Chapter 4

Grape

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CONTENTS

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I. INTRODUCTION

A. GRAPE PRODUCTION

Grapevines are the most widely planted fruit crop worldwide and are cultivated on all continents except Antarctica.[1] Grapevine acreage as of 1988 was greater than 10 million ha.[2] The widespread distribution of grapevines is due to a large genetic diversity of available species and cultivars and a low chilling requirement for the release of buds from dormancy. However, a single species, *Vitis vinifera* L., of which there are currently over 10,000 cultivars accounts for greater than 90% of the annual production worldwide. Sixty percent of the world production of grapes (>63 Tg) is produced in Europe with Spain, Italy, and France each having more than 1 million ha of land devoted to grapevines.

Grapes are primarily used for wine, juice, distilled liquors, dried fruit (raisins) and fresh consumption fruit (table grapes). Italy, France, and Spain produce more than 50% of the world's wine; European countries together with the Commonwealth of Nations (former Soviet Union) account for 80% of the world's production.[1] The production of raisins worldwide is approximately 800 Gg (dried fruit); the United States and Turkey are the top two producing countries. Annual world production of table grapes is approximately 7 Tg. Italy, the Commonwealth of Nations, and Turkey comprise the top table grape producing nations. Fruit juice is concentrated when production exceeds demand.

B. CLIMATIC CONSTRAINTS TO GRAPE PRODUCTION

V. vinifera is a temperate climate species adapted to hot summers with mild winters. The suitability of a given grape cultivar to a local environment is based upon day length, heat summation, rainfall, length of the growing season, and minimum winter temperatures. On a broad scale the main grape production areas are found between 30 and 50°N and 30 and 40°S latitudes, corresponding to the 10 and 20°C yearly isotherms.[1] Grapes can be commercially grown in other areas where climate is moderated due to local geographical conditions (mountains, land masses, and ocean currents). Raisin production is limited to the latitudes of 30 and 39°N in the Northern Hemisphere and between 28 and 36°S in the Southern Hemisphere. This is due to the fact that the best suited raisin cultivars, 'Thompson Seedless' (syn. 'Sultinina') and 'Zante Currant', require warm temperatures for fruit bud differentiation and fruit maturation. In addition, the production of natural raisins (sun-dried grapes) requires high temperatures and lack of rainfall following harvest. Warm, dry weather also favors the production of table grapes as the incidence the fungal diseases is much reduced under these conditions.

C. CYCLE OF VINE GROWTH

Vineyards are planted via vegetative means such as cuttings, rootings, or grafted vines. Vineyards commonly produce a harvestable crop in the third growing season, subsequent to establishment of a root system and training the vines to fit a specific trellis system.[2] Trellis choice depends upon intended use of the grapes (wine, raisin, or table grape production), methods of pruning and harvest (manual or mechanical),[3] and climate and soil conditions.

Current season's vegetative and reproductive growth occurs from compound buds (consisting of a primary, secondary, and tertiary bud) in the spring. The primary bud consists of eight to ten leaf primordia with zero or more cluster primordia. Budbreak is followed by rapid shoot growth. Flower differentiation on the cluster primordia begins prior to budbreak and continues up until anthesis. Anthesis occurs approximately eight weeks after budbreak, therefore, considerable leaf area has developed before pollination, fertilization, and berry set takes place. Berry growth of both seeded and "seedless" cultivars is of the double sigmoid type in which growth occurs in three stages. Vegetative growth commonly continues until veraison (the end of Stage II; characterized by softening of the fruit and change in color for red and black cultivars). Wine and raisin grapes are harvested when the soluble solids (°Brix) concentrations are between 16 and 25 °Brix. Table grapes are generally harvested when the soluble solids levels are 15 to 17 °Brix.

Leaves remain photosynthetically active and will remain such until the first killing freeze. Periderm will have formed on the main axis of the shoot throughout the growing season. Once the leaves abscise the vine goes dormant and the leafless shoots, now called canes, will be pruned during the winter to regulate next year's crop.

Cluster differentiation (for the next year's crop) within the compound buds of spur pruned cultivars (four basal nodes on a shoot) begins around anthesis and is complete prior to veraison for spur-pruned table grape cultivars in California (L.E. Williams, unpublished data). Cluster differentiation is complete at node 15 by late summer. Therefore, environmental conditions and stress during these periods can dramatically affect the next season's yield. Further details on the physiology, anatomy, and morphology of the grapevine can be found in Mullins et al.[1]

II. IRRADIANCE

Solar radiation induces various biological responses through changes in light quality, quantity, direction, and periodicity.[4] Plant responses include thermal effects, photosynthesis, photomorphogenesis, and mutagenesis. Viticulturists have become increasingly aware of the positive effects of light on both the quantity and quality of the harvested fruit due in large part to the pioneering work of Dr. Nelson Shaulis and co-workers at the New York State Agricultural Experiment Station, Geneva, NY.

A. INTERCEPTION BY GRAPEVINE CANOPIES

1. Effect of Canopy Height and Row Direction

Light interception is dependent primarily upon canopy shape and orientation. Smart[5] predicted that sunlight interception by grapevine canopies declines rapidly as canopy height decreases and the distance between walls of foliage (i.e., distance between vine rows) is increased. While a smaller distance between rows increases solar radiation interception on an area basis, cross-row shading becomes a significant factor limiting sunlight interception of individual foliage walls as the distance between rows is reduced. A value of 1:1 for the ratio of canopy height to distance between canopies is recommended to avoid cross shading.[5]

Row direction also has a pronounced effect on solar radiation interception. Greater amounts of direct light are absorbed by the canopy walls in the mid-morning and mid-afternoon in rows oriented north-south compared to east-west.[5] Canopies 1 and 3 m in height and spaced 4 m apart intercepted approximately 10 and 22% more sunlight, respectively, when rows were oriented north-south compared to the east-west row orientation.

2. Effect of Trellis and Canopy Management

The amount of solar radiation intercepted by the grapevine canopy, as well as the light environment within the canopy interior, is largely determined by the training and trellis system employed and vine leaf area.[6] These factors, combined with such cultural practices as shoot positioning and basal leaf removal, determine shoot orientation, canopy surface area, and vine foliage density.[7] Shaulis and co-workers[8] were among the first to recognize the influence of vine training and trellis design on the light environment within grapevine canopies, and its effect on vine productivity and fruit composition. Vegetative growth normally increases as canopy width expands, thereby increasing the total amount of leaf surface available for solar radiation interception.[9] As a result of greater sunlight interception per unit row or canopy length, increasing both canopy height and width via vineyard layout and training/trellising generally increases vine yield.[10–12]

Solar radiation interception and penetration to the canopy's interior has been substantially increased by the separation of the canopy into two vertical curtains.[8] The Geneva double curtain training system has often resulted in greater bud fruitfulness and vine productivity, and improved fruit quality. Carbonneau and Huglin[13] reported that the surface of an open lyre or "U" shaped canopy with two distinct curtains of foliage intercepted 10% more solar radiation per day than a non-separated, single row canopy at wide row spacing. Light measured in the fruiting zone was 21% of ambient for the separated lyre canopy, compared to 6.4% of ambient for the single canopy. Kliewer et al.[14] reported that photosynthetic photon flux density (PFD) within the fruiting zone of a non-divided canopy of 'Sauvignon blanc' was approximately 4% of ambient, while the fruit zone PFD of this cultivar with a divided canopy was greater than 30% of ambient.

Additional canopy management practices may be employed to increase solar radiation interception and penetration into the canopy interior. Shoot positioning, either performed manually or mechanically, can be used to separate tangled foliage within the interior of divided canopies. Shoot positioning prevents shading and improves sunlight interception by maintaining canopy separation throughout the growing season.[7] Basal leaf removal, influences the light microclimate in the canopy interior. Bledsoe et al.[15]

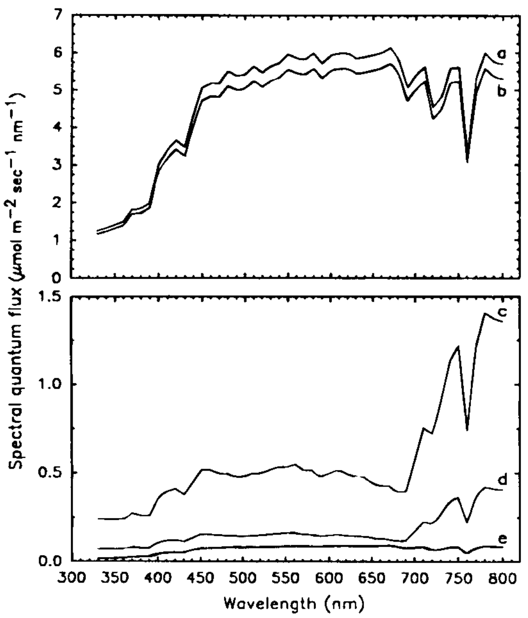

Figure 1 Spectral quantum flux of radiation between the wavelengths of 330 and 800 nm for: ambient sunlight (a), a sunfleck within the interior of a grapevine canopy (b), and for canopy light in the fruiting zone of 'Cabernet Sauvignon' grapevine canopies with 2.1 (c), 5.6 (d) and 12.2 (e) m^2 leaf area m^{-1} canopy length. Each curve represents the mean of five separate scans. Determinations were made at 2-nm wavelength intervals using a scanning spectroradiometer with the sensor positioned horizontally near solar noon under clear skies in Oakville, CA. (N.K. Dokoozlian, unpublished data.)

reported that basal leaf removal following berry set increased PFD within the fruiting region of 'Sauvignon blanc' grapevines by approximately 20% when compared to the untreated control.

B. LIGHT ENVIRONMENT WITHIN GRAPEVINE CANOPIES

Of the PFD arriving perpendicular to the surface of a grape leaf, 80 to 90% is absorbed and the remainder is either transmitted or reflected.[16] The low levels of PFD (5% of ambient or less) commonly measured within the interior of dense grapevine canopies is a result of this high degree of absorption.[17] The spectral quality also is altered when compared to ambient solar radiation in that the blue (400 to 500 nm) and red (650 to 700 nm) wavelengths are absorbed by the vine's canopy to a greater extent than the far-red (710 to 800 nm) wavelengths (Figure 1). This results in a decrease in the amount of blue light in the canopy interior relative to other wavelengths, as well as a decrease in the red (R) to far-red (FR) ratio (R:FR). The spectral composition of sunflecks, which occur when direct solar radiation penetrates through gaps in the canopy, closely resembles that of incident radiation (Figure 1).[18]

The relationship between canopy leaf area and PFD, R:FR, and sunflecks within the canopy of wine grapes grown under the standard (non-separated) training/trellis system used in California is presented in Figure 2. PFD decreased to 10% or less of its ambient value approximately 0.5 m below the canopy surface. PFD was lowest near the fruiting zone, with values of 7.0 and 0.3% of ambient, for vineyards with 2.2 and 12.2 m^2 of leaf area per meter canopy length, respectively. PFD increased below the fruit zone, and ambient values of PFD were found at ground level of canopies with low leaf area densities. Patterns of the R:FR ratio and sunfleck attenuation within low and high leaf area density canopies were similar to those observed for PFD (Figures 2B and 2C, respectively). The R:FR ratio decreased immediately below the canopy surface, and reached its lowest level at or near the fruit zone. The R:FR also increased gradually moving downward along the vertical transect from the fruit zone to the ground. Sunflecks illuminated about 20% of the fruit zone at harvest within the low density canopy, but were nearly absent along the vertical transect in a high density canopy. This study also revealed that the patterns of PFD, R:FR, and sunfleck attenuation changed little during the course of fruit development, despite an approximate doubling of canopy leaf area in various vineyards during this same time period.[19] A close, positive relationship exists between PFD and the R:FR ratio (Figure 3). In very dense canopies PFD may approach 0.1% of ambient sunlight and the R:FR ratio may drop as low as 0.05.

C. EFFECTS ON VINE GROWTH AND METABOLISM

1. Cluster Differentiation

The differentiation of anlagen into either cluster or tendril primordia is dependent upon the irradiance level reaching the compound bud during development as demonstrated by experiments conducted under

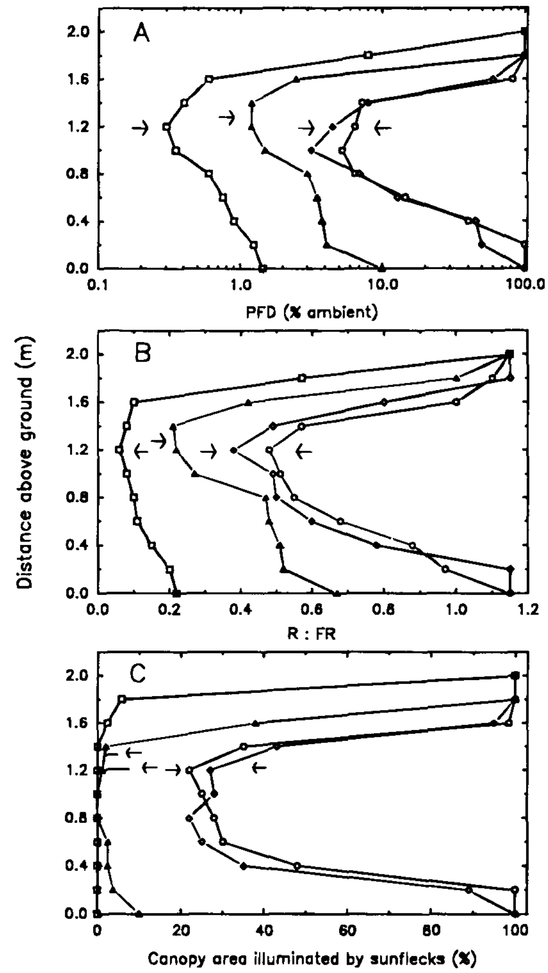

Figure 2 Relationship between photosynthetic photon flux density (PFD) (A), the red:far red (R:FR) ratio (B), and the percent canopy area illuminated by sunflecks (C) as a function of canopy depth for 'Cabernet Sauvignon' canopies at harvest. Symbols correspond to the following canopy leaf areas: (○) 2.2, (◇) 3.3, (△) 8.7, and (□) 12.1 m^2 leaf area m^{-1} canopy length. Readings were taken with sensors positioned vertically upward, at solar noon under clear skies. Arrows indicate the locations of the fruit zone in each canopy. (N.K. Dokoozlian, unpublished data.)

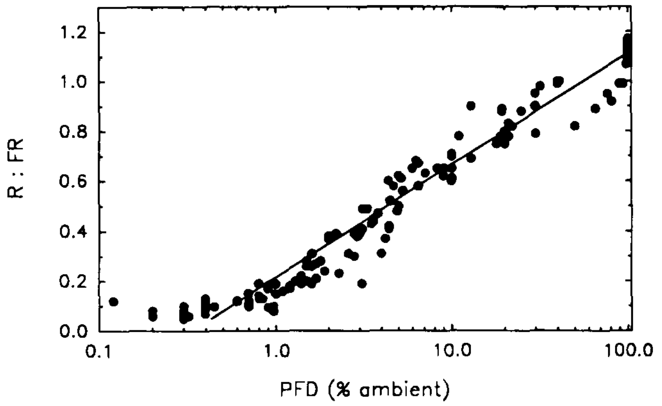

Figure 3 Relationship between the red:far red (R:FR) ratio and photosynthetic photon flux density (PFD) (% ambient, log scale) within grapevine canopies. Values represent a wide range of vineyard sites and canopy densities and depths. Measurements were made with light sensors positioned horizontally at solar noon under clear skies. Data were fitted to a linear function: $y = -0.431 + 2.147x$, $r^2 = 0.96$. (N.K. Dokoozlian, unpublished data.)

controlled environmental conditions[20,21] and in the field.[22,23] Low irradiance favors the differentiation of tendril primordia. The number and size of cluster primordia generally increase with an increase in irradiance level.[20] Bud fruitfulness and subsequent yield are increased by improving the light environment of developing buds by the use of divided canopies[8] or retention of spurs or canes developing at the top of the canopy.[1]

The specific mechanisms responsible for the regulation of bud fruitfulness by light are unknown. However, increased cluster initiation under well-exposed conditions appears to be primarily due to increased light quantity; the R:FR ratio was shown to have no effect on bud fruitfulness.[24,25] Although shading individual buds decreases cluster initiation, some controversy remains regarding the influence of irradiance on the leaves immediately subtending the bud on fruit bud differentiation.

The irradiance required to maximize bud fruitfulness varies among *Vitis vinifera* cultivars.[26] 'Sultana' (syn. 'Thompson Seedless') and 'Ohanez' require relatively high irradiance (approximately one third full sunlight) for notable cluster initiation. In comparison, significant cluster differentiation of 'Rhine Riesling' buds was obtained with only 10% of full sunlight.

It is generally accepted that photoperiod has little effect on cluster differentiation of *V. vinifera.*[1] However, American *Vitis* species will respond to increased day length. For example, the *Vitis* × *labruscana* cultivar 'Delaware' had three times more clusters when grown under long days compared to those grown under short days.[27,28]

2. Leaf Gas Exchange

As for other C_3 species, the relationship between leaf net CO_2 assimilation rate (A) and PFD for grapevine leaves can best be described as a rectangular hyperbole. Light saturation for individual leaves of grapevines may change due to conditions under which the vines are grown.[29,30] However, recent studies using field-grown grapevines indicate that light saturation occurs at approximately 1500 μmol quanta m^{-2} s^{-1}.[1,31,32] The light compensation point for A of grapevines is between 10 and 20 μmol quanta m^{-2} s^{-1}.[32,33]

Stomatal conductance to water vapor (g_s) of well-watered vines showed a hyperbolic response to PFD.[34,35] Maximum stomatal opening of an individual leaf has been recorded at a PFD of 130 to 300 μmol quanta m^{-2} s^{-1}.[30,34,35] Canopy conductance of a grapevine at full canopy, unlike single leaf g_s, is linearly related to PFD (Figure 4). This is expected as individual leaves located throughout the canopy are simultaneously exposed to different PFDs due to shading, leaf angle, zenith angle of the sun, and row and shoot direction. Therefore, maximum canopy conductance is associated with maximum PFD and occurs when the greatest proportion of the leaf canopy is exposed to direct solar radiation.[37]

It has been suggested that there is a high PFD-stress effect on *V. vinifera* leaves that causes an afternoon depression of A independent of leaf temperature.[38,39] This contradicts studies on well-watered field-grown grapevines in which there was no midday depression of A at high irradiance levels.[31,40,41] Data demonstrating the midday depression of A, though, were collected on potted vines either without a measure of vine water status[38] or grown in a glasshouse with measurements taken in the lab.[39] Düring[33] has shown that A of potted glasshouse-grown but not field-grown Riesling vines was slightly depressed at high PFD.

