Fruit Ripening in *Vitis vinifera* L.: Responses to Seasonal Water Deficits

MARK A. MATTHEWS[1*] and MICHAEL M. ANDERSON[2]

The response of fruit ripening to vine water status was investigated in a hillside Cabernet franc vineyard in the North Coast region of California. Treatments were imposed by drip irrigation at 2 X the standard practice rate (continual) to maintain high water status, by withholding water before (early deficit) or after (late deficit) veraison, or by withholding water throughout most of the season (full deficit). Midday leaf water potential of continual vines decreased from approximately –0.3 MPa before bloom to –1.13 MPa at veraison and to -1.32 MPa at harvest. Leaf water potentials of early deficit and late deficit vines were approximately 0.3 MPa more negative than continual vines at veraison and harvest, respectively. After veraison, water status of early deficit vines recovered to the level of continual vines. These moderate differences in water status at different phenological stages altered fruit composition at harvest. The concentrations of phenolics in juice and dermal extracts and of anthocyanins in dermal extracts were increased by all treatments which withheld water. Malate concentrations were significantly lower in treatments which imposed low vine water status before veraison. Low vine water status after veraison increased proline concentration significantly. There were no treatment effects on the onset of veraison, the duration of ripening, juice pH, or potassium levels, and little difference in °Brix or titratable acidity. Thus, irrigation to obtain seasonal water deficits may offer a cultural control of winegrape composition without significant effects on the time required to reach maturity.

KEY WORDS: water stress, irrigation, malate, proline, phenolics, potassium

The North Coast region of California is recognized for the production of premium winegrapes. In this region, many vineyards are irrigated weekly, while others are totally dependent upon stored soil water. Plantings have expanded from the valley floors, where soils are often of adequate depth and some growers have ample irrigation water, to the hillsides where soils are shallow and reservoirs limited. Hence, the water status of vines is likely to vary among vineyards and during the season.

It is clear that water status affects a myriad of plant functions (4). The importance of understanding physiological responses to water status is magnified in wine grapes, where the composition of fruit challenges yield as the primary parameter of productivity. However, there are no reports of vine responses (*e.g.*, growth or fruit composition) to irrigation or to vine water status in North Coast vineyards. Indeed, the role of vine water status in determining the reproductive development and composition of winegrapes is, in general, not known (27,33). Therefore, this study was conducted to determine the extent to which reproductive development, including the ripening process, is sensitive to vine water status. In this paper, we report that the levels of selected juice solutes of potential importance in winemaking respond differentially to seasonal water deficits.

[1,2]Department of Viticulture and Enology, University of California, Davis, CA 95616-5270.

*Author to whom correspondence should be addressed.

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Materials and Methods

The site of the study was selected for its shallow, light soil (gravelly loam), southwestern aspect, premium winegrape variety, and vine uniformity. Six-year-old vines (*Vitis vinifera* L., cv. Cabernet franc on Ganzin (A × R1) rootstock) in a commercial hillside (approx. 20% grade) vineyard near Saint Helena, California, were cultured and irrigated as previously described (15). Briefly, irrigation was supplied weekly by a drip system at approximately 45 L/vine in the standard practice treatment (SP) and at 90 L/vine/week in all other treatments. In the SP and continual (C) treatments, water was supplied throughout the season. Water was withheld before veraison in the early deficit (ED) treatment, withheld after veraison in the late deficit (LD) treatment, and applied twice (2 wk) before veraison and twice (2 wk) before harvest in the full deficit (FD) treatment. The total volume of water applied per vine was approximately 320, 640, 730, 820, and 1500 L in the FD, ED, SP, LD, and C treatments, respectively. No measureable rain occurred during the treatment period in any season. (Total evapotranspiration during the growing season for a full-canopied vineyard can be estimated roughly from the work of Pruitt *et al.* (23) as 3000 L/vine during treatment application). Treatments were applied to three-row × seven-vine plots. Data were collected only from the middle five vines of the middle row. Each treatment was replicated five times.

Midday leaf water potential was determined with a pressure chamber as previously described (15). Two or three leaves per replicate plot were sampled; a total of 10 to 15 leaves were used to estimate treatment water potential for each sample date.

The air temperature at a central, internal site in

individual clusters was determined by carefully inserting a long (10 cm) thermistor probe into representative basal clusters without damage to berries. Ambient temperature within the canopy was determined with similar sensors suspended near the cluster with an internal probe. Sensors were read several times throughout the day (day 200, approx. veraison).

