anthesis and the subsequent rate and duration of cell division and expansion (Coombe 1976). There are approximately 0.2 million cells in the ovary at anthesis and 0.6 million 40 days later (Harris et al. 1968). Coombe (1976) calculated that the number of cell doublings to achieve these numbers was 17 before anthesis and 1.5 after anthesis. Cell division in the pericarp begins 5 to 10 days before anthesis (Coombe 1960). Harris et al. (1968) concluded that berry pericarp growth was a product of both cell division and expansion up to 3 weeks after anthesis with subsequent growth due to cell expansion alone. Tissue of the pericarp represented 64% of the final volume of the Sultana (syn. Thompson Seedless) berry (Harris et al. 1968).

The majority of berry growth occurs at night. During the day there is no berry expansion; more likely there is contraction (Greenspan 1994). In that study it also was demonstrated that diurnal berry expansion and contraction differed before and after veraison; there was less contraction during the day post veraison. The enlargement of the berry during stages I and II is not associated with dermal tissue extensibility or turgor (Matthews et al. 1987). They also demonstrated that berry expansion subsequent to stage II was not due to changes in berry turgor; however, there was an increase in plastic extensibility of the dermal tissue.

The accumulation of fresh or dry fruit biomass on a whole vine basis occurs rapidly subsequent to berry set. The accumulation of cluster dry biomass has been shown to be a linear function of degree days (Gutierrez et al. 1985; Wermelinger et al. 1991; Williams et al. 1985a; Williams 1987a) and calendar days (Alexander 1958). The accumulation of cluster dry biomass followed a sigmoid curve for Riesling grafted onto rootstock 26G (Lohnertz 1988); it followed an exponential curve for Cabernet Sauvignon grafted onto rootstock 5C (Williams and Biscay 1991); both were based on calendar days. The preceding results indicate that the biphasic growth curve of individual berries is indistinguishable when the growth of all the fruit on a vine is quantified in the field. This may be due to asynchrony in the

growth of individual berries on a cluster and asynchrony in the growth of individual clusters on a vine or to sampling frequency (Coombe, 1992).

5. Daily CO_2 Requirements for Biomass and Carbohydrates

Utilizing the data found in tables 4.1 and 4.2 of Mullins et al. (1992), one can calculate carbon requirements of these grapevines at three stages of vine growth (Table 2). It was assumed that the carbon content of vine dry matter was close to 45% (Downton and Grant 1992). Approximately 98% of the carbon is utilized for dry matter accumulation at anthesis, while during fruit maturation 83% of the carbon is utilized for the accumulation of nonstructural carbohydrates. This demonstrates a shift over the growing season from a vine utilizing carbon for structural purposes to that of a vine accumulating sugars and starch.

B. Source-Sink Relationships in Grape

1. Fruit as a Sink

The fruit is the largest sink on the vine once fruit set has occurred (Mullins et al. 1992). The proportion of biomass partitioned to the fruit from budbreak until fruit maturity ranged from 44% to 69% of the total biomass accumulated during that period for Thompson Seedless grapevines (Table 3). This proportion was independent of the cultural practices employed to grow the vines and is probably more a function of the fruitfulness of the canes retained at pruning. The proportion of biomass partitioned to the fruit as a function of standing biomass at fruit harvest is dependent upon the age of the vines and the way in which they were trained. For nonirrigated Cabernet Sauvignon approximately 20% of the standing biomass at harvest was found in the fruit (Williams and Biscay 1991), while for Chenin blanc approximately 30% of the standing biomass was allocated to the fruit (Table 4).

Growth of the fruit after veraison is associated with the uptake of both water and hexose sugars. The uptake of water into the berry after veraison is probably from the phloem sap as there is an apparent loss of xylem function at veraison (During et al. 1987; Findlay et al. 1987). A nearly exclusive role of the

Table 2 The Change in Total Dry Weight and Nonstructural Carbohydrates of Chenin Blanc Grapevines from Budbreak Until Harvest and Calculated Values of CO_2 Uptake Required to Meet Those Demands (g $vine^{-1}$ day^{-1})

			CO_2 required	
Day of year[a]	Δ dry wt	Δ NSC	for dry wt[b]	for NSC[c]
88-147	64.7	1.5	106.8	2.2
148-206	31.0	19.0	51.3	27.9
207-253	10.0	55.3	4.5	81.3

[a]Budbreak, anthesis, and harvest correspond to day of year 88, 141, 253, respectively. Changes in dry wt and NSCs were calculated from tables 4.1 and 4.2 in Mullins et al. 1992. NSC, nonstructural carbohydrate.

[b]Carbon in dry matter was assumed to be 45%. CO_2 required for dry matter was determined by multiplying the dry wt column by 0.45 and that value by 3.67 (molecular wt CO_2/molecular wt C).

[c]CO_2 required for NSC was calculated by multiplying NSC column by 1.47 (molecular wt CO_2/molecular wt CH_2O)

Table 3 Current Year's Dry Biomass Production of Thompson Seedless Grapevines Grown in the San Joaquin Valley of California from Budbreak to Harvest, g vine^{-1}[a]

	1988		1989		1992	
Organ	Dry wt	%	Dry wt	%	Dry wt	%
Roots	495	6	308	2	293	2
Trunk	501	6	828	7	623	5
Stems	2056	26	2227	18	1891	14
Leaves	1458	18	1554	13	1308	10
Clusters	3568	44	7302	60	9173	69
Total	8078		12209		13288	

[a]Vines in 1988 and 1989 were harvested from a furrow-irrigated vineyard planted in 1984. Vines in 1992 were harvested from a drip-irrigated vineyard planted in 1987. Vine and row spacings from the furrow- and drip-irrigated vineyards were 2.44 and 3.66 and 2.1 and 3.55 m, respectively. Each value is the mean of at least five individual vine replicates. The percentage (%) column represents individual values in the dry wt columns divided by total weight.

xylem for water transport to the fruit is evident prior to veraison while the phloem is clearly dominant for the berry's postveraison water budget (Greenspan, 1994). It is unknown whether the uptake of water required for the growth of the berry after veraison is due to that accompanying sugars in the phloem, or to the decrease in berry water potential due to increasing solutes with a subsequent water inflow via the apoplast.

