Implications of Seasonal Canopy Management and Growth Compensation in Grapevine*

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The effect of eight seasonal canopy management treatments on yield and growth compensation of a vertically trellised *Vitis vinifera* L. cv. Sauvignon blanc/110 Richter vineyard was investigated. East-West orientated rows were spaced 2.75 x 1.5 m. Spurs were spaced 15 cm apart. Intensive micro-irrigation was applied. Canopy management comprised better accommodation of foliage on the trellising system and different means of reducing foliage during the berry set to pea berry size period of the growth season. Combinations of shoot positioning-suckering-topping and shoot positioning-suckering-topping-leaf removal resulted in the highest yields; substituting leaf removal with lateral (secondary shoot) removal noticeably decreased yields. No canopy management resulted in the lowest yields. Based on production (and labour), lateral shoot removal cannot be considered an economically viable canopy management practice. Significant compensatory growth was induced by the removal of lateral shoots. That would have impacted on the distribution of carbohydrates and probably counterbalanced the positive effects of an improved microclimate and related reactions. Lateral removal reduced bunch development compared to treatments that included leaf removal instead. Yield differences between treatments showed no obvious relationship with fertility or budding. Neither bunch rot nor soluble solid accumulation played a role in the yield reduction found with lateral removal. Total hexose content in the berries at ripeness was, however, reduced by lateral removal, decreasing further the earlier lateral removal was applied. For the treatments where no laterals were removed, lateral leaves made the highest contribution to the total sugar content of the leafy part of the canopy. The ratio between the total output of the main shoot leaves and that of the lateral shoots was reversed when laterals were removed. Sugar content of leaves on main shoots of lateral removal treatments complied with the compensation theory of source:sink relationship. Apparently, shading had a pronounced effect on the total carbohydrate content of non-treated canopies. Although root starch content was not affected by lateral removal during the study period, root density was decreased, indicating limited root development. A positive relationship between root density and yield was found. Although the presence of particularly medium and small leaves and therefore the contribution of these leaves to yield was reduced by lateral removal, the total leaf area/g fruit was never less than the generally accepted norm of 12 cm^2. The results indicated that available leaf area (even when well-exposed) cannot generally be accepted as the norm, but that the composition of the leaf area should be taken into account, as it has a critical role in the efficiency of the canopy and the nourishing of the bunches. Ratios of main shoot leaf area to lateral shoot leaf area as well as practical canopy composition criteria are presented. Results are also argued as to the role of hormonal activity in growth compensation and trigger mechanisms. The results provide new perspectives on existing canopy composition criteria and implications of growth compensation. The study clearly indicates the beneficial effects of correct seasonal canopy management.

Ultimately, grapevine canopy management is aimed at optimising carbon allocation to fruit sinks without disturbing growth and development in other parts of the grapevine, e.g. perennial structures such as the roots. Given the complexity of the grapevine canopy and pronounced effect it may have on microclimate, photosynthetic activity, yield, grape composition, and wine quality (Koblet, 1984; Kliewer & Bledsoe, 1987; Smart *et al.*, 1985, 1990; Hunter *et al.*, 1995a), canopy management should be applied with great care and thorough consideration of the partitioning of assimilates between sites of production, accumulation and utilisation in order to reach this goal. In addition to primary effects, e.g. changing of translocation patterns (acropetal/basipetal movement), when seasonal practices such as topping and different levels of defoliation are applied (Quinlan & Weaver, 1970; Hunter & Visser, 1988a; Koblet *et al.*, 1993), secondary effects include compensatory growth (Kliewer & Antcliff, 1970; Kliewer & Fuller, 1973; Marangoni *et al.*, 1980; Candolfi-Vasconcelos & Koblet, 1990; Hunter & Visser, 1990a). Different leaf age groups also play a major role in the continuous changing of the import/export kinetics in the canopy as the growth season progresses (Koblet, 1975; Hunter & Visser, 1988a, 1988b; Ruffner *et al.*, 1990; Hunter *et al.*, 1994) and growth compensa-

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tion (e.g. the formation of lateral shoots) resulting from alterations to the canopy would therefore directly affect the assimilate distribution dynamics, which are critical for continued, predictable yields and favourable grape composition for high quality wine. Growth compensation seems to be an integral part of the balancing act of the grapevine canopy upon manipulation and may impact directly on the total leaf area/g fruit of approximately 12 cm^2, which is generally accepted as being required to adequately ripen the fruit in terms of soluble solid accumulation (Hunter & Visser, 1990b, and references therein).