Berry samples (approx. 125), comprised of berries representing each vine and all positions on the shoots and within clusters, were obtained biweekly from each plot. Subsamples (100 berries) were wrapped in double-layer cheesecloth and crushed with a small hand press. The resulting juice was centrifuged at 3000 *g* for two minutes to remove debris. Aliquots of the supernatant were retained for immediate analysis of pH, titratable acidity (TA) by titration with NaOH (9), and soluble solids by refractometry (1). Potassium was determined by emission spectroscopy. The remaining juice was immediately frozen and stored for further analysis.

After thawing to lab temperature, aliquots of juice were taken for determination of malate, proline, and soluble phenolics. Malate content was determined enzymatically according to Hohorst (10). Proline was determined with ninhydrin from the A_{520} as described by Ough (19). Total phenolics were estimated using the methods of Singleton and Rossi (25) as modified by Slinkard and Singleton (26). Gallic acid standards included glucose and fructose (1:1) at concentrations equivalent to °Brix of the juice samples to avoid overestimates of phenols caused by the positive reaction of sugars with the alkaline Folin-Ciocalteu reagent (25).

Disks of dermal tissue (0.20 cm^2) were removed from 10-berry subsamples with a cork borer. Anthocyanins were extracted with acidified methanol and estimated from the A_{535} according to Kliewer (13). Total phenolics of skin extracts were estimated from the A_{280} using gallic acid standards. Precipitation with trichloroacetic acid had no measureable effect on absorbance; no correction was made for chlorophyll absorption.

Fruit growth was determined by repeated determinations of berry diameter with a hand-held micrometer as previously described (15). Berry volume was calculated assuming a spherical berry. In order to determine berry water content, five-berry subsamples were weighed, frozen, and lyophilized until no further decrease in weight was observed.

Results

Midday leaf water potential (Ψ) was approximately −0.30 MPa in all treatments at the onset of the experiment (Table 1). Vine water status declined until veraison in all treatments, but more in ED vines than in other treatments. At veraison, Ψ was greater than -1.20 MPa in C and LD vines, but was −1.43 MPa in ED vines (Table 1). Thereafter, Ψ was relatively stable in C vines, but decreased in FD and LD vines (which had water withheld after veraison) and increased in ED vines (which had water supplied after veraison). Ψ declined more after veraison in LD vines than in FD vines (Table 1). At harvest, Ψ was highest in ED vines and lowest in LD vines (Table 1). Thus, withholding water during different phenological stages (*i.e.*, before and after the onset of ripening) created significant deficits in plant water status in comparison with C vines. The ripening consequences of these differences were the focus of the following measurements.

Table 1. Midday leaf water potential at early, mid-, and late season of vines receiving various irrigation treatments (described in **Materials and Methods**). Budbreak occurred at approximately day 75. Data are means of 10 to 15 samples per treatment. The standard error of the mean never exceeded 0.10 MPa.

Treatment	Julian date 106	200 (veraison)	242 (harvest)
	Midday leaf water potential		
Standard practice	-0.29	-1.18	-1.35
Continual	-0.29	-1.13	-1.32
Early deficit	-0.31	-1.43	-1.24
Late deficit	-0.31	-1.18	-1.64
Full deficit	-0.30	-1.23	-1.48

Diurnal measurements of the cluster interior air temperatures were conducted during fruit ripening. No differences among treatments in cluster temperatures or between ambient air temperatures and cluster temperatures were observed until afternoon. Readings at 1300 (Table 2) and 1600 hours indicated slightly higher temperatures in the vines which had been exposed to preveraison water deficits, but no differences were greater than 1.5°C at any sample time. Cluster temperatures did not increase measurably when clusters were exposed to direct sunlight by restraining the foliage throughout the diurnal measurement period.

Table 2. Midday (1300 h) cluster temperature and internal canopy ambient temperature in plots receiving different irrigation treatments. Values are the mean of two samples (clusters) in each treatment.

Treatment	Interior air temperature (°C) Cluster	Canopy
Continual	32.4	33.1
Late deficit	31.5	32.5
Early deficit	32.9	32.4
Full deficit	33.1	32.7

Fruit growth responded to plant water status. At harvest, berry volume was significantly less in vines from which water was withheld than in C vines (inset table, Fig. 1). The volume of C berries was approximately 31% and 39% greater than LD and ED berries, respectively. In all treatments, berry water content decreased similarly throughout the season, reaching approximately 72% of the fresh weight at harvest (Fig. 1).