Sucrose is purported to be the primary sugar translocated from the leaves of *V. vinifera* to other organs (During and Alleweldt 1980). The metabolism of sucrose within the cell and its loading into the phloem and subsequent translocation within grapevines are probably similar to those described elsewhere in this book. Individual flowers are served by five or six vascular bundles in the pedicel

Table 4 Standing Biomass at Fruit Harvest and Current Year's Biomass and Nonstructural Carbohydrate Production of Chenin Blanc Grapevines Grown in the San Joaquin Valley of California, g vine^{-1}[a]

	Standing biomass		Current year's production			
Organ	Dry wt	%	Dry wt	%	NSCs	%
Roots	2984	16	220	3	625	17
Trunk	3015	16	263	4	217	6
Cordons	3421	18	-41	0	143	4
Stems	2539	13	2383	33	156	4
Leaves	1732	9	1641	23	91	2
Clusters	5199	28	2696	37	2503	67
Total	18890		7162		3375	

[a]Data were generated from tables 4.1 and 4.2, Mullins et al. 1992. The percentage (%) column represents individual values in the dry wt and NSC columns divided by total of each column.

which separate in the receptacle, giving rise to branches serving the flower parts and the ovary (Mullins et al. 1992). Once fruit set has occurred, the ovary bundles give rise to vascular traces within the developing berry; two serve the seeds and placenta, while the third is the peripheral bundles located between the dermal tissues and the pericarp (berry flesh). The peripheral bundles are joined to the central bundles (Mullins et al. 1992). The vascular strands are composed of tracheids, sieve cells, and elongated cells (Pratt 1971). The number of cells in the pericarp between the periphery and the central vascular bundles after veraison ranges from 15 to 20 cells (Harris et al. 1968).

The concentration of sucrose in *V. vinifera* berries is very low, comprising less than 4% of the total sugars (Hawker et al. 1976). It also was found that the sucrose concentration in easily expressed juice is less than that occurring in the rest of the berry, indicating that sucrose was compartmentalized in tissue that would have included the vascular system. Before veraison the highest concentrations of glucose and fructose are found in the skin and berry center, while after veraison highest concentrations of these two sugars are found in the berry core and below the peripheral vascular bundles (Possner and Kliewer 1985). These results indicate rapid hydrolysis of sucrose once it leaves the vascular tissue.

The majority of the increase in fruit biomass occurs after the inception of veraison (Coombe 1992). Veraison occurs after the lag phase of berry growth and is associated with berry softening and change in color of red- and black-fruited cultivars. The accumulation of glucose and fructose begins suddenly, on the same day that berry softening begins (Coombe 1989). Once it has begun, the concentrations of these two sugars increase linearly. Sugar accumulation rates into berries of field-grown grapevines have been calculated to be 1.1 μmol h^{-1} g^{-1} fresh weight (Hawker 1969). Similar rates have been reported in vitro (Brown and Coombe 1984). Hypotheses about the accumulation of hexose sugars in the pericarp of the berry recently have been reviewed (Coombe 1992). They include (a) active transport of sugars through the tonoplast of pericarp cells, (b) sucrose unloading from the phloem into the apoplast, and (c) sugar flow caused by leakiness of the plasma membrane in the pericarp cells.

Results derived from compartmental analysis in grape berries indicate that high concentrations of sugars can be found in the apoplast (Coombe 1989). As the concentration of hexose sugars increases during berry maturation, diffusible sugars in dermal segments increased (from 40% to 75%, beginning of ripening to 16% soluble solids), while the compartmented space increased only slightly (Brown and Coombe 1985). These results suggest that active uptake is not responsible for the dramatic sugar increase in pericarp cells but do support phloem loading of the berry. In further support of phloem unloading into the apoplast, Kriedemann (1969) demonstrated that labeled glucose moved from the phloem to the apoplast before entering pericarp cells. Finally, it has been shown that sugar import into the berry can continue after growth ceases (Matthews and Anderson 1988, 1989), even when berry volume decreases (Coombe 1973).

The third hypothesis was proposed by Lang et al. (1986). The breakdown of the apoplast-symplast compartmentation during berry ripening would establish a gradient of water potential between source and sink that would favor the movement of phloem sap into the berry (Coombe 1992). There is some evidence that cells in the pericarp develop some leakiness, such as a decrease in extractable gas, increased proportion of diffusible sugars, and increased translucency of the pericarp after veraison (Coombe 1992). However, the increase in berry sugar late in the growing season without a concomitant increase in volume would indicate that increasing concentrations of sugar in the apoplast of the berry does not create an osmotic gradient which would promote water uptake as implied by this hypothesis.

At present it is unknown what triggers the massive accumulation of sugars in the berry after veraison. Increased invertase activity has been shown to be associated with the increase in berry sugar accumulation (During and Alleweldt 1984). This increase would establish a gradient of sucrose from the phloem to the apoplastic space in the pericarp. Both soluble and cell-wall-associated forms of invertase have been localized in leaf and berry tissues of grape (Hawker 1969; Ruffner et al. 1990). However, invertase activity has been shown to exist in the berry before veraison, arguing against the activation of invertase as the triggering mechanism (Coombe 1989). Finally, phytohormones also have

been implicated as possible triggering mechanisms in other fruit crops (predominantly ethylene in climacteric fruit). The leading candidate for grape (a nonclimacteric fruit) appears to be abscisic acid (ABA) (Coombe 1989).

2. Seasonal Source-Sink Relationships

The initial growth of the shoot is dependent upon carbohydrate reserves in the permanent structures of the vine. Between budbreak and anthesis, the decrease in nonstructural carbohydrates amounted to approximately 350 g $vine^{-1}$ for Thompson Seedless grapevines (Fig. 3). It is assumed that the decrease in carbohydrate content in the roots and trunk was utilized to support growth of the new shoots and to meet the respiratory demands of the rest of the vine. This value is similar to the utilization of carbohydrates during this period when modeling the growth of grapevines (Gutierrez et al. 1985; Wermelinger et al. 1991). As mentioned earlier, the shoot is able to meet growth and respiratory demands of a single node cutting once the leaf area exceeds 50 cm^2 (Buttrose 1966). Therefore, when all individual shoots on the entire vine exceed this leaf area, utilization of reserve carbohydrate diminishes and the vine becomes dependent upon recently assimilated photosynthate. This occurs sometime before anthesis (Scholefield et al. 1978; Yang et al. 1980).