The most extensive research investigating photoinhibition of A in grapevines has been conducted on the native California species *V. californica* Benth. At high PFD both the light and dark reactions of A were more severely inhibited at high (41.5°C) and low (22.7°C) temperatures than at intermediate temperatures.[42] The inhibition of A at high PFD was greater for growth chamber grown vines relative to vines grown outside. Exposure to either high light or high temperature caused reductions in PSII photochemical activity with a subsequent recovery the following day.[43] However, exposure of *V. californica* leaves to both high light and high temperature caused PSII inhibition that was severe and persistent. Finally, field studies using unrestrained and horizontally held leaves of this species confirmed that high PFD (>1800 μmol quanta m^{-2} s^{-1}) had no adverse impact on A.[44]

3. Berry Growth and Composition

Much of the recent information regarding the influence of light on grape berry growth and composition has been obtained from studies investigating the influences of training-trellis systems and other canopy management practices on grapevine yield and fruit composition.[13,14,45,46] In cool climates canopy management practices which improve the exposure of vine foliage and fruit to solar radiation have generally improved grape and wine composition. Fruit of vines in which the canopy interiors are well exposed

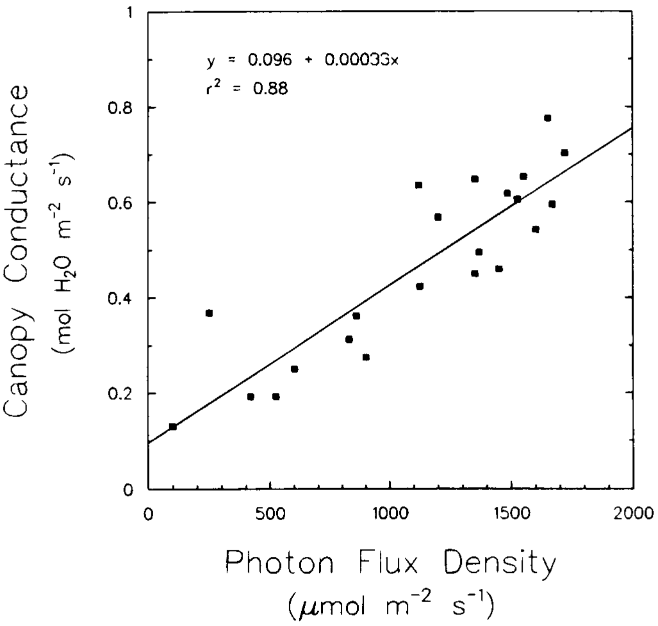

Figure 4 The relationship between canopy conductance and photosynthetic photon flux density. Total vine conductance was calculated according to the method of Grantz and Meinzer.[36] Canopy conductance was calculated as the difference between total vine conductance and aerodynamic conductance.[37] The data were collected on two separate days during the month of August, 1992. (L.E. Williams, unpublished data.)

to sunlight have normally exhibited increased rates of sugar accumulation, greater concentrations of anthocyanins, and total phenols, yet decreased levels of malic acid, potassium, and pH compared to fruits produced from vines with little interior canopy exposure. The above-mentioned practices are used to alter the fruiting zone light environment and have likely influenced other aspects of vine microclimate. For example, training-trellis systems, shoot positioning, and other canopy management practices, alter the light environment of both shoots (leaves) and clusters thus creating uncertainty as to whether improvements in berry composition are attributable to increased fruit exposure, leaf exposure, or both. In addition, increased levels of solar radiation exposure can result in substantial increases in both berry[47] and leaf[8] temperatures.

Recent investigations have shown that a photoreceptor localized in the grape berry is responsible for the detection of the light environment and thus the photoregulation of grape berry growth and composition.[19] The exclusion of light to fruit of field-grown 'Sultana' (syn. 'Thompson Seedless') for a period 2 weeks prior to softening until harvest increased berry weight and soluble solids compared to fruit exposed to natural light in the canopy.[48] Fruit of 'Thompson Seedless' vines exposed to direct solar radiation had similar soluble solids (°Brix), but were lower in weight and acidity and had a higher pH than fruit that ripened in the canopy interior.[49] Anthocyanin concentrations and soluble solids of 'Emperor' berries were decreased when they received 15% compared to berries receiving 54 or 100% of ambient solar radiation.[50] Field-grown 'Cabernet Sauvignon' berries exposed to sunlight had lower berry weights but higher concentrations of tartrate, malate, glucose, fructose, and anthocyanins compared to berries ripened in the canopy interior.[51,52] Morrison[53] reported on the independent effects of cluster shading and leaf shading on the growth and composition of fruit from field-grown vines of 'Cabernet Sauvignon'; cluster shading reduced fruit anthocyanin and total soluble phenolic concentrations, while leaf shading reduced berry weight and decreased the rate of sugar accumulation.

During Stage I of the double sigmoid curve of grape berry growth,[54] berry pericarp growth is rapid due to both cell division and cell expansion while growth during Stage III is due to cell enlargement. Light affects grape berry growth and composition differently during the three stages of fruit development. It was found that when sunlight was excluded from clusters during Stages I and II, berry growth was significantly less compared to those which received 20% of ambient sunlight during these two stages (Figure 5). It is unknown whether the reduction in berry growth was due to a reduction in cell division,

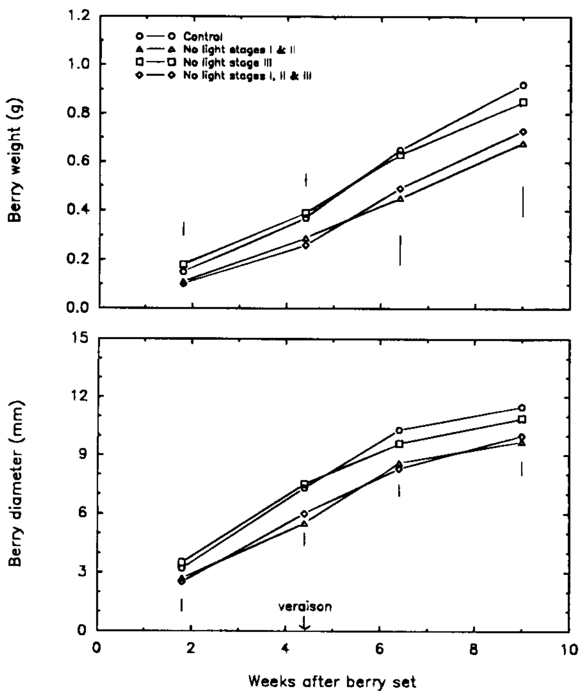

Figure 5 The influence of solar radiation exclusion during various stages of fruit development on the fresh weight (upper) and diameter (lower) of 'Cabernet Sauvignon' grape berries. Sunlight was excluded from the clusters by enclosing the fruit in aluminum lined, paper bags at the appropriate stage of growth. Data represent the mean of four, single-cluster replicates grown on potted vines in a phytotron. Bars represent LSDs ($p < 0.05$) on each sample date. (N.K. Dokoozlian, unpublished data.)

cell enlargement, or both. Berries of these clusters also exhibited reduced rates of solute and color accumulation during Stage III compared to berries exposed to sunlight during Stages I and II. Exclusion of sunlight during Stage III had little effect on berry weight, berry diameter, or solute accumulation. However, berries from these clusters exhibited lower rates of anthocyanin and phenol accumulation indicating that light has the greatest effect on both berry growth and fruit composition during Stages I and II.

The importance of phytochrome in the control of grape berry growth and composition is a topic of interest. Smart et al.[55] reported that 'Cabernet Sauvignon' vines shaded with neutral shade cloth and receiving supplemental red light in the fruiting zone (i.e., exposed to 10% of ambient PFD, and a R:FR ratio of 3.0) produced fruit with greater concentrations of glucose, fructose, and anthocyanins than shaded vines which received no supplemental red light. In a similar study, 'Cabernet Franc' vines grown under artificial (neutral shade cloth) and natural (foliage) shade received similar levels of PFD, but the R:FR ratios of the two treatments were 0.7 and 0.07, respectively.[56] Compared to the controls, both shading treatments reduced berry weight, soluble solids, and anthocyanin concentrations. The effects of natural shade on fruit growth and composition were partially reversed by supplemental red light (R:FR ratio of 3.0) in the fruiting zone indicating the involvement of phytochrome.

By contrast, a study of 'Cabernet Sauvignon' and 'Pinot Noir' fruit exposed to various combinations of light quantity (20 and 1% of ambient PFD) and light quality (R:FR = 1, 0.6, 0.3, or 0.1) indicated that light quantity rather than light quality was of primary importance. A reduction in light quantity from 20 to 1% of ambient PFD, regardless of the R:FR ratio, decreased berry weight and diameter, and delayed the accumulation of sugars, anthocyanins, and phenolics. Also, varying the R:FR ratio under continuous illumination had no influence on anthocyanin accumulation and did not reverse the R to FR mediated anthocyanin synthesis. These results indicate that a photoreceptor which is dependent upon light quantity is most likely involved in the regulation of anthocyanin accumulation in grape berries.

4. Nitrogen Metabolism

The nitrate concentration of grapevine petioles and leaf blades has been shown to be inversely related to the PFD environment.[57] The petiole NO_3 concentrations of 'Chardonnay', 'Zinfandel', and 'Malbec' vines were five-fold higher and nitrate reductase activity was lower in vines grown at 8% of ambient PFD compared to vines grown in full sunlight. Smart et al.[55] reported that shading increased the concentration of NO_3^- in petioles and leaf blades, and the concentration of NH_4^+ in the leaf blades, peduncles and juice of 'Cabernet Sauvignon'. In addition, supplemental red light partially restored leaf nitrate reductase activity of heavily shaded vines, suggesting a phytochrome mediated regulation of nitrate reductase. However, red light has not stimulated leaf nitrate reductase activity of field-grown *V. vinifera* cultivars (Dokoozlian, unpublished data).

III. TEMPERATURE

Temperature is the environmental factor primarily responsible for the distribution of *V. vinifera* throughout the world. Grapes are produced in some of the hottest cultivated areas of the earth. Air temperatures in the Jordan Valley of Israel and the interior valleys of California during the summer often exceed 35°C with maximum temperatures approaching 43°C. Over 40% of the grapes produced in China are grown in the Turpan depression of Xinjiang Province, Northwest China, the mean temperature during July is 33°C, daily temperatures exceed 35°C and the maximum is 48°C.[58,59] While the loss of a grape crop due to high temperatures is rare, partial yield loss in individual vineyards can occur. When the daily high temperature increased from an average of 30 to 47°C over a 3-day period in the Coachella Valley of California, clusters of 'Thompson Seedless' grapevines, which had just been girdled (the removal of a strip of phloem from around the trunk), in several vineyards became desiccated and resulted in crop loss (L.E. Williams, personal observation). It is unknown whether this crop loss was due solely to the high temperatures or a combination of high temperature and improper irrigation applications.

Potential crop loss of grapes due to low temperatures is far greater than that for high temperatures. "Potential crop loss" is used because in many cases, the result of a winter freeze is reported as the percent primary bud loss.[60–62] The interpretation of crop loss is often complicated by the adjustment in pruning practices made by the vineyard managers to compensate for bud injury or compensation by the vine producing fruitful shoots from secondary or tertiary buds, or by increasing total fruit set and berry size.[62,63] Losses due to late spring and especially early fall freezes are less likely to be compensated for by either the vineyard manager or the grapevine. For instance a spring freeze in 1985 caused a reduction in 'Concord' grape yield in the state of Washington from 151,000 tons in 1984 to only 90,000 tons in 1985.[64]

The growth and productivity of many crops are temperature dependent in the range of 5 to 20°C assuming all other factors are non-limiting.[65] One of the first attempts to use this concept was the development of a relationship between air temperatures and the dates of grape harvest.[65] In viticulture, temperature summations (i.e., termed in the literature as degree-days, growing degree days, day degrees, or heat summations) have been used as dependent variables in describing the timing of various grapevine phenological events and growth.[1] Amerine and Winkler[66] used accumulated degree-days above 10°C to formulate recommendations for the growing of wine grape cultivars in California.

While their method has gained wide acceptance, recent studies have indicated that degree-days may not be the most accurate basis for viticultural recommendations.[67,68] A major limitation in calculating degree-days, by taking the mean of the daily maximum and minimum temperatures and subtracting a base temperature, is that periods of fog, cloud cover, or wind, factors which may not affect the daily maximum and minimum temperatures but undoubtedly will affect vine growth. Degree minutes calculated with dataloggers may improve the accuracy of degree-days.[69]

A. EFFECTS ON GAS EXCHANGE

Every aspect of plant growth, such as physical processes, enzyme reactions, ion and carbohydrate transport, and membrane permeability, is controlled by temperature. Vine growth and productivity are dependent upon the assimilation of carbon via photosynthesis and subsequent carbon translocation and allocation. The production of biomass is the result of a balance between carbon gains and losses due to respiration, organ death, and other means where biomass may be lost (i.e., pruning, herbivory).

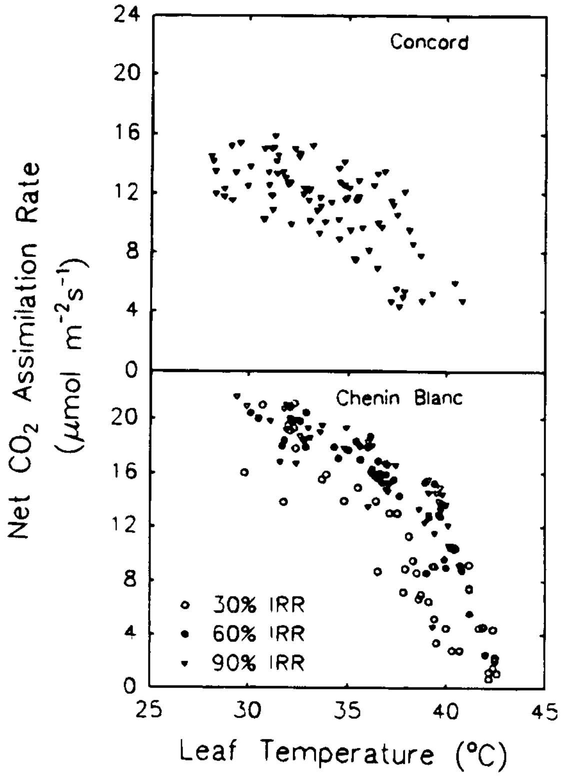

Figure 6 The effect of leaf temperature on net CO_2 assimilation of 'Concord' and 'Chenin blanc' grapevines grown in Washington, USA. The 'Chenin blanc' vines were irrigated with 30, 60, or 90% of daily evapotranspiration. (R. Wample, unpublished data.)

The optimum leaf temperature for photosynthesis of field-grown grapevines is quite broad; generally between 25 and 35°C[1,29] while other studies have demonstrated a more narrow temperature optimum (25–30°C).[29,30] This variation may be due to cultivar, growth conditions or seasonal variation.[70] This could perhaps also explain some of the variation in the data presented in Figure 6 since it is a compilation of data from several seasons and dates of measurement. Photosynthesis generally declines at temperatures above 35°C, for both American and European species of grapevines, yet a positive A occurs even up to 40°C (Figure 6).[1,30,43,44] It is also noteworthy that the leaf temperature of 'Chenin blanc' vines receiving 90% evapotranspiration replacement barely exceeded ambient temperature, i.e., 40°C, as a result of evaporative cooling. The temperature dependency of A of 'Concord' leaves appeared to be similar to 'Chenin blanc' and reports of other *V. vinifera* cultivars.[1] Thus, air temperatures up to 40°C, unless experienced for an extended period of time would not appear to be a major limiting factor in grape production.

Plants grown in thermally contrasting habitats exhibit photosynthetic temperature responses that reflect an adaptation to the temperature regimes of their respective habitat.[71] The photosynthetic temperature response curves of 'Chenin blanc' grapevines grown in two thermally contrasting climates in California are presented in Figure 7. Although fitted curves for the two data sets were similar at temperatures greater than 32°C, the decrease in A occurred more rapidly for vines grown in the San Joaquin Valley as leaf temperature decreased.

