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Differential effects of shading fruit or foliage on the development and composition of grape berries

by

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Effets différentiels de l'ombrage du fruit ou du feuillage sur le développement et la composition des baies de raisin

Résumé : Pour étudier les effets respectifs de l'ombrage des grappes ou du feuillage sur la croissance du fruit et l'accumulation des sucres, anthocyanes, malate, tartrate et potassium dans le fruit, des portions de vignes (*Vitis vinifera* L. cv. Cabernet Sauvignon) ont été ombragées à l'aide de toiles de polypropylène. La croissance du fruit est retardée et réduite par l'ombrage du feuillage, qui affecte aussi la séquence et l'intensité de l'accumulation des sucres. La quantité totale de sucre par baie de raisin est comparativement plus réduite par l'ombrage que la concentration en sucre à cause de l'effet simultané de l'ombrage sur la taille du fruit.

Le taux d'accumulation de malate avant véraison, la quantité maximale de malate à la véraison et le taux de réduction de malate dans les baies après véraison sont les plus élevés dans les vignes entièrement exposées au soleil et diminuent à mesure que l'intensité de l'ombrage à l'intérieur de la vigne augmente. L'acide tartrique est significativement moins élevé dans le fruit des vignes ombragées que dans celui des vignes exposées. L'ombrage du feuillage est aussi correlé avec la concentration de potassium dans le fruit. A la récolte, le pH du jus est mieux correlé avec les concentrations d'acide tartrique et de potassium qu'avec la concentration de malate. Les grappes des vignes fortement ombragées ont le pH le plus élevé.

L'accumulation des anthocyanes est plus affectée par l'ombrage des grappes que par l'ombrage du feuillage. Le fruit ombragé contient significativement moins d'anthocyanes que le fruit exposé au soleil.

Key words: light, shading, leaf, bunch, berry, growth, maturation, sugar, acidity, tartaric acid, malic acid, anthocyanin, potassium.

Introduction

Factors controlling the development and composition of grape berries are multiple and complex. Even among clusters on a single vine and among berries within a cluster there is always a high degree of variability in berry composition and in stage of development. Differences in microclimate within the canopy are thought to contribute significantly to this variability (SMART *et al.* 1985). Light is one microclimatic variable that has been reported to affect grape development and composition (SHAULIS and SMART 1974). Artificial (KLENERT 1975; KLIEWER 1977) and natural shading (CRIPPEN and MORRISON 1986 a) were found to reduce concentrations of soluble solids in the fruit. The reduction in sugar concentration has been related to the effects of shading on berry growth (KLENERT 1974; CRIPPEN and MORRISON 1986 a). Shading also reduced anthocyanin content of pigmented varieties, even when shaded fruit was compared to sun-exposed fruit of similar sugar content (KLIEWER 1977; CRIPPEN and MORRISON 1986 b). Increases in potassium concentration and juice pH have also been correlated with shaded canopy microclimates (SMART *et al.* 1985). Although most work has concentrated on cluster microclimate, it has been suggested that leaf shading may play an important role in the compositional changes in fruit from shaded shoots (CRIPPEN and MORRISON 1986 a). The experiments reported here were designed to separate the effect

of shading clusters from that of shading foliage on the development and composition of grape berries.