The redistribution pattern of recent photosynthate was initially studied with $^{14}CO_2$ labeling and autoradiography, providing qualitative results (Hale and Weaver 1962; Koblet 1977). More recent studies have provided more quantitative data (Hunter and Visser 1988a; Matsui et al. 1985; Yang and Hori 1979, 1980). An interesting result obtained from these studies is the large proportion of ^{14}C label that remains in the source leaf up to 72 hours after exposure to $^{14}CO_2$, whether the vines were potted or were grown in the field. The data indicate a slow turnover of recently assimilated photosynthate in the leaves of grapevines. However, data obtained with both annual and perennial plants demonstrate that carbon export rates range from 5 to 10 μmol C m^{-2} s^{-1} under controlled environmental conditions (Li et al. 1992; Moing et al. 1992; Servaites et al. 1989). An export rate of 5.1 μmol C m^{-2} s^{-1}, averaged over an 8-hour period, can be calculated for field-grown Thompson Seedless grapevines by using the carbohydrate data in Fig. 4 and the net photosynthesis rates given in the text.

Generalizations can be made about the distribution of ^{14}C-labeled photosynthate. Young leaves, less than 50% of their final size, retain most of the carbon they assimilate. Once leaves are larger than 50% of their final size they begin to export carbohydrates (Hale and Weaver 1962; Koblet 1977), although there may be cultivar differences (Yang and Hori 1980). Before anthesis, translocation of photosynthates from grapevine leaves is toward the apical portion of the shoot. Just before and after anthesis movement of photosynthates from the leaves on the basal two-thirds of the shoot is toward the clusters and back into the permanent organs of the vines. After berry set, the fruit becomes a very large sink. Of the ^{14}C-labeled photosynthate that moved from the source leaves, no less than 71% of that label was recovered in the clusters, regardless of the position of the source leaf along the shoot, once berries were 8 to 10 mm in diameter (Hunter and Visser 1988a). The carbon isotope composition of immature berries would indicate that most of the carbon found in the fruit is imported from the leaves (Di Marco et al. 1977); little is derived from berry photosynthesis. After harvest, most of the recently assimilated photosynthate is translocated back to the permanent structures of the vine.

The flush of roots during the growing season, one beginning before anthesis and the other after harvest (McKenry 1984; van Zyl 1984), indicates little allocation of carbon to the root system during initial shoot growth and again once the fruit becomes the major sink. Moreover, dry matter and nonstructural carbohydrates in the root system did not increase until after anthesis, with a smaller increase again after fruit harvest (Williams 1991; Fig. 3). For very young vines, the accumulation of dry matter in the root system did not occur until the canopy was well developed, regardless of treatment (Araujo and Williams 1988). However, once initiated, the growth of the root system for these young vines was maintained throughout the remainder of the growing season. In addition, root dry matter

increased from budbreak to fruit maturity for Chenin blanc vines (Mullins et al. 1992) and from anthesis to fruit maturity for Cabernet Sauvignon vines (Williams and Biscay 1991). It also has been demonstrated that ^{14}C-labeled photosynthate is translocated to the root system during all stages of berry growth (Matsui et al. 1985). In fact, the proportion of label found in the ethanol insoluble fraction in the root system was greater than that found in all other sinks on the vine. While root dry matter increased throughout the season in these examples, it should be stressed that this increase is much less than the dry matter partitioned to the fruit during that time.

There also appears to be an alteration in the partitioning of carbon to the other permanent structures of the grapevine. The increase in trunk diameter during the season mimics root flushes (van Zyl 1984). Trunk biomass does not increase until after anthesis; it levels off during stage III of berry growth and then increases again after fruit harvest (Williams 1991; Fig. 3). Apparently trunk growth does not begin early in the season until there is excess, recent photosynthate. Diminished growth during phase III of berry growth and increased growth after the fruit is removed indicate that the trunk does not compete well for carbon once berries become a strong sink.

Growth of vegetative organs is greater when clusters are removed from the vine compared to those with crop (Table 5). The increased biomass partitioned to leaves, stems, canes, and trunk ranged from 50% to 73%, while the increase in root biomass was 350% greater when the two treatments were compared. The data indicate that the root system is the organ most severely affected because fruit is such a large sink. The results also illustrate that vegetative organs do not have the same sink potential that clusters have, at least under the conditions of this experiment. Total biomass accumulation on vines without fruit, during the period from anthesis to 28 August, was only 53% that of vines with fruit. It should be pointed out that midday, photosynthesis measurements of leaves exposed to direct solar radiation were not different for the two treatments throughout the study (unpublished data). Possible explanations for this apparent anomaly are (1) time of day photosynthesis measurements were made (see Downton et al. 1987), (2) less photosynthesis of leaves elsewhere in the canopy of vines without fruit than on vines with fruit such that whole vine photosynthesis was less, (3) changes in canopy architecture which may reduce whole vine CO_2 assimilation, (4) more shoot biomass removed through mechanical hedging to allow equipment down the row, or (5) higher maintenance respiration rates of vegetative than reproductive organs (see next section).

3. Utilization of Carbon for Respiration

It has been estimated 25% to 75% of the CO_2 assimilated by woody plants and perennial crops is lost via respiration (Amthor 1989; Kramer and Kozlowski 1979; Vogt 1991). This would include respiration associated with growth of new tissue, maintenance respiration, and respiration needed for other metabolic processes. Respiration needed for growth has been estimated to be approximately 30% of net

Table 5 The Effect of Crop Removal at Anthesis on Subsequent Growth of 3-Year-Old Thompson Seedless Grapevines

	Organ, Δ g dry wt vine^{-1}[a]						
Treatment[b]	Leaves	Stems	Canes	Trunk	Roots	Fruit	Total
w/Fruit	759	797	237	557	252	6250	8852
w/o Fruit	1137	1358	388	962	872	-	4717

[a]Values represent the increase in biomass after anthesis. Data were generated from six individual vine replicates harvested on 5 September.