Preconditioning temperatures may also influence photosynthetic processes. Balo et al.[72] found that 3 to 6 h of chilling (6 ± 2°C) had little effect on gas exchange, fluorescence kinetics, and water relations of rooted cuttings of 'Merlot' grapevines. However, durations of over 24 h of chilling caused significant reductions in these variables. Chilling stress (6°C) for 4 h under low light reduced A by 10% for leaves of 'Leanyka' and 20 to 70% in 'Zold veltelini'.[73] The effect was reversible and longer exposure resulted in acclimation and improved A rates. Stomata of 'Leanyka' closed in response to chilling while the

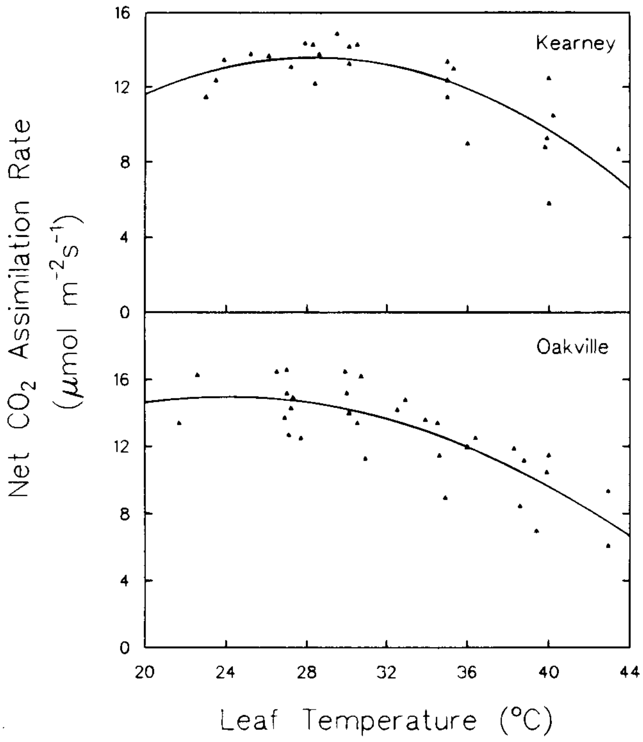

Figure 7 The effect of leaf temperature on net CO_2 assimilation of 'Chenin blanc' grapevines grown either in the Napa Valley (UC-Davis Oakville Field Station) or in the San Joaquin Valley (UC Kearney Ag Center) of California. Leaves were placed inside temperature controlled cuvettes and net CO_2 assimilation was measured after CO_2 exchange reached steady state (approximately 30 to 45 minutes after the temperature was changed). Data were fit to nonlinear functions: Kearney $y = -9.4 + 1.62x - 0.029x^2$, $r^2 = 0.62$; Oakville $y = 2.9 + 1.0x - 0.021x^2$, $r^2 = 0.65$. (L.E. Williams, unpublished data.)

more chilling-sensitive 'Zold veltelini' showed a loss of stomatal control. Both cultivars developed more negative water potentials in response to chilling stress. Sherer[74] found the time for the induction curve of light induced chlorophyll fluorescence to return to a stationary level at 5°C was longer in cold-susceptible cultivars of grapevines than in cold-tolerant cultivars; an indication of a greater effect of chilling on the photosynthetic mechanism of chill-sensitive cultivars.

It is probable that respiration by an entire grapevine commands a large portion of the daily photosynthate as the percentage of photosynthate utilized in respiration by other woody perennial species ranges from 38 to 65%.[75] Respiration can be divided into two components: respiration required for growth and respiration needed for organ maintenance. Carbon requirements for growth and maintenance respiration during the 3 weeks prior to anthesis of an individual grape flower was 0.23 mg CO_2 (3 J) and 0.83 mg CO_2 (10.8 J), respectively.[76] Maintenance respiration costs of mature organs may vary from 0.015 to 0.6 kg CO_2 kg^{-1} dry mass d^{-1}. Even when little growth is occurring, grapevines still demand large amounts of carbon for maintenance respiration and the larger the plant the greater the carbon requirement.

Temperature is the most important abiotic factor affecting respiration under most conditions.[72] The Q_{10} of respiration is approximately 2 in the range of physiological relevant temperatures.[77] For example, respiration rate of mature leaves of Perlette grapevines growing in southern California was close to zero at a leaf temperature of 10°C and doubled with each 10°C increase in temperature (Figure 8). Several factors may affect the Q_{10} and actual rate of respiration such as organ type and age, tissue N content, availability of carbon substrates and growth temperature. For example, leaves of 'Chardonnay' grapevines grown in a cool climate continued to respire down to a leaf temperature of 7°C, at which time respiration rates were too small to quantify (L. E. Williams, unpublished data). It also has been found that the Q_{10} of grapevine leaf respiration may change during leaf ontogeny (H. Schultz, personal communication).

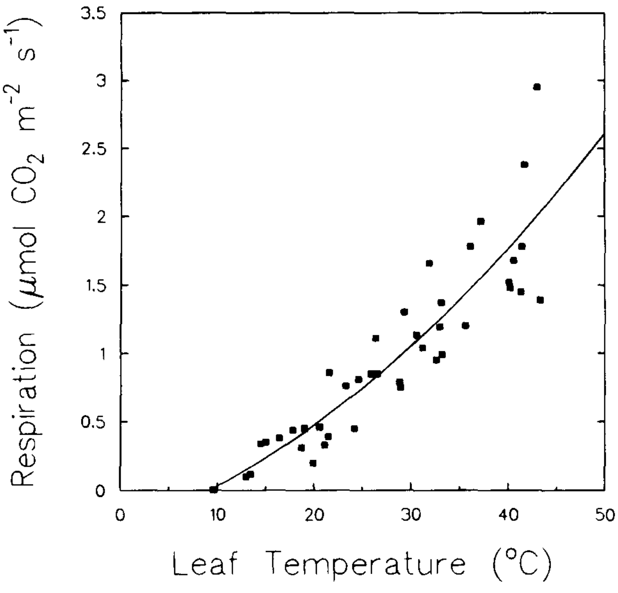

Figure 8 The effect of leaf temperature on respiration rate (CO_2 evolution) of mature leaves of 'Perlette' grapevines grown in the Coachella Valley of California. Measurements were made in temperature controlled cuvettes. (L.E. Williams, unpublished data.)

B. EFFECTS ON ROOT GROWTH

There is generally little information regarding the effects of high root temperatures on grapevine growth and development or physiology due largely to the depth of rooting and the smaller variations in root, compared to shoot, temperatures. In addition, in many of the hottest viticultural areas, irrigation is a normal practice minimizing root zone temperature fluctuations. Furthermore, the shade provided by the grapevine canopy would reduce the heat load on the soil as will the presence of a cover crop. Thus, high temperature effects on roots of grapevine have received relatively little attention.

By contrast, low temperatures may result in root injury or death. Several reports have shown differences in cold hardiness between rootstock selections[78] and for own rooted commercial cultivars.[79,80] In the colder regions of grape production, temperatures as low as −13°C at 20-cm depth have been recorded.[78] Low soil moisture results in lower soil temperatures and increased chance of root injury. Thus, late season irrigation is recommended in viticultural areas that routinely experience low winter temperatures accompanied by low fall and winter precipitation.

C. HIGH TEMPERATURES

1. Species and Cultivar Differences

There has been no comprehensive survey of the high temperature tolerance of *Vitis* species or cultivars, although several species or cultivars have been classified into different groups requiring varying levels of heat units to mature.[81] It was shown that the temperature at which heat injury occurred in leaf discs of 'Venus' was 48°C while that for 'Veeblanc' was only 44°C. The same two hybrids in tissue culture were both injured at 42°C. Damage resulted from irreversible changes in the plasma membrane for both. The loss of membrane function leads to symptoms of water stress.

Fanizza and Ricciardi[83] noted a decline in shoot growth of *in vitro* propagated grape cultivars when subjected to sequential subculture at 35 or 38°C. Four of the seven cultivars examined showed no apex growth or died at 35°C; all cultivars died at 38°C.[83] Growth rates recovered when temperatures were lowered to 25°C. The authors were not certain if the reduction in growth was due to a loss in an unknown heat tolerance mechanism of the apices or ageing of the cultures. Pre-rooted cuttings of 'Muscat of Alexandria' grown in growth chambers showed maximum growth and dry weight at 25/20°C day/night temperatures followed by 30/25°C.[20] During the 13 weeks of this study, leaves represented an increasing percentage of total dry weight; the apparent level of apical dominance with increasing temperature within the temperature range of this study (20 to 30°C).

Buttrose[21] demonstrated that high temperatures increased the number of clusters per shoot. Cluster initiation in 'Muscat of Alexandria' was almost nonexistent at 20°C but increased between 25 and 35°C.[84] Stem dry weight at 20°C increased indicating a change in the sink strength or allocation pattern at this temperature that was not conducive to fruit bud initiation.

The effect of the previous season's temperatures, particularly during the initiation period, on current seasons vine fruitfulness has not been thoroughly researched. Smit[85] studied this in the production of 'Sultana' vines and recognized the potential effect on a commercial level. Unfavorable conditions during the period of bud initiation and early development of the inflorescence primordia lead to a reduction in the crop potential the following year. This reduction in flower initiation and development may be misinterpreted as a reduction in fruit set. Very little is known about the effect of high temperatures on flower buds following initiation, although there appears to be no major detrimental effects on crop production in regions of the world where temperatures often reach 35 to 40°C after flower bud initiation has occurred.

Bud fruitfulness may be affected even during the period just prior to and following budbreak. For example, the number of clusters per shoot was greater at higher temperatures and the number of flowers per cluster was reduced.[86] Hence there is an extended period of time, prior to anthesis, over which the potential productivity of a grapevine can be influenced by temperature.

Cluster development following budbreak of container-grown 'Cabernet Sauvignon', 'Shiraz', 'White Riesling', and 'Clare Riesling' potted vines was increased at 32/27 and 38/33 compared to 14/9, 20/15, and 26/21°C, day/night temperatures.[87] The number of days to flowering was reduced from 70 to 18 over this temperature range. There was a difference of only 2 days between the 26/21 and the 38/33 treatments suggesting a reduction in flowering at the higher temperature. In this same paper, maximum fruit set occurred at 20/15°C with no fruit set occurring at either 14/9 or 38/33°C for the cultivar 'Cabernet Sauvignon'. While the above information may not be directly transferable to field-grown vines, the authors note that in most areas where grapes are grown, the temperature rarely reaches these higher levels during the period from budbreak to bloom.

Numerous reports indicate that fruit set in grapes is inhibited by high temperatures.[88–92] Potential causes of reduced set include a reduction in ovule or pollen viability and/or in pollen tube growth, changes in hormonal status and, indirectly, water stress. Kliewer[88] demonstrated a loss of ovule viability for 'Pinot Noir' and 'Carignane' grapes at 35 and 40°C compared to 25°C. Reduced ovule viability, which results in fewer seeds per berry, could contribute to smaller berries and yield based on the known relationship of seed number, hormones, and berry size.[93] Pollen germination and pollen tube growth in Petri dishes was unaffected in 'Muscat of Alexandria' at 35°C compared to 22 or 25°C[94] while that for 'Delaware' (*V. labruscana*) was reduced to about 30% at 30°C compared to 24°C.[89]

Thirteen years of data collected at over 100 vineyard sites in the Yakima Valley of Washington, showed that high temperatures during bloom did not generally reduce the number of berries per cluster for 'Concord' vines (Figure 9). In fact temperatures above 25°C often gave higher berry set than lower temperatures. This data clearly shows that low temperatures are more detrimental to berry set than high temperatures in this cultivar.

Matsui et al.[95] investigated the effect of plant hormones and high temperature effects on fruit growth of 'Thompson Seedless' and 'Napa Gamay' grapevines. Four-year-old potted vines, with the root temperature being controlled, were subjected to 40/22°C (day/night) for 4 days and fruit development compared to plants held in a greenhouse (temperature range 22 to 32°C). Pre-stress treatment with gibberellic acid (GA_3) or GA_3 plus a cytokinin (benzyladenine) partially overcame the negative effect of high temperature on berry size and total soluble solids accumulation. Only GA_3 overcame the effect on berry weight. Estimates of total endogenous GA_3 levels from 'Thompson Seedless' berries indicated a reduction in the level and a change in the qualitative nature due to heat stress and suggests the reason for recovery with GA_3 applications.

High root temperatures (20 vs. 11°C) have also reduced the number of berries per cluster in 'Cabernet Sauvignon'.[96] High air temperatures do not always have a deleterious effect on fruit development. For example during 1992, the U.S. Pacific Northwest experienced two periods of 10 days or greater when the temperature was 35°C or higher (Figure 10). However, fruit maturation occurred from 2 to 4 weeks earlier than average with normal crop loads for this grape production area.

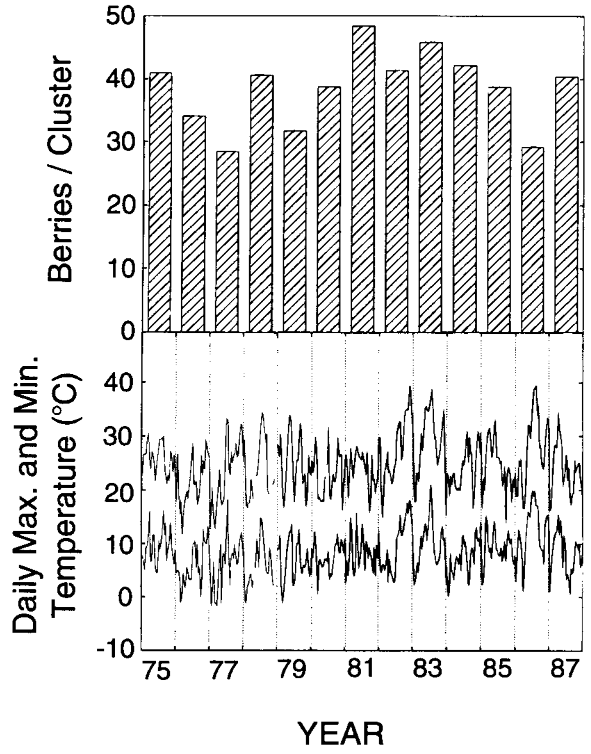

Figure 9 Number of berries per cluster and daily maximum and minimum temperatures for 2 weeks before and 2 weeks after full bloom of 'Concord' grapevines grown in the Yakima Valley of Washington, US, from 1975 to 1987. Data represent the mean of approximately 100 different vineyard sites. (R. Wample, unpublished data.)

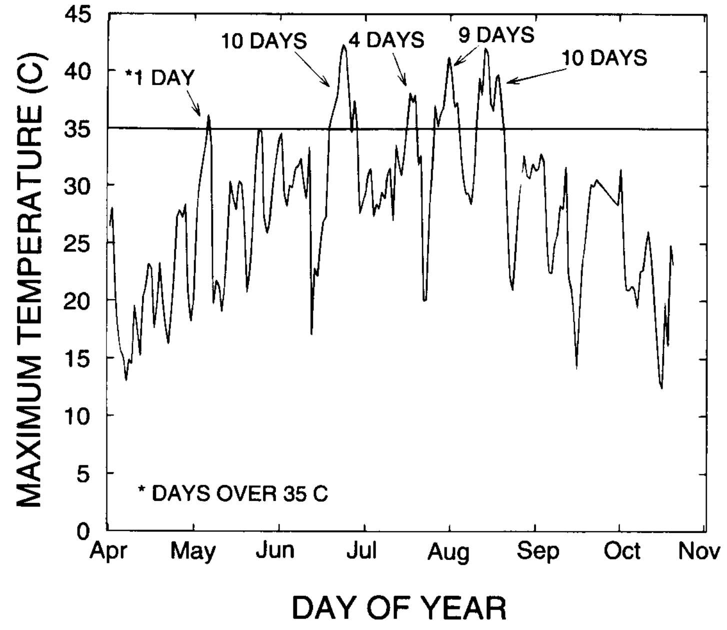

Figure 10 Daily maximum, ambient temperatures during the 1992 growing season at Paterson, Washington, US. The number of days in which the maximum temperature exceeded 35°C are at the top of the graph. (R. Wample, unpublished data.)

2. Effects on Water Relations

Differences have been found in the stomatal response of grape cultivars to temperatures ranging from 34 to 43°C.[97] 'Cardinal' showed the least response to heat stress although the control treatment (25 to 29°C) had a relatively low g_s compared to the other cultivars studied. The response of 'Chardonnay' and 'Chenin blanc' to heat stress was similar whether measured on a diurnal basis or over 4 to 12 days. This work underscores the influence of vapor pressure deficit when evaluating g_s in heat-stressed vines (see Humidity Section).

3. Other Physiological Processes

Growth of grapevines, as well as other plants, at constant high temperatures (>35°C) for extended times (>30 days) is also important as an essential procedure in the elimination of viruses, viroids, mycoplasmas, and perhaps some bacteria. The effect of such treatment appears to have more effect on the microorganism than the grapevine. The response of grapevines to high temperatures and elevated CO_2 concentrations has been examined.[98] Rooted cuttings of 'Cabernet Sauvignon' subjected to heat treatment and elevated (1200–1300 ppm) CO_2 levels manifested a reduced transpiration (E), elevated A and growth rates and a change in the allocation of photosynthates that promoted more root growth. Increased A was apparently due to reduced nonstomatal limitations of carboxylation and a lower level of photorespiration since g_s was lower.

Excessively high temperatures for extended periods of time generally result in a delay of fruit maturation, and a reduction in fruit quality.[99–103] Both of the above characteristics have been associated with a decline in total titratable acidity and increased pH[104] caused primarily by a reduction in the synthesis and the increased catabolism of malic acid;[105] increased mono- and di-basic salts of tartaric acid and di-basic salt of malic acid have also been noted.[101] High temperatures also reduce color development of grape berries.[88,102] For example, at 35°C pigment development was completely inhibited in 'Tokay' and reduced in 'Cardinal' and 'Pinot Noir' compared to 20 or 25°C.[106] In general, cool nights or days improve coloration and a beneficial effect of night cooling by sprinkling has been found[103,107,108] and has become a commercial practice in other fruit crops such as apple. Such a practice in grapes should be carefully managed to prevent disease problems from developing in the fruit and canopy.

High temperatures can also affect the partitioning of photosynthates within the leaf. As temperature increased the concentration of starch within the leaves of 'Cabernet Sauvignon' vines decreased.[109] For example, leaf starch concentrations of vines grown in growth cabinets and exposed to day temperatures of 18, 25, and 35°C were 23.3, 10.9, and 1.3% of dry weight, respectively. Increasing leaf temperature resulted in a shift in lipids from 5.8 to 16% of dry weight over this same temperature range. Interestingly, total chlorophyll content increased from 0.6% of dry weight at 18°C to 1.2% (equivalent to 5.6 mg dm^{-2}) at 35°C. Roper and Williams[40] reported that the starch levels in field-grown grapevine leaves from a warm climate also remained very low. However, it is not clear if changes in lipids and chlorophyll will occur under field conditions.

Translocation of photosynthates, a major factor in fruit development and maturation, may be influenced by high temperatures. Sepulveda et al.[110] exposed a mature leaf of non-bearing 'Chenin blanc' and bearing 'Chardonnay' grapevines to $^{14}CO_2$ for 30 minutes after 4, 8, or 12 days in a greenhouse (29/15°C) or a phytotron (40/20°C). Twenty-four h after $^{14}CO_2$ exposure, heat stress enhanced the transport of ^{14}C photosynthates to the shoot tip at the expense of the roots, trunk, and clusters. High temperatures did not reduce A. Sucrose concentrations increased in all vine organs due to heat stress in both cultivars. Heat-stressed 'Chardonnay' vines had lower concentrations of glucose and fructose in the fruit.