Materials and methods

4-year-old Cabernet Sauvignon vines on A × R 1 rootstock were selected for uniformity of growth and bearing habit from a commercial vineyard in Oakville, CA. The vines were vertically trained such that little shading took place within the canopy. The experimental shading treatments were established 2 weeks after anthesis, using neutral polypropylene shade cloth (McAllister, Burbank, CA) attached to 30 cm crossarms on the trellis posts (Fig. 1). The four shading treatments included a totally exposed control (TE); a treatment in which fruit and surrounding leaves were shaded, but the upper 80 % of the canopy was exposed to sunlight (CE); a treatment in which fruit was exposed (FE) but 60 % of the foliage was shaded, with only the leaves at cluster level and the shoot tips remaining exposed; and an extreme shade treatment (TS), with both clusters and leaves shaded and only about 20 % of the canopy at the shoot tips receiving sunlight. Each treatment was replicated 4 times with 3 entire vines per replicate, randomly distributed in the block. Light incidence was measured continuously with 4 quantum sensors (LI-Cor 190SB, Lincoln, NE), and air and tissue temperature with thermistor probes attached to a micrologger (Campbell Scientific, Logan, UT). Light incidence under the shade cloth was approximately 8 % of ambient; the spectral distribution was not significantly altered by the shade cloth. Air temperature under the polypropylene was higher than ambient during the day (Fig. 2 A). Shading had less effect on fruit temperature, which was slightly higher in exposed fruit during the early part of the day, probably due to radiational heating, and higher in the shaded treatments in the afternoon, probably because of the higher air temperatures (Fig. 2 B).

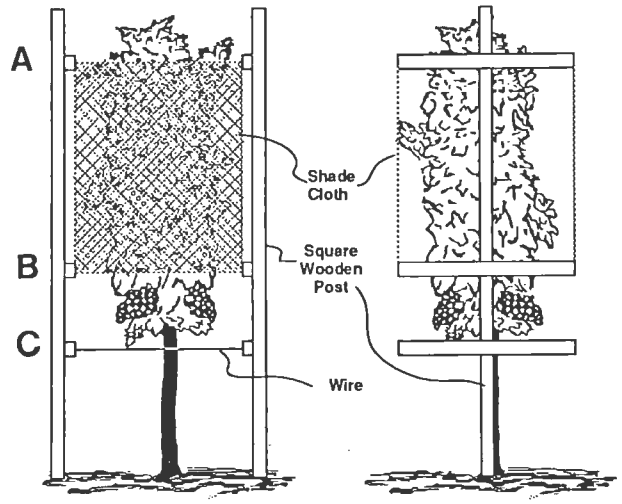

Fig. 1: Shading treatments used in this experiment. Left: view facing row; right: view from end of row. For leaf shading polypropylene cloth was attached to crossarms A and B; for fruit shading to crossarms B and C; for total shade to crossarms A and C.

Les traitements expérimentaux. Côté gauche: vue sur le rang; côté droit: vue du bout du rang. Pour ombrager le feuillage, les toiles de polypropylène sont attachées entre A et B, pour ombrager les grappes, entre B et C; pour l'ombrage total entre A et C.

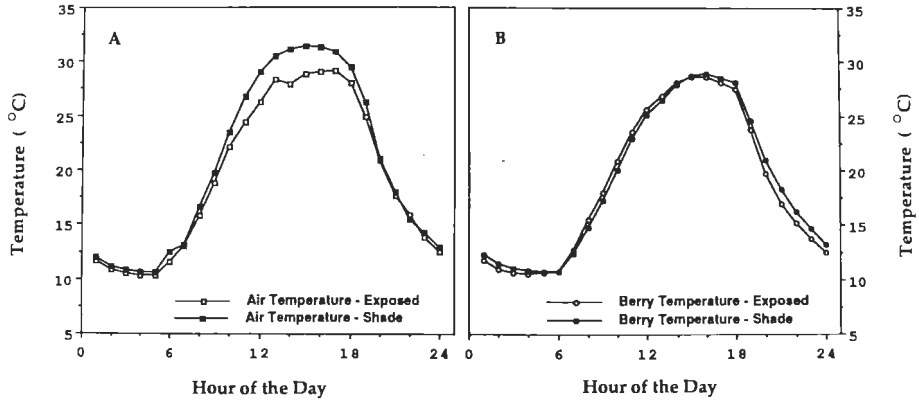

Fig. 2: Effects of the polypropylene shade cloth on air and berry tissue temperatures. Mean hourly temperatures for the month of July.

Effets des toiles de polypropylène sur les températures de l'air et des tissus. Températures moyennes pour le mois de juillet.