[b]Clusters were removed at anthesis (14 May). Dry weights for leaves, stems, canes, trunk, roots, and fruit at anthesis were 524, 474, 370, 561, 481 and 150 g vine^{-1}, respectively.

CO_2 assimilation (Penning de Vries et al. 1983), and this value was recently used to model grapevine growth (Wermelinger et al. 1991). The actual respiratory demand would depend upon tissue composition (Amthor 1989). Maintenance respiration also is dependent upon tissue composition, most notably N content (Ryan 1991). Measurements indicate that "normal values" of maintenance respiration in vegetative tissues range from 0.015 to 0.06 kg CO_2 kg^{-1} dry matter d^{-1} (Penning de Vries 1983) but may be substantially lower in fruit and storage organs. Other factors which would influence respiration rates include temperature and respiratory substrate levels. Schultz (1991) found that shade leaves have a lower specific rate of respiration than leaves grown in full sunlight; the lower rate may have been due to reduced carbohydrate levels in the shade leaves.

Dark respiration rates of grapevine leaves decrease with age; this effect is no longer apparent after vegetative growth ceases (Schultz 1991). This may be due to a decrease in the growth component once the leaves are fully expanded. The Q_{10} of dark respiration is above 3 early in the season and at the beginning of fruit ripening (Schultz 1991). At other times the Q_{10} ranged between 2.4 and 2.7 in that study. Using fully expanded leaves, a Q_{10} of 2 was measured in the temperature range of 10°C to 42°C (Williams et al. 1994). Leaf respiration was negligible at 10°C for Perlette vines grown in the desert, whereas it was measurable down to 5°C for Chardonnay vines grown in a cool climate (unpublished data). Absolute rates of dark respiration in mature leaves at 20°C range from 0.15 to 0.5 μmol CO_2 m^{-2} s^{-1} (Schultz 1991; Williams et al. 1994). Specific respiration rates of other vegetative tissues of grapevine are less well known.

Fruit respiration of grapevines has been studied much more thoroughly (Frieden et al. 1987a; Geisler and Radler 1963; Koch and Alleweldt 1978; Leyhe and Blanke 1989; Kriedemann 1968). Before anthesis individual flower respiration ranged from 1 to 5 μg CO_2 h^{-1}; after set berry respiration ranged from 5 to 60 μg CO_2 h^{-1}(Leyhe and Blanke 1989). Specific berry respiration can be as high as 600 μg CO_2 g^{-1} fresh wt h^{-1} early in berry development, decreasing to approximately 40 μg CO_2 g^{-1} h^{-1} at fruit maturation (Frieden et al. 1987a; Geisler and Radler 1963; Koch and Alleweldt 1978). An increase in berry temperature increases berry respiration, with a Q_{10} of approximately 2.0 (Frieden et al. 1987b).

The estimated daily CO_2 demand of Chenin blanc grapevines grown in the San Joaquin Valley of California is presented in Table 6. The daily requirement of CO_2 for dry matter and nonstructural carbohydrates is taken from Table 2. Maintenance respiration of the trunk and root system was determined by using the starvation method on mature grapevines (unpublished data), while that for

Table 6 Daily, Calculated CO_2 Requirements of Chenin Blanc Grapevines at Three Different Phenological Stages of Vine Growth, mol CO_2 $vine^{-1}$ day^{-1}

			Vegetative[b]		Fruit[c]	
Day of year	Dry matter	NSCs	R_g	R_m	R	Total
147	2.43	0.05	0.73	0.86	0.34	4.41
206	1.17	0.63	0.35	0.98	0.66	3.79
253	0.38	1.85	0.11	1.32	0.58	4.24

[a]See Table 2 for further details.

[b]Growth respiration (R_g) was assumed to be 30% of the cost of dry matter production. Maintenance respiration (R_m) costs were assumed to be 25.9, 11.6, 100.8, and 154.4 ng CO_2 g^{-1} dry wt s^{-1} for roots, trunk, stems, and leaves, respectively. See text for further details.

[c]Specific fruit respiration was taken from Geisler and Radler (1963). Rates for days 147, 206, and 253 were 240, 84, and 40 μg CO_2 g^{-1} fresh weight h^{-1}, respectively.

current season's stems and leaves was taken from a study on peach trees (Grossman 1993). It was assumed that fruit respiration, taken from Geisler and Radler (1963), encompassed both growth and maintenance components, while the accumulation of reserves had no conversion costs (Wermelinger et al. 1991). The costs of carbohydrate translocation were not taken into account. Approximately, 50% of the total CO_2 required by Chenin blanc grapevines on these three dates was used for respiratory purposes. This percentage is similar to the estimates of whole tree respiratory costs mentioned above. The cost of growth respiration diminished as the season progressed; however, as standing biomass increased, so did maintenance respiration. Between days 147 and 253 the increase was 53%. It should be emphasized that the estimates of daily whole vine CO_2 requirements using this data set are similar to the modeled estimates of whole vine photosynthesis presented in Fig. 1.