Seasonal canopy management practices, consisting of different combinations of suckering, shoot positioning, topping, leaf removal, and lateral removal, were therefore applied in order to determine their effect on yield and related parameters as well as their impact on growth compensation. The study also presented an opportunity to re-evaluate existing canopy composition criteria by quantifying the whole canopy in terms of contribution of different leaf size groups to yield. Possible trigger mechanisms for compensatory reactions are discussed.

MATERIALS AND METHODS

Vineyard and viticultural practices: A vigorously growing *Vitis vinifera* L. cv. Sauvignon blanc (clone SB10) vineyard, grafted onto 110 Richter (clone RQ28A), and situated in the Robertson area (Western Cape) on a Hutton soil was used. Vines were orientated approximately East-West, spaced 2.75 m x 1.5 m and cordon trained to a Lengthened Perold System. Two-bud spurs were spaced 15 cm apart. Intensive micro-irrigation was scheduled according to A-pan evaporation figures. Treatments are presented in Table 1. Except for the control, shoot positioning was done on all treatments and comprised positioning of shoots in line with spurs. Suckering consisted of the removal of shoots not located on spurs at approximately 30 cm main shoot length. Topping (30 cm above the top wire) was done once or twice during the period berry set to pea size and comprised the removal of up to 30 cm of shoots. Partial defoliation (33%) was done evenly on all shoots from side to side in the canopy (approximately 30% of leaves removed during leaf removal comprised leaves situated on lateral shoots – data not shown). All lateral shoots, irrespective of size, were removed. Leaf and lateral removal were done as described at a particular stage and in a particular zone.

TABLE 1

Canopy management treatments as applied in a vertically trellised Sauvignon blanc vineyard situated in the Robertson area on a Hutton soil.

Treatments	
No treatment (control)	
Suckering & topping	
Leaf removal (33%):	Berry set (bunch zone)
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)
Lateral removal (all):	Berry set (bunch zone)
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)
Lateral removal (all):	Berry set
Lateral removal (all):	Pea size

Shoot positioning was done on all treatments (excluding control vines), whereas leaf and lateral removal treatments were also suckered and apically topped. Shoots of control vines grew in all directions.

Measurements: Seven shoots (including bunches) per vine were sampled in order to determine total leaf area, primary and secondary leaf area, remaining leaf area, number of lateral shoots, shoot lengths, bunch mass, berry volume and bunch rot (visual score). Leaf area was determined by means of a LICOR Model 3100 area meter. Budding percentage (number of shoots/number of buds allocated during pruning x 100) and fertility (number of bunches/number of shoots originating from buds allocated during pruning) were determined at the end of the season following treatment. Yield values represent total yield from all replications per treatment. Treatments were harvested on the same day and soluble solids (°Balling) were determined from a representative bunch sample comprising at least seven bunches. Light intensity in the bunch zone of the canopy was measured during mid-morning by means of a LICOR Line Quantum Sensor and expressed as a percentage of ambient light level determined in the vine row. Canopy density was determined after the point quadrat method described by Smart (1982). Photosynthetic activity of mature (large) leaves was measured during mid-morning using an open system ADC portable photosynthesis meter (The Analytical Development Co., Ltd., England). Leaf water potential of mature (large) leaves was determined from early to mid-afternoon using a Scholander pressure chamber (Scholander *et al.,* 1965).

Root density was determined using the profile wall method of Böhm (1979) as described by Hunter (1998). Starch content of the different root sizes was determined enzymatically (Hunter *et al.,* 1995b).

Hexose (glucose and fructose) concentrations in large (> 70% of mature leaf size), medium (> 30%, but < 70% of mature leaf size) and small (< 30% of mature leaf size) leaves was determined using the equipment and conditions described by Hunter *et al.* (1991).

Statistical analyses: Treatments were replicated five times with five vines per replicate in a randomised block design and applied for three years. Mean values of the last two years of the experiment (1994/95 and 1995/96) are presented. Root density and starch were determined during the winter of the last growth season. Student's t-LSD test was used to determine significant differences.