The double-sigmoid growth habit of the berry creates a minor complication in interpretation of differences in solute concentrations, since fruit ripening and growth occur simultaneously. A dilution of inorganic constituents (decrease in concentration) without a net loss thereof may occur in berries during Stage III growth. On the other hand, solute accumulation may

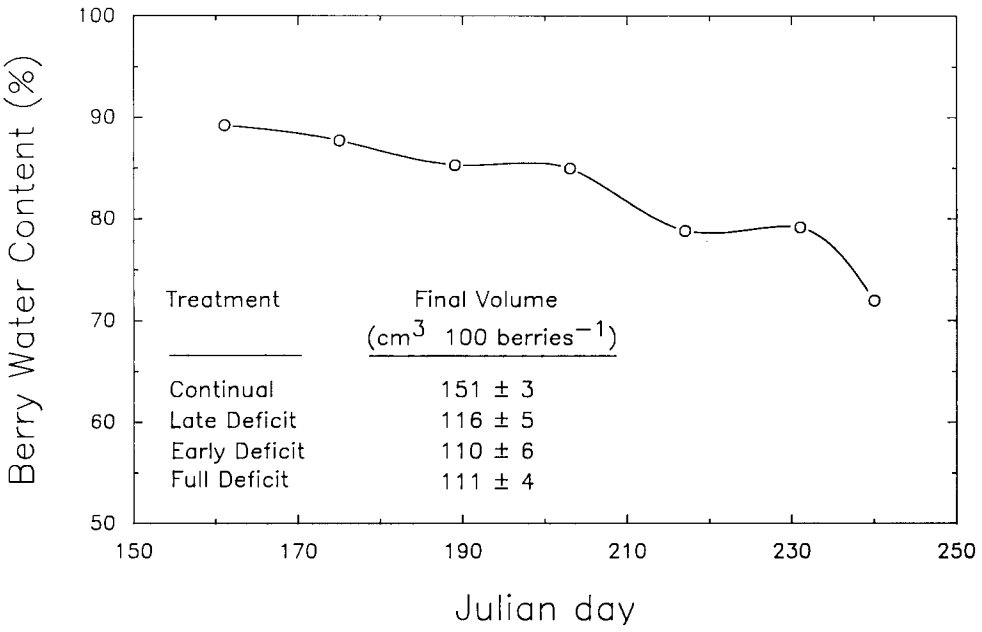


Fig. 1. Water content (% fresh wt) of Cabernet franc berries during ripening. Continual treatment shown only; other treatments exhibited the same pattern and were omitted for clarity. Final (harvest sample) water content was within 1.5% of 72% of berry fresh weight for all treatments. Inset table shows the final berry volume for vines receiving different irrigation treatments. Data shown are means ±standard error (n = 5).

occur during expansive growth despite a constant (or even decreasing) concentration. Consequently, juice composition was analyzed on the bases of concentration and content per berry. In most cases, the final juice concentration is the parameter of significance for wine-making and sensory attributes.

The rate of increase in sugar concentration was initially similar in all treatments but slowed near harvest in LD vines (Fig. 2). At harvest, the concentration of soluble solids was 22.0 ± 0.1, 21.9 ± 0.1, and 20.8 ± 0.3 °Brix (x ± s.e.m., n = 5) in C, ED, and LD treatments, respectively (Fig. 2). The final concentrations of soluble solids in FD and SP treatments (21.5 and 21.7°Brix, respectively) were intermediate to the ED and LD treatments. The amount of sugar in each berry was always greatest in the C vines, and this difference increased near harvest when the rate of growth (14) and accumulation of sugar per berry (inset, Fig. 2) slowed in ED and LD vines.

Juice TA increased slightly before and then declined approximately 10X after veraison in all treatments (Fig. 3). At veraison, the TA of ED vines was slightly greater than in treatments irrigated weekly (Fig. 3), although the difference was not statistically significant. In all treatments, the TA decreased significantly before an increase in soluble solids was detectable (cf. Fig. 2, 3). At harvest, mean TA was slightly lower in ED juice (0.37 mg tartrate equiv/100 mL, respectively). Final TA levels of FD and SP vines were intermediate and did not differ from other treatments. TA per berry followed a pattern similar to that of juice TA (inset, Fig. 3). All berries lost approximately 75% of the TA present before veraison, but TA per berry at harvest was significantly greater in C berries than in ED berries (inset, Fig. 3).

