The Effect of Partial Defoliation on Quality Characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon Grapes 1. Sugars, Acids and pH

J.J. Hunter[1], O.T. de Villiers[2] and J.E. Watts[2]

1) Viticultural and Oenological Research Institute (VORI), Private Bag X5026, 7600 Stellenbosch, Republic of South Africa
2) Department of Botany, University of Stellenbosch, 7600 Stellenbosch, Republic of South Africa

Submitted for publication: November 1990
Accepted for publication: February 1991
Key words: *Vitis vinifera*, defoliation, grapes, sugars, acids, pH

The effect was studied of partial defoliation (33% and 66%) on the sugar and acid accumulation and pH in grapes of *Vitis vinifera* L. cv. Cabernet Sauvignon. Although the total soluble sugar (TSS) in grapes of partially defoliated vines was significantly higher than that of non-defoliated vines in some cases, no significant differences were generally found. No significant differences in total titratable acidity (TTA) were found between treatments. The timing of defoliation had no effect on TSS in grapes, whereas TTA tended to be higher the earlier partial defoliation was commenced. In general, 33% and 66% defoliated vines respectively produced approximately 33% and 200% more TSS and TTA in the fruit per cm^2 leaf area than non-defoliated vines. No significant differences between defoliation treatments were found on a per gram dry berry mass or per berry basis for glucose and fructose or tartaric and malic acid. However, 66% defoliated vines had significantly less soluble solids in berries per shoot, which was probably caused by a lower total berry mass per shoot. Although no significant differences in sugar composition could be found between defoliation treatments, tartaric acid levels tended to be higher and malic acid levels lower as a result of partial defoliation. Partial defoliation had no effect on the accumulation patterns of sugars and acids. Glucose dominated in berries at véraison, with fructose dominating at ripeness. The highest total tartaric and malic acid concentrations occurred at pea size. Malic acid content decreased rapidly from véraison, whereas the decrease in tartaric acid was not pronounced. Must pH was not affected by partial defoliation. The results seem to suggest that the general metabolism of vines was favourably changed by partial defoliation, mainly in terms of a more favourable source: sink ratio, more efficient photosynthesis, and an improved canopy microclimate.

South African vineyards generally suffer from excessive vegetative growth. This results, among others, in disturbances in source:sink relationships, an increase in canopy density and an inferior canopy microclimate for the continuous maximum photosynthetic activity of leaves (Hunter & Visser, 1988a, 1988b, 1988c, 1989). These factors all interrelate and may detrimentally affect grape and wine composition in particular, resulting in, e.g., too low concentrations of sugar, tartaric acid and anthocyanins, and too high malic acid, potassium and nitrogen contents and must pH (Smart, 1982; Smart *et al.*, 1985; Smart, Smith & Winchester, 1988). According to Champagnol (1977) the quality of a harvest may be defined as its aptitude to yield a wine of quality, and this is dependent on the composition of the numerous constituents of berries.

Ethyl alcohol in wines is derived solely from the fermentation of sugars, and sugar concentration is the most important single measure of grape maturity. Sugars are therefore qualitatively the most important constituents of grapes (Amerine, 1956; Champagnol, 1977), with glucose and fructose the primary sugars (Kliewer, 1967b). Acids in wines favourably effect fermentation, flavour, colour, taste and ageing (Amerine, 1964). Tartaric and malic acids are the major organic acids in grapes (Kliewer, 1967b). Although malic acid contributes greatly to the acidity of musts, it posesses an aggressive, less desirable taste than tartaric acid. The disappearance of malic acid through malolactic fermentation is therefore favourable to quality and contributes organoleptically to the acceptability of fresh grapes and to must and wine quality (Philip & Kuykendall, 1973). Cleanness of fermentation and the colour, taste, and disease resistance of finished wines are strongly affected by pH (Amerine, 1956).

Leaves have the greatest effect on the constituents of grapes and should therefore be managed in such a way that their full potential is explored. Young leaves produce more organic acids, whereas mature leaves produce greater amounts of sugars. Tartaric acid is synthesized only by young leaves whose lamina are still expanding. Young as well as old leaves produce less sugar than mature leaves (Kriedemann, 1977). Leaf photosynthesis depends upon demand for assimilates. Reduced rates of utilization lower photosynthetic rates, an effect related to the accumulation of photosynthetic products in leaves (Wareing, Khalifa & Treharne, 1968; Koblet, 1984). Mesophyll resistance, the content of carboxylating enzymes, and competition between leaves for mineral nutrients and possibly specific hormones, as supplied by roots, may all affect photosynthetic activity (Wareing *et al.*, 1968) and thus an accumulation of photosynthetic products in grapes. At low light intensities Rubisco activity in leaves is highly regulated by feedback processes and probably quantum efficiencies of photosystems I and II (Woodrow & Berry, 1988). Light conditions in the canopy would therefore greatly affect the accumulation of photosynthates in sinks.

Partial defoliation, in an endeavour to alter grape composition favourably, has been widely applied. Different meth-

Acknowledgements: The technical assistance of A.J. Heyns, D.J. le Roux, W.J. Hendricks and L.M. Paulse is appreciated.

ods, levels and time of defoliation, however, led to divergent results. Some investigators found that partial defoliation increased total soluble solids and reduced titratable acidity, malic acid, pH and potassium levels in fruit (Wolf, Pool & Mattick, 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). Others, however, either failed to demonstrate any significant effects on grape composition (Koblet, 1987; Williams, Biscay & Smith, 1987) or even found a reduction in total soluble solids (May, Shaulis & Antcliff, 1969; Kliewer, 1970; Kliewer & Antcliff, 1970; Sidahmed & Kliewer, 1980). The timing of leaf removal had no significant effect on fruit composition (Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). Sugar concentration was, however, slightly higher with early defoliation, as opposed to later defoliation (Koblet, 1987; Kliewer *et al.*, 1988).

In general, studies dealt mainly with the effect of selective defoliation in canopies in which normal translocation patterns within shoots were most probably disturbed. Recommendations regarding the amount of leaves and the time during the growth season when foliage should be removed are frequently omitted. Partial defoliation as conducted in this study, i.e. evenly over the whole canopy, had no effect on the patterns of photosynthate distribution within shoots, but increased accumulation in bunches (Hunter & Visser, 1988b). It can therefore be expected that differences in solute accumulation in fruits between partially defoliated and non-defoliated vines would reflect solely deviations in source/sink activity and canopy/sink microclimate. It was also established that partially defoliated vines compensated adequately in terms of photosynthetic activity, provided that defoliation was not too severe (Hunter & Visser, 1988b, 1988c, 1989), and differences in canopy and fruit microclimate were also found (Hunter & Visser, 1988c, 1990a, 1990b). These differences were reflected in significant effects on vegetative and reproductive growth and leaf:fruit ratios between non-defoliated vines and vines defoliated 33% and 66% over the whole canopy from different developmental stages during the growth season (Hunter & Visser, 1990a, 1990b).