RESULTS AND DISCUSSION

Yield: Highest yields were obtained by applying combinations of shoot positioning-suckering-topping and shoot positioning-suckering-topping-leaf removal; substituting leaf removal with lateral removal consistently decreased yields (Table 2). No treatment (control) resulted in the lowest yields. The application of shoot positioning-suckering-topping increased yield by 21%, whereas removing leaves at berry set and at pea size in addition to shoot positioning, suckering and topping resulted in 30% higher yields, compared to that of non-treated vines. Similar results were found with Cabernet Sauvignon (Hunter *et al.,* 1995a). Removing leaves (in the bunch zone) at berry set increased yield by 18%. However, removing lateral shoots (in the bunch zone) instead of leaves increased yield by only 5%. Any additional lateral shoot removal increased yield only up to a maximum of 7% [Lateral shoot removal was also found to be much more labour intensive than leaf removal (data not shown), e.g. lateral removal in the bunch

TABLE 2

Yield parameters as affected by different seasonal canopy management combinations.

Treatment		**Yield (ton/ha)**	**Fertility index**	**Budding (%)**	**Bunch mass (g)**
No treatment (control)		16.8c	1.8ab	99.9a	150.9c
Suckering & topping		20.3b	1.9a	95.9a	184.2ab
Leaf removal (33%):	Berry set (bunch zone)	19.8b	1.8ab	98.1a	180.0b
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)	21.9a	1.8ab	97.6a	203.6a
Lateral removal (all):	Berry set (bunch zone)	17.7c	1.7ab	97.1a	173.9b
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)	17.8c	1.7ab	99.0a	179.6b
Lateral removal (all):	Berry set	17.9c	1.8ab	97.4a	172.6b
Lateral removal (all):	Pea size	17.0c	1.6b	97.7a	173.0b

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

TABLE 3

Canopy (bunch zone) light intensity and density as affected by different seasonal canopy management combinations.

Treatment		**Canopy light intensity (% of ambient)**	**Canopy density (number of leaf layers)**
No treatment (control)		0.4d	4.7a
Suckering & topping		0.5d	4.0b
Leaf removal (33%):	Berry set (bunch zone)	0.6d	3.8bc
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)	0.8cd	3.5cd
Lateral removal (all):	Berry set (bunch zone)	1.0bcd	3.4cd
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^{1}/_{2}$ of canopy)	2.2bc	2.9d
Lateral removal (all):	Berry set	2.3b	3.0d
Lateral removal (all):	Pea size	3.9a	3.0d

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

zone increased labour by almost 30% compared to leaf removal in this part of the canopy (Hunter & Le Roux, 1997; Hunter, 1999), rendering it an economically non-viable practice and clearly showing that production from vines that are non-treated and those where laterals are removed will decrease profit margins].

It is known that photosynthetic activity of leaves as well as export of photoassimilates increase as a result of improved canopy microclimate and lower source:sink ratio (Koblet, 1975; Hofäcker, 1978; Johnson *et al.,* 1982; Hunter & Visser, 1988b, 1988c; Candolfi-Vasconcelos & Koblet, 1990; Hunter *et al.,* 1995a; Koblet *et al.,* 1996). However, in this study an improved light intensity (Table 3), apparent enhancement in photosynthetic activity of mature leaves (Table 4) and the possibility of delayed senescence and abscission of remaining leaves (Candolfi-Vasconcelos & Koblet, 1990; Hunter & Visser, 1989) as a result of lateral shoot removal had no marked stimulating effect on yield. A possible constant distribution of energy to activated compensatory growth areas, acting as strong sinks and counteracting generally found positive effects from microclimate improvement and lower source:sink ratio on the utilisation of photosynthesis-related products (Koblet, 1975; Hunter & Visser, 1988a; Hunter *et al.,* 1995a, 1995b), probably played a role in this regard. Mostly young, active leaves were removed during lateral removal, whereas leaf removal comprised a random removal of leaves of all ages on both main and lateral shoots, thereby stimulating activity of all leaves without changing normal distribution dynamics in the canopy (Hunter & Visser, 1988b). Therefore, although bunch development was still stimulated by lateral shoot removal compared to the non-treated vines, it was reduced when compared to the treatments that included leaf removal. It is noticeable that these results were found under vigorous conditions. It is expected that lateral removal under less vigorous conditions will result in poorer performance.