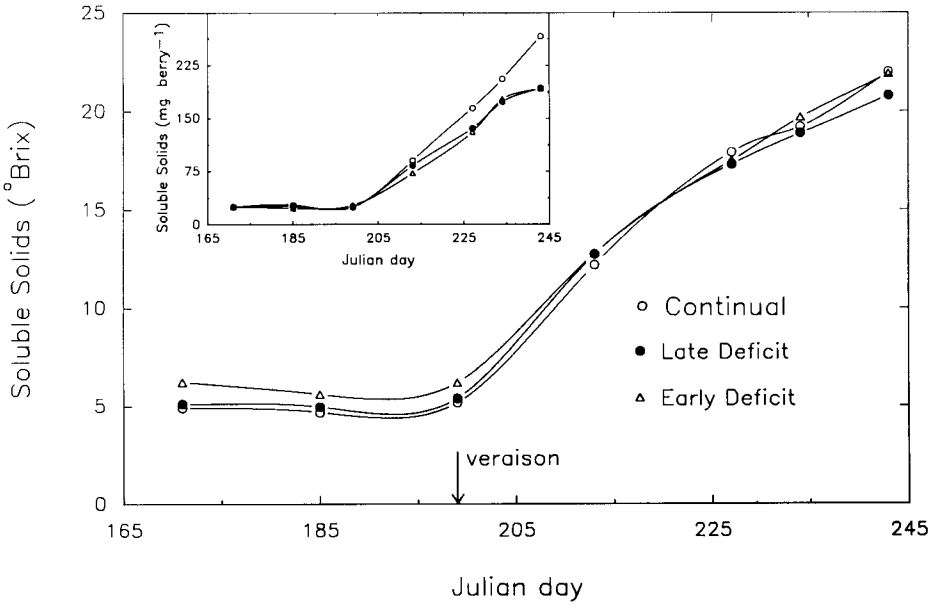


Fig. 2. Soluble solids (expressed as °Brix) in the juice at various times of the season for Cabernet franc vines which received different irrigation treatments during fruit development. There were no significant differences until the final sample date. Final °Brix given in text, except full deficit and standard practice treatments (not shown), which were 21.5 and 21.7 °Brix, respectively. Inset figure shows accumulation of soluble solids on a per berry basis. All data are means for the juice of 100-berry samples taken from each of 5 replicate plots.

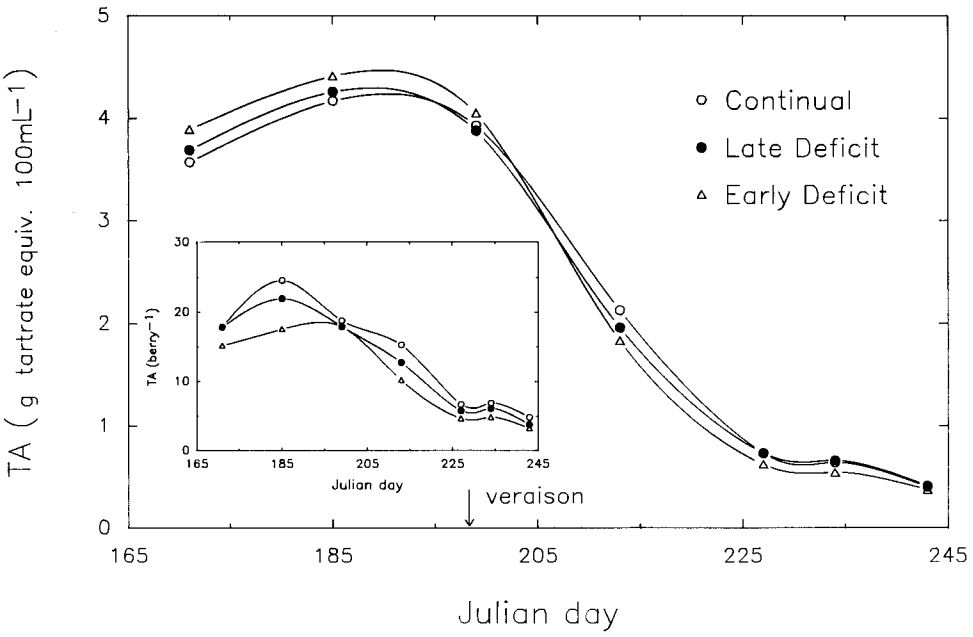
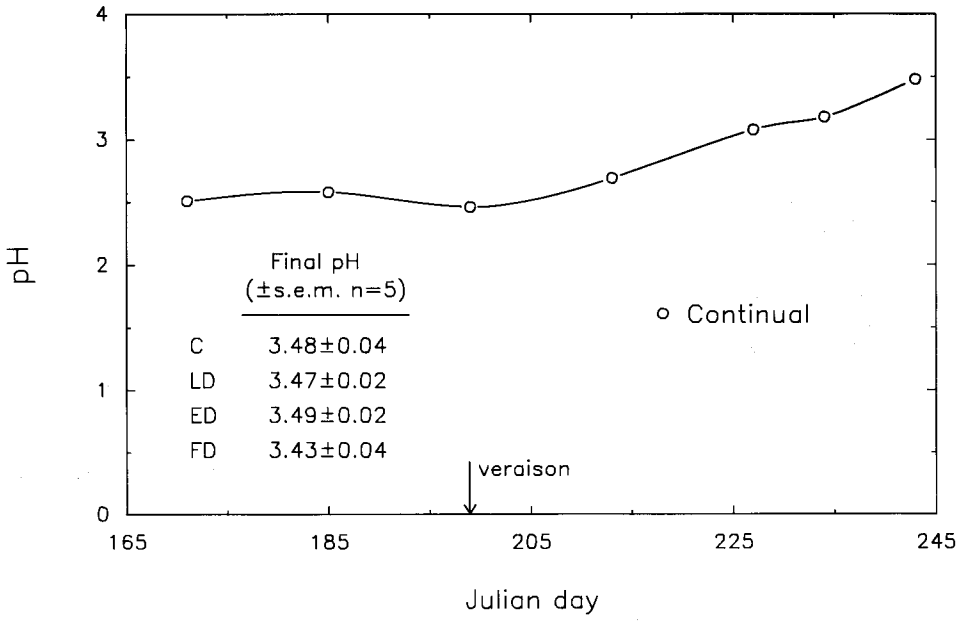