This study deals with the effects of partial defoliation on grape composition in general, the time at which defoliation should be applied for optimal accumulation in bunches, and interrelationships between source size/activity and sink size/activity. The effect of partial defoliation on sugar and acid accumulation and pH in *Vitis vinifera* L. cv. Cabernet Sauvignon grapes was studied. Another paper deals with skin colour and wine quality (Hunter, De Villiers & Watts, 1991).

MATERIALS AND METHODS

Experimental vineyard: An eight-year-old *Vitis vinifera* L. cv. Cabernet Sauvignon, clone CS 46, vineyard, on the experimental farm of the Viticultural and Oenological Research Institute near Stellenbosch, in the Western Cape was used. The cultivar was grafted onto rootstock 99 Richter, clone RY 30. Vines were planted (3,0 x 1,5 m spacing) on a Glenrosa (Kanonkop series 13) soil (MacVicar *et al.*, 1977) and trained onto a 1,5-m slanting trellis as described by Zeeman (1981). Further details of the experimental vineyard were given by Hunter & Visser (1988a).

Experimental design: The experiment was laid out as a completely randomized design comprising 24 treatments and nine replications. Three defoliation levels were applied to the whole canopy, i.e. 0%, 33% and 66%. The 0% defoliation treatment (control) was analysed at four different stages (berry set, pea size, véraison, ripeness), and 33% and 66% defoliation levels consisted of 10 treatments each, as described by Hunter & Visser (1990a). The defoliation treatments were implemented as follows: Four from approximately one month after bud break, three from berry set, two from pea size and one from véraison. These treatments were analysed at the remaining subsequent stages. Organic acid contents in grape samples were determined at berry set, pea size, véraison and ripeness, whereas sugar determinations were conducted only at véraison and ripeness. Total titratable acidity (TTA) and total soluble sugar (TSS) were determined at ripeness. There were nine replications, comprising one-vine plots, for each of the 24 treatments. In the case of organic acid and sugar determinations, equal quantities of 3 replications were combined and a representative sample analysed, resulting in three replications for each organic acid and sugar. Véraison in this study refers to full colour expression, which is later than physiological véraison, i.e. maximum acid accumulation and the start of sugar accumulation.

Defoliation treatments: Defoliation treatments consisted of removing the first leaf out of every three (33%) and the first two leaves out of every three (66%) starting at the basal end of the shoot. All shoots, including lateral shoots, were treated likewise. Defoliation percentages were maintained until each sampling stage, i.e. leaves emerging after initial defoliations were removed as described above at approximately monthly intervals.

Analyses: Total soluble sugars (°Balling), total titratable acidity (g/dm^3) and must pH were determined according to standard VORI methods. Individual sugars (glucose and fructose) and organic acids (tartaric acid and malic acid) were determined in freeze-dried grape samples according to methods described by Hunter, Visser & De Villiers (1990). Leaf areas were determined with a LI-COR LI 3000 portable area meter.

Statistical analyses: A one-way analysis of variance (standard VORI statistical software packages) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using Scott-Knott and Student analyses. Data were obtained during the third year after partial defoliation was applied for three consecutive growth seasons.

RESULTS AND DISCUSSION

TSS and TTA: Although TSS in berries of partially defoliated vines was significantly higher than in those of non-defoliated vines in some cases, no significant differences were generally found (Fig. 1). Koblet (1987) and Kliewer *et al.* (1988) found that sugar concentration increased slightly with early defoliation. That was not confirmed in this study. Kliewer & Bledsoe (1987) also found that timing of leaf removal had no effect on sugar accumulation. Owing to the severe defoliation applied in this study, the high sugar concentrations found are of special importance. Many investigators found that partial defoliation increased the total soluble solids in berries (Wolf *et al.*, 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). Many explanations for this have been given, such as a remobilization of stored carbohydrates, an increase in the photosynthetic activity of remaining leaves, an improvement in the light microclimate of remaining leaves, and an increased sink strength (Kliewer & Antcliff, 1970; Kliewer & Bledsoe, 1987). Furthermore, changes in the red:far-red radiation ratio in the canopy and therefore phytochrome stimulated responses on certain enzymes involved in maturation processes (Kliewer & Bledsoe, 1987), a change in the pattern of assimilate movement, and increased fruit temperatures (Bledsoe *et al.,* 1988) were suggested. Kliewer & Lider (1970), Klenert (1975) and Brown & Coombe (1985) also found decreases in the accumulation of sugars under shaded conditions.

It was previously found that partial defoliation, as applied in this study, had no effect on the pattern of photosynthate movement in shoots (Hunter & Visser, 1988b), but significantly increased the photosynthetic activity of remaining leaves as well as photosynthetically active radiation received by all leaves in the canopy (Hunter & Visser, 1988c). The microclimate of grapes in terms of canopy density, light intensity at the cordon, relative humidity and windspeed in the canopy was also improved (Hunter & Visser, 1990a, 1990b). All these factors could have contributed to the still high TSS found for partially defoliated vines, in spite of the severity of defoliation.

No significant differences in TTA in berries were generally found (Fig. 2). Except for defoliation from véraison, however, TTA in grapes of partially defoliated vines was seemingly slightly higher. This is in contrast to the findings of Kliewer & Lider (1970) that shaded conditions increased TTA as well as to other investigators that partial defoliation reduced TTA (Wolf *et al.,* 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.,* 1988). The apparently higher TTA found in the grapes of partially defoliated vines in the present study can be ascribed to the increase in lateral shoot growth reported by Hunter & Visser (1990a), which resulted in an increase in the number of young and newly matured leaves in the canopy. The relationship, if any, between the amount of TTA in grapes and the presence of young leaves must, however, still be established. The higher TTA in grapes found with earlier defoliation may also suggest a delay in ripening. Furthermore, since light intensity in the canopy was significantly increased by partial defoliation (Hunter & Visser, 1988c), photosynthetic activity in these leaves would also have increased. According to Kriedemann (1977) these leaves produce more organic acids