4. Vine Adaptations

Like many other living organisms, the genus *Vitis* is presumed to produce heat-shock proteins (HSP) which apparently play a role in the metabolism of other proteins and in their protection against thermal degradation.[111] Despite the apparent heat tolerance of *Vitis* spp. the authors are not aware of any reports that demonstrate the importance of HSP in grapevines.

D. LOW TEMPERATURES

1. Chilling

Grapevines vary greatly in chilling tolerance. A brief period of chilling (4 h) caused only a 10% reduction in A in the cultivar 'Leanyka' but as much as a 70% reduction in 'Zold veltelini' but in both

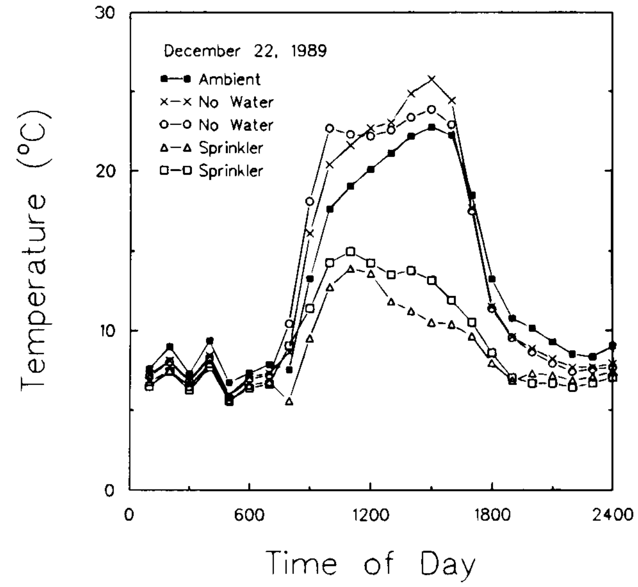

Figure 11 The effect of evaporative cooling on bud temperature of 'Perlette' grapevines grown in the Coachella Valley of California. Vines were either cooled with overhead sprinklers while the controls were not sprinkled with water. Bud temperatures were measured with hypodermic thermocouples connected to a data logger. Individual data points are the hourly means of bud or ambient temperatures measured every minute. (L.E. Williams, R. A. Neja, and E. A. Walker, unpublished data.)

cases this was reversible within 24 h.[76] Some recovery in photosynthetic capacity occurred following chilling periods longer than 12 h. McIntyre et al.[67] working with 100 cultivars of grapes in Davis, CA reported that differences in susceptibility to either spring or fall frosts were dependent upon phenology (i.e., date of budbreak or fruit maturation). This demonstrates the possibility of two levels of tolerance to chilling temperatures. First is the inherent genetic tolerance to low temperatures and the second the effect of environmental and management factors on vine phenology which may confer more or less risk to a low temperature event.

2. Effects on Growth

Although there is some controversy regarding the absolute chilling requirement of grapevines,[112] evaporative cooling and other practices are used to achieve more rapid and uniform budbreak in many warm grape growing areas.[113,114] Evaporative cooling reduced bud temperatures by 10 to 15°C (Figure 11), and resulted in increased yield, and advanced, more uniform berry maturity.[113,114] Chilling has also been linked to decreased catalase enzyme activity in grapevine buds and this has been associated with release from dormancy.[115] Weaver and Iwasaki[116] reported that 4 to 8 weeks of chilling (0°C) were required for rapid and uniform budbreak of 'Zinfandel' grape. They were unable to establish any meaningful relationship between either free or bound ABA and bud response to chilling or calcium cyanamide treatment. Takeno et al.[117] showed that chilling somatic embryos of hybrid grape (*V. vinifera* × *V. rupestris*) for 1 week at 4°C caused an increase in GA-like activity which declined during the second and third week of chilling.

Roubelakis and Kliewer[91] reported cultivar differences in fruit set at day/night temperatures of 15/10°C. Higher light intensities enhanced fruit set at those temperatures. Fruit set in 'Concord' appeared more sensitive to high (32–35°C) than to low (15–18°C) temperatures.[90,118] The temperature range associated with maximum fruit set for most species/cultivars has been between 20 and 30°C.

Several studies have reported an improvement in vine microclimate with evaporative cooling during the growing season.[103,108,109] Evaporative cooling during this stage of vine growth results in changes in vine temperature and vapor pressure deficit (VPD) and may improve vine water relations, photosynthesis, and fruit quality. In Montpellier, France, it was observed that maximum shoot growth occurred at 28°C and that growth ceased at 10°C and below.[120]

3. Effects on Water Relations

Chilling of container-grown *V. vinifera* cvs. in controlled environment chambers for more than a few hours decreased plant water potential (Ψ) despite a significant reduction in g_s indicating that water uptake and/or transport might have been affected.[75,76] However, it is possible that increased water stress was the result of much lower root temperatures (or a greater rate of temperature reduction) in the growth chamber than would have been experienced under field conditions. Cold nights (<10°C) have also induced higher leaf resistances the following day in 'Concord' vines grown in New York. This inhibition of stomatal opening appeared to be independent of Ψ_l and it was speculated that this might be due to a chilling-induced reduction in starch hydrolysis and an inhibition of A.

Thus it seems that chilling may have both direct and indirect effects on plant water relations. Unfortunately, there are few field studies on the effects of chilling on grapevines to help clarify our understanding. This research could be valuable in viticultural areas where low (0–10°C) temperatures are common during the growing season.

4. Other Physiological Processes

Ahmedullah[121] found that exposing 1-year-old 'Cardinal' grapevines to 15°C, as compared to 25°C, led to increased basipetal transport of photosynthates. He also found a higher rate of total recovery of ^{14}C-labelled photosynthates at 15°C indicating a lower respiration rate (see Figure 8). In some viticultural areas, the night time temperatures often, even in mid summer, drop to 15°C or lower. Increased basipetal transport of photosynthates coupled with lower rates of respiration at night may contribute to more rapid fruit maturation and may account for the ability to mature some cultivars of grapes in areas that would not appear to have enough heat units.

To our knowledge there has been very little research designed specifically to evaluate grapevine adaptations to chilling. However, the above-mentioned reports indicate that grapevines can acclimate and adjust to changing temperatures.

E. FREEZING TEMPERATURES

1. Cultivar Tolerance

A wide range of cold hardiness exists in the genus *Vitis* and this genetic variation has been utilized in breeding and cultivar evaluation programs.[122] In a report covering 88 European, 34 American, and 14 French Hybrid cultivars, Clore et al.[123] ranked grapevine cold hardiness and demonstrated the wide range in genetic cold hardiness potential.

Cold hardiness may encompass mid-winter hardiness as well as spring and fall frost hardiness. Mechanisms of cold hardiness may involve tolerance and/or avoidance. For instance, avoidance of spring frost damage due to late budbreak is an important distinction from the ability to survive (i.e., tolerate) frost. Species as well as cultivar differences in timing of budbreak, flowering, and fruit maturation are important in the selection of grapes for a given vineyard. McIntyre et al.[67] found up to 25 days difference in budbreak and more than 100 days difference in the maturity date among 100 cultivars. Often, cultivars with early budbreak are susceptible to spring frost but are also early maturing thereby avoiding crop losses due to fall frost. It appears that vines whose origins are further from the equator are more sensitive to changes in photoperiod and thus less susceptible to fall frost.[124]

An example documenting the need to understand this relationship was reported by Wolf and Cook[125] who found that 'Cabernet Franc' was 1 to 2°C more hardy throughout the winter than 'Cabernet Sauvignon'. However, 'Cabernet Franc' deacclimated more rapidly in the spring and was more susceptible to spring frost or late winter freeze. Comparable results also were found examining the deacclimation of 'Concord', 'White Riesling', and 'Cabernet Sauvignon'.[125] Similarly, Proebsting et al.[126] reported that although cold hardiness of 'Concord' buds was much greater than either 'White Riesling' or 'Cabernet Sauvignon', they deacclimated 1 to 2 weeks earlier thereby explaining the greater crop loss for 'Concords' compared to wine grapes in Washington during a major spring frost on April 28, 1985.

Differences in cold hardiness within a *Vitis* species may be influenced by changes in temperature and water content. Damborska[127] found that warm temperatures induced a cultivar and/or season-specific reduction in cold hardiness. 'Riesling' maintained its hardiness better than 'Muller-Thurgau' in mid-winter after exposure to 10, 12, or 15°C, although 'Riesling' was less cold hardy in the spring. Such cultivar- and species-specific changes were also evident during a winter freeze in the U.S. Pacific Northwest during December 1990. Bud injury following a brief (36 h) period of high temperatures

Table 1 **Percent of primary and secondary bud injury of seven cultivars of *Vitis vinifera* and *V. labruscana* cv. Concord as affected by irrigation**

	Bud injury (%)			
	Irrigated		Stressed	
Cultivar	Primary	Secondary	Primary	Secondary
Chenin Blanc	98.8	64.3	97.5	60.5
Chardonnay	96.0	64.3	87.0	67.0
Cabernet Sauvignon	96.3	73.5	81.3	52.5
Gamay Beaujolais	59.0	16.0	56.0	26.0
Meunier	58.0	27.0	39.0	13.0
Pinot Noir	71.0	39.0	53.0	33.0
Semillon	100.0	97.0	100.0	96.0
Concord	<19.9	<5.0	<10.0	<5.0

Note: Data were collected following a severe winter freeze in December, 1990. Percentages represent the mean of 10 or more vines and 100 or more dissected buds per vine. Stressed vines had received only one irrigation compared to 4 or more for irrigated vines.

From Wample, R., unpublished data.

(10°C) was followed by temperatures as low as −28°C is presented in Table 1. A consistent reduction in primary bud injury was associated with less irrigation the previous season for all but 'Concord' grapevines. Mild water stress during bud development appears to improve winter survival and is associated with smaller cane diameter and shorter internodes. Wolpert and Howell[128] noted the importance of low water content on cold hardiness development during early acclimation. Our understanding of temperature and water interactions on grapevine bud, cane, and trunk cold hardiness is incomplete and in need of additional research.

2. Effects on Vine Growth

Growth following freezing injury may be separated into events that occur pre- and post-budbreak. In a pre-budbreak state, low temperature injury may influence one or more of the following: the primary, secondary, or tertiary bud; the phloem of the trunk and canes or roots; the xylem parenchyma of the trunk and canes or roots; and/or the vascular and cork cambia of the permanent structures. The simplest and perhaps the most frequent case, low temperature injury of the primary bud, results in very few changes in overall growth of the vine, but frequently results in a significant loss of yield for that season. Some cultivars such as 'Tokay' and 'Folle blanche' have fruitful secondary buds and may still produce nearly a full crop.[129,130] Loss of more than the primary bud is often accompanied by damage to other vine organs, frequently resulting in the loss of permanent structures and requires retraining of the vine if it survives. This is a major problem in grafted vines and either regrafting or replanting may be required if the scion is completely killed.

Situations have been recorded where the root system has been injured by low temperature while the majority of the shoot system has been undamaged. This occurred during the winter of 1978–79 in the Pacific Northwest of the United States when a shortage of irrigation water was combined with very little rainfall after harvest. This led to dry soils and resulted in freezing to a depth of 30 to 40 cm. Air temperature varied between 0 and −20°C which resulted in a minimum of bud damage but significant root damage. In the spring, budbreak occurred and shoot growth began normally. After a few weeks of shoot growth, and during a very warm period, the injured root system was unable to meet the water requirements of the shoot system and resulted in the collapse of the green shoots and in many cases vine death. Although not confirmed, there appeared to have been effects of this root damage as much as 3 to 5 years later, as the root system became infected by soil born pathogens.

Low temperature injury may facilitate the development of crown gall [*Agrobacterium tumefaciens* (E.F. Smith and Townsend) Conn, biovar 3] in grapevines which may be more deleterious than low temperature injury itself. Therefore, propagation wood should be from crown gall free vines when possible. Methods of eliminating this bacteria from grapevine cuttings are proceeding.[131-134]

The extent of injury when freezing occurs after budbreak depends upon the severity of the freeze and the subsequent management of the vines. Winkler[129] studied frost injury to 'Thompson Seedless', 'Malaga', and 'Tokay' grapes during the spring of 1932 and 1933. He concluded that if the injury did not extend basipetally beyond the clusters there was little need to adjust the vine. However, if the injury extended below the clusters in cultivars with fruitful secondary and tertiary buds, removal of the shoots to stimulate the growth could result in increased yields. In cultivars with non-fruitful secondary and tertiary buds it made little difference to the present year's crop whether or not the frosted shoots were removed. However, the development of the next years fruiting wood was improved by shoot removal if the injury were such that an excessive number of axillary buds began to grow. Lider[135] in a similar study in the spring of 1964 on 'Folle blanche', 'Cabernet Sauvignon', and 'White Riesling', found that doing nothing was the most economical practice following frost injury. He was unable to confirm the benefit of shoot removal in 'Folle blanche' which reportedly has fruitful secondary buds. A study of 'Chardonnay', 'White Riesling', and 'Cabernet Sauvignon' in Washington (Stimson Lane Wine and Spirits, personal communication) confirmed the results of Lider in that "no treatment" was the most economical practice following frost injury. Despite some significant differences in the number of clusters per vine and cluster weight due to post-frost treatments, there was no difference in yield for 'Cabernet Sauvignon' or 'White Riesling' (Figure 12). For 'Chardonnay', however, shoot removal following frost injury significantly reduced yield.

Pratt and Pool[136] have provided an anatomical description of the recovery of canes of *V. vinifera* from simulated freezing. They found that recovery was dependent upon a sufficient quantity of viable undifferentiated tissues (cork and vascular cambia, and xylem and phloem parenchyma) capable of undergoing cell division. In the case of bud injury, a surviving lower-order bud was required to replace those injured since adventitious buds in grapes have not been reported. The apparent required characteristics for recovery included an apical meristem and at least two vascular traces.

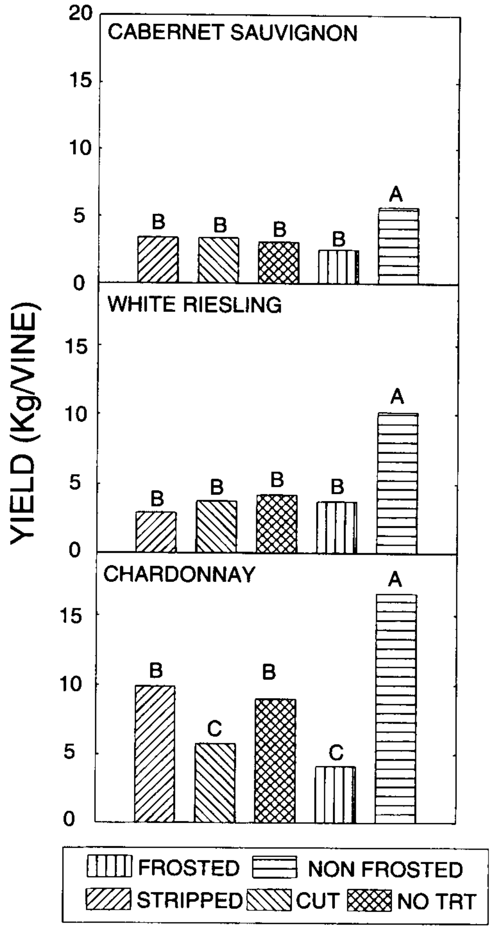

Figure 12 Yield response of 'Cabernet Sauvignon,' 'White Riesling' and 'Chardonnay' vines following spring frost injury during May 1992 in Washington, US. Treatments included removal of the partially frosted shoots by hand (stripped), removal of the frosted portion of the shoot with hand shears (cut), no treatment of partially frosted shoots (no trt), vines that were severely frosted with no additional treatment (frosted), and control (non-frosted) vines. Columns with different letters are significantly different at the p = .05 level or better. (R. Wample, unpublished data.)

3. Effects on Water Relations

Continuous periods of below freezing, non-lethal temperatures often result in the formation of extracellular ice which has the consequence of establishing a strong vapor pressure gradient between the extracellular water and the liquid water in the cells. The slow, continuous diffusion of water out of the cells to the extracellular ice results in an increase in grapevine cold hardiness.[126,127,138-140] This occurs through a combination of reduced cellular water content, a concentration effect of the cellular solutes and additional physiological changes in membrane and protein structure.[158] This "water transfer" process appears to occur in buds but may not take place in cane and trunk tissues.[141] Results similar to these for *V. riparia* have been noted for several cultivars of *V. vinifera* including 'Cabernet Sauvignon', 'White Riesling', and 'Chenin blanc'.

As a part of the acclimation process, the formation of tyloses and other vascular blockages play a role in the reduction of vine water content.[142,143] Vascular blockages also have the effect of inhibiting the rehydration process during the winter and may be important in the maintenance of low water content throughout most of the dormant period. One of the hazards near the end of dormancy is the rehydration of cane and bud tissues which if followed by subfreezing temperatures results in significant vine injury.

4. Other Physiological Processes

Nitrogen nutrition is related to grapevine performance, and may influence cold hardiness.[144] A review of the literature found little evidence to support the contention that high nitrogen nutrition resulted in direct loss of grapevine cold hardiness.[145] Nitrogen metabolism in grapevines during the acclimation and dormant periods is known to be dynamic.[146-148] Total and protein nitrogen levels rise at the onset of acclimation and continues into the second phase of hardening.[147] Higher levels of total nitrogenous substances were found in the more cold hardy cultivars.[147] Higher nitrogen concentration may have resulted from the slower growth rate of these cultivars, and are thus indirectly related to cold hardiness. Similarly, it has been shown that grafting European grapevines onto winter-hardy American rootstocks led to higher mid-winter nitrogen levels and improved cold hardiness.[149] High protein to total nitrogen ratios have also been linked with more winter-hardy cultivars.[148] Despite these reports, two recent publications indicate little or no effect of different nitrogen nutrition levels on the cold hardiness and survival of 'Chardonnay'[150] or 'White Riesling'[151] grapevines.