Berry sampling (4 replicates of 45 berries each) was done biweekly from 6 weeks after anthesis through commercial harvest. The berries were weighed, measured with calipers, then frozen until analysis. The thawed samples were homogenized in an Omni-Mixer (Sorvall, Norwalk, CT), then centrifuged (1000 *g*, 20 min). The pellet was extracted sequentially with 1N HCl (10 ml/g) and acidified 95 % ethanol (10 ml/g). Quantitation of glucose, fructose, tartaric acid and malic acid in the juice fraction and 1N HCl extract was by HPLC (Waters, Milford, PA), using the method of McCord *et al.* (1984). Potassium content of the juice fraction and the 1N HCl extract was determined by emission spectroscopy using a Perkin-Elmer model 2380 atomic absorption spectrophotometer (Perkin-Elmer, Norwalk, CT), following the method of Crippen and Morrison (1986 a). Anthocyanin content of juice, HCl and ethanol fractions was determined by absorbance at 520 nm at pH < 1 (Somers and Evans 1977). The juice and extract values were combined to give the total content of each component per berry. Titratable acidity of the juice fraction was determined by titration with NaOH to a pH 8.2 endpoint.

Data were analyzed by analysis of variance; Duncan's multiple range test was used for comparisons among treatment means. Polynomial regressions were performed for the data of berry weights and diameters.

Results

The period of rapid fruit growth accompanying veraison was delayed by approximately 2 weeks in the treatments with shaded leaves (FE and TS) compared to the treatments with exposed leaves (TE and CE). Growth rate curves for fruit from vines with shaded foliage had a more gradual slope (Fig. 3), indicating a slower, more prolonged growth period. Fruit from these treatments were still enlarging at commercial harvest. Growth rates were significantly different ($P < 0.01$) among treatments. Berry size was decreased in treatments with shaded foliage, but cluster shading did not significantly affect fruit size (Table 1).

Anthocyanin accumulation began 10 weeks after anthesis in fruit from the two treatments with exposed foliage and 12 weeks after anthesis in treatments with shaded

Table 1

The effects of shading on berry weight and diameter · Values followed by the same letter are not significantly different ($P < 0.05$)

Effets de l'ombrage sur le poids et le diamètre des baies · Les valeurs suivies par la même lettre ne sont pas différentes au seuil de 5 %

Treatment	Berry weight (g)		Berry diameter (mm)	
	8 weeks post bloom	16 weeks post bloom	8 weeks post bloom	16 weeks post bloom
Totally exposed (TE)	0.50 a	1.18 a	9.44 a	12.31 a
Canopy exposed (CE)	0.48 a	1.15 a	9.35 a	12.26 a
Fruit exposed (FE)	0.43 ab	0.99 b	8.92 a	11.70 b
Total shade (TS)	0.32 b	0.71 c	8.02 b	10.29 c

foliage. Leaf shading did not significantly affect anthocyanin content at maturity, however. At harvest, the two treatments with shaded fruit had significantly less anthocyanins than the exposed fruit, but there was no difference between the foliage shade and control treatments (Table 2).

The accumulation of sugar was also delayed by 2 weeks in treatments with shaded foliage (Fig. 4). Fruit from treatments with exposed leaves (TE and CE) were not significantly different from each other, but both had higher concentrations of sugars from veraison through harvest than the treatments with shaded foliage ($P < 0.05$). The concentration of sugars was higher in the totally shaded treatment than in the treatment