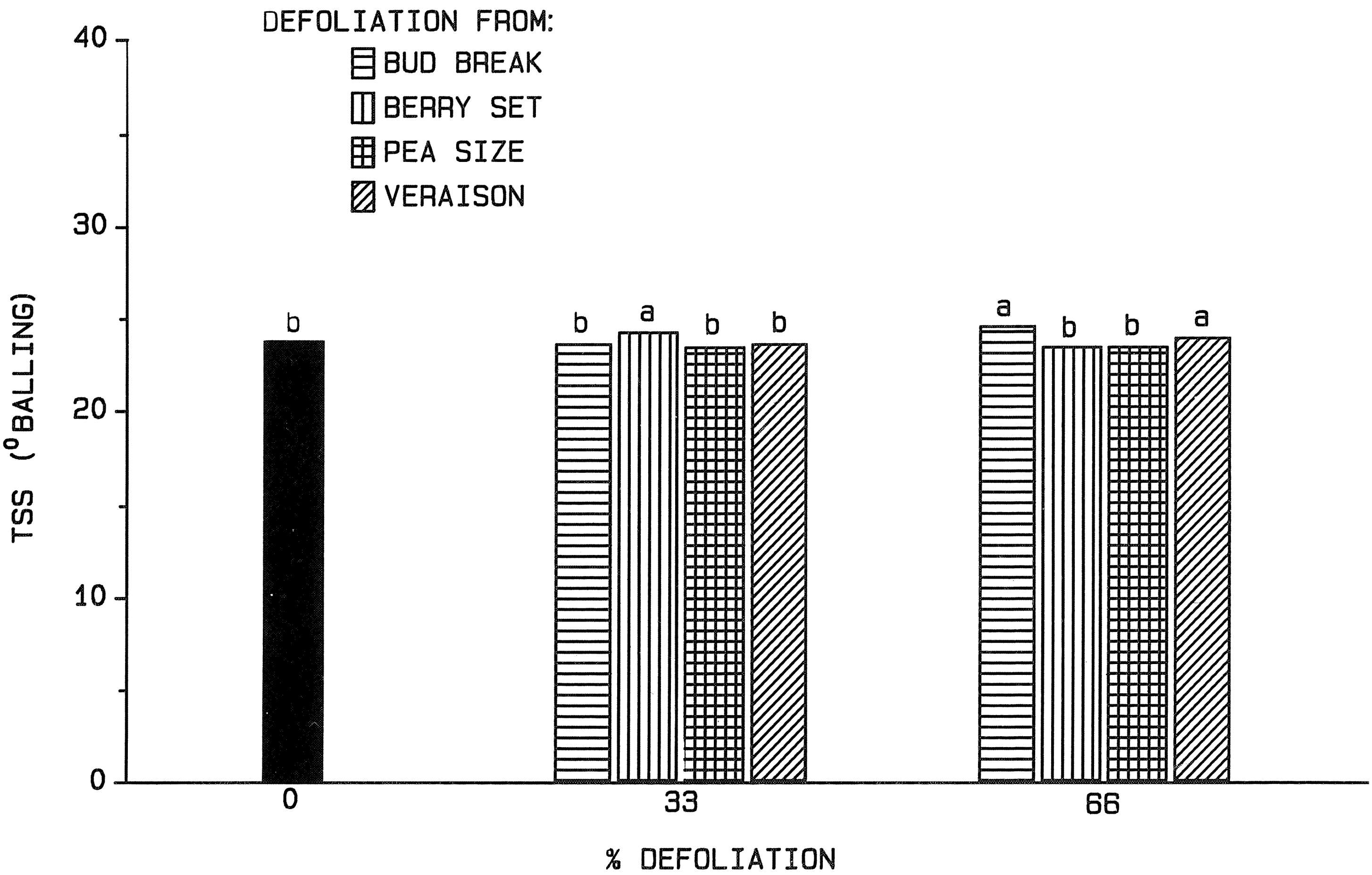

FIGURE 1

The effect of defoliation at different developmental stages of the vine on total soluble sugars (TSS) in berries at ripeness. Bars designated by the same letter do not differ significantly ($p \leq 0,05$).

in relation to sugars. Koblet (1987) suggested that a higher proportion of young leaves on lateral shoots would increase grape quality.

It is evident that TTA apparently decreased the later partial defoliation was commenced during the season, resulting in a significantly lower acidity in grapes of vines defoliated from véraison, compared to non-defoliated vines. This may be explained by the fact that the earlier partial defoliation commenced, the more lateral shoot growth was stimulated (Kliewer & Fuller, 1973; Hunter & Visser, 1990a).

TSS and TTA/cm² leaf area: Vines maintained at 33% and 66% defoliation during the entire growth season respectively produced approximately one third and two times more TSS and TTA in the berries/cm² leaf area, compared to control vines (Fig. 3). The leaf areas of the treated vines were given by Hunter & Visser (1990a) and data on reproductive growth by Hunter & Visser (1990b). Similar results were found by Kliewer (1970). The leaves of partially defoliated vines were therefore metabolically stimulated by partial defoliation, resulting in more efficient photosynthesis. Furthermore, since the size of sinks was not altered, but only the size of sources, the demand for photosynthetic products from sinks was increased, resulting in an increased photosynthetic activity. The latter was found by Hunter & Visser (1988b, 1988c, 1989). Because of the improved sink microclimate (Hunter & Visser, 1990b), however, sink activity could also have increased, affecting accumulation in bunches. According to Brown & Coombe (1985), the major limitation to the accumulation of photosynthetic products in grapes might be unloading from the phloem into vascular bundles. Ho (1988), however, stated that there was no evidence that rates of import were limited mainly by rates of unloading; the potential sink strength is, rather, determined genetically and can be expressed fully when the supply of assimilate is sufficient to meet the demand and when environmental conditions for the metabolic activity of sink organs are optimal.

The data (Fig. 3) are, however, not indicative of photosynthetic products being used for respiration and vegetative growth, as well as those translocated to and from storage parts of the vine such as the roots, trunk, arms and canes. Kliewer & Antcliff (1970) found that as much as 40% of the total sugar in fruits of grapevines may come from storage parts. A remobilization of stored carbohydrates could have contributed to accumulation in grapes of vines defoliated from just