Cold acclimation and near freezing temperatures have been associated with increases in the soluble carbohydrate levels found in bud and cane samples of grapevines.[151-156] Low temperatures influence the magnitude of the apparent conversion of starch reserves into soluble carbohydrates, but the absolute nature of this relationship is not fully understood. The concentrations of soluble carbohydrates are slightly lower in cane tissues than in buds, but relative seasonal changes were similar.[151,156] Sucrose is the primary soluble carbohydrate with glucose and fructose making up the majority of the balance. Sucrose levels appeared to peak during late winter and early spring while glucose and fructose declined during this time.[155,156] Starch levels showed an inverse relationship to soluble carbohydrates.[151,156]

Increased solute concentrations have been correlated with cold hardiness and deep supercooling (the presence of water in a liquid state below the normal ice nucleation point) of grapevine tissues.[157] Although some reports have associated the rise in soluble carbohydrates with a cause and effect relationship with grapevine cold hardiness, the increase in soluble carbohydrates is probably responsible for only a few degrees freezing point depression and therefore cannot account for the changes in hardiness observed.[151,156,158] Deep supercooling, the primary cold hardiness mechanism in grape,[157,159] is not known to be directly related to the level of soluble carbohydrates.[151,156]

5. Vine Adaptations

Supercooling has been associated with the geographic distribution of some plants.[158] However, because the temperature at which the low temperature exotherms occur varies with different species and cultivars, precise distribution limits have not been established for all *Vitis* species. It may be possible to estimate the limits of distribution for a given cultivar if its minimum exotherm temperature were known and were compared with low temperature isotherms for a geographical area. Other adaptations that exist in some *Vitis* species are the deposition of callose and suberin in the phloem and phellem, which reduces the uptake of water during dormancy and limits mechanical injury due to intracellular ice formation.[142]

The ability of different cultivars of grape to respond to photoperiod is important to survival in cold climates. A synergistic effect of photoperiod and temperature enhanced the development of cold hardiness in 'White Riesling' grapes.[160] Fennell and Hoover[161] reported similar responses for *V. labruscana* and

V. riparia but with distinctions between these species. Interruption of the dark period did not significantly affect the cold hardiness of 'Concord' buds out to the 12th node or in the extent of cane maturation.[162] They did record more actively growing shoots on the night interrupted vines.

IV. WATER STRESS

Grapevines are often cultivated in regions of low rainfall and high evaporative demand and if irrigation is limited vines may experience some water stress during the growing season. Reviews of the effects of water stress on various aspects of grapevine growth and physiology have recently been published.[1,2,163,164] Therefore, in this section we will review much of the basic aspects of vine water stress and whatever new information has been published since 1989. In addition, preliminary data from an irrigation experiment with treatments varying from 0 to 140% of vine water use, determined with a weighing lysimeter, will be included to demonstrate trends between available water and vine response.

A. HUMIDITY

Experimental evidence indicates that the reduction in g_s induced by abscisic acid causes heterogeneous stomatal closure in many plant species[165] including *V. vinifera.*[166] Heterogeneous stomatal closure in response to ABA may be associated with the species' mesophyll anatomy.[165] It appears that plant species having their leaf mesophyll separated into intercellular chambers hermetically sealed from other areas (heterobaric type as compared to homobaric type mesophyll anatomy) will respond to ABA applications or stress with non-uniform stomatal closure[167] although there are exceptions.[168] Heterogeneous stomatal behavior will provide erroneous infrared gas analyzer-calculated values of intercellular CO_2 concentrations (C_i) as a result of the nonlinear relationship of g_s and A.[166]

Stomata are controlled by numerous environmental factors (in addition to internal factors). Generally an increase in VPD above a certain threshold, causes a reduction in g_s in most plant species[169] including *Vitis* spp.[170] The effect of VPD on g_s of grapevines is cultivar dependent.[35,170] Düring[167] recently has shown that high VPD in addition to ABA causes non-uniform stomatal closure in *Vitis* species as determined by the water infiltration technique.

The response of A to VPD may differ from that of g_s in *V. vinifera* depending on where on the curve of the relationship between A and g_s the measurements were taken. The relationship between A and g_s of field-grown 'Thompson Seedless' grapevines is curvilinear with maximum A leveling off at a conductance to water vapor of approximately 500 mmol m^{-2} s^{-1} (Figure 13). Thus, there may be a reduction in g_s due to an increase in VPD without a concomitant decrease in A when measurements are taken beyond the linear portion of the curve. Düring[170] found a linear decrease in both A and g_s with increasing VPD, however, he also found that A and g_s were linearly related up to a g_s of 160 mmol m^{-2} s^{-1}, the maximum g_s measured in that study. This would be equivalent to the linear portion of the curve in Figure 13.

Decreases in g_s due to increases in VPD may also be more pronounced for vines grown under drought conditions.[171,172] Stomatal conductance decreased significantly when 'Müller-Thurgau' and 'Riesling' vines were grown with an aerial environment kept at 50% relative humidity (RH) and soil water content maintained at 60% of field capacity compared to vines grown at 50% RH and a soil water content held at 95% of field capacity.[172] This response can also be measured on field-grown vines. Stomatal conductance decreased as VPD increased throughout the day for vines receiving less than full vineyard evapotranspiration (ET_c) (Figure 14). An increase in VPD from 1 to 3 kPa reduced g_s 50 and 75% for vines irrigated at 60 and 20%, respectively, of vine water use determined with a weighing lysimeter. In semi-arid environments, such as found in the San Joaquin Valley of California, VPD and ambient temperature are highly correlated.[174] Therefore, the relationship between g_s and ambient temperature are similar to the relationship found in Figure 14 for this particular data set.

Investigations into the response of grapevine growth and development to VPD are limited. If carbon assimilation is decreased due to VPD effects on g_s then one would expect a reduction in vine growth. In addition, high evaporative demand may also induce water stress again limiting the uptake of CO_2. A study conducted in growth cabinets demonstrated that vines grown under low RH (50 compared to 95% RH) produced more leaf but less stem (main axis of shoot) biomass than vines grown under the higher humidity.[172] There was no effect on dry matter partitioning to the root. It also was shown that budbreak occurred earlier and more buds broke at 95% RH than at 50% RH in that study for both

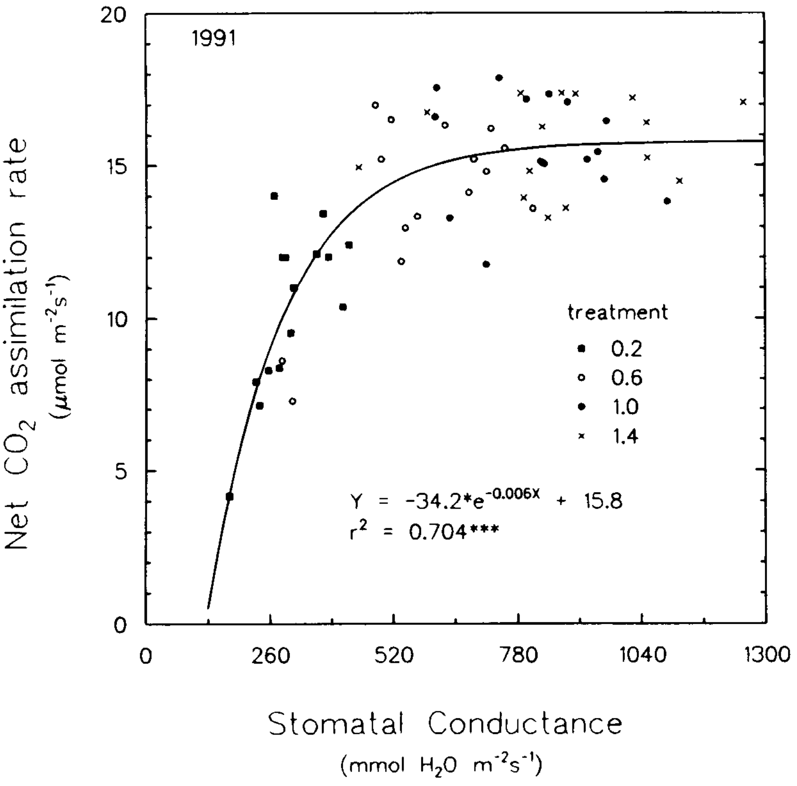

Figure 13 The relationship between net CO_2 assimilation rate and stomatal conductance of 'Thompson Seedless' grapevines measured at solar noon approximately every 2 weeks throughout the 1991 growing season. Vines were irrigated daily at various fractions (treatments 0.2, 0.6, 1.0, and 1.4) of vine water use determined with a weighing lysimeter. A complete description of the weighing lysimeter is found in Phene et al.[173] (L.E. Williams, unpublished data.)

'Müller-Thurgau' and 'Riesling'. The effect of VPD on reproductive development of the current season's crop in grape is unknown.

B. DROUGHT

As mentioned earlier in this chapter the majority of the grape production areas of the world are characterized by Mediterranean type climates having warm to hot temperatures and little rainfall during the summer. Supplemental irrigation, therefore, is necessary if one is to produce a harvestable crop of high quality. However, irrigation generally is not permitted in European Community (EC) vineyards where grapes are destined for "quality wine" while in many other viticultural areas throughout the world the availability of supplemental water is limited. Therefore, vines may undergo a considerable amount of water stress sometime during the growing season in these viticultural production areas.

1. Species and Cultivar Tolerance

It is thought that the cultivation of the grapevine began during the Neolithic era (6000–5000 BC) in the region known as Transcaucasia.[1] By 4000 BC grape growing extended from Transcaucasia to Asia Minor and into the Nile Delta. Many of these regions today are characterized by low summer rainfall and periods of drought. It is probable that many of today's grape cultivars evolved in warm climates with little rainfall during the growing season and therefore may have indirectly been selected early for drought tolerance.

There have been attempts to classify both *V. vinifera*[175] and rootstock cultivars[176] with regards to drought tolerance although the basis for the rankings are not necessarily given. It is thought that *V. vinifera* is very drought-tolerant, and the American species *V. berlandieri* and *V. cordifolia* also are

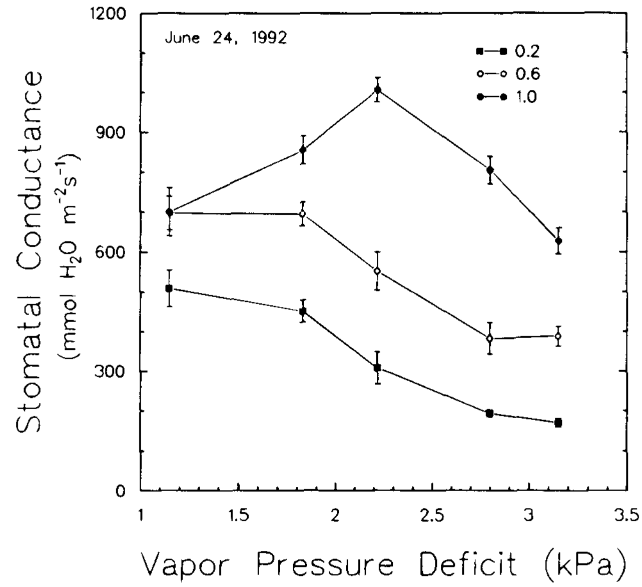

Figure 14 The relationship between stomatal conductance of 'Thompson Seedless' grapevines and vapor pressure deficit (VPD). Measurements were taken at 2-h intervals during the day. Thus, the measurements obtained at the highest VPDs were collected subsequent solar noon (at 1500 and 1700 h) at which time solar radiation may have become a limiting factor. Each value is the mean of nine individual leaf replicates. The numbers in the upper right corner of the figure represent the fraction of full vine-water use the treatments received. (L.E. Williams, unpublished data.)

known for their drought tolerance.[177] Galet[178] has classified the performance of the hybrids of *berlandieri-rupestris* as the most satisfactory in very dry soils. *V. riparia* and *V. rupestris* are thought to be sensitive to soil-water deficits.[177]

2. Effects on Vine Water Relations

Grapevine Ψ_l will undergo diurnal fluctuations[1,2] regardless of the amount of water available to the vine.[179] Vines with adequate soil moisture will have a pre-dawn Ψ_l between −0.01 and −0.1 MPa while those with less available water will have a more negative Ψ_l (Figure 15). The daily minimum Ψ_l potential typically occurs after midday (solar noon) and then increases as solar radiation and evaporative demand decrease in the late afternoon. Pre-dawn Ψ_l of well-watered vines will remain relatively constant throughout the growing season while that of deficit irrigated vines will become less.[179,180] For the data set in Figure 15, vines which had not been irrigated throughout the season had a pre-dawn Ψ_l close to −0.9 MPa on August 18. While midday Ψ_l is dependent upon evaporative demand, this value should not become much less than −1.0 MPa if the vines are irrigated at full vineyard ET even under semi-arid conditions.[181] Midday Ψ_l of deficit irrigated vines will continue to decrease as soil-water content decreases.[179,181]

Stem and cluster water potentials also will fluctuate on a diurnal basis.[34,179] Pre-dawn cluster water potential ($\Psi_{cluster}$) is more negative than Ψ_l and remains such until evaporative demand increases after sunrise with Ψ_l decreasing more rapidly as the day proceeds.[34,179] Clusters will reach their minimum water potential values later in the afternoon than leaves and may ameliorate changes in Ψ_l by supplying water to leaves especially during midday. As with Ψ_l, $\Psi_{cluster}$ is more negative for deficit irrigated vines compared to those receiving adequate water on both a diurnal and seasonal basis.[179,182]

It has been suggested that drought avoidance rather than tolerance is the mechanism by which grapevines respond to soil water deficits.[164] However, there are a few studies that indicate *V. vinifera* cultivars are able to osmoregulate.[181,183,184] Experiments conducted in the lab and field indicate that a decline in the osmotic potential (Ψ_π) of between 0.4 and 0.7 MPa can occur in drought stressed vines.[181,184] The ability to adjust the vine's Ψ_π appears to be cultivar/species dependent.[185]

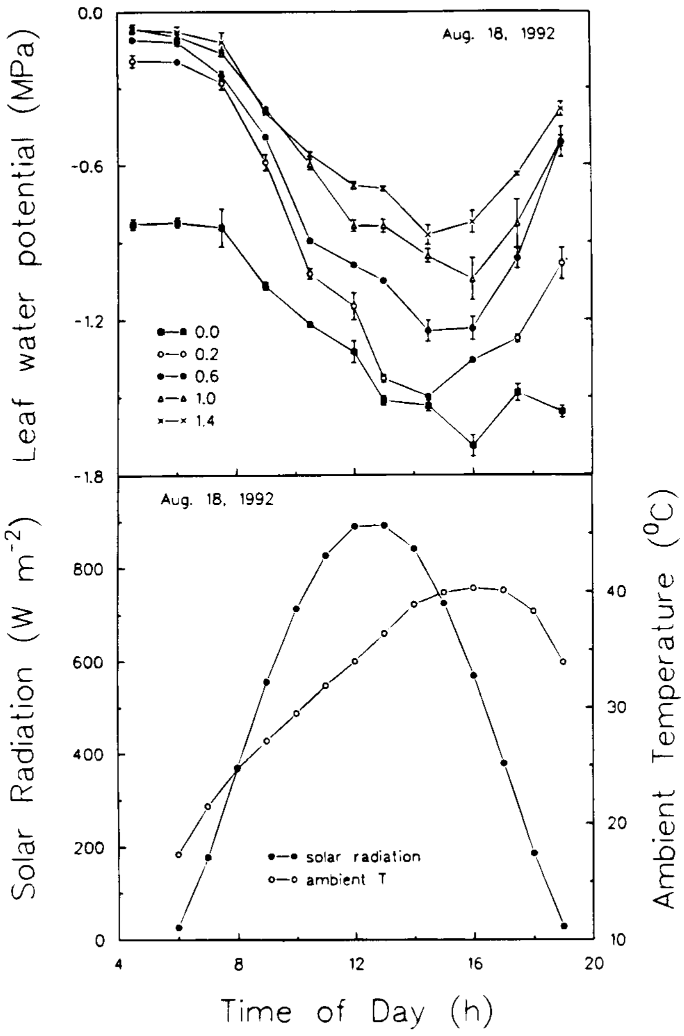

Figure 15 The diurnal time course of leaf water potential for 'Thompson Seedless' grapevines receiving various fractions of full vine water use (top). The diurnal time course of ambient temperature and solar radiation for this day also is included (bottom). Leaf water potential values represent the means of six individual leaf replicates per treatment. Treatments represent irrigation amounts at various fractions of full vine-water use (1.0 treatment). (L.E. Williams, unpublished data.)