Noticeably, yield differences between treatments showed only a relationship with bunch mass, but no obvious relationship with either fertility or budding (Table 2). Therefore, although light

TABLE 4

Photosynthetic activity and water potential of large (>70% of mature leaf size) leaves as affected by different seasonal canopy management combinations.

Treatment		Photosynthetic activity (mg $CO_2/dm^2/h$)	Water potential (MPa)
No treatment (control)		11.5a	-1.40c
Suckering & topping		12.4a	-1.21abc
Leaf removal (33%):	Berry set (bunch zone)	13.0a	-1.32bc
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower ½ of canopy)	12.8a	-1.10a
Lateral removal (all):	Berry set (bunch zone)	12.1a	-1.22abc
Lateral removal (all):	Berry set (bunch zone) Pea size (lower ½ of canopy)	13.5a	-1.08a
Lateral removal (all):	Berry set	14.3a	-1.12ab
Lateral removal (all):	Pea size	13.5a	-1.16ab

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

TABLE 5

Berry soluble solid and hexose content as affected by different seasonal canopy management combinations.

Treatment		Berry soluble solid accumulation (°B)	Total berry sugar content (glucose & fructose) (g/vine)
No treatment (control)		21.1a	69.5c
Suckering & topping		21.4a	92.6ab
Leaf removal (33%):	Berry set (bunch zone)	21.1a	94.2ab
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower ½ of canopy)	21.0a	100.1a
Lateral removal (all):	Berry set (bunch zone)	21.1a	80.9abc
Lateral removal (all):	Berry set (bunch zone) Pea size (lower ½ of canopy)	21.4a	84.5abc
Lateral removal (all):	Berry set	21.2a	75.1bc
Lateral removal (all):	Pea size	21.3a	79.4abc

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

intensity and duration of exposure of buds are important requirements for continued fertility and budding (May, 1965; Smart *et al.*, 1982), the expected positive effect of the improved canopy light exposure of particularly the vines where laterals were removed (Table 3) was probably outclassed by a continuous redistribution of photosynthetic products and/or stimulating agents (such as hormones) to sinks other than the buds, thereby limiting bud reaction to light exposure and eventually production. The fact that the additional lateral (and leaf) removal was applied later than the period for the formation of inflorescence primordia and their initiation and differentiation (before bloom) (Swanepoel & Archer, 1988) could have contributed to this situation. The decrease in bunch rot found with lateral removal (and also with the rest of the canopy management treatments) is in agreement with the improved disease control normally found with better canopy microclimate (Koblet, 1987; Stapleton & Grant, 1992) and is evidence that bunch rot did not play a role either in the yield reduction found with lateral removal, compared to those treatments that included leaf removal instead. Soluble solid accumulation in the fruit was also not affected (Table 5). Similar results were found by Candolfi-Vasconcelos & Koblet (1990) and Koblet *et al.* (1993) and may either be the result of active transport from the canopy to this obviously important sink and/or may represent mobilisation of reserves from the cordon, trunk and roots.

However, regarding the latter possibility, starch values of the different root sizes would seem to indicate an opposite tendency during the period of study (Table 6), rather in line with previous results demonstrating the stimulating effect of an improved canopy microclimate and source:sink ratio by discriminative, judicious canopy management on root reserve accumulation (Hunter *et al.*, 1995a, 1995b). However, in spite of the possible equalising effect of the favourable soil conditions (data not shown) and intensive irrigation in this vineyard, lateral shoot removal ostensibly decreased root density, indicating a limitation of root development and distribution with a possible highlighting of existing negative effects through malnutrition in the long term (Freeman, 1983; Richards, 1983) (Table 6). The data also seem to be further evi-

TABLE 6

Starch content of roots of diffferent sizes and root density as affected by different seasonal canopy management combinations.