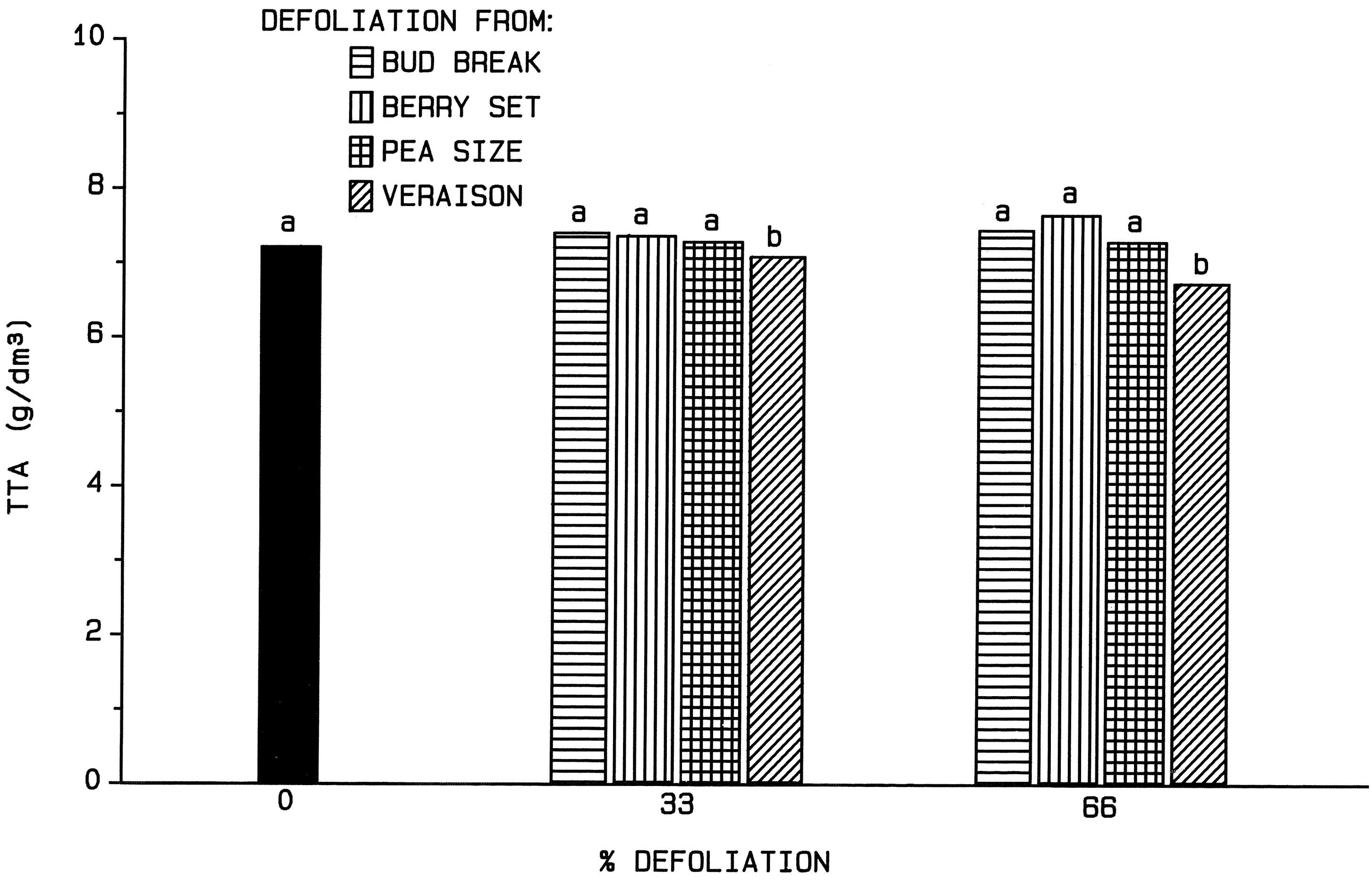

FIGURE 2

The effect of defoliation at different developmental stages of the vine on total titratable acidity (TTA) in berries at ripeness. Bars designated by the same letter do not differ significantly ($p \leq 0,05$).

after bud break in particular. Nevertheless, as vegetative growth was not strikingly affected by partial defoliation (Hunter & Visser, 1990a), the results demonstrated a more efficient use of the aerial parts of these vines. This confirms the findings of Hunter & Visser (1988b, 1988c, 1989).

Specific sugars: No significant differences on a mg/g dry berry mass or mg/berry basis between partially defoliated and non-defoliated vines were found for either glucose or fructose at véraison or ripeness. Mean glucose concentrations amounted to 317 and 340 mg/g dry mass and mean fructose concentrations to 303 and 349 mg/g dry mass at véraison and ripeness, respectively. Glucose dominated in berries at véraison, whereas fructose dominated at ripeness. These results verify those found for various species and cultivars (Amerine, 1956; Kliewer, 1966, 1967a, 1967b). However, 66% defoliation treatments generally had significantly less glucose and fructose on a g/shoot basis than 33% defoliated and non-defoliated vines (Fig. 4). Since no significant differences were found on a concentration or per berry basis, these differences mainly reflected lower total berry mass per shoot, especially for vines defoliated early during the season. The latter was fully discussed by Hunter & Visser (1990a).

Specific acids: It seemed that defoliation from early developmental stages (bud break and berry set) significantly affected tartaric and malic acid concentrations prior to véraison in some cases (Table 1). No significant differences between defoliation treatments were, however, found at véraison and ripeness. Partially defoliated vines therefore compensated adequately, probably as a result of increased photosynthetic activity (Hunter & Visser, 1988b, 1988c, 1989). Although no significant differences in tartaric or malic acid were generally found between partially defoliated and non-defoliated vines, it seemed that grapes of the former apparently had higher tartaric acid and lower malic acid concentrations. According to Philip & Kuykendall (1973) this suggests higher grape quality. The acidity balance was therefore apparently changed favourably by partial defoliation. Since only the ratio between tartaric and malic acid was changed, this might explain why no significant differences in TTA were found (Fig. 2). A decrease in malic acid concentration with partial defoliation was found by Wolf *et al.* (1986), Kliewer & Bledsoe (1987) and Kliewer *et al.* (1988).

Partial defoliation had no effect on the pattern of acid accumulation in berries. Irrespective of defoliation or the time of defoliation, the highest tartaric and malic acid concentrations were reached during the rapid growth phases (berry set and pea size) of berries. This is in accordance with concentrations found by Johnson & Nagel (1976). The highest total acid concentration occurred at pea size. Although malic acid concentrations declined rapidly from véraison to ripeness, the decrease in tartaric acid concentration was not pronounced and eventually resulted in a concentration approximately four times that of malic acid. This verifies the findings of Amerine (1956), Kliewer, Howarth & Omori (1967), Kliewer (1971) and Van Zyl (1984). Since tartaric acid concentrations are usually higher than those of malic acid during ripening, Kliewer (1964) suggested that tartaric acid is metabolized very slowly, either owing to the lack of an active metabolizing enzyme system during this period or because of enzyme inhibition. Saito & Kasai (1968) stated, however, that the accumulation of tartaric acid during ripening is due to its conversion to an insoluble salt, which is barely affected by