Fig. 3. Titratable acidity (TA) of juice at various times of the season from Cabernet franc vines which received different irrigation treatments during fruit development. There were no significant differences among treatments until the final sample date (see text). Inset table shows TA on a per berry basis at various times of the season. All data are means for the juice of 100-berry samples taken from each of 5 replicate plots.

Table 3. The concentration of malate, proline, and total soluble phenolics in juice and total soluble phenolics in dermal extracts for fruit of vines which received different irrigation treatments. Data are means ± standard error, n = 5.

Treatment	Malate (g/100mL)	Proline (mM)	Phenolics (gallic acid equiv.) Juice (μM)	Phenolics (gallic acid equiv.) Dermal (μmol/cm²)
Continual	0.19 ± 0.01	3.9 ± 0.2	0.88 ± 0.70	2.70 ± 0.14
Late deficit	0.16 ± 0.01	5.8 ± 0.6	1.19 ± 0.80	3.09 ± 0.11
Early deficit	0.12 ± 0.01	4.7 ± 0.6	1.14 ± 0.80	3.29 ± 0.24
Full deficit	0.11 ± 0.01	4.8 ± 0.2	1.17 ± 0.70	3.34 ± 0.08

Fig. 4. The pH of juice at various times of the season from Cabernet franc vines. Continual treatment shown only; other treatments exhibited the same pattern and were omitted for clarity. The inset table shows the final juice pH of vines which received different irrigation treatments during fruit development (C, continual; LD, late deficit; ED, early deficit; and FD, full deficit). All data are means for the juice of 100-berry samples taken from each of 5 replicate plots.



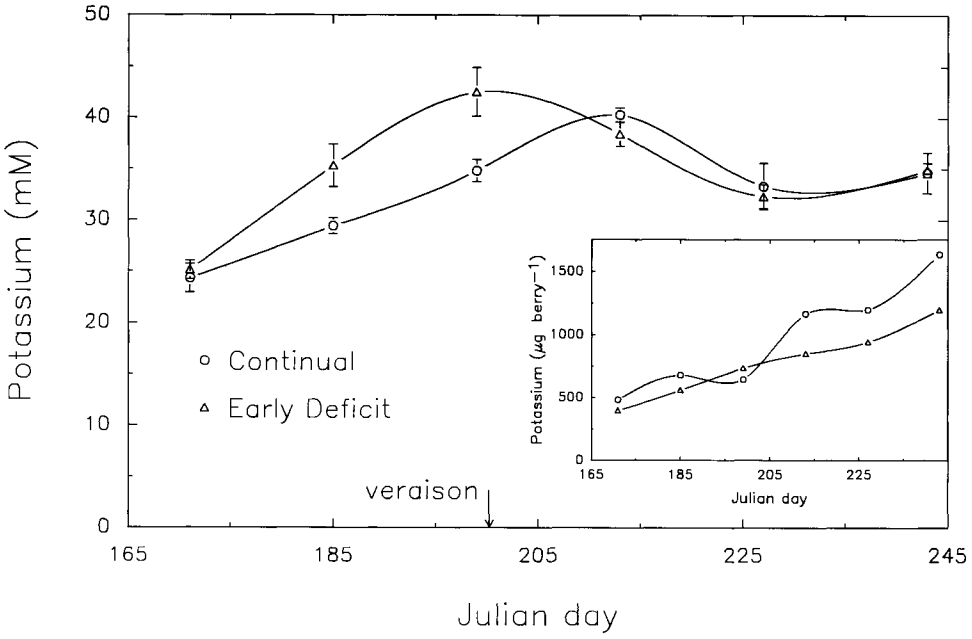


Fig. 5. The concentration of potassium in the juice at various times of the season from Cabernet franc vines which received different irrigation treatments during fruit development. Data from the late deficit, full deficit, and standard practice treatments were similar to the continual treatment and were omitted for clarity. Inset figure indicates the potassium content on a per berry basis. All data are means ± standard error (n = 5).