Treatment		**Starch content/root size (mg/g dry mass)**				**Root density/ m^2 profile wall**
		<0.5mm	**0.5–2mm**	**2–5mm**	**5–10mm**	
No treatment (control)		97.8ab	114.0a	117.7b	119.9a	351.7ab
Suckering & topping		120.0a	138.6a	168.4a	120.4a	347.0ab
Leaf removal (33%):	Berry set (bunch zone)	103.5ab	121.1a	148.1ab	165.3a	419.5a
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)	94.7ab	121.7a	134.5ab	151.8a	331.0ab
Lateral removal (all):	Berry set (bunch zone)	119.0ab	150.1a	138.3ab	159.4a	297.7ab
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)	100.5ab	111.8a	165.8a	152.6a	292.0b
Lateral removal (all):	Berry set	102.1ab	133.5a	165.4a	170.9a	264.5b
Lateral removal (all):	Pea size	85.9b	146.0a	158.3ab	173.0a	301.3b

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

dence of the positive relationship between root density and yield found in previous studies (Hunter & Le Roux, 1992; Swanepoel & Southey, 1989; Van Zyl, 1988). The decrease in root density with lateral shoot removal is interesting given the relatively high starch content of the roots. Root development must therefore have been affected by factors other than reserve availability, possibly regulatory reactions originating in the canopy.

Given the higher light intensity in the canopy (Table 3) and generally more exposed canopy of the lateral removal treatments, transpiration of the berries may have increased, concentrating the solutes, particularly during the very last stage of the ripening period (see McCarthy & Coombe, 1999). Water loss from the berry could therefore have balanced a possible reduction in soluble solid accumulation with this treatment, compared to the rest of the treatments. In fact, despite the lack of differences in total soluble solids, total contents of individual sugars in the berries at ripeness (g glucose plus fructose/total vine berry dry mass) were decreased by lateral removal, compared to the rest of the canopy management treatments (Table 5); though closely related in terms of the different groups of treatments, no direct relationship between yield and sugar accumulation occurred (Tables 2 & 5). Given the involvement of particularly glucose in the formation of several quality compounds and glycosides, a decrease in sugar content will eventually lead to lower grape and wine quality. It seems that the earlier and more severe the removal of laterals, the more the sugar content was reduced.

The decrease in sugar accumulation in the bunches of the treatments where lateral shoots were removed is conceivable considering the closeness of the laterals to the bunches and the very important role of leaves in this position in phloem unloading into the bunches throughout the season (Quinlan & Weaver, 1970; Hunter & Visser, 1988a, 1988b; Hunter *et al.,* 1994). Furthermore, younger and/or recently matured leaves in the top half of the canopy contribute to the photosynthetic and carbon distribution capacity of the canopy as a whole during the latter part of the season in particular (Hunter *et al.,* 1994), impacting on the availability of carbohydrates for bunch development and quality, as determined by studies involving radioactive labelling and removal of lateral shoots (Koblet & Perret, 1971; Koblet, 1987, 1988; Candolfi-Vasconcelos & Koblet, 1990). Total production (per vine) of individual sugars in the leaves on the main shoot at ripeness surprisingly showed little variation between treatments (Table 7). However, total sugar contents of the leaves on lateral shoots of lateral removal treatments were clearly reduced compared to those of the rest of the treatments, even when laterals were only removed in the bunch zone. Those treatments where no laterals were removed also had a higher sugar production of lateral shoots *versus* main shoots, whereas this production ratio was reversed for the lateral removal treatments. Clearly, in the case of the lateral removal treatments these effects relate to a shift in the main shoot leaves:lateral shoot leaves output ratio and the physical reduction in lateral shoot leaf area as a result of treatment, compared to the rest of the treatments. The lateral removal treatments had generally higher carbohydrate accumulation in the main shoot leaves (none of which were removed during treatment), which corresponds to the enhancement in photosynthetic activity and compensation theory mentioned with a reduction in source quantity. The source:sink differences between older and younger leaves (Ruffner *et al., 1990;* Hunter *et al.,* 1994) are also evident, sugar levels decreasing from mature/large to young/small leaves.

Considering their total remaining leaf area, the non-treated vines were expected to have higher total carbohydrate contents; the relatively low contents are, however, evidence of the well-known limiting effect of shade on leaf performance and shoots not being optimally accommodated on the trellising system to allow better leaf exposure and leaf area:yield ratio. The lateral shoots of the non-treated and leaf removal treatments noticeably contributed to the carbohydrate pool of the canopy, resulting in higher total carbohydrate contents compared to those of the lateral removal treatments. As for the lateral shoot removal treatments, the carbohydrates available in the leaves of especially the secondary lateral shoots were probably mostly hoarded for their own growth and development, limiting transport to the bunches. Despite an ostensible increase in photosynthetic activity (Table 4), the carbohydrate in particularly the main shoot leaves of the lateral removal treatments may also have been mobilised from

TABLE 7

Sugar content (glucose plus fructose) of different leaf sizes on main and lateral shoots at ripeness as affected by different seasonal canopy management combinations.