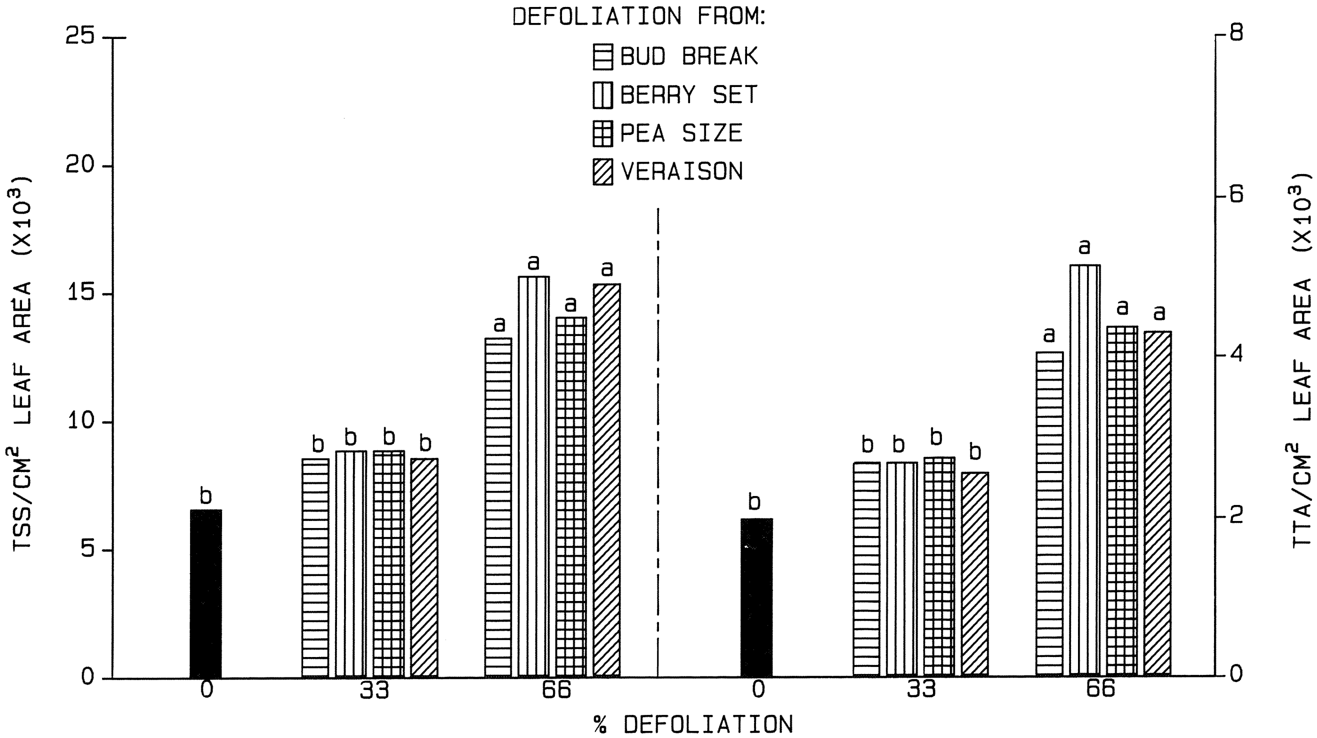

FIGURE 3

The effect of defoliation at different developmental stages of the vine on TSS and TTA per cm^2 leaf area in berries at ripeness. Bars designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

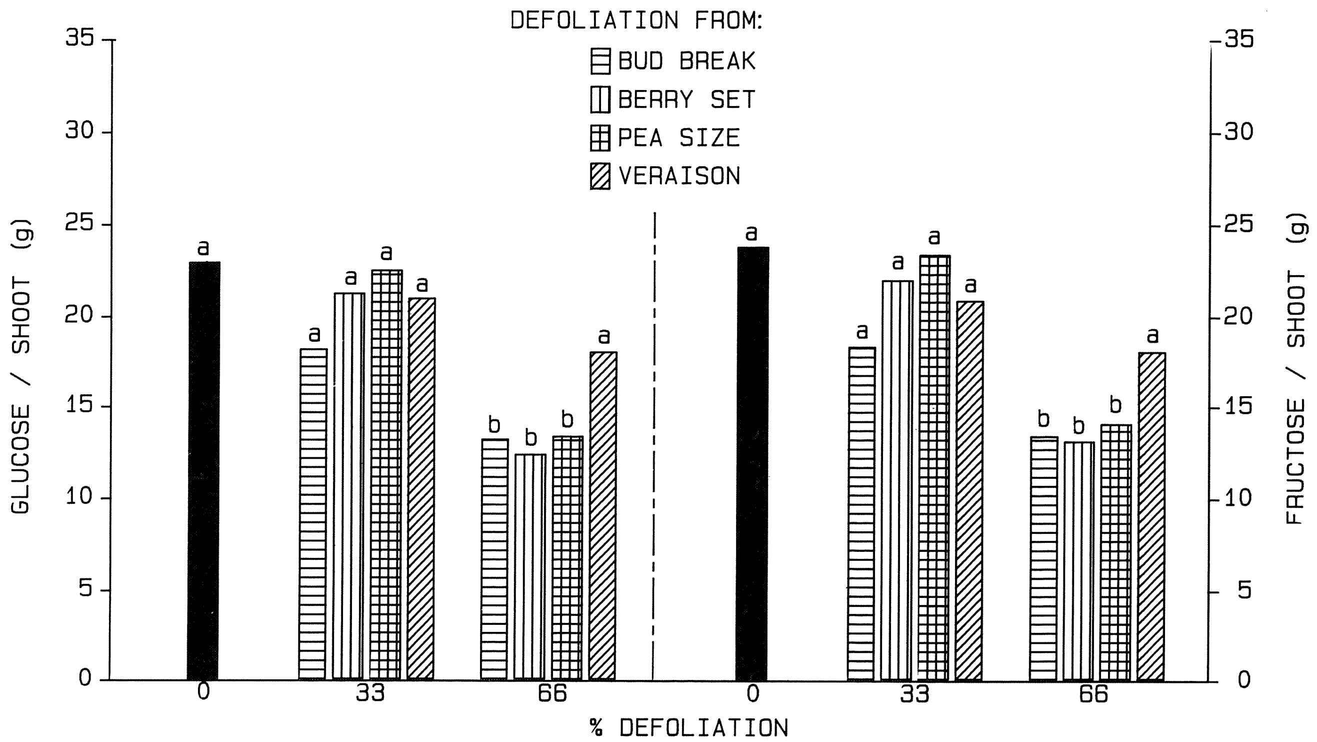

FIGURE 4

The effect of defoliation at different developmental stages of the vine on glucose and fructose contents per shoot in berries at ripeness. Bars designated by the same letter do not differ significantly (p≤ 0,05) for each sugar.

TABLE 1

The effect of defoliation at different developmental stages of the vine on tartaric acid and malic acid concentration in the berry, expressed in mg/g dry mass.

Developmental stage defoliation commenced	Developmental stage analysed	Tartaric acid			Malic acid		
		*0	*33	*66	*0	*33	*66
Bud break	Berry set	163,00b	168,67a	173,33a	68,00d	66,33d	64,67d
	Pea size	137,33d	140,67d	152,00c	169,67a	149,33b	152,33b
	Véraison	37,00e	37,33e	42,33e	36,67e	29,33e	35,00e
	Ripeness	23,00f	23,33f	24,00f	6,00f	5,00f	5,67f
Berry set	Pea size	137,33d	152,67c	148,33c	169,67a	155,00b	142,00c
	Véraison	37,00e	37,00e	38,33e	36,67e	32,33e	34,00e
	Ripeness	23,00f	23,67f	25,00f	6,00f	6,00f	5,33f
Pea size	Véraison	37,00e	37,67e	40,33e	36,67e	35,67e	34,00e
	Ripeness	23,00f	23,00f	24,00f	6,00f	6,00f	5,67f
Véraison	Ripeness	23,00f	23,67f	23,33f	6,00f	5,33f	5,67f
Cv(%)		6,24			6,15		

* Percentage defoliation.