3. Effects on Leaf Gas Exchange

Water stress will cause a reduction in g_s of grapevines. The Ψ_l at which stomatal closure begins varies between −0.9 and −1.6 MPa[30,34,179,180,182] depending upon environmental conditions and the rate of water stress imposition (i.e., rapid for potted vines; slow for field-grown vines). The relationship between midday Ψ_l and g_s throughout the 1991 growing season for 'Thompson Seedless' vines irrigated at various fractions of vine water use (ET), however, results in a linear reduction in g_s with a decrease in Ψ_l (Figure 16). The low coefficient of determination indicates that other factors (either internal or environmental) must contribute to the reduction in g_s. It was demonstrated in Figure 14 that vines experiencing soil water deficits are more sensitive to changes in VPD than well-watered vines. A similar r^2 value for the relationship between midday Ψ_l and g_s of 'Colombard' grapevines has been reported by van Zyl.[179]

Studies during the past decade on numerous plant species indicate that the reduction in stomatal conductance and growth of plants due to soil water deficits may be a response to some sort of "root signal".[186] This signal probably arises due to the roots sensing a reduction in soil water content or an

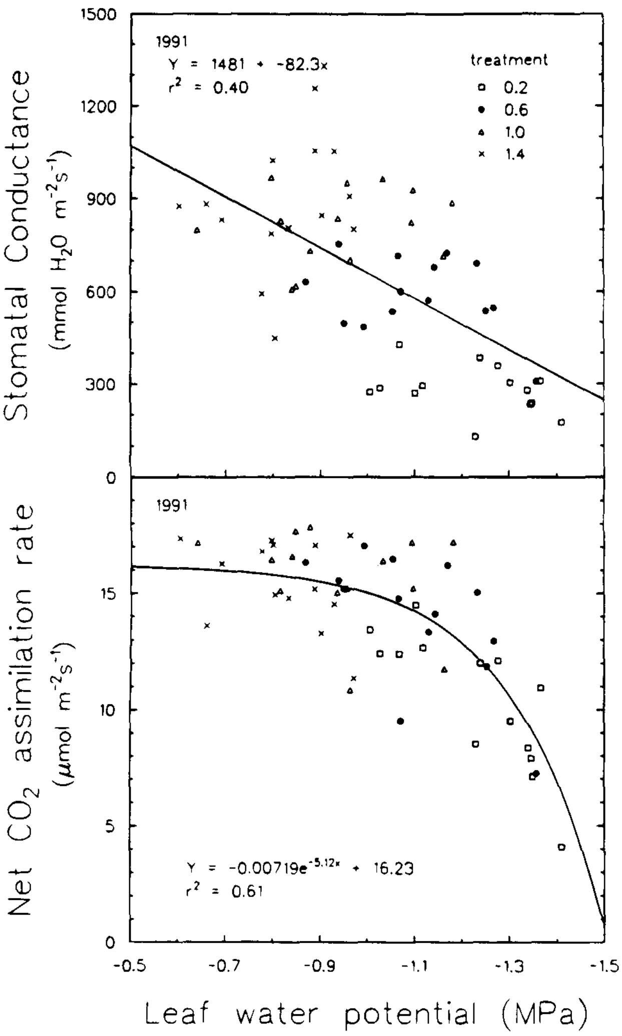

Figure 16 The relationship between midday measurements of net CO_2 assimilation rate and stomatal conductance and leaf water potential of 'Thompson Seedless' grapevines grown in the San Joaquin Valley of California. Data were collected throughout the 1991 growing season. Each data point is the mean of nine individual measurements of A and g_s and six individual Ψ_l measurements. Treatments are as outlined in Figure 13. (L. E. Williams, unpublished data.)

increase in the mechanical impedance as the soil dries out. The most likely candidate for this signal is ABA produced in the roots or an as-yet unidentified regulator.[186,187]

It has been found in grapevines under well-irrigated conditions and exposed to a minimum level of stress that the ABA content of leaves increases after sunrise and peaks at approximately twice the predawn level at midday.[188,189] Decreases in g_s during the day were correlated with ABA accumulation in the leaves. Loveys[190] suggested that ABA is exported from leaves to roots, and then transported back to the leaves via the xylem which ultimately controls g_s optimizing water use efficiency.[189] ABA also will increase in the leaves of water-stressed grapevines.[191-193] The involvement of ABA in stomatal regulation of grapevines is further supported by the fact that water stress causes heterogeneous stomatal closure in grapevine[193] which also has been shown to occur in grapevine leaves supplied with ABA.[166]

van Zyl[179] found that pre-dawn and midday Ψ_l were highly correlated with both soil water content and soil water potential (Ψ_{soil}). Coefficient of determinations were highest between Ψ_{soil} and both predawn and midday Ψ_l. Studies on other plant species indicate that soil water content is the factor responsible for eliciting root sensed responses in the shoot.[194,195] Data in Figure 17 demonstrates that

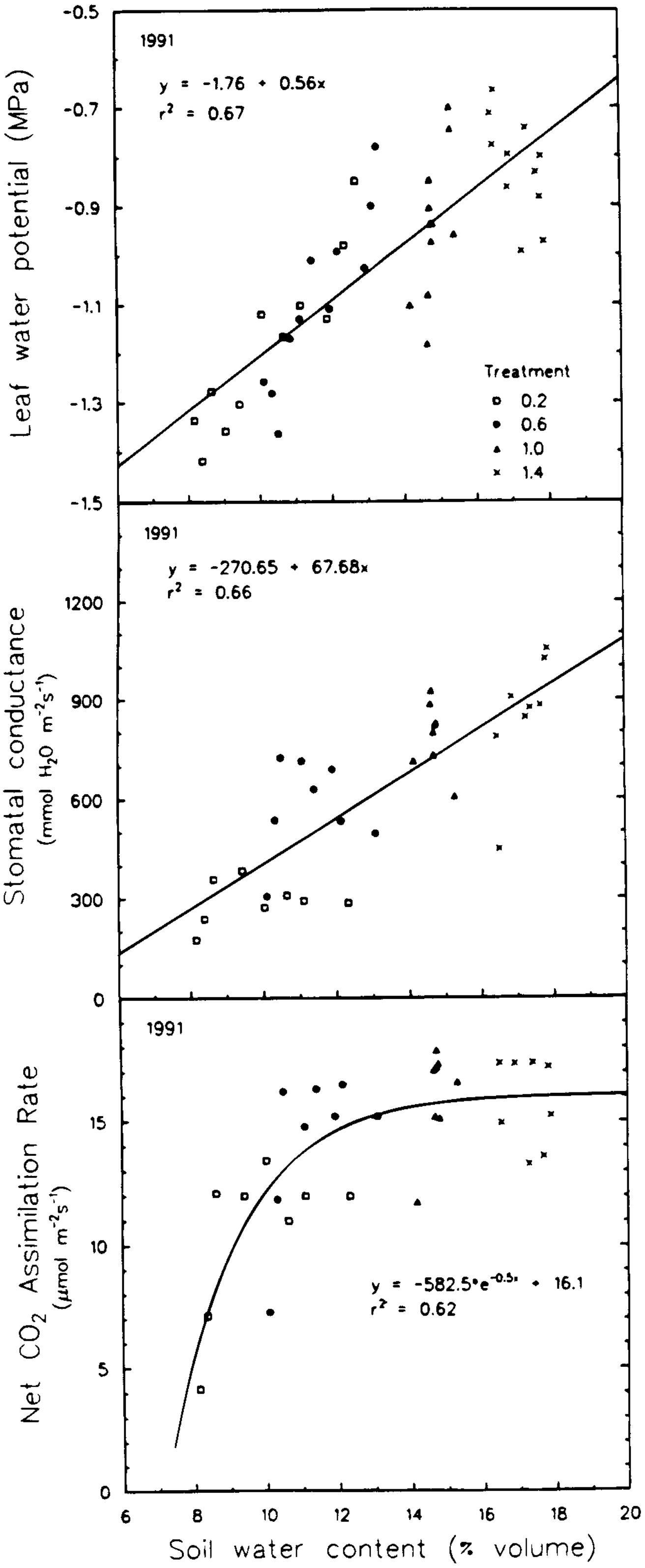

Figure 17 The relationship between midday measurements of net CO_2 assimilation rate, stomatal conductance, and leaf water potential of 'Thompson Seedless' grapevines and soil water content. Treatments are the same as those outlined previously (Figure 13). Soil water content was measured as described in Grimes and Williams.[181] The nine access tubes per individual vine were replicated three times in each irrigation treatment. Soil water content is the mean of those three replicates (nine access tubes measured to a depth of 3 m per individual vine replicate). (L.E. Williams, unpublished data.)

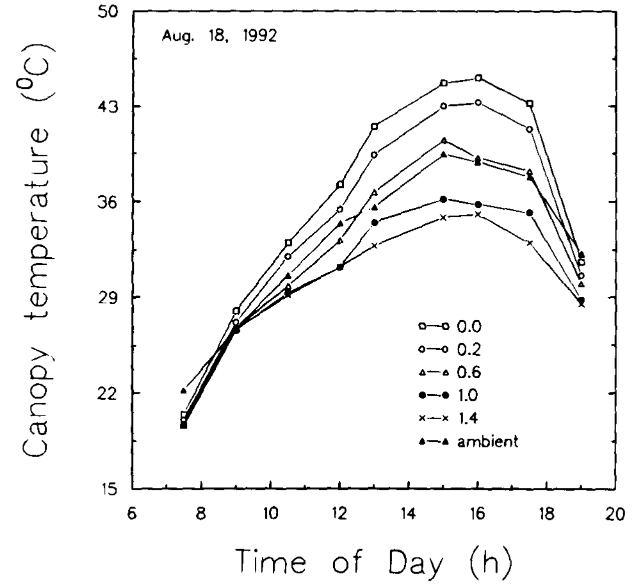

Figure 18 The diurnal time course of 'Thompson Seedless' canopy temperature as a function of irrigation treatment on August 18, 1992. Canopy temperature was measured with an infrared thermometer. Each value is the mean of nine individual measurements per irrigation treatment. Ambient temperature was measured 0.5 m above the canopy. Other information as given in Figure 13. (L.E. Williams, unpublished data.)

during the growing season midday Ψ_l and g_s were highly correlated with soil water content (SWC). Soil water content accounted for up to two thirds of the variation of both plant-based measures of vine water status. It should be pointed out that measurements were taken on vines irrigated at various fractions of full vine ET throughout the season and that only the 0.2 and 0.6 ET_c treatments experienced decreasing soil water content as the season progressed. In a study where water was withheld for 13 days for drip irrigated vines, there also was a linear relationship between SWC and midday Ψ_l (Ψ_l decreased as SWC decreased), and the coefficient of determination was 0.91.[196] The results found in Figure 17 and those of Araujo,[196] would indicate that the rapidity in which the soil dries out affects the degree of coupling between root sensed responses and the aerial portion of the vine.

Water stress is associated with a reduction in A and E of grapevine leaves.[164] The exponential relationships found in Figures 16 and 17 do indicate that A will decrease once the plant or soil water status reaches a particular level. A relationship similar to that shown between Ψ_l and A in Figure 16 previously has been demonstrated on leaves from excised shoots of grapevines.[30] It appears that stomatal control of A occurs during the early stages of drought, perhaps due to ABA's (irrespective of site of origin) effect on stomatal closure. The previously reported non-stomatal limitation to A when Ψ_l exceeds -1.3 MPa may actually be due to non-homogeneous stomatal closure.[193] For example, PSII photochemical efficiency was not a primary target of water stress in *V. californica.*[43]

Canopy temperature (measured via portable infrared thermometers) has often been used to rapidly evaluate plant water status.[181,197,199,200] If plants are well supplied with water and stomata are open, transpiration will proceed at the maximum rate determined by soil and plant hydraulic conductance and by climatic evaporative demand. As VPD increases, transpiration of nonstressed plants will increase with greater evaporative cooling resulting in foliage that is cooler than the surrounding air. As water becomes limiting, transpiration will decrease and the canopy temperature will increase, becoming greater than that of the nonstressed plants. Canopy temperatures of vines irrigated at full vineyard ET or greater always were lower than ambient temperature throughout a hot, summer day in the San Joaquin Valley of California (Figure 18). Vines irrigated at less than full ET had canopy temperatures greater than ambient at least during some portion of the day. Canopy temperature is an average of all of the leaves in the field of view of the infrared thermometer, therefore, individual, sunlit leaf temperature will be warmer than that of the canopy.[197] Canopy-to-ambient temperature differentials of up to 10°C have been measured on grapevines.[198] The concept of a Crop Water Stress Index (CWSI) based upon the difference between canopy and air temperature eventually may be used as a means to schedule irrigations.[201]

Diurnal measurements of A indicate that vines with less soil water availability can be as great as that of well-irrigated vines early in the morning.[202] However, as the day progresses A of stressed vines will decrease as opposed to a near constant rate of A of the nonstressed vines.[202]

4. Effects on Vegetative Growth

Few studies have determined the effects of soil moisture deficits on the growth of the permanent structures (i.e., roots, trunk, and cordons) of field-grown grapevines.[164] A recent study using field-grown 'Chenin blanc' vines demonstrated that dry biomass of the roots was reduced approximately 30% for vines irrigated at 52% of vineyard ET when compared to vines irrigated at full ET_c after the completion of a 4-year experiment. Root growth of container-grown vines was affected less than shoot growth.[203] It has been shown that the number of actively growing root tips diminish due to soil water deficits.[204]

Soil water deficits, due to irrigation at 52% of calculated ET, decreased trunk and cordons biomass by 17 and 30%, respectively. van Zyl[204] concluded that trunk circumference measured annually was a reliable indicator of vine water stress. While there were reductions in biomass of the roots, trunk, and cordons due to deficit irrigation, there was no significant difference in the concentration of non-structural carbohydrates (glucose, fructose, sucrose, and starch).[1]

The effects of soil water deficits on budbreak and subsequent phenological events have been assessed in a few studies. Water stressed vines generally have earlier budbreak than those receiving greater amounts of irrigation water[205,206] whether vines are deficit irrigated throughout the season[205] or subsequent to fruit harvest on vines grown in the desert.[206] In the first year of a timing-of-irrigation study it was shown that differences in vine water status had no significant effect on the duration of vine developmental periods (i.e., between anthesis and veraison) expressed either on calendar days or degree days.[207]

Growth inhibition and final growth cessation due to water stress was shown to be similar among internodes, leaves, and tendrils of container-grown White Riesling.[208] The relative partitioning of growth among these three organs was unaltered when growth was inhibited due to water stress. The pre-dawn tissue Ψ of leaves, internodes, and tendrils which completely inhibited growth of each was -1.0, -1.2, and <-1.2 MPa, respectively. The growth of each organ was inhibited initially at a Ψ_{soil} of -0.065 MPa and ceased completely at a Ψ_{soil} of -0.54 MPa. It was concluded that the sensitivity of growth to water stress increased with ontogeny as some growth was maintained in younger tissues when inhibition was complete in older tissues.

These data contrast with those of field-grown vines. Soil matric potentials (Ψ_m) of -0.05 MPa were insufficient to decrease midseason shoot growth in a cool environment,[209] while the same soil Ψ_m decreased shoot growth in a hot environment with shoot growth ceasing at a $\Psi_m = -0.065$ MPa measured at a depth of 0.3 m.[210] Kliewer et al.[180] found that the rate of shoot elongation of 'Carignane' was reduced by water stress before any differences were detected in pre-dawn Ψ_l and that water stress reduced shoot growth but had no effect on the growth rate of leaves. The differences in results between field- and container-grown vines could possibly be because soil water status in the field was measured only in a limited portion of the root zone and therefore may not reflect the soil Ψ_m of the entire rooting profile. In addition, the study on container-grown vines was conducted on vegetative vines while those in the field had a crop.[208]

A reduction in shoot growth is the first visible symptom of vine water status in the field[211] and may be more sensitive to Ψ_{soil} than physiological processes occurring within the leaf (Figure 17), and recent studies on annual crops indicate that non-hydraulic signals from the roots in drying soil may inhibit leaf elongation without influencing g_s.[212] Such a response may act to conserve water as the soil dries but before the onset of water stress in the aerial portion of the plant. The reduction in shoot elongation is clearly demonstrated on vines irrigated daily at various fractions of vine ET (Figure 19). The soil Ψ_m, for the 1.0, 0.6, and 0.2 irrigation treatments on day-of-year 150 were -0.025, -0.05, and -0.06 MPa, respectively.

Weights of canes pruned from the vine during the dormant portion of the growing season is often used as a measure of shoot growth the previous season. Pruning weights may increase up to 137% with irrigation;[164] the relative increase in pruning weight being largely dependent on the volume and timing of irrigation throughout the season.[213] When vines were irrigated daily at various fractions of full vineyard ET (from 0 to 140%) pruning weights increased linearly with irrigation quantity (L. E. Williams,

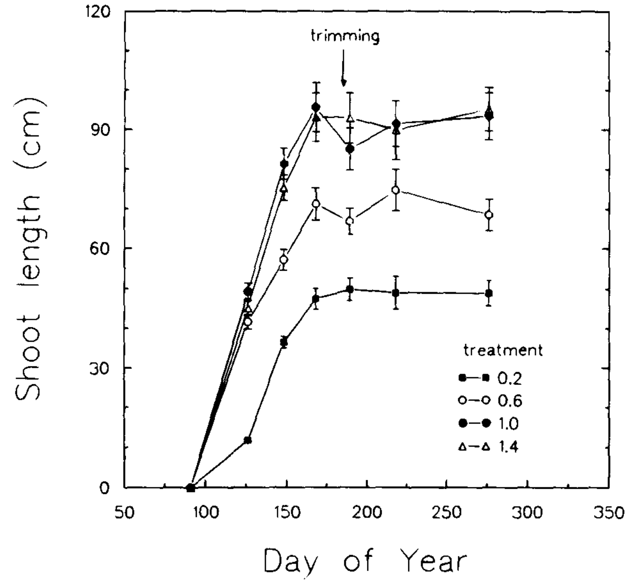

Figure 19 Average shoot length of 'Thompson Seedless' grapevines throughout the 1991 growing season as a function of irrigation treatments. Each value is the mean (± SE) of all shoots on three individual vine replicates per irrigation treatment measured repeatedly during the season. (L.E. Williams, unpublished data.)

unpublished data). Irrigation at full ET, under the conditions of this study, increased pruning weights to almost three times that of the non-irrigated control.

Water use efficiency (WUE) is the amount of plant biomass produced per amount of water transpired and is a useful parameter in assessing the effects of water stress on productivity and drought tolerance.[214] WUE can be constant despite differences in crop water use due to different irrigation regimes.[215] However, the WUE (g dry wt produced per kg water transpired) of container-grown vines ranged from 1.5 to greater than 5 for different cultivars of *V. vinifera*.[216] The authors concluded that WUE increased with increased vegetative growth (vigor) of the vine. The WUE decreased as vine ET increased for 'Thompson Seedless' vines grown in a semi-arid environment over the period from budbreak to veraison (Figure 20) despite increased vine vigor with greater irrigation amounts. WUE decreased from 5.85 for the 0.2 irrigation treatment to 1.84 for the 1.4 treatment. These values are similar to those calculated by Smart and Coombe[164] with data from a study by van Zyl and van Huyssteen.[217] One may expect differences in WUE due to differing amount of applied water with 'Thompson Seedless' grapevines as the relationship between A and g_s is curvilinear (Figure 13). The greatest efficiency between A and transpiration in this study occurred at a g_s of approximately 500 mmol H_2O m^{-2} s^{-1}. Most of the midday values of g_s for vines irrigated at 100 and 140% of vine water use are greater than 500 mmol m^{-2} s^{-1}.