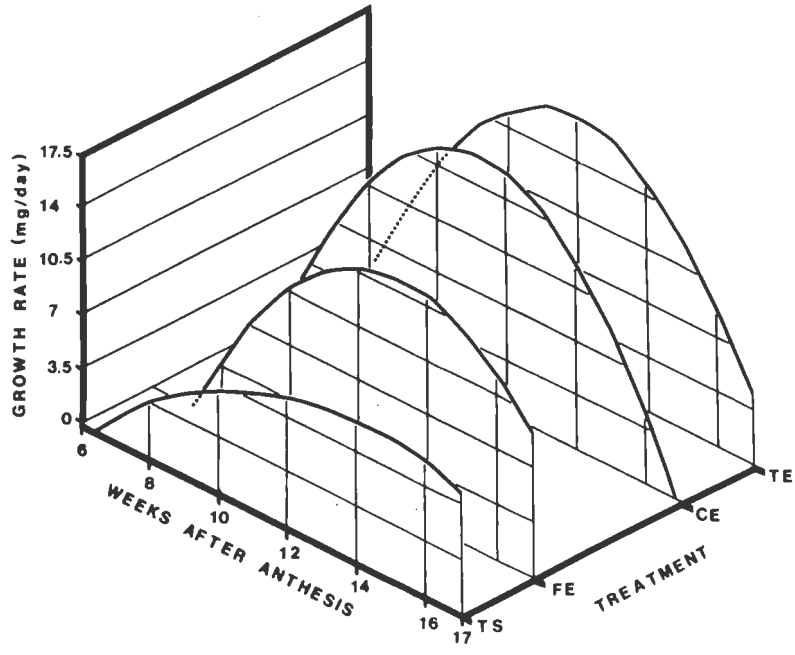

Fig. 3: Effects of foliage and cluster shading on berry growth rate.

Effets de l'ombrage du feuillage ou des grappes sur le taux de croissance des baies.

Table 2

Effects of shading on anthocyanin content of mature fruit · Numbers followed by the same letter are not significantly different ($P < 0.05$)

Effets de l'ombrage sur la quantité des anthocyanes des baies mûres · Les valeurs suivies par la même lettre ne sont pas différentes au seuil de 5 %

Treatment	Anthocyanins	
	mg/g fresh wt.	mg/berry
Totally exposed (TE)	1.59 a	1.80 a
Canopy exposed (CE)	0.95 b	1.01 b
Fruit exposed (FE)	1.57 a	1.49 a
Total shade (TS)	1.02 b	0.63 c

with exposed fruit (Fig. 4), even though the total amount of sugar per berry was lower (data not shown). The smaller berry size in the totally shaded vines contributed to the concentration differences.

The malate content of fruit from vines with exposed foliage (TE and CE) reached its highest concentration at color change, 10 weeks after anthesis (Fig. 5). The highest concentration measured for the exposed fruit treatment (FE) was also on that date, even though color change and the start of rapid sugar accumulation occurred 1—2 weeks later. The malate peak may have occurred between sampling dates for treatment FE. The totally shaded treatment (TS) reached its highest malate concentration at color change, 12 weeks after anthesis, which was 2 weeks later than the more exposed treatments. If the peak value of malate concentration is compared regardless of calendar date, treatment TE had the highest peak concentration of malic acid. Treatments FE and CE were not significantly different from each other, but the maximum concentration of treatment TS was significantly lower ($P < 0.05$), suggesting that malate synthesis was reduced in this treatment preveraison. During the period of rapid accumula-

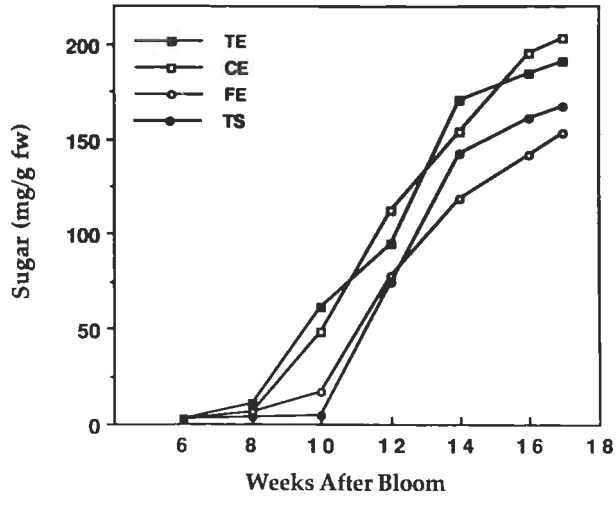

Fig. 4: Effects of foliage and cluster shading on the concentration of sugars in the ripening fruit.

Effets de l'ombrage du feuillage ou des grappes sur les concentrations des sucres dans le fruit.