Values designated by the same letter do not differ significantly for each organic acid.

such enzymes. According to Johnson & Nagel (1976), Coombe (1987) and Iland (1987) the small decline in tartaric acid concentration during ripening is the result of dilution, whereas the decline in malic acid concentration resulted from water uptake and metabolic reactions, causing malic acid to decrease in absolute amounts in the berry. Ruffner (1982) stated that malic acid is very much involved in sugar metabolism through processes of glycolysis and gluconeogenesis. According to Selvaraj *et al.* (1978), the decrease in total acidity during ripening might be due to the oxidation of acids or the preferential utilization of organic acids during respiration.

Although no significant differences for either of the acids on a per berry basis were found between partially defoliated and non-defoliated vines, berries of 66% defoliated vines had significantly lower tartaric and malic acid contents per shoot (Fig. 5). As for sugar content per shoot (Fig. 4), these results also primarily reflect differences in total berry mass between partially defoliated and non-defoliated vines.

pH: No significant differences in must pH were found between any of the treatments. A mean pH of 3,19 was recorded. This is in contrast to the finding of Bledsoe *et al.* (1988) but confirms that of Williams *et al.* (1987) and is probably due to the fact that no differences in canopy temperature could be found between defoliation treatments (Hunter & Visser, 1990a). According to Amerine (1956), tartaric acid is a stronger acid than malic acid and should buffer the pH lower. The differences between treatments in tartaric and malic acid, however, were apparently not pronounced enough.

General: Although temperature has a preponderant effect on grape composition (Ruffner, 1982; Hofäcker, Alleweldt & Khader, 1976; Kliewer, 1973; Lakso & Kliewer, 1978), canopy temperatures did not differ between defoliation treatments (Hunter & Visser, 1990a) and the results of the present study therefore reflect mainly differences in vine capacity and light microclimate. Berry temperatures could, however, still be different, but were not measured.

The sugar, acid and pH results indicated that defoliation as applied in this investigation did not affect the ability of vines to still ripen grapes to a similar and apparently better composition than in non-defoliated vines with a much higher leaf area, as found by Hunter & Visser (1990a). The capacity of vines was therefore effectively explored to maintain an acceptable grape quality. This was also verified by the fact that no significant differences in sugar:acid ratios could be found. The mean sugar:acid ratio was 3,30.

The results confirm the general conception that an optimal canopy microclimate necessary is in the cultivation of wine grapes. This can only be beneficial to the general metabolic activity of vines and contribute to establishing the capacity of vines and finding the perfect balance between the vegetative and reproductive growth and accumulation of reserves. From the results it is evident that 66% defoliation over the whole canopy of grapevines is too severe regarding the total accumulation of important sugars and organic acids in bunches. Nevertheless, it seems that partial defoliation can safely be applied in practice, provided that defoliation is not too severe (66%).

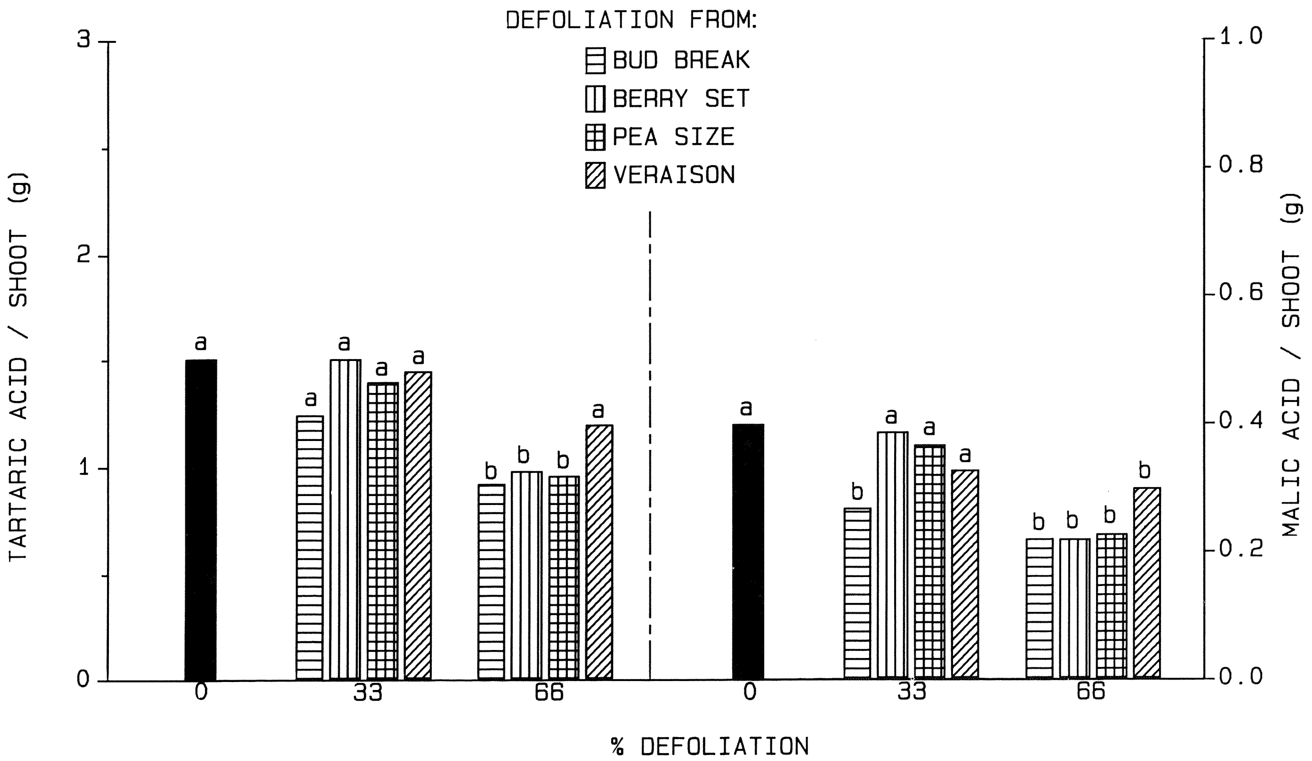

FIGURE 5

The effect of defoliation at different developmental stages of the vine on tartaric acid and malic acid contents per shoot in berries at ripeness. Bars designated by the same letter do not differ significantly (p≤ 0,05) for each organic acid.