4. Root/Shoot Ratios

The root/shoot ratio is used to provide a quantitative relationship between below- and above-ground growth of plants. However, the usefulness of such a relationship for woody perennial crops under intensive cultivation has yet to be determined. The root to shoot (or aerial) ratio in grapevine varies with vine age, growth stage, environmental conditions, crop load, and management practices. For example, the root/aerial ratio (aerial = trunk, cordons, and shoots) of Chenin blanc grapevines at fruit maturity in South Africa varied from 0.71 to 1.1, depending upon how the soil was prepared before planting (Saayman and van Huyssteen 1980). The calculated root/aerial ratio also varied when vines were planted at different row spacings and trellis heights (Mullins et al. 1992; see table 6.1). The root/aerial ratio (based on standing vegetative biomass) of Chenin blanc vines grown in the San Joaquin Valley of California varied from 0.36 at budbreak to 0.28 at fruit maturity (Mullins et al. 1992). When just the current season's accumulation of biomass is used for the calculation (Table 4), the ratio becomes 0.15 at fruit harvest. The root/aerial, root/shoot (stems + leaves) or root/leaves ratio of the current season's accumulation of Thompson Seedless biomass varied considerably from year to year (data taken from Table 3). The preceding data indicate that when modeling the growth of the grapevine root system, one cannot assume that root growth is a particular fraction of the biomass allocated to the shoots (Gutierrez et al. 1985; Wermelinger et al. 1991). However, as shown in Fig. 6, there appears to be a constant relationship between allocation of biomass to the root system and allocation to the trunk of Thompson Seedless grapevines.

The small amount of biomass allocated to the root system of grapevines (see previous discussion) differs from estimates of C (or biomass) allocated to root systems of trees in a forest (Cannel 1985; Vogt 1991). From 24% to 66% of the assimilated carbon is allocated to the roots of trees, most of this for fine root turnover. However, the amount of carbon allocated to the roots of Pinus sylvestris decreased from 59% to 31% with improved soil fertility (Linder and Axelsson 1982). Therefore, high soil fertility and availability of water for irrigation purposes in vineyards (Tables 3 and 4) and orchards (Miller and Walsh 1988), as would be the practice in a commercial situation, may decrease the carbon demand of roots for intensively managed tree and vine crops, resulting in low root/aerial or root/shoot ratios.

V. EFFECTS OF MANAGEMENT PRACTICES ON SOURCE-SINK RELATIONSHIPS

A. Canopy Management and Crop Load

Many different cultural practices are performed on grapevines in order to enhance fruit or wine quality (Jackson and Lombard 1993). These include the use of different trellises, planting densities, pruning practices, leaf and shoot removal, and adjustment of crop load. These management practices will alter the source-sink ratio of the vines. Many of them are used presumably to favor carbon transport to the fruit at the expense of that to the vegetative structures.

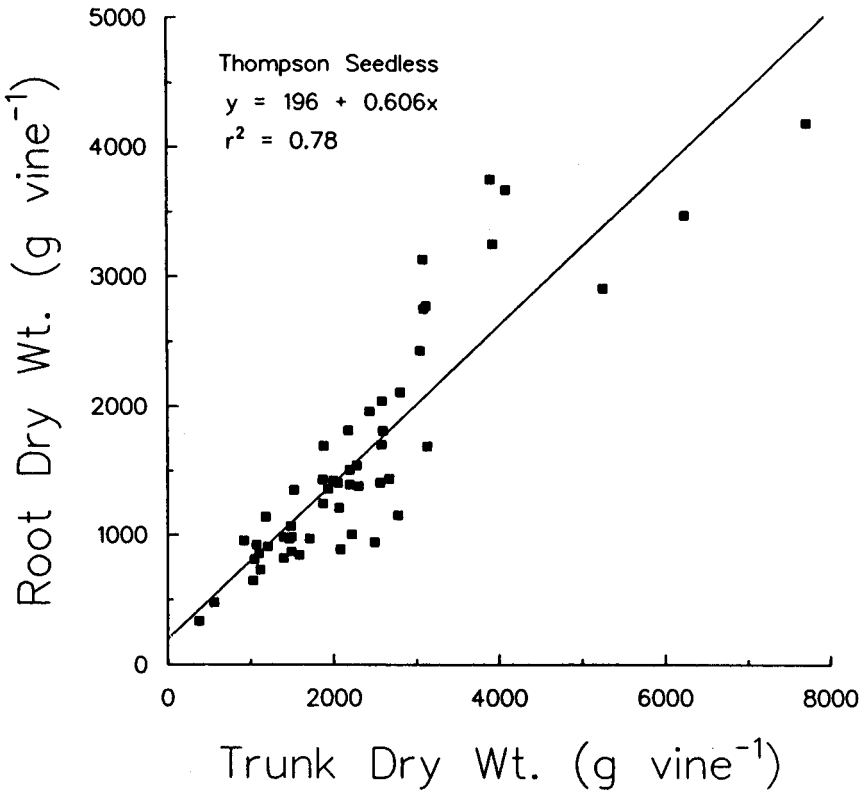

Figure 6 The relationship between trunk and root dry biomass of Thompson Seedless grapevines. Each data point is the mean of at least four individual vine replicates. See text for further details.

The presence or absence of sinks on a grapevine may or may not affect individual leaf net CO_2 assimilation rate. The removal of sinks (either the fruit or actively growing shoot apices) from potted grapevines results in a significant decrease in the net CO_2 assimilation rate of individual leaves (Candolfi-Vasconcelos and Koblet 1991; Hofacker 1978; Kriedemann and Lenz 1972). Net CO_2 assimilation rate of leaves that remain on shoots on which defoliation has occurred is greater than that of leaves on shoots on which no defoliation took place (Candolfi-Vasconcelos and Koblet 1991; Hunter and Visser 1988b). It should be emphasized that fruit removal may have no effect on individual leaf (Williams 1986) or whole vine CO_2 assimilation (Edson et al. 1993). It appears that sink effects on grapevine leaf photosynthesis are a function of the time of day (Downton et al. 1987) and time during the season when measurements were taken (Candolfi-Vasconcelos and Koblet 1991). The presence of other sinks, especially on large, field-grown vines, apparently mitigates any depressing effect fruit removal may have on leaf CO_2 assimilation under those conditions (L. E. Williams and F. Araujo unpublished data).

Crop level affects berry and cluster size, accumulation of sugar and other flavor components in the fruit, and various aspects of vegetative growth (Weaver and McCune 1960; Weaver and Pool 1968; Winkler 1954). As yield per vine increases, berry size and cluster weight decrease (Clingeleffer 1984, 1989; Kliewer and Weaver 1971; Weaver and Pool 1968). It is thought that high yields on vines reduce the quality of the fruit (Jackson and Lombard 1993). This effect is due in part to the fact that "overcropping" delays the accumulation of sugar in the fruit when compared to that of vines with less

crop. However, there are reports indicating that the amount of crop per vine does not affect sugar accumulation and fruit quality (Clingeleffer 1989) or that there is a specific amount of crop a vine will mature before further yield increases delay maturation and affect quality (Bravdo et al. 1985; Kliewer and Antcliff 1970).