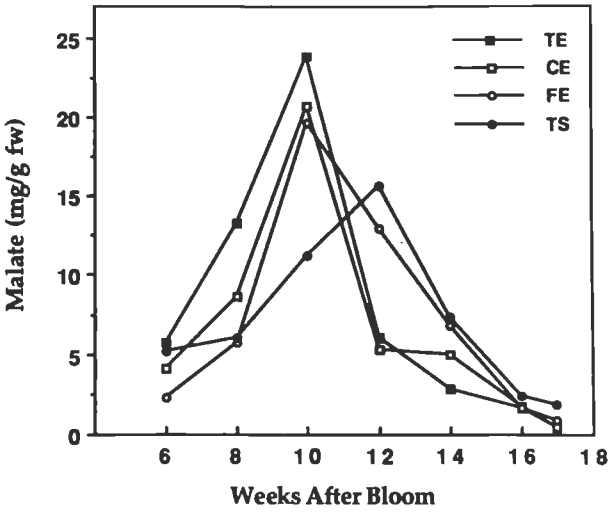

Fig. 5:Effects of foliage and cluster shading on the concentration of malate in the fruit during ripening.

Effets de l'ombrage du feuillage ou des grappes sur la quantité d'acide malique dans le fruit.

tion, fruit from treatment TS accumulated only 1.5 mg malate berry^{-1} week^{-1}, compared to rates from 3.5 to 4.0 mg berry^{-1} week^{-1} for the three more exposed treatments. At harvest, there was no significant difference between the two treatments with exposed foliage, but both were significantly lower ($P < 0.05$) than the shaded foliage treatments. Faster rates of malate decline (4.5 and 3.3 mg berry^{-1} week^{-1} in treatments TE and CE, respectively, compared to 1.0 and 1.2 mg berry^{-1} week^{-1} in FE and TS)

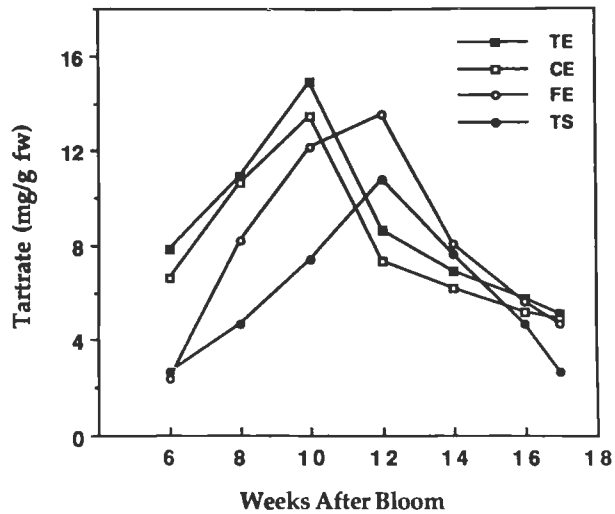

Fig. 6: Effects of foliage and cluster shading on the concentration of tartrate in the fruit during ripening.

Effets de l'ombrage du feuillage ou des grappes sur la quantité d'acide tartrique dans le fruit.

resulted in lower malate at harvest despite the higher maximum concentration at veraison in the exposed canopy treatments.

Tartaric acid concentrations were highest immediately before the rapid burst of growth at veraison in all treatments (Fig. 6). The decline in tartrate concentration after veraison was much slower than that of malic acid. When the same data were recalculated as tartrate per berry, there was little change during ripening, suggesting that the changes in concentration can be attributed to the dilution effect of berry growth. The partially shaded treatments were not significantly different in tartrate content from the totally exposed control, but were all significantly higher than the totally shaded treatment ($P < 0.05$).

Berry potassium content increased during the ripening period (Fig. 7). At harvest, the highest concentration of potassium was seen in fruit from the most heavily shaded treatment, and the lowest concentration in fruit from the totally exposed treatment, with the partially shaded treatments intermediate between the extremes. The higher potassium concentration in the heavily shaded vines may be partially due to the concentration effect of reduced berry growth, because the potassium content per berry was lower in treatment TS than in the more exposed treatments.