In contrast to TA, malate concentration was markedly dependent upon vine water status. At harvest, malate levels in juice were 0.19, 0.16, and 0.13 g/100 mL in C, LD, and ED vines, respectively (Table 3). Malate level was also low in FD vines (0.11 g/100 mL) and significantly less in ED and FD vines than in LD and C vines (Table 3).

The concentration of the primary cations in grape juice (H^+ and K^+) differed little among treatments. The pH of C juice at various times during ripening is shown in Figure 4 to indicate the seasonal pattern. The pH of juice was virtually identical and increased after veraison in concert in all treatments. Final juice pH did not differ by more than 0.06 pH units among the treatments (inset table, Fig. 4). There were no significant differences nor apparent trends among treatments.

Potassium concentrations in juice during ripening were also similar among treatments, increasing before veraison and decreasing after veraison until reaching a stable value *ca* 15 days before harvest (Fig. 5). There were no significant differences in K^+ concentration at harvest. However, K^+ concentration consistently increased more rapidly and peaked earlier in ED vines than in vines irrigated weekly until veraison, *i.e.*, C and LD treatments (Fig. 5). K^+ per berry increased throughout ripening in all treatments (inset, Fig. 5). The rate of increase was similar and relatively constant in ED and LD vines but was significantly greater in C vines after veraison (inset, Fig. 5).

The concentration of anthocyanins extractable from

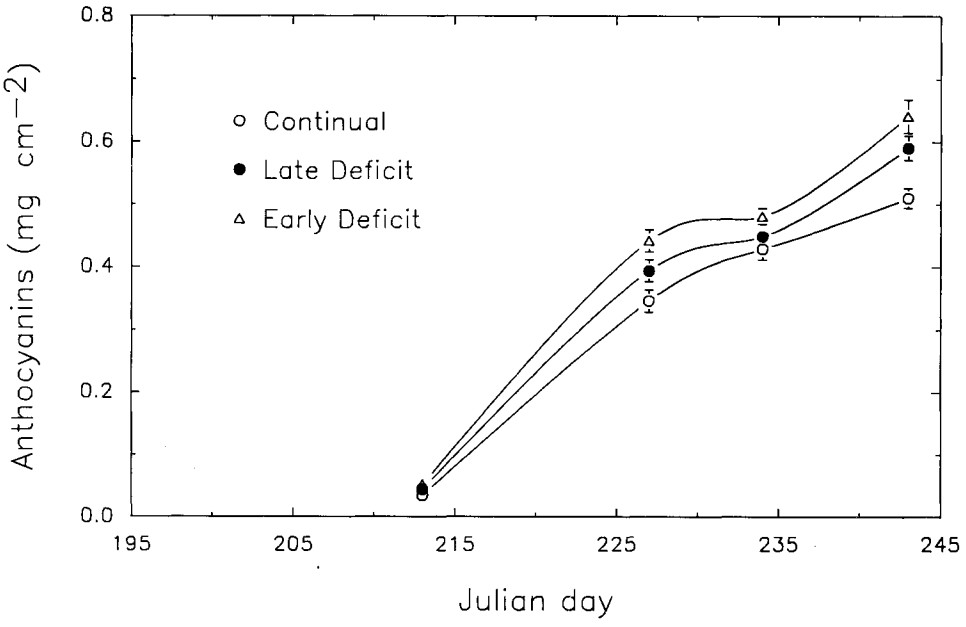


Fig. 6. The concentration (area basis) of anthocyanins extracted from dermal tissue of berries at various times of the season for Cabernet franc vines which received different irrigation treatments during fruit development. All data are means ± standard error (n = 5).

dermal tissue began to increase rapidly at approximately day 212 in all treatments (Fig. 6). During the subsequent 30 days, anthocyanins increased more than 10× (Fig. 6). The rate of increase during the initial 15 days was approximately 2× that of the final 15 days in all treatments (Fig. 6). Treatment differences were established during the initial 15 days of rapid increase in anthocyanin content when the increase in concentration was most rapid in ED vines and slowest in C vines (Fig. 6). Concentrations of anthocyanins at harvest were 0.51, 0.59, and 0.64 mg/cm^2 in C, LD, and ED vines, respectively (Fig. 6).

The concentration of total phenolics in juice and dermal extracts were increased significantly by withholding water at different times of the season. When water deficits were imposed before or after veraison, phenolic concentration at harvest was approximately 1.15 μ*M* (Table 3), whereas in C vines, phenolic concentration was *ca* 0.88 μ*M* (Table 3). Similarly, concentration of phenolics in dermal extracts of C vines was significantly less than in vines which experienced water deficits (Table 3). Phenolics in FD juice and dermal extracts were virtually identical to ED levels (Table 3).