CONCLUSIONS

Although no significant differences in TSS in berries were generally found between partially defoliated and non-defoliated vines, the TSS of the former was significantly higher in some cases. This could be ascribed to an improved canopy microclimate and photosynthetic activity created by partial defoliation. The timing of partial defoliation had no effect on TSS. In contrast to the findings of other investigators, TTA was slightly higher in the grapes of partially defoliated vines and also increased the earlier defoliation commenced, albeit not significantly. The latter may suggest a delay in ripening. Nevertheless, TSS and TTA/cm^2 leaf area results clearly indicated that vines were metabolically stimulated by partial defoliation, resulting mainly in more efficient photosynthetic processes.

Although no significant differences on a per gram dry mass or per berry basis for glucose and fructose or tartaric and malic acid were generally found between defoliation treatments, the contents in berries per shoot decreased significantly for 66% defoliated vines. This mainly reflected a lower total berry mass per shoot, as was previously found. No significant differences in the quality of sugars could be found. Partial defoliation had no effect on the accumulation pattern of sugars during the growth season. Glucose dominated in the berry at véraison, whereas fructose dominated at ripeness. However, although significant in only some cases, the grapes of partially defoliated vines generally had slightly higher tartaric acid and slightly lower malic acid contents than those of non-defoliated vines. This is generally accepted to present a higher grape quality for wine-making purposes. Therefore, partial defoliation, and particularly improved canopy microclimates created, apparently changed the acid balance in grapes for the better. It is noticeable that this could still be achieved under warm South African climatic conditions.

Partial defoliation did not change the accumulation pattern of sugars and acids during the growth season. The highest tartaric and malic acid concentrations occurred during rapid growth phases of berries, whereas the highest total concentrations were reached at pea size. Malic acid decreased rapidly from véraison to ripeness, but the decrease in tartaric acid was not pronounced. No significant differences in must pH were found between partially defoliated and non-defoliated vines.

Although more pronounced differences in sugars, acids and must pH were expected in some cases, it is important to note that, in spite of the severe defoliations applied in this study, vines still had the ability to support similar concentrations and amounts of these compounds in berries than those of vines with much larger leaf areas. The 66% defoliated vines were, however, not capable of accumulating similar total amounts in the grapes on a per shoot basis. Nevertheless, the results stressed the fact that non-defoliated vines were more passive, not metabolizing to their full capacity. It would seem that partial defoliation, as applied in this study, favourably changed the general metabolism of vines, mainly in terms of more favourable source:sink ratios, resulting in more efficient photosynthesis and canopy microclimate. This favoured the production of grapes needed for quality wine.

LITERATURE CITED

AMERINE, M.A., 1956. The maturation of wine grapes. *Wines & Vines* **37,** 27-38.

AMERINE, M.A., 1964. Acids, grapes, wines and people. *Am. J. Enol. Vitic.* **15,** 106-115.

BLEDSOE, A.M., KLIEWER, W.M. & MAROIS, J.J., 1988. Effects of timing and severity of leaf removal on yield and fruit composition of Sauvignon blanc grapevines. *Am. J. Enol. Vitic.* **39,** 49-54.

BROWN, S.C. & COOMBE, B.G., 1985. Solute accumulation by grape pericarp cells III. Sugar changes *in vivo* and the effect of shading. *Biochem. Physiol. Pflanzen* **180,** 371-381.

CHAMPAGNOL, F., 1977. Physiological state of the vine and quality of the harvest. In: Proc. Int. Symp. on the Quality of the Vintage, 14-21 Feb., Cape Town. pp. 107-116.

COOMBE, B.G., 1987. Influence of temperature on composition and quality of grapes. *Acta Hort.* **206,** 23-35.

HO, L.C., 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **39,** 355-378.

HOFÄCKER, W., ALLEWELDT, G. & KHADER, S., 1976. Einfluss von Umweltfaktoren auf Beerenwachstum und Mostqualität bei der Rebe. *Vitis* **15,** 96-112.

HUNTER, J.J., DE VILLIERS, O.T. & WATTS, J.E., 1991. The effect of partial defoliation on quality characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon grapes II. Skin colour, skin sugar and wine quality. *Am. J. Enol. Vitic.* 42, 13-18.

HUNTER, J.J. & VISSER, J.H., 1988a. Distribution of ^{14}C-Photosynthetate in the shoot of *Vitis vinifera* L. cv. Cabernet Sauvignon I. The effect of leaf position and developmental stage of the vine. *S. Afr. J. Enol. Vitic.* **9** (1), 3-9.

HUNTER, J.J. & VISSER, J.H., 1988b. Distribution of ^{14}C-Photosynthetate in the shoot of *Vitis vinifera* L. cv. Cabernet Sauvignon II. The effect of partial defoliation. *S. Afr. J. Enol. Vitic.* **9** (1), 10-15.

HUNTER, J.J. & VISSER, J.H., 1988c. The effect of partial defoliation, leaf position and developmental stage of the vine on the photosynthetic activity of *Vitis vinifera* L. cv. Cabernet Sauvignon. *S. Afr. J. Enol. Vitic.* **9** (2), 9-15.

HUNTER, J.J. & VISSER, J.H., 1989. The effect of partial defoliation, leaf position and developmental stage of the vine on leaf chlorophyll concentration in relation to the photosynthetic activity and light intensity in the canopy of *Vitis vinifera* L. cv. Cabernet Sauvignon. *S. Afr. J. Enol. Vitic.* **10,** 67-73.

HUNTER, J.J. & VISSER, J.H., 1990a. The effect of partial defoliation on growth characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon I. Vegetative growth. *S. Afr. J. Enol. Vitic.* **11,** 18-25.

HUNTER, J.J. & VISSER, J.H., 1990b. The effect of partial defoliation on growth characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon II. Reproductive growth. *S. Afr. J. Enol. Vitic.* **11,** 26-32.

HUNTER, J.J., VISSER, J.H. & DE VILLIERS, O.T., 1990. Preparation of grapes and extraction of sugars and organic acids for determination by high performance liquid chromatography. *Am. J. Enol. Vitic.* Accepted for publication.

ILAND, P.G., 1987. Interpretation of acidity parameters in grapes and wine. *Aust. Grapegrow. Winemak.* **4,** 81-85.

JOHNSON, T. & NAGEL, C.W., 1976. Composition of Central Washington grapes during maturation. *Am. J. Enol. Vitic.* **27,** 15-20.

KLENERT, M., 1975. Die Beeinflussing des Zucker- und Säuregehaltes von Traubenbeeren durch künstliche Veränderung der Umweltbedingungen. *Vitis.* **13,** 308-318.

KLIEWER, W.M., 1964. Influence of environment on metabolism of organic acid and carbohydrates in *Vitis vinifera* I. Temperature. *Plant Physiol.* **39,** 869-880.

KLIEWER, W.M., 1966. Sugars and organic acids of *Vitis vinifera. Plant Physiol.* **41,** 923-931.