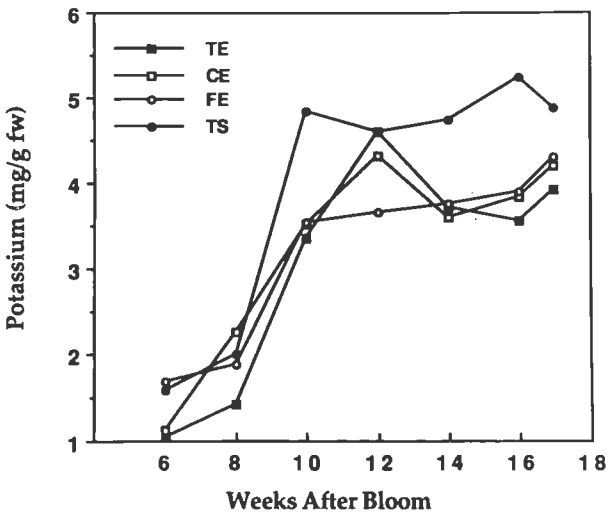

Fig. 7: Effects of foliage and cluster shading on the concentration of potassium in the fruit during ripening.

Effets de l'ombrage du feuillage ou des grappes sur la quantité de potassium dans le fruit.

Discussion

Vines with shaded foliage had smaller berries than exposed vines or those with shaded fruit, even though vines and clusters had been chosen for uniformity at the time of shading. The effect of shading on berry size is in agreement with KLENERT (1974). The two treatments with exposed canopies (TE and CE) did not differ in berry size at any time during the growing season, even though the fruit and approximately 20 % of the foliage were shaded in treatment CE. It would appear that above some critical level of canopy exposure additional sun interception has minor importance for fruit

growth, and that both of these treatments exceeded the critical exposure levels required for normal fruit development. The two treatments with shaded canopies were significantly different, both from the exposed canopy treatments and from each other. This suggests that both of these treatments were below the critical level of solar interception, and that under low light conditions the additional 20 % of the canopy shaded in treatment TS had an additional impact on fruit size. It is less likely that the differences between treatments FE and TS are due to an influence of fruit shading, because of the lack of response in treatment CE.

A high coincidence was found between the effects of leaf shading on the start of anthocyanin and sugar accumulation and on the start of the final stage of fruit growth. This is in agreement with KLENERT (1974, 1975) and ALLEWELDT *et al.* (1984), who similarly found that shading delayed both ripening and growth. The differences among growth rate curves suggest that both the pre-veraison and post-veraison growth periods may be prolonged under heavily shaded conditions.

Anthocyanin content was significantly reduced by cluster shading, but not by leaf shading. This is consistant with previous reports that anthocyanin content is reduced in shaded clusters (KLIEWER 1977), although sensitivity to shading varies with cultivar (KATOAKA *et al.* 1984).

The delay and the decreased rate of sugar accumulation with increased canopy shade is in agreement with KLIEWER and LIDER (1970), SHAULIS and SMART (1974), REYNOLDS *et al.* (1986), and others. The higher sugar content per berry in the exposed fruit treatment (FE) than in the totally shaded treatment (TS) despite a lower concentration suggests that the relatively few exposed leaves in the cluster zone in treatment FE made an important contribution, not only to berry size, but also to total sugar accumulation in these otherwise heavily shaded vines.

The faster rate of malate decline in the exposed canopy treatments is in agreement with KLIEWER and LIDER (1970), SHAULIS and SMART (1974) and REYNOLDS *et al.* (1986), who similarly reported decreased acidity under conditions of higher light exposure.