Treatment		**Leaf sugar content (g/vine)**								
		Main shoot				**Lateral shoot**				**TOTAL**
		L	**M**	**S**	**Total**	**L**	**M**	**S**	**Total**	
No treatment		5.0	3.3	0.6	8.9	1.0	5.8	6.9	13.7	22.6
Suckering & topping		8.1	2.7	1.3	12.1	1.4	5.6	13.4	20.4	32.5
Leaf removal (33%):	Berry set (bunch zone)	5.4	1.8	0.5	7.7	1.6	5.0	4.6	11.2	18.9
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower ½ of canopy)	5.7	2.0	0.8	8.5	0.5	4.7	3.9	9.1	17.6
Lateral removal (all):	Berry set (bunch zone)	6.3	3.5	0.9	10.7	0.6	2.7	3.4	6.7	17.4
Lateral removal (all):	Berry set (bunch zone) Pea size (lower ½ of canopy)	5.3	2.4	0.5	8.2	0.3	3.0	4.0	7.3	15.5
Lateral removal (all):	Berry set	5.9	3.8	0.5	10.2	0.5	2.9	3.1	6.5	16.7
Lateral removal (all):	Pea size	5.8	2.2	1.2	9.2	0.3	1.0	2.4	3.7	12.9

L = Large leaves (> 70% of mature leaf size).
M = Medium leaves (30–70% of mature leaf size).
S = Small leaves (<30% of mature leaf size).

Values represent the means of five replications.

perennial storage organs, represents altered distribution patterns in order to preferentially direct energy to compensatory growth, or may be evidence of a reduction in carbon drain from these leaves in order to maintain functionality.

It is evident that accumulation of sugar in the ripening bunches not only depends on available sugar in the leaves (Tables 5 & 7), but also on bunch microclimate conditions conducive to sugar accumulation *via* e.g. a stimulation in enzyme activity (invertase) as well as berry transpiration, affecting the water potential gradient and phloem sap flow to the bunches (Ollat & Gaudillère, 1996; Dreier *et al.,* 1998, and references therein) along with the proposed apoplast/symplast compartmentation breakdown in the berry (Lang & Düring, 1991; Dreier *et al.,* 1998). Efficient and well-timed canopy management would therefore greatly affect the translocation and accumulation of photoassimilates in berries and eventual grape and wine quality.

Growth compensation: When seasonal canopy management practices (removal of shoot tips or leaves) are applied to the grapevine, compensation normally occurs in the form of additional lateral shoot growth (Kliewer & Fuller, 1973; Candolfi-Vasconcelos & Koblet, 1990; Hunter & Visser, 1990a). In this experiment, the remaining lateral shoot leaf area, number of lateral shoots, and total shoot (main plus lateral) length per vine were decreased by lateral shoot removal (Table 8). However, considering the leaf area removed during treatment as well as the total remaining leaf area per vine, it is evident that considerable compensatory growth was induced by lateral shoot removal (Table 9). This is particularly striking when total lateral leaf area produced during the growth season is taken into account, which in most cases was more than 30% higher than that of leaf removal treatments. Minimal compensatory growth occurred for leaf removal treatments. Although topping stimulated the growth of laterals (cf. also Kliewer & Bledsoe, 1987; Koblet, 1987), lateral removal *per se* also had a stimulatory role. The growth compensation can under severe conditions, in addition to the formation of lateral shoots, also represent an increase in leaf mass (Candolfi-Vasconcelos & Koblet, 1990; Hunter & Visser, 1990a) and lamina expansion (Fournioux, 1997) of the remaining leaves. As mentioned before, the additional compensatory growth and thus energy demand brought about by lateral removal would have impacted directly on the metabolic processes of the grapevine and particularly the availability and distribution of carbohydrates for bunch development. As shown, this will not occur when judicious leaf removal, instead of lateral removal, is applied (Hunter *et al.,* 1995a).