The proline concentration in juice at harvest was least in C vines (3.95 m*M*), intermediate in ED vines (4.66 m*M*), and greatest in LD vines (5.76 m*M*) (Table 3). FD vines also had a significantly higher proline level (4.79 m*M*) than C vines. An exception to this occurred in 1985 when the proline level of C vines was greater than those of ED and FD vines (data not shown).

Discussion

The results show that vine water status was readily manipulated by altering the amount and timing of water applications to a drip-irrigated, hillside vineyard in Napa Valley, California. Differences in vine water status, established before and after veraison, led directly to differences in the size and composition of Cabernet franc winegrapes. Berry solutes sensitive to vine water status included organic acids, amino acids, anthocyanins, and total soluble phenolics.

°Brix, TA, and K were slightly higher in ED vines than in C or LD vines before veraison. This may have been due to the moderate preveraison water deficit having a greater effect on fruit growth than on fruit metabolism. Since TA was slightly lower in ED vines at harvest, the rate of acid loss was probably greater in ED vines (and somewhat slower in C vines) than in other treatments, although differences in fruit growth may confound this interpretation. The high malate concentration at harvest in C juice and low concentration in ED juice support this conclusion, since most of the acid lost during fruit ripening is malate (11).

The malate concentration at harvest was also low in FD juice, which indicates that preveraison water deficits decreased the final malate concentration independent of vine water status during fruit ripening. The pattern of decline in TA after veraison suggests that the differences in malate may have been due to differences in catabolism after veraison rather than to the malate level at veraison. These observations are relevant to vineyard management and winemaking decisions, since the large effect on malate and relatively small effect on TA suggest that early season water deficits result in increased tartrate to malate ratios. Van Zyl (29) clearly showed that the tartrate to malate ratio increased when water was withheld from drip- irrigated Colombar in South Africa. This may be important in determining the method of deacidification of musts with high TA (3) and in the stability of pH and TA during malolactic fermentations.

Although K uptake continued throughout fruit ripening treatments, K concentration increased before veraison and decreased slightly after veraison in all treatments. Thus, juice pH increased as K was decreasing. Coombe (5) also showed a decrease in K concentration from 17 to 26°Brix in Muscat Gordo. The responses of juice K and pH to seasonal water deficits were similar in that there were no treatment effects evident at harvest, although early-season water deficits caused a slight decrease in juice TA. Thus, under the conditions of this study, there appears to be limited potential to manipulate juice pH status with irrigation scheduling, whether via K uptake from the soil, K transport to fruit, or other mechanisms.

Similar results have been observed with other cultivars and experimental protocols (16,29,32). Although irrigation studies have shown increased (8,28) and decreased (17) juice pH as a results of supplemental irrigation, the effects have almost always been marginal. For example, significant differences were observed in one out of two years (27) or in one out of three years (8). Therefore, the general sensitivity of juice pH to vine water status is not high and may be site- and variety-specific.

The concentration of phenolics was dependent upon vine water status. Both early- and late-season water deficits resulted in phenolic concentrations in the juice and dermal extracts which were more than 30% and 15% greater, respectively, than in vines maintained at a higher water status throughout the season. At present, no assay of soluble phenolics can discriminate between phenols which impart bitterness and astringency and those that do not (31). Changes in phenolic concentration in the juice suggest that the nonflavonoid (24) phenolics, present predominantly in the vacuoles of the mesocarp cells (31), were particularly sensitive to vine water status. Sensory research has shown that the nonflavonoids contribute little to wine flavor (18,30). Hence, the differences in phenolics of dermals extracts, albeit less than in the juice, may be of greater importance to the sensory characteristics of the wine, since there is a high proportion of flavonoids in the phenolics of the dermal cells (2). The increase in phenolic concentration in the juice was similar to the decrease in fruit volume caused by low water status. However, the phenolic concentration in dermal extracts also increased when expressed on a surface area basis. These differences are of clear importance due to the prominent role

of phenolics in determining the color, bitterness, and astringency of table wines (24,31).

The observation of increased anthocyanin content in juice or wine in treatments which decrease (or were likely to have decreased) vine water status can now be considered commonplace (33). The results here indicated that color development was most rapid during the first two weeks after the onset of anthocyanin synthesis and that color development was more sensitive to vine water status in the early rather than late stages of the ripening process. The general response to water deficits and recognition of the importance of the early phase of fruit ripening in the synthesis of anthocyanins may facilitate improved winegrape production for cultivars and environments in which color production is a concern.