Differences in results among the studies mentioned indicate the importance of quantifying all aspects of vine growth before concluding that high vine yields decrease fruit quality. As expected, leaf area per vine would be a major determinant in explaining the differences with regard to crop level. This has led many to conduct studies in which vines are defoliated to a certain level to determine the leaf area required to mature a given amount of fruit. A ratio of 0.7 to 1.0 m^2 kg^{-1} fruit is usually reported to be the value required so that sugar accumulation is not delayed (Jackson and Lombard 1993). Ratios as low as 0.5 have been reported for field-grown Thompson Seedless grapevines in which sugar accumulation is not affected (May et al. 1969; Williams et al. 1987). The usefulness of this ratio in a field situation is probably minimal as trellis type, row direction, seasonal canopy development, and diurnal path of solar radiation alter the proportion of leaves contributing the major portion of a vine's daily production of photosynthate. Indices such as leaf area index (Grantz and Williams 1993), leaf area per meter canopy length, or canopy leaf area to canopy surface area (Dokoozlian 1990) may be more appropriate and useful especially with regard to modeling vine C gain.

It must be stressed that fruit maturation also is affected by the microclimate in the fruiting zone (Williams et al. 1994). One means to increase yield per vine is to leave more buds per vine at pruning. Increased bud numbers without expanding the vine's framework result in more shoots per vine, creating a canopy microclimate that may decrease the accumulation of sugar in the fruit and other aspects of fruit quality, such as color (Smart 1985). The removal of the basal leaves on shoots up to the node positions of the clusters is increasingly being used in California to alter the microclimate in the fruiting zone in the hope of affecting fruit composition. This practice enhances sugar accumulation in the berries through an increase in berry temperature under those conditions (Bledsoe et al. 1988).

Retaining varying numbers of buds on a vine, through differential pruning, usually is the means to assess the effects of crop load on reproductive and vegetative growth (Miller et al. 1993; Weaver and Pool 1968). Current season aerial, vegetative growth and leaf area increase much more rapidly early in the season for vines in which higher number of buds are retained (Downton and Grant 1992). However, leaf area measured at fruit harvest (Downton and Grant 1992) or pruning weight taken during the dormant portion of the season (Clingeleffer and Krake 1992; Miller et al. 1993) is equal to or greater than on vines with low bud numbers retained at pruning than on those that initially have more count buds. Increased vegetative growth and leaf area per vine may be due to increased growth of shoots derived from noncount buds (Table 7). Note that for vines in which two canes were retained half of the entire vine's leaf area originated from the head of the vines and that those shoots also had greater leaf area on lateral shoots. These results would indicate that increased accumulation of sugar in the fruit of vines with lowered cluster numbers is the result of an alteration in the source/sink ratio; much greater source for the vines pruned to two canes. Interestingly, the leaf area (derived only from shoots on the fruiting canes) to fruit ratios for all three treatments were similar, ranging from 0.81 to 0.85 m^2 kg^{-1}.

There have been a few field studies which examined the effects of pruning level on biomass partitioned to the permanent structures of the vine. The root biomass of Cabernet franc vines was significantly less for mechanically pruned compared to spur-pruned vines after the treatments had been imposed for 5 years; however, there were no differences in biomass of the trunk among treatments (Clingeleffer and Krake 1992), there were only slight differences in the concentration of nonstructural carbohydrates in the trunk and roots of these vines (Ruhl and Clingeleffer 1993). Over a 3-year period Thompson Seedless grapevines pruned to four canes produced almost 28 kg more fruit than those pruned to two canes; however, there was almost no difference between the two with regard to the partitioning of biomass to the trunk (Table 8). Biomass partitioning to the root system of vines with yields greater than double those pruned to two canes was reduced by 21% over the 3-year period.

Table 7 Effect of Pruning Level on Yield and Leaf Area of Thompson Seedless Grapevines 3 Weeks Before Fruit Maturity in 1987

Pruning level, (no. of canes)[a]	Yield, kg vine^{-1}	Leaf area (m^2 vine^{-1}) Canes[b] 1°	Canes[b] 2°	Head[b] 1°	Head[b] 2°	Total
2	10.9	6.5	2.8	5.7	5.6	20.6
4	19.3	12.2	3.5	3.8	1.9	21.4
8	25.7	15.4	5.7	3.3	1.3	25.7

[a]Vines were planted in 1968 and were flood-irrigated each growing season. Vine and row spacing were 2.44 and 3.66 m, respectively. Treatments were imposed for a single season.
[b]Leaf area was subdivided into that derived from the fruiting canes (canes) and the head of the vine and from primary (1°) and lateral (2°) shoots.

As demonstrated by Clingeleffer and Krake (1992) there was little effect of pruning level on the partitioning biomass to the trunk. The preceding results would indicate that the extreme, deleterious effect of overcropping reported previously in California may be cultivar-specific (Weaver and McCune 1960) or due to lack of regular irrigation and fertilization programs (Winkler 1954, 1958).