The plant hormones such as cytokinins (produced in the roots), abscisic acid (ABA) (produced in the roots and mature leaves), gibberellic acid (GA) (produced in the young shoots and possibly roots) and auxin (produced in young shoots) (Davies, 1995) may be involved in compensatory growth. Working with Brussels sprouts, Thomas (1983) stated that the leaves may produce substances inhibitory to bud growth or they may deprive the buds of, for example, growth-promoting hormones such as cytokinins and gibberellins translocated from the roots; removal of leaves stimulated the outgrowth of axillary buds. Bud inhibition may also be due to basipetal movement of auxin from the shoot apex (Phillips, 1975). This inhibitory influence of the leaf on axillary bud growth apparently diminishes with increase in age (Snow, 1929; Thomas, 1983). That would explain the apparently later initiation of lateral shoots in the case of the non-topped control vines (large-leaf lateral shoot leaf area is smaller compared to that of leaf removal treatments) in this study (Table 8). Hunter & Visser (1990a) also found that the later leaf removal was applied, the fewer lateral shoots were formed. According to Fournioux (1998) young leaves control the growth of buds (lateral growth) through basipetal inhibition, which continues for the duration of leaf

TABLE 8

Vegetative growth as affected by different seasonal canopy management combinations.

Treatment		**Lateral shoot leaf area (dm^2/vine)**			**Number of lateral shoots/ main shoot**	**Number of lateral shoots/ vine**	**Total shoot length (m/vine)**
		L	**M**	**S**			
No treatment		25.1a	397.4ab	337.3a	10.0a	202.0a	69.2a
Suckering & topping		45.6a	408.6ab	252.6c	10.0a	187.0a	61.3a
Leaf removal (33%):	Berry set (bunch zone)	43.6a	417.3a	301.2ab	10.0a	194.0a	68.0a
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)	15.7a	333.6ab	279.9bc	9.5a	181.5a	60.0ab
Lateral removal (all):	Berry set (bunch zone)	18.0a	273.8bc	262.4bc	9.0a	165.0a	51.2bc
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)	10.2a	170.1c	208.7d	5.5b	108.5b	43.2cd
Lateral removal (all):	Berry set	10.4a	179.3c	204.1d	3.5b	70.0b	40.8d
Lateral removal (all):	Pea size	9.6a	158.7c	148.8e	4.5b	81.5b	41.9cd

L = Large leaves (> 70% of mature leaf size).
M = Medium leaves (30–70% of mature leaf size).
S = Small leaves (<30% of mature leaf size).

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

TABLE 9

Vegetative growth compensation as affected by different seasonal canopy management combinations.

Treatment		**Total leaf area removed (dm^2/vine)**		**Total remaining leaf area (dm^2/vine)**	**Total lateral shoot leaf area produced during the growth season (dm^2/vine)**
		Main shoot & lateral shoot	**Lateral shoot**		
No treatment (control)				1359.3a	706.8b
Suckering & topping				1192.6bc	759.8b
Leaf removal (33%):	Berry set (bunch zone)	146		1229.4b	*803.0b
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)	458		1083.7cd	*757.4b
Lateral removal (all):	Berry set (bunch zone)		252	1028.7d	806.6b
Lateral removal (all):	Berry set (bunch zone) Pea size (lower $^1/_2$ of canopy)		1017	876.0e	1406.4a
Lateral removal (all):	Berry set		1072	856.2e	1466.2a
Lateral removal (all):	Pea size		1118	823.1e	1435.4a

*Approximately 30% of leaves removed during leaf removal consisted of leaves situated on lateral shoots (data not shown).

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

growth; once lateral growth is activated, the laterals and the apical young leaves are in competition in a non-polarised way. Using Riesling vines, Palma & Jackson (1989) found that gibberellins elongated the primordial shoot by increasing internode length, but tended to depress leaves, inflorescences and tendrils, whereas cytokinins and abscisic acid may balance GA and overcome these depressive effects. Auxins had opposite effects to GA_3. In a review, Phillips (1975) presented evidence that auxin originating in the young leaves of the apical bud serves as the signal influencing either cytokinin synthesis or utilisation within lateral buds or distribution of root synthesised cytokinins; the inhibition of lateral bud growth is suggested to be a consequence of cytokinin deficiency. It is, however, stated that not only cytokinins, but also other growth regulators (auxin, gibberellin) plus nutrients and water are ultimately required for full outgrowth of laterals.