The decline in tartaric acid concentration was much slower than that of malic acid in all treatments and can be attributed to the dilution effects of berry growth. JOHNSON and NAGEL (1976) and CRIPPEN and MORRISON (1986 a) similarly found that tartrate content per berry changed relatively little during ripening, despite rapid decreases in malate. Unlike malic acid, which is an intermediate of primary metabolism, tartaric acid displays the behavior of an end product (SAITO and KASAI 1968) and can be considered a secondary metabolite (RUFFNER 1982 a). The relatively constant amount per berry after veraison suggests that either tartrate does not turn over after accumulation, or that the rates of synthesis and breakdown are essentially equal. Labelling studies have indicated a relatively static pool with little tartrate synthesis (SAITO and KASAI 1968) or turnover (HARDY 1968) during the ripening period.

SAITO and KASAI (1969) demonstrated that light was required for tartrate synthesis in grape berries, although malate was synthesized under both light and dark conditions. This suggests that the lower tartrate content in treatment TS was due to the influence of extensive shading on tartrate synthesis.

The higher potassium concentration in fruit from the heavily shaded vines is in agreement with SMART *et al.* (1985) and BLEDSOE *et al.* (1988), who similarly reported a negative correlation between potassium concentration and sun exposure. Potassium content per berry continued to increase throughout the ripening period, but was lower in treatment TS than in the more exposed treatments, suggesting that the higher concentration in treatment TS may partially be due to the concentration effect of reduced berry growth. STOREY (1987) similarly found that potassium concentrations were signficantly higher in the skin of small grape berries than in large berries.

BOULTON (1980) identified potassium as a major factor in determining the pH of wines and grape juice. In this study, juice pH was positively correlated with potassium concentration, and both potassium concentration and pH were highest in the most densely shaded treatment (TS). Both were also high in the shaded foliage treatment relative to the low sugar concentration at harvest. Other reports have similarly found a correlation between higher potassium concentrations and higher pH (SMART *et al.* 1985) in vines grown under shaded conditions. Our results suggest that the leaf shading in treatments FE and TS had more of an effect on potassium and pH than the cluster shading in treatment CE.

No consistent correlation was found between the concentration of sugars in the fruit and either juice pH or titratable acidity. The observation that excessive tartness is normally correlated with low sugar concentration (RUFFNER 1982 a) did not hold for the leaf shading treatments. This indicates that, in addition to the general delay in maturity observed under conditions of leaf shading, there were specific effects of shading on individual components contributing to juice pH and titratable acidity. Malate and potassium content appeared to be the compounds most affected, and both appeared to be influenced more by leaf shading than by cluster shading.

The results of the experiments reported here suggest that leaf shading and cluster shading had different effects on grape berry development. Leaf shading both delayed and reduced the rate of berry growth and sugar accumulation, while cluster shading had little effect on these processes. Cluster shading did significantly affect anthocyanin accumulation, which was little affected by leaf shading.

Summary

Grape vines (*Vitis vinifera* L. cv. Cabernet Sauvignon) were selectively shaded with polypropylene cloth to separate the effects of shading fruit from the effects of shading foliage on berry development and on the accumulation patterns of sugar, anthocyanins, malate, tartrate and potassium in the fruit. Shading the foliage led to both a delay and a decrease in berry growth. Leaf shading also affected the timing and the magnitude of sugar accumulation. Total sugar per berry was reduced more by shading than was sugar concentration because of the simultaneous effect of shading on fruit size.

The rate of pre-veraison malate accumulation, the maximum malate content at veraison, and the rate of post-veraison malate loss in the berries were all highest in the fully sun-exposed vines and were progressively lower with increasing foliage shade. Tartaric acid was significantly lower in fruit from heavily shaded vines than in fruit from the more exposed treatments. Leaf shading was also significantly correlated with an increase in potassium concentration in the fruit. At harvest, juice pH was more closely correlated with the concentrations of tartaric acid and potassium in the berries than with malate content. Grapes from heavily shaded vines had the highest pH. Anthocyanin accumulation in the fruit was affected more by cluster shading than by leaf shading. Shaded fruit had significantly less anthocyanin than sun exposed fruit. These results indicate that in addition to a general delay in ripening there were also specific effects of shading on individual components of berry composition, and that the specific effects were different for leaf and cluster shading.

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