Increasing vine density within the vineyard decreases yield and vegetative growth per vine but increases yield per unit land area without an apparent effect on fruit quality (Archer and Strauss 1991; Lavee and Haskel 1982; Mullins et al. 1992). Increasing vine density from 1120 to 1680 vines ha^{-1} decreased shoot biomass by 30%, but there was no effect on biomass partitioned to the root system (Mullins et al. 1992). However, vine densities greater than 2000 vines ha^{-1} reduced root growth (Archer and Strauss 1985). It has been demonstrated that vines planted to higher densities reduce soil water

Table 8 The Effect of Pruning Level Imposed for Three Growing Seasons on the Increase in Trunk and Root Dry Weight of Thompson Seedless Grapevines During That Period

Pruning level, no. of canes	Yield,[a] kg vine^{-1}	Increase in dry biomass, g vine^{-1} Trunk[b]	Roots[b]
2	12.9	1921	2365
4	22.2	2105	2285
8	29.0	1949	1865

[a]Values in this column are the 3-year mean of each treatment.
[b]Initial biomass, measured at budbreak in 1988, of the trunk and root system was 1981 and 1385 g vine^{-1}, respectively. Biomass at the conclusion of the study was determined after leaf fall, 20 November 1990. Four single-vine replicates were used in determining biomass at the end of the study. Other information is in Table 7.

content more rapidly than those at wider spacings, resulting in more negative leaf water potentials (Archer and Strauss 1989) and reduced rates of photosynthesis (Archer and Strauss 1990). Therefore, the reduction in vine growth at closer spacings may be due to effects of a less favorable vine water status if these density experiments are not irrigated or irrigated with the same amount of water regardless of treatment. The ability to maintain fruit quality at higher densities may be due to a greater leaf area to fruit weight ratio (Archer and Strauss 1991) or to the positive effects of mild water stress (Williams et al. 1994).

B. Irrigation and Fertilization Management

Vineyard water management is probably the best tool with which to manipulate vine growth and fruit quality. Reproductive growth of grapevines appears to be less sensitive to water stress than is vegetative growth (Williams and Matthews 1990; Williams et al. 1994). For example, as applied water decreased from 100% to 80% to 60% of vineyard evapotranspiration (ET), pruning weights decreased 15% and 39% for the latter two irrigation treatments, respectively, compared to the 100% treatment (Fig. 7). However, the corresponding reduction in vine yield was only 1% and 10% for the 80% and 60% irrigation treatments, respectively. Another point illustrated in this data is related to the purported reduction in vegetative growth due to the increasing carbon demands of the fruit as the season progresses (as discussed in previous sections). While there were no significant differences in yield for the 80%, 100%, and 120% irrigation treatments, pruning weights continued to increase linearly. Thus water management and not sink strength of the fruit determined continued growth of the shoots in this study. It should also be pointed out that vines in this study are mechanically hedged in order to facilitate the movement of equipment down the rows. Therefore, pruning weights reported here are less than actual vegetative growth that occurred during the season, especially for vines irrigated at 100% of ET or greater. Finally, the results also indicate that increased leaf area does not always advance fruit maturation as there were no significant differences in soluble solids at fruit harvest for irrigation treatments between 80% and 140% (unpublished data). An alternate conclusion would be that the increased vegetative growth occurring at the higher irrigation levels did not detract from sugar accumulation in the fruit.

Vineyard water stress also will affect the amount of carbon partitioned to the permanent structures of the vine. Root, trunk, and cordon biomass was reduced 31%, 17%, and 26%, respectively, for vines irrigated at 52% of vineyard ET compared to those at 100% ET after 5 years (Mullins et al. 1992; see table 6.6). The concentration of nonstructural carbohydrates in those organs differed only slightly for the two treatments. Water stress generally increased the concentration of carbohydrates in the stems and roots of cuttings of several wine grape varieties (Ruhl and Alleweldt 1.990). While the data differ in the preceding two studies with regard to carbohydrate concentrations, it is agreed that total carbohydrate content in those organs decreased on a per vine basis as a result of reduced growth brought about by water stress.

The application of fertilizers in nutrient-deficient soils increases both vegetative and reproductive growth. Continued application of excessive nitrogen fertilizer favors vegetative over reproductive growth. Reduction in the accumulation of sugar in the fruit of vines growing on fertile soils or those fertilized with high rates of N (Spayd et al. 1994) is probably associated with excessive vegetative growth affecting the microclimate in the vine's fruiting zone (Smart 1991).

C. Plant Growth Regulators and Girdling

Plant growth regulators (PGRs) are frequently used in grape culture, especially for the production of seeded and seedless table grapes. The two most commonly used PGRs are (2-chloroethyl) phosphonic acid (Ethephon) and gibberellic acid (GA_3). Ethephon is used to enhance berry color and maturation, induce cluster abscision, and influence budbreak and vegetative growth (Szyjewicz et al. 1984). The

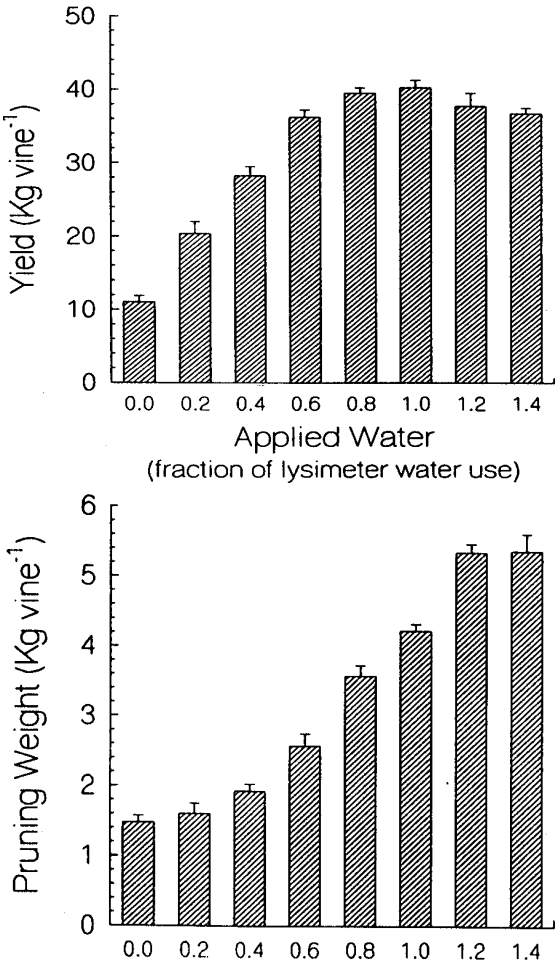

Figure 7 The effect of various amounts of applied water on vine productivity and vegetative growth (pruning weights) of 6-year-old Thompson Seedless grapevines. Full vine ET (1.0 applied water treatment) was determined with the use of a weighing lysimeter (Phene et al. 1991). Vines were irrigated daily at various fractions of the amount of water vines in the lysimeter used.

movement of Ethephon within the vine and its exact mode of action are unclear. Application of Ethephon increases maturity of the fruit in some instances and either has no effect or decreases it in others (Szyjewicz et al. 1984). The contrasting results probably are related to concentration used, time of application, environment, and cultivar. It inhibits the growth of primary and lateral shoots; inhibition wears off with time. It is unknown whether the advancement of berry maturation is due to the inhibition of shoot growth or the maintenance of a canopy microclimate favorable to fruit maturation due to less shoot growth.