Proline is the primary free amino acid in the juices of many winegrape cultivars, including Cabernet Sauvignon, Merlot, Petit Sirah, and Zinfandel (12). Although there are no reports for Cabernet franc, it is likely that proline is also the primary free amino acid for this variety, since the amino acid profiles of the above varieties (which are similar to Cabernet franc) were very similar (12). Kliewer (12) showed that the concentration of proline in juice increases during ripening of many cultivars. In Cabernet franc, the proline concentration at harvest was higher in vines which were at low water status and lower in vines at high water status. However, withholding irrigation decreased the accumulation of proline in Carignane at Davis, California (8). The cause of the increase in proline concentration during ripening and of the different responses to low vine water status is not clear.

Proline is unlikely to play a direct role in fermentation or wine flavor, since proline is flavorless and is utilized only when other amino acids have become limiting (21). However, amino nitrogen clearly plays an important role in yeast growth during fermentation (20), and proline levels have been correlated positively with summed amino acid concentrations in ripening grapes (6).

There are several indirect mechanisms by which seasonal periods of low water status could alter fruit composition. The potential confoundment of water-status-induced differences in "crop load" (7,21) was effectively avoided by considering data from the initial season of the study only. It was only in the initial season, in which yields differed but due only to differences in berry size (15), that the cumulative effects of water deficits on reproductive development (14) could be avoided. However, the reported treatment differences in vine water status and fruit composition were observed in each of three seasons (with one exception, noted in **Results**).

Fruit size may be important in determining the extraction (dilution) of dermal cell contents, which are clearly the primary site of several important solutes for winemaking (5). Large diameter fruit would have a greater solvent (mesocarp cell sap) to solute (dermal cell sap) ratio as a result of the lower surface to volume ratio compared to smaller fruit. Hence, the inhibition of fruit expansion by water deficits may diminish the dilution of dermal solutes in the must.

The differences in fruit composition reported here are unlikely to be attributable to the simple inhibition of fruit expansion (decrease in solvent) or to an indirect effect of increased fruit temperature (due hypothetically to increased exposure of clusters to solar radiation). First, the levels of berry solutes did not change in one direction which would have been consistent with simple altered volume or temperature hypotheses. Components exhibited unchanged (°Brix, K), decreased (malate), or increased concentrations (phenolics, proline) as a result of low water status. Second, the direction of the change in solute concentrations was not always consistent with that predicted by these hypotheses. For example, although water deficits increased the concentration of proline, the proline concentration was not greatest in the ED or FD treatments, which had the smallest fruit and inhibited canopy growth (15). Also, the increase in phenolics in the treatments which experienced water deficits is inconsistent with an increased fruit temperature (18). Finally, we obtained little evidence of increased fruit temperature (at least at the cluster interior) as a result of water deficits, although small differences may have occurred.

Water deficits might also alter the onset or duration of the ripening period. Differences in vine water status before veraison had no effect upon the onset of veraison (15; Fig. 6). Withholding water after veraison eventually slowed the increase in soluble solids, but this effect was not evident until water deficits were maximal (shortly before harvest in the LD treatment). All treatments were harvested on the same date and were within 1.2°Brix. Smart and Coombe (27), citing studies with yield differences of up to 131% (irrigated compared to nonirrigated), suggested that the time required for ripening was inversely related to yield increases brought on by increased water status. In this study, the water status and yield of C vines were greater than those of other treatments (15), but there was no delay of fruit maturation in C vines compared to any treatment. Consequently, the differences in composition discussed below cannot be attributed to any general effect on the duration of the ripening period. There are evidently direct effects of vine water status on berry metabolism during ripening.

The water deficits encountered in the LD treatment were at the margin of that which would significantly delay fruit maturation. However, it may be important to note that the increase in soluble solids was not delayed in FD vines which received much less water than LD or other vines. Consistent with this observation was the lower water status of LD vines compared to FD vines at harvest (Table 1). This suggests that the water deficits created by supplying water at a relatively high rate before veraison and withholding water after veraison

were near the maximum achievable in that vineyard. This also demonstrates the importance of quantitating vine water status in investigations of vine responses to water deficits, since LD vines received more than twice the total amount of water applied to FD vines.

The developmental period during which water deficits were imposed selectively determined the solutes affected. Therefore, in vineyards in which vine water status is sensitive to irrigation, irrigation scheduling offers the grower an opportunity to control the composition of the raw material and, hence, of the product wine. However, these results relate fruit composition to vine water status only. The irrigation scheduling required to obtain various vine water statuses in different mesoclimates has not been addressed. It may also be important to note that although some of the compositional responses to water deficits shown here may be perceived as positive, inhibition of floral development may be a simultaneous consequence of low water status.

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