5. Effects on Reproductive Growth

Reproductive growth of grapevines is less sensitive to water stress than vegetative growth.[2,163,164,204,218] Information on the effects of water stress on bud fruitfulness of grapevines is limited due to the inability of separating specific effects of water stress from those of temperature and light intensity in the field.[1] Water stress has decreased bud fruitfulness of container-grown vines under controlled environmental conditions.[219] However, it was suggested that bud fruitfulness is not adversely affected by the levels of water stress experienced in the field,[220] and may even increase bud fruitfulness.[213] Increased fruitfulness may be due to the reduction in vegetative growth which improves the exposure of the buds to light (see Section II.C). However, severe reductions in shoot growth due to water stress will result in fewer buds available for next year's fruiting canes for cane pruned cultivars if there is not sufficient shoot growth.

Using 3-year-old, container-grown vines, it was demonstrated that severe water stress (predawn Ψ_l <0.6 MPa) for the 3-week period after anthesis, induced cluster abscission and reduced berry set.[221] While severe water stress at anthesis in the field is uncommon, cluster abscission did occur early in the season (shoot length 30 cm) for vines irrigated at 0 and 20% of full vineyard ET the previous

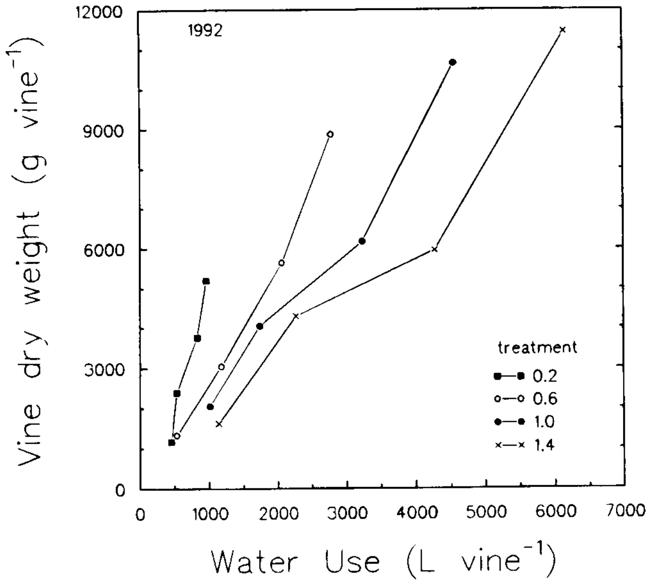

Figure 20 The relationship between the accumulation of dry biomass (leaves, main axis of shoots, and clusters) of 'Thompson Seedless' grapevines and water use throughout the 1992 growing season. Water use of each irrigation treatment was determined by adding the amount of water applied via drip irrigation to each vine and the amount of water depleted in the soil. Each value is the mean of three individual vine replicates. (L.E. Williams, unpublished data.)

growing season (L. E. Williams, unpublished data). Vines in these two treatments lost 70 to 90% of the clusters present on the vines during the period of delayed shoot growth noted in Figure 19.

Water stress will reduce the growth of berries, but does not influence the characteristic double-sigmoid growth curve.[204] A given water deficit during Stage I (when cell division is occurring) will generally reduce final berry size more than water deficits during Stages II and III (growth by cell expansion).[2,54,204,207,221,222] Also, the reduction in berry size due to soil moisture deficits during Stage I cannot be reversed by supplemental irrigation during Stages II and III.[213,223,224]

The sink potential of the fruit, determined during Stage I, appears to dictate the amount of carbon allocated to the cluster regardless of water stress. GA_3 applied at berry set will increase final berry size in seedless cultivars due to increased cell division.[225] An application of GA_3 to non-irrigated 'Thompson Seedless' vines at berry set resulted in comparable berry size and yield to the irrigated control vines (Table 2) underscoring the importance of events occurring during Stage I in determining final berry size. Final yields were similar between the irrigated control vines and the non-irrigated vines that were sprayed with GA_3 at berry set despite large differences in leaf area per vine at harvest. In addition, the ability of the water stressed vines (with reduced leaf area) to mature a crop, similar to that of irrigated vines indicates that alterations in source/sink relationships may be able to overcome the detrimental effects of water stress. Berry growth rate of irrigated and non-irrigated vines is similar subsequent to

Table 2 **The interaction of irrigation amount and gibberellic acid (GA_3) applied at berry set on berry size and yield of 'Thompson Seedless' grapevines**

Irrigation treatment	Berry weight (g)		Yield (kg vine^{-1})	
	Control	GA_3	Control	GA_3
Irrigated	2.0	2.8	16.5	23.4
Nonirrigated	1.2	1.8	9.0	16.1

Note: Mean leaf area per vine at harvest for the irrigated treatment was 20.3 m^2 while that for the nonirrigated treatment was 6.2 m^2. There were no significant differences in berry weight and yield between the irrigated control vines and the nonirrigated vines sprayed with GA_3.

From Williams, L.E., unpublished data.

Stage I despite differences in vine water status.[205] These results indicate that the involvement of plant hormones, other than ABA, should also be studied in plants under water stress.

The effects of water stress on berry growth are reflected in final yield.[164,205] Post-veraison water deficits had less of a detrimental effect on final yield than pre-veraison water deficits when compared to a continuous weekly irrigation treatment.[207,222] Hepner et al.[226] reported no significant differences in yield due to different irrigation amounts for 'Cabernet Sauvignon' vines between May and July 15th or subsequent to July 15th until harvest. There was a linear increase in yield for 'Thompson Seedless' grapevines irrigated daily at fractions of full ET_c, 40 to 100%.[181] Thus, both the timing and degree of water stress will have an important effect on the yield of field-grown grapevines.

6. Effects on Fruit Quality

Vine water status affects fruit solute composition throughout berry development. However, the literature contains conflicting data as to the exact effects of water stress on the berry composition. The accumulation of sugars is less affected by water deficits than is berry growth[2] although severe water stress may decrease sugar accumulation.[205,221] Sugar accumulation may also be delayed by increased water applications or by increased vegetative growth resulting in a less favorable light environment in the fruit zone (see Section II.C).

Organic acids contribute to the quality of the harvested fruit. A decrease in titratable acidity may occur with vine water stress.[204,223,227] Malic acid is the primary acid affected by water deficits; its concentration is dependent upon the specific time the deficit is imposed in relation to veraison.[204,227] The reduction in malate may be due to increased fruit temperature, and therefore increased respiration, as clusters become more exposed because of lack of leaf shading. The losses of malate may be balanced by similar decreases in counter-balancing cations or by accumulation of other acidic moieties such as amino acids.[2] The effects of water deficits on pH of the juice is less clear as some studies report that pH is increased by irrigation while others found no effect of supplemental irrigation.[2]

Water deficits will improve fruit color of red- and black-fruited cultivars.[2] The increase in color is the result of an increase in the production of anthocyanins. It is unknown whether this is a direct effect of water stress or an indirect one due to increased fruit exposure as a result of a reduction in vegetative growth.

Both early and late season water deficits increased juice and skin phenolics in berries of 'Cabernet franc' vines.[228] Wine sensory characteristics also can be manipulated by vineyard irrigation amounts and timings.[229] Wine made from continually irrigated vines differed from those irrigated only before or after veraison while the early season water deficit differed from the late season water deficit in appearance, flavor, taste, and aroma.[229] The wine effects may be associated with reduced berry size and increased skin content.

C. FLOODING

Waterlogging is a serious problem of grapevines.[230] Some species used for rootstocks may have tolerance to excessive soil water. *V. rupestris* is the most sensitive species to low soil 0_2.[177] Less sensitive species are *V. solonis, cinerea, candicans*, and the *riparia* × *rupestris* hybrids. For example, the rootstock (Couderc) 3306 (a *V. riparia* × *rupestris* hybrid) has been shown to tolerate poor soil drainage in Australia.[231]

Sensitivity of grapevines to waterlogging depends upon the time of year. Subsequent to leaf fall, grapevines are little affected by waterlogging conditions. In fact, flooding a vineyard in midwinter for a period of up to 6 weeks has been used as a means to control grape phylloxera (*Daktulosphaira vitifoliae* Fitch).[232] Waterlogging after budbreak will cause reduced shoot growth, leaf chlorosis, and death.[233] Excessive irrigation, resulting in saturated soils reduces new root initiation[234] and inhibits the growth of roots into water saturated soil layers.[204]

Webber and Jones[235] have recently summarized the indirect effects of waterlogged conditions on vine growth. Many of the American *Vitis* species used for rootstocks are intolerant of lime and they will suffer from chlorosis,[231] which is aggravated by waterlogging. In addition, waterlogging can change soil pH and affect the availability of nutrients.

While waterlogged soils may have deleterious effects on vine performance, over-irrigation (water applications slightly greater than vineyard ET) has more subtle effects on growth, productivity and fruit quality. Such vines have reduced bud fruitfulness and yields but increased pruning weights (L. E. Williams, unpublished data). Excessive irrigation generally will reduce fruit sugar concentration, titratable acidity and delay color development.[204] This is thought to be due to competition for photosynthates between the fruit and post-veraison vegetative growth.[164] However, much of the negative effects of over-irrigation may actually be due to shading effects due to excessive vegetative growth (see Section II.C).

V. MISCELLANEOUS ENVIRONMENTAL FACTORS

A. SALINITY

Grapes are grown in areas where salinity is a problem, most notably in areas of Australia, Israel, and portions of southwestern United States. Grape has been classified as moderately sensitive to salinity (chloride) based upon vegetative growth measurements.[239] Most annual crops are affected by the reduction in Ψ_π of the soil solution due to salinity while woody perennial crops are primarily affected by specific ion toxicities.[236] Grapevines accumulate chloride readily either via the root system[237] or through the leaf.[238]

The visible symptoms of salt stress on grapevines first appear as marginal chlorosis on the leaves followed by necrosis progressing towards the center of the leaf blade. These toxicity symptoms are probably due to the uptake of the chloride ion as grapevines grown on sodic soils rarely exhibit these symptoms.[240] The maximum permissible chloride in soil water without leaf injury was shown to range from 60 to 80 mol m^{-3} for three container-grown, commercial rootstocks.[236] However, Prior et al.[241] found that symptoms of leaf damage (marginal necrosis) in the field were more closely related to the onset of hot dry weather than with reaching a particular Cl or Na concentration in the lamina. Under severe salt stress the entire vine may defoliate.

There is variability in the uptake of salt among *Vitis* species, cultivars, and rootstocks.[1] Downton[242] categorized *V. rupestris* as the most salt tolerant species followed in order of descending tolerance by *berlandieri, riparia, candicans, champinii, longii, cinerea, cordifolia,* and *vinifera.* Antcliff et al.[243] found the order of *V. berlandieri, champinii,* and *cinerea* similar to that of Downton[242] but that the only clone of *V. rupestris* used by Downton, 'Rupestris du Lot' (syn. 'Rupestris St. George'), was atypical of that species. Their data indicated *V. rupestris* salt tolerance as comparable to that of *V. cinerea.* The variation in Cl exclusion both among and within species indicates there may be a genetic basis for this characteristic.[244] The ability to exclude Cl by the *V. champinii* species (the 'Ramsey' rootstock, syn 'Salt Creek') is probably due to the action of many genes.[245] The genetic basis for Cl exclusion in *V. berlandieri* may be due to a single dominant gene.[246] In that study, Cl exclusion was independent of both yield and berry weight.

V. champinii rootstocks 'Dogridge' and 'Ramsey'[242,243,247,248] and the *berlandieri* × *rupestris* hybrids '110 Richter', '140 Ruggeri', and '1103 Paulsen'[243,247] are effective Cl excluders.[243,247] Salt tolerant *V. vinifera* cultivars include 'French Colombard' (most tolerant) > 'Grenache', 'Chenin blanc', 'Thompson Seedless' > 'Barbera', 'Muscat of Alexandria', or 'Ribier' (susceptible).[1,240]

Reductions in growth and A have been observed to occur in response to soil salinity before any toxic symptoms appear in grapevines.[249] Prior et al.[241] found that the response of A to salinity of field-grown grapevines was almost identical to that found by Downton[249] on container-grown vines and was more strongly correlated with leaf Cl than leaf Na. The reduction in A is due to a uniform decrease in g_s up to a tissue concentration of 165 m*M* Cl.[250] It also was found that at tissue concentrations above 165 m*M* Cl non-stomatal inhibition of A was actually due to non-uniform stomatal closure (determined visually using $^{14}CO_2$ uptake and autoradiograms). It has been observed that ABA levels in the leaves of salt-stressed grapevines increase rapidly and remain such for several weeks.[251] Therefore, in grapevines the salt-induced reductions in A (mediated by the increase in ABA levels) are a result of heterogeneous stomatal closure.

Container-grown grapevines exposed to saline water are able to osmotically adjust shortly after exposure.[252] Osmotic adjustment is due to the accumulation of Na, K, and Cl ions and an increase in reducing sugars.[251] It was concluded that the maintenance of turgor pressure and osmotic adjustment during salt stress prevents immediate damage to PSII activity. However, the continued accumulation of chloride eventually causes membrane permeability changes, cell damage, and the loss of turgor.

As mentioned above, grapevine tissue ion content will change with the use of saline water. Prior et al.[253] found that the accumulation of Na and Cl in leaves and petioles of field-grown vines was not linear but tapered off at high irrigation water electrical conductivity (EC) values, indicating that the tissue was becoming saturated with salt. K concentrations in petioles and leaf blades generally are reduced due to elevated levels of NaCl in the rooting medium.[240,241] However, it was shown that leaves of container-grown grapevines began to accumulate K^+ and Cl within 6 h of exposure to high levels of NaCl while the uptake of Na was not evident until the next day.[251] The accumulation of K^+ and Na generally balanced the accumulating Cl ion. The effect of saline water on the accumulation of other mineral nutrients in vine tissues is less clear and differs depending whether the study is conducted on container-grown vines over a short period or on field-grown vines over a long-term period.

Vegetative growth (shoot length, pruning weights, and leaf weight) of 'Sultana' (syn. 'Thompson Seedless') was reduced by salinity to a much greater extent than yield.[241] In that study, all vegetative growth parameters measured were reduced by salinity with the effects of salinity were more severe on heavier soils. Growth reductions occurred despite the fact that there were no differences in Ψ_l among salinity treatments. Root density was reduced to a greater extent than the reduction in total leaf area.[253] Root growth was severely restricted on container-grown 'Cabernet Sauvignon' even in concentrations of NaCl as low as 20 m*M* in the rooting medium.[254] Soil salinity has also reduced starch levels in the canes and increased the concentrations of reducing sugars.[241,250] It was concluded that the reduction in vegetative growth and photosynthetic area was the primary reason for a reduction in yield in the study of Prior et al.[241,253,255]

A 6-year study on own-rooted 'Sultana' vines conducted in the River Murray flood basin of Australia[241,253,255] showed that vine performance declined with the duration of exposure to salinity and was strongly influenced by soil texture.[255] Yield response to salinity levels in the lightest textured soil resembled the model developed by Maas and Hoffman,[239] although more severe losses than predicted occurred in the heavier soils. Yield was correlated with EC[253] of the soil extract, but that relationship was not as good as that derived between yield and plant-based measures (lamina content) of salinity.[241] For own-rooted 'Sultana': (1) there was no evidence of a yield threshold in response to soil salinity when averaged across all soil texture types; (2) there was a 10% yield loss when EC at the end of the winter exceeded 1.0 dS m^{-1}; (3) vine-based measurements of salinity effects were better than soil-based measurements as they were able to integrate the rootzone salinity over space and time; (4) the best relationship between yield and vine tissue concentrations was obtained using petiole Cl and Na values; and (5) petiole Cl and Na values should be kept below 420 and 191 mmol kg^{-1} dry weight, respectively, to avoid the detrimental effects of salinity on vine productivity.

There are instances when salt in the irrigation water may be present only for a short period of time. A study investigating transient (two-month period), soil salinization of a Colombard vineyard on 'Ramsey' rootstock found that the treatments increased EC values and petiole Na and Cl concentrations and decreased Ψ_l[256]; however, vegetative growth or yield were not affected.[256] The authors concluded that the lack of growth or yield response in this vineyard was not due the use of the 'Ramsey' rootstock as other studies have found that growth of various scion/rootstock combinations will decline over a range of saline water.[257] Thus, it appears that transient exposure to high EC levels (3 to 6 dS m^{-1}) for 2-month periods may not necessarily reduce vine productivity. Of significant importance in minimizing the effects of salinity is to ensure that adequate leaching of salts take place sometime during the growing season.[253]

Fruit composition may be affected by salinity. The accumulation of sugars in the fruit was not affected for the first 3 years of soil salinization,[255,258] but declined subsequently. Juice titratable acidity increases with salt treatments as does the concentrations of Na, K, and Cl ions; wines made from the fruit were similarly affected.[242] The use of rootstocks, known to exclude Cl, reduced the levels of Cl in the wine.[242]

B. WIND

Wind can affect the physiology and growth of plants in numerous ways.[259] Wind speed is of significant importance as it affects heat and mass transfer of individual leaves and the vine canopy as a whole. High wind velocities can lead to structural damage of plant tissue while constant winds at low to medium velocities can lead to deformation and disruption of physiological processes. Vineyards in many regions may be exposed to chronic low- to medium-wind velocities; the effects of chronic wind exposure on vine physiology and productivity have not been quantified.