KLIEWER, W.M., 1967a. The glucose-fructose ratio of *Vitis vinifera* grapes. *Am. J. Enol. Vitic.* **18,** 33-41.

KLIEWER, W.M., 1967b. Concentration of tartrates, malates, glucose and fructose in the fruits of the genus *Vitis. Am. J. Enol. Vitic.* **18,** 87-96.

KLIEWER, W.M., 1970. Effect of time and severity of defoliation on growth and composition of "Thompson Seedless" grapes. *Am. J. Enol. Vitic.* **21,** 37-47.

KLIEWER, W.M., 1971. Effect of day temperature and light intensity on concentration of malic and tartaric acids in *Vitis vinifera* L. grapes. *J. Am. Soc. Hort. Sci.* **96,** 372-377.

KLIEWER, W.M., 1973. Berry composition of *Vitis vinifera* cultivars as influenced by photo- and nycto-temperatures during maturation. *J. Am. Soc. Hort. Sci.* **98,** 153-159.

KLIEWER, W.M. & ANTCLIFF, A.J., 1970. Influence of defoliation, leaf darkening, and cluster shading on the growth and composition of Sultana grapes. *Am. J. Enol. Vitic.* **21,** 26-36.

KLIEWER, W.M. & BLEDSOE, A.M., 1987. Influence of hedging and leaf removal on canopy microclimate, grape composition, and wine quality under California conditions. *Acta Hort.* **206,** 157-168.

KLIEWER, W.M. & FULLER, R.D., 1973. Effect of time and severity of defoliation on growth of roots, trunk, and shoots of "Thompson Seedless" grapevines. *Am. J. Enol. Vitic* **24,** 59-64.

KLIEWER, W.M., HOWARTH, L. & OMORI, M., 1967. Concentrations of tartaric acid and malic acids and their salts in *Vitis vinifera* grapes. *Am. J. Enol.* **18,** 42-54.

KLIEWER, W.M. & LIDER, L.A., 1970. Effects of day temperature and light intensity on growth and composition of *Vitis vinifera* L. fruits. *J. Am. Soc. Hort. Sci.* **95,** 766-769.

KLIEWER, W.M., MAROIS, J.J., BLEDSOE, A.M., SMITH, S.P., BENZ, M.J. & SILVESTRONI, O., 1988. Relative effectiveness of leaf removal, shoot positioning, and trellising for improving winegrape composition. In: Proc. Sec. Int. Cool Climate Vitic. Oenol. Symp., Jan. 1988, Auckland, New Zealand. pp. 123-126.

KOBLET, W., 1984. Influence of light and temperature on vine performance in cool climates and applications to vineyard management. In: Heatherbell, D.A., Lombard, P.B., Bodyfelt, F.W. & Price, S.F. (eds.). Proc. Int. Symp. on Cool Climate Vitic. Enol., 25-28 June 1984, Oregon. pp. 139-157.

KOBLET, W., 1987. Effectiveness of shoot topping and leaf removal as a means of improving quality. *Acta Hort.* **206,** 141-156.

KRIEDEMANN, P.E., 1977. Vineleaf photosynthesis. In: Proc. Int. Symp. on the Quality of the Vintage, 14-21 Feb. 1977, Cape Town. pp. 67-87.

LAKSO, A.N. & KLIEWER, W.M., 1978. The influence of temperature on malic acid metabolism in grape berries II. Temperature responses of net dark CO_2 fixation and malic acid pools. *Am. J. Enol. Vitic.* **29,** 145-149.

MacVICAR, C.N. & SOIL SURVEY STAFF, 1977. Soil classification. A binomial system for South Africa. Scientific Pamphlet 390. Dep. Agric. Developm., Private Bag X116, 0001 Pretoria, Republic of South Africa.

MAY, P., SHAULIS, N.J. & ANTCLIFF, A.J., 1969. The effect of controlled defoliation in the Sultana vine. *Am. J. Enol. Vitic.* **20,** 237-250.

PHILIP, T. AND KUYKENDALL, J.R., 1973. Changes in titratable acidity, °Brix, pH, potassium content, malate and tartrate during berry development of Thompson seedless grapes. *J. Food Sci.* **38,** 874-876.

RUFFNER, H.P., 1982. Metabolism of tartaric and malic acids in *Vitis:* A review - Part B. *Vitis* **21,** 346-358.

SAITO, K. AND KASAI, Z., 1968. Accumulation of tartaric acid in the ripening process of grapes. *Plant & Cell Physiol.* **9,** 529-537.

SELVARAJ, Y., PAL, D.K., DIVAKER, N.G., PUROHIT, A.G. AND SHIKHAMANY, S.D., 1978. Sugars, organic acids and amino acids in Anab-E-Shahi grape during growth and development. *J. Food Sci. Tech.* **15,** 136-139.

SIDAHMED, O.A. & KLIEWER, W.M., 1980. Effects of defoliation, gibberellic acid and 4-chlorophenoxyacetic acid on growth and composition of Thompson Seedless grape berries. *Am. J. Enol. Vitic.* **31,** 149-153.

SMART, R.E., 1982. Vine manipulation to improve wine grape quality. In: Proc. Grape and Wine Centennial Symp., June 1980, University of California, Davis. pp. 362-375.

SMART, R.E., ROBINSON, J.B., DUE, G.R. & BRIEN, C.J., 1985. Canopy microclimate modification for the cultivar Shiraz II. Effects on must and wine composition. *Vitis* **24,** 119-128.

SMART, R.E., SMITH, S.M. & WINCHESTER, R.V., 1988. Light quality and quantity effects on fruit ripening for Cabernet Sauvignon. *Am. J. Enol. Vitic.* **39,** 250-258.

VAN ZYL, J.L., 1984. Response of Colombar grapevines to irrigation as regards quality aspects and growth. *S. Afr. J. Enol. Vitic.* **5,** 19-28.

WAREING, P.F., KHALIFA, M.M. & TREHARNE, K.J., 1968. Rate-limiting processes in photosynthesis at saturating light intensities. *Nature* **220,** 453-457.

WILLIAMS, L.E., BISCAY, P.J. & SMITH, R.J., 1987. Effect of interior canopy defoliation on berry composition and potassium distribution in Thompson Seedless grapevines. *Am. J. Enol. Vitic* **38,** 287-292.

WOLF, T.K., POOL, R.M. & MATTICK, L.R., 1986. Responses of young Chardonnay grapevines to shoot tipping, etephon, and basal leaf removal. *Am. J. Enol. Vitic* **37,** 263-268.

WOODROW, I.E., & BERRY, J.A., 1988. Enzymatic regulation of photosynthetic CO_2 fixation in C_3 plants. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **39,** 533-594.

ZEEMAN, A.S., 1981. Oplei. In: Burger, J.D. & Deist, J. (eds.). Wingerdbou in Suid-Afrika, VORI, 7600 Stellenbosch, Republic of South Africa. pp. 185-201.