The application of GA_3 has long been used in California to increase the size of seedless table grape cultivars (Weaver and McCune 1959). Application at anthesis reduces the number of flowers that set, reducing potential sinks; an additional application a few weeks later also increases berry size by enhancing cell division in the pericarp (Sachs and Weaver 1968). GA_3 also may affect the movement of recent photosynthate (Weaver et al. 1969). For example, its effect on increasing berry size differs, depending on the portion of the vine that is sprayed (Harrell and Williams 1987a; Weaver et al. 1969). Berry size is greater when individual clusters as opposed to entire vines are sprayed with GA_3. It is unknown whether this is due to better coverage of the material when just individual clusters are sprayed or to reduced competition for carbohydrates with shoots, which are covered on whole vine applications. The latter would be the case if GA_3 were able to direct the movement of photosynthate to newly formed vegetative sinks. The application of GA_3 to the vine results in lower concentrations of nonstructural carbohydrates in leaf tissue shortly after treatments are imposed, compared to the control (Roper and Williams 1989). However, no differences in nonstructural carbohydrates were observed in other vegetative organs 2 months later (unpublished data). Therefore, GA_3 is able to increase berry size by decreasing total sink size of the fruit cluster, increasing sink potential by increasing cell division, and possibly manipulating the direction of recent photosynthate. It is interesting to note that berry size and yield of nonirrigated Thompson Seedless grapevines sprayed with GA_3 were similar to those of vines that were irrigated but not sprayed with GA_3 (Williams et al. 1994). This was despite the fact that the leaf area of the nonirrigated vines was less than one third that of the irrigated vines.

Trunk girdling (the removal of a strip of phloem, 6 mm in width) has been used even longer than GA_3 in California to increase the size of seedless table grape cultivars and to advance fruit maturation (Jacob 1929). Girdling is performed at berry set (same time as the second GA_3 application) to increase size and also at veraison to advance fruit maturation. Trunk girdling effectively disrupts the movement of carbohydrates to the root system, resulting in an increase in total carbohydrates above the girdle and a diminishing reserve in the root system (Roper and Williams 1989). Girdles heal under California growing conditions in 4 to 5 weeks. The increased availability of carbohydrates above the girdle is hypothesized to be the reason for the effect on increasing berry size and advancing maturity.

Girdling potted and field-grown grapevines results in decreased rates of photosynthesis as long as the girdle remains open (During 1978; Harrell and Williams 1987b; Hofacker 1978; Kriedemann and Lenz 1972). It is thought that the reduction in photosynthesis is due to the accumulation of carbohydrates in the leaves (Kriedemann and Lenz 1972), but recent work on field-grown vines indicates that this is not the case (Roper and Williams 1989; Fig. 4). The reduction in photosynthesis in response to girdling may be due to the accumulation of ABA in the leaves (During 1978), which decreases stomatal conductance (Downton et al. 1988). When grapevines are both girdled and sprayed with GA_3, the reduction in photosynthesis due to girdling is not as great as with girdling alone (Harrell and Williams 1987b). The specific mode of action of GA_3 on grape leaf photosynthesis under these conditions is unclear.

VI. SUMMARY

There are more than 10,000 cultivars of *V. vinifera* grown commercially under a wide range of climatic conditions. The differences among cultivars presented in this chapter with regard to source-sink relationships would indicate that efforts to model the growth of a specific cultivar under a given set of environmental conditions will require further, extensive studies. In addition, the use of different cultural practices by grape growers indicates that potential sources and sinks of the same cultivar will differ from vineyard to vineyard. Therefore, vine growth (including root growth) must be quantified as a function of vine training, trellis system, and irrigation and fertilization management practices to gain a better understanding of source-sink relationships in grape.

The data presented in this review demonstrate that even during the portion of the growing season

when large amounts of carbohydrate reserves in the permanent structures of the vine continue. This would be expected of this perennial crop as carbohydrates are needed for maintenance of the vine during dormancy and for initial shoot growth in the spring. The ability of vines to partition carbohydrates to the permanent structures during fruit growth would be especially advantageous in cooler regions, where the first freeze may occur shortly after harvest. It was also demonstrated that the amount of carbohydrates found in those structures is only a small portion of the total required to produce the new vegetative and reproductive structures. Therefore, only under extreme pest or disease pressure would one expect the vine not to have adequate carbohydrate reserves. Finally, the amount of reserve carbohydrates found in the permanent structures' of grapevines (presented in this chapter) would provide only a small portion of the total C required to grow and mature a grape crop. Therefore, it is doubtful that a vine would deplete these reserves to sustain continued fruit growth in instances in which the vine's canopy could not supply adequate carbohydrates.

Further research is needed to elucidate the mechanism by which grapes accumulate massive amounts of sugars and the stimulus that triggers that event in berries at veraison. The role of phytohormones in regulating sink potential and their effect on carbohydrate translocation need additional study. Grapevines, especially of seedless grape cultivars, may prove to be an excellent system in which to conduct such experiments.

It is hoped that the information presented in this chapter will dispel some of the myths associated with the culture of grapevines. It has been the author's experience that many individuals attribute various maladies of grape growth and delayed sugar accumulation to vegetative sinks' diverting carbohydrates from the fruit. Many of the examples presented indicate that is not the case. More likely, continued vegetative growth alters the microclimate within the fruiting zone, which may then alter berry metabolism (Smart 1985; Williams et al. 1994). Continued quantitative research on vine growth and modeling efforts by viticulturists will provide much needed information on what we do and do not know about this perennial fruit crop.

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