Vineyards are considered aerodynamically rough as their surfaces are covered by discontinuous canopies. Wind will determine the depth of the boundary layer which ultimately affects the exchange of CO_2 and water vapor between the plant and the atmosphere. Weiss and Allen[260] did not find a constant flux zone over the vineyard in which their measurements were made as has been found for other crops. They concluded that the vineyard boundary layer actually consisted of an inner and outer zone. Wind direction also influences the degree of roughness of a vineyard. The drag coefficient, which is a nondimensional measure of the roughness of a surface, is higher for cross-row flow than for down-row flow of air in a vineyard.[260,261] Wind speed also has been shown to be more important than wind direction in maintaining between-row circulations.[262]

An increase in wind speed will increase the boundary layer conductance which generally increases the rate of transpiration from leaves and plant canopies.[215] Hicks[261] found that vineyard ET increased 10 to 20% with cross-row flow as compared with down-row flow of air. This indicated that ET increased due to an increase in the drag coefficient (see above). However, studies conducted both in the lab and the field on individual leaves of grapevines have shown that g_s and transpiration is decreased when wind speed exceeds a given threshold;[263-265] wind velocities greater than 3 m s^{-1} were required to significantly decrease g_s and transpiration. Preliminary results from Australia indicate that ABA increases in leaves of grapevines exposed to chronic, low- to medium-wind velocities (B.R. Loveys, personal communication). The reduction in g_s of grapevines exposed to wind may be due to the accumulation of ABA as others have found that ABA increases in plant tissues that are exposed to wind.[266]

Wind has been reported to have little effect on the water relations of various plant species[215,259] including *V. vinifera.*[264] However, in studies examining the differences in water relations between sheltered and non-sheltered, field-grown grapevines in windy locations, Ψ_l of the sheltered vines always was more negative than that of the controls.[263,265] This may be expected as g_s was always greater for the sheltered vines.

The only report documenting a wind-induced reduction of A of grapevines did not include g_s measurements.[267] Many of the authors who have studied the effects of wind on grapevines suggest that the reduction in g_s due to increased wind speeds also will reduce A. The degree in which A is reduced due to increased wind speeds is largely dependent (although not linearly dependent) upon the extent that g_s is reduced. However, preliminary assessment of wind-breaks on vine physiology and growth indicates that there may not always be a large reduction in A when g_s is reduced due to chronic wind exposure (Figure 21).

Kobringer et al.[264] reported a carryover effect on g_s by wind velocities greater than 10 m s^{-1} but not at 3.6 m s^{-1}. Stomatal conductance remained depressed for up to 4 days after the treatment stopped, however, there were cultivar differences. A similar type of response has been observed in the field using windbreaks in a 'Chardonnay' vineyard (L. E. Williams, unpublished data). Wind has been shown to both increase and decrease the density of stomata on leaves of other plant species.[259] The carryover effect on g_s reported by Kobringer et al.[264] was not due to a reduction in stomatal densities as measurements were made only on mature leaves over a short period. It is uncertain whether this was true for the field study as the leaves had been exposed to chronic wind stress throughout the growing season.

While extremely high winds can cause physical damage in vineyards,[268] constant exposure to medium velocity winds (i.e., 1 to 2 m s^{-1}) also may affect vine growth and productivity.[269] At vineyard sites planted perpendicular to prevailing winds the vines will have an asymmetric growth habit (i.e., growth is much reduced on the windward side). The reduction in shoot growth is primarily due to a reduction in internode length (Table 3). There also is a reduction in individual leaf size and it is this parameter which is principally responsible for the reduction in total vine leaf area. The reduction in total vine leaf area is probably a more important determinant of reduced vine growth due to wind than the small decreases in leaf A. The reduction in growth may be the result of physiological and/or mechanical effects.[215] The production of ethylene in response to mechanical perturbation may be responsible for thigmomorphogenic responses of plants.[270]

Yields are greater for vines grown within windbreaks (Table 3) or close to windbreaks in vineyards when compared to vines grown further away or upwind from the break.[268,269] Simon[271] found that growth and productivity of vines increased when grown within a distance of five times the height of the windbreak. The reduction in yield was due both to reduced berry weight and cluster numbers per vine. Fruit soluble solids were lower for exposed vines when compared to the sheltered vines.[269] Other differences in fruit composition measured between sheltered and non-sheltered vines may be the result of differences in maturity between the treatments.

C. AIR POLLUTION

Extensive reviews of the effects of airborne pollutants on the grapevine were published in the early 1980s.[272-274] Therefore, this section will briefly review the effects of air pollutants on vines and present some more recent data on this subject.

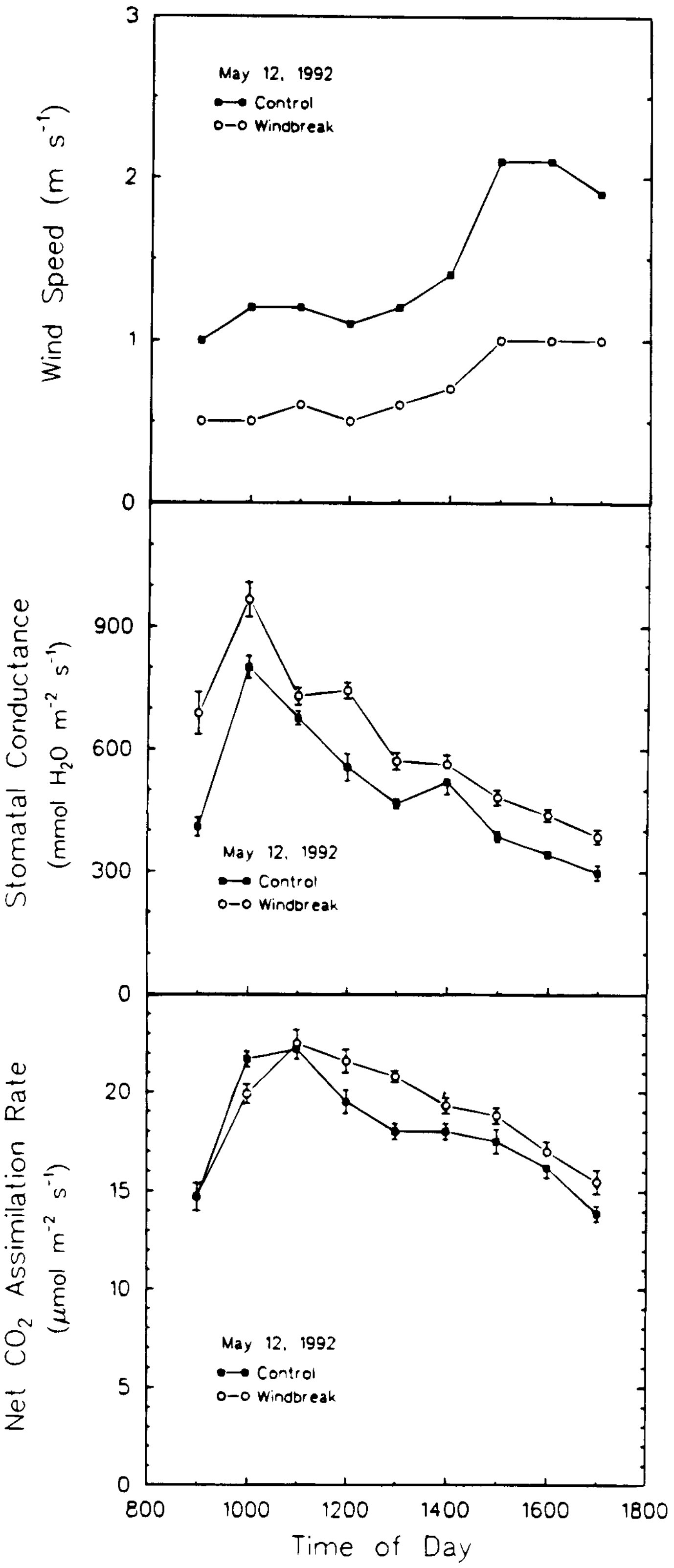

Figure 21 The effect of a windbreak on the diurnal time course of net CO_2 assimilation rate, stomatal conductance, and wind speed of 'Chardonnay' grapevines grown in the Salinas Valley of California. Control vines were exposed to ambient wind velocities. For an explanation of the windbreak see Table 3. Each value of A and g_s are the means of eight individual leaf measurements. Wind speed values are the hourly means of measurements taken every minute by a datalogger. (L.E. Williams, N.K. Dokoozlian, and L. Bettiga, unpublished data.)

Table 3 **The influence of windbreaks on the growth and yield of 'Chardonnay' grapevines grown in the Salinas Valley**

Treatment	Internode length (cm)	Shoot length (cm)	Individual leaf area[a] (cm^2)	Total vine leaf area (m^2)	Vine yield (kg)
Control	3.3	62	77	8.5	6.8
Windbreak	4.6	99	112	11.7	7.6

Note: The windbreak consisted of 50% density shade cloth surrounding seven vines. The shade cloth extended from the soil surface up to 3.05 m into the air. Each plot was replicated eight times.

[a] These values represent the area of individual leaves from the primary shoot. Leaves from lateral shoots are not included.

From Dokoozlian, N. K., Bettiga, L., and Williams, L. E., unpublished data.

Airborne pollutant injury to grapevines was first reported in France early in the Twentieth Century.[272] Pollution injury in the Western Hemisphere was first reported to occur in the 1950s in Southern California.[275] Since those times there have been numerous reports of air pollution affecting grapevines in vineyards throughout the industrialized world. Exposure of grapevines to air pollutants results in foliar symptoms as these molecules are taken up through the stomata.[276] Symptoms of pollution injury may vary among cultivars and might be confused with mineral nutrient deficiencies or toxicities. Exposure of grapevine leaves to ozone results in small patches of necrotic tissue surrounded by healthy green tissue and is termed 'Oxidant stipple'.[275] These lesions are localized in the palisade tissue of the leaf. Severe injury will result in chlorosis, bronzing, and premature leaf senescence and abscission. Older leaves are more susceptible to O_3 than younger leaves.

There is evidence of tolerance to airborne pollutants by native *Vitis* species, various cultivars of *V. vinifera*, and some French and American hybrids.[272] Tolerance is based upon foliar symptoms. For example, it was found that grape oxidant stipple (symptom of ozone exposure) was more prevalent on 'Carignane' and 'Grenache' than on 'Zinfandel' and 'Thompson Seedless'.[275] Similar categories have been established for susceptibility to hydrogen fluoride and sulfur dioxide.[272] Unfortunately, foliar symptoms of grapevines in response to air pollutants are dependent upon concentration and dose of the particular pollutant, stage of shoot development, leaf age, and cultural practices. Thus, there is some disagreement among studies with regard to the tolerance classification of individual cultivars.

Ambient partial pressures of O_3 (12-h mean 50 to 60 μPa Pa^{-1}) will reduce grapevine A anywhere from 5 to 13%.[41] The authors concluded that reductions in A were due to an O_3-induced decline in g_s which resulted in decreased C_i. This differs from the findings of Shertz et al.[277] who found that stomata of grapevine were opened by exposure to O_3. Studies on other plant species have shown ambient partial pressures of O_3 will reduce g_s to a greater extent than mesophyll conductance.[278,279] Even O_3 partial pressures greater than ambient levels significantly reduced g_s while having no significant effect on grapevine A over a 5-h fumigation period.[41] The exact mode of action of O_3 on grapevine g_s is unknown. ABA may be produced in response to pollutant exposure.[280,281] As discussed previously, the reduction in grape A when ABA is taken up is due solely to its effect on g_s and results in heterogeneous stomatal closure.[166] Heterogeneous stomatal closure in response to ozone fumigation has been shown on other plant species.[282] The symptoms of O_3 damage in grape leaves, oxidant stipple, would be consistent with heterogeneous stomatal closure upon exposure to this air pollutant. Stomata which remain open allow ozone to diffuse into the mesophyll and may result in acute damage to cells; stomata which remained closed would ostensibly protect the tissue from damage.

Most studies characterizing the effects of air pollutants on growth and productivity of grapevines have been conducted on container-grown plants.[272] However, there have been three studies conducted in the field assessing the effects of ambient oxidants (O_3) using open-top chambers. The chambers are constructed around mature vines and then either charcoal-filtered air or ambient air is forced through the chambers and out the top. Studies conducted on 'Zinfandel'[283,284] and 'Thompson Seedless'[285] grapevines in California, indicate that ambient pollution reduced pruning weights ca. 25 and 12%, respectively, compared to the charcoal-filtered controls. A study conducted on 'Concord' vines in New York found no significant effects of ambient oxidants on vegetative growth although there was a trend for less growth in the ambient air chambers.[286,287]

Thompson and co-workers[283,284] found that yields of 'Zinfandel' vines exposed to ambient air were reduced 12 and 61% when compared to vines in the charcoal-filtered chambers in the first and second years of the study, respectively. Yields of 'Thompson Seedless' were reduced 28 and 17% after the second and third years of exposure to ambient oxidants, respectively.[285] The number of clusters per vine was the yield component affected most for 'Thompson Seedless'.[285] It appears that O_3 exposure affects the differentiation of clusters within the compound bud; however, it is unknown whether O_3 directly affects the differentiation of cluster primordia or indirectly affects the process via a reduction in available vine carbohydrates due to a reduction in A.

Berry weight and the accumulation of soluble solids within the fruit of 'Zinfandel' were reduced due to exposure of vines to ambient oxidants.[283,284] Apparently, the reduction in A on both a single leaf basis[41] and whole vine basis (foliage levels estimated) reduced the amount of photosynthate available for growth of the fruit. In addition to a reduction in A, premature leaf abscission and loss of effective leaf area due to toxic levels of O_3 can cause a reduction in plant biomass.[288]

Sulfur dioxide injury results in grayish-brown lesions along the margins or tip of the leaf with middle-aged leaves most susceptible.[272] The first symptom of fluoride injury is a gray-green color at the margins of young leaves which then becomes brown or reddish-brown in color.[272]

The effects of sulfur dioxide and hydrogen fluoride on grapevine productivity is less clear.[272] Sulfur dioxide and ozone may exert a synergistic effect on vine physiology.[289] Reduced yields due to exposure to hydrogen fluoride may depend less on the degree of foliar injury than on characteristics of exposure over one or more growing seasons and stage of vine development.[272]

There have been no studies assessing the effects of air pollutants on the post-harvest storage of fruit used for table grapes (fresh market). This is crucial as appearance and storeability are important quality characteristics of table grapes. Crisosto et al.,[290] found that elevated partial pressures of O_3 decreased wax deposition and cuticle thickness of plum fruit (*P. salicina*, cv. Casselman) and the highest O_3 partial pressures resulted in a greater weight loss. Unfortunately, no data are available for grapevines.

VI. SUMMARY

The world-wide distribution of grapes (*Vitis* sp.) attests to the large genetic diversity both across the genus and within a species. The diverse climates, under which grapevines are grown, has resulted in a remarkable selection of cultivars that meet a variety of uses. Fortunately, there has been a minimum of "gene pool" reduction within the *Vitis* genus which will provide opportunities for grape breeding programs in the future.

Although there are several commercially-grown species, *V. vinifera* constitutes the majority of the acreage in the United States and around the world. The major limitations in the distribution of *Vitis* are low temperatures, seasonal heat accumulation, and water availability. Despite the fact that low temperature stress is the predominant limitation to the distribution of grapevines, little is known about the acclimation and deacclimation processes that are important for continued production in geographically and climatically extreme areas. For *V. vinifera*, high temperatures are clearly not a limiting factor and this species may have some unique characteristics as a crop plant in this regard. This species is also very tolerant to drought stress although irrigation may improve vine productivity.

A major theme present throughout this chapter is the mechanism by which grapevine leaves respond to various environmental stresses. It has been documented that heterogeneous stomatal closure in the leaves of grapevines occurs due to applied ABA, increases in VPD, soil water deficits, and salinity. A similar response may occur when grapevines are exposed to air pollutants and wind. It is tempting to suggest a causal relationship between the accumulation of ABA in grape leaves and the vine's response to environmental stresses as ABA causes heterogeneous stomatal closure.[166] Interestingly, a recent study has shown that ABA accumulates in the leaves of grapevines and grape callus tissue in response to high temperatures.[291] The authors suggested that ABA may be a factor in high-temperature acclimation and heat-tolerance induction in grape.

While the involvement of ABA in mediating environmental stresses at the leaf level in grapevines is apparent, other phytohormones may also play a role.[292] This is exemplified in the data from Table 2. It was demonstrated that the application of GA_3 at berry set of the seedless cultivar, 'Thompson Seedless', was able to overcome the negative effects of soil water deficits on berry growth. Further studies are needed to clarify how stress affects phytohormones in grape and other horticultural fruit crops.

Temperature extremes and fluctuations and availability of water will determine in large part the global distribution of species and cultivars of grapevines used for commercial purposes. However, it is possible to manipulate a vine's microclimate with the use of various training and trellising systems. While temperature, VPD and wind are ameliorated to some degree by the use of these cultural practices, it is the light microclimate within and at the surface of the canopy that is most impacted by training and trellising systems. Beginning with the pioneering work of Shaulis and co-workers, great advances have been made regarding our understanding of the effects of irradiance on vine growth, productivity, and fruit composition. Much attention has also been given to canopy management practices such as basal leaf removal and shoot positioning, for the improvement of the canopy's light environment.

Although some uncertainty remains regarding the location of the photoreceptor responsible for the regulation of bud fruitfulness, it is generally believed that irradiance received directly by the bud governs cluster initiation. Existing evidence suggests that light quantity rather than quality regulates fruit bud differentiation. Recent work also has revealed that many aspects of grape berry growth and composition are regulated by light and that the photoreceptors are located in the fruit. Much speculation has centered around the involvement of phytochrome for the photoregulation of berry metabolism. Again, it has been shown that light quantity rather than light quality is responsible, suggesting that chlorophyll or the putative blue light photoreceptor cryptochrome, may be involved in the regulation of grape berry growth. The elucidation of the exact location and nature of the photoreceptor(s) regulating vine growth and metabolism should be of high priority for future research.

Further improvements in vine productivity and fruit quality may only be possible by increasing our basic understanding of the interactions of solar radiation interception by the vine and other environmental factors. Therefore, future studies in viticultural research must be conducted under a wide variety of vine training and trellising systems in contrasting mesoclimates. With this knowledge and a subsequent expanded database, modelling vine performance will be enhanced, and the use of expert systems in viticulture will become common place.

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