It seems likely that restricted root development, which seems to be the case in this study for the lateral removal treatments (Table 6), may limit the production and transport of cytokinins to leaves and reduce photosynthetic activity, similar to effects found with soil-drying of maize plants (Davies *et al.,* 1986). A reduction in supply of cytokinins to the canopy may affect canopy expansion, photosynthetic capacity and thus carbohydrate accumulation in the bunch. Results of Tamas *et al.* (1979) on *Phaseolus vulgaris* indicated that fruits play a major role in the regulation of shoot growth and total plant size through control of axillary bud dormancy. It is therefore possible that the reverse situation can also occur, i.e. axillary bud growth controlling yield capacity. Hayes & Patrick (1985) found that GA, indole-3-acetic acid (IAA) and kinetin application to decapitated stems of *Phaseolus vulgaris* increased the pool size of free-space sugars at the hormone-treated region of the stem and deduced from that that hormonal action promoted the processes determining the rates of sugar unloading from sieve element companion cell complexes. Quinlan & Weaver (1970) showed that treatment of a bearing grapevine shoot with GA_3 increased sink capacity and induced a compensatory movement of photoassimilates from an adjacent shoot to the treated shoot. This mechanism would also be possible when axillary buds are growing and hormones accumulate in the young shoots, thus redirecting flow of sugar from bunches.

It is quite conceivable that stress conditions as a result of compensatory growth were induced, particularly by the severe lateral removal treatments in this study. Although ABA accumulation is generally associated with stress conditions, the role of ABA in the growth of lateral buds is controversial – a stimulatory role seems more apparent than an inhibitory role (Walton, 1980). Apparently, IAA plays a role in maintaining ABA levels and this relationship may be involved in apical dominance; however, this hypothesis is far from being elucidated. Koussa *et al.* (1998) found that the removal of leaves before leaf fall resulted in an increase in free ABA (*cis*-ABA) in the buds and internodes, indicating that free ABA was translocated from buds and internodes to leaves during this period. The roots also supplied ABA to the shoots during this period. The ABA may inhibit stomatal opening (Loveys & Kriedemann, 1973; Liu *et al.,* 1978). The source of ABA regulating leaf gas exchange was suggested to be leaves rather than roots, but the continued presence of ABA in the xylem is dependent on supply from the roots; transport to roots and back to leaves occurs naturally (Loveys, 1984). The raising of ABA levels appears to be under control of turgor pressure (Walton, 1980; Davies *et al.,* 1986; Zeevaart & Creelman, 1988). Our field-grown plants, however, did not show any marked water potential differences between canopy management treatments (Table 4); in fact, the non-treated plants were the most stressed, probably as a result of their larger leaf area (Table 9). Loveys & Kriedemann (1974) found stomatal resistance and ABA levels of Cabernet Sauvignon mature leaves to increase independently of decreased water potential after photoperiod extension, fruit removal and stem cincturing. Fruit removal increased ABA levels in nearly all cases, while photosynthesis was reduced. Düring (1977) found IAA in the berries to increase during the first phase of berry growth and to decrease before the start of ripening, whereas ABA accumulated during ripening parallel to the increase in sugar accumulation. Investigating the role of ABA in the distribution of sucrose and asparagine, Porter (1981) suggested that endogenous ABA in plant organs could serve as an important factor in the directional control of assimilate transport in plants. This hormone is therefore firmly involved in the regulation of photosynthetic performance and leaf-fruit communication (Coombe, 1989; Eschrich, 1989).

Canopy composition: It is evident that, although main shoot leaf area/g fruit was similar between treatments (albeit lower than that of the control), the contribution of lateral leaf area, particularly that of medium and small leaves, to yield was generally decreased by lateral shoot removal (Table 10). In spite of this, total leaf area/g fruit was never less than 12 cm^2 (Table 11), which is accepted as being required to adequately ripen the fruit in terms of soluble solid accumulation (Hunter & Visser, 1990b, and references therein). In fact, it was mostly similar to that of the leaf removal treatment which produced the highest yield (Table 2) and individual sugar accumulation (Table 5) and yet yields and hexose accumulation of the lateral shoot removal treatments were noticeably lower than those of the shoot positioning-suckering-topping and shoot positioning-suckering-topping-leaf removal treatments.

Collectively, the results clearly indicate that 12 cm^2 leaf area/g fruit (or for that matter any leaf area), even if this leaf area is well

TABLE 10

Main and lateral shoot leaf area per gram fresh fruit as affected by different seasonal canopy management combinations.

Treatment		**Main shoot leaf area (dm^2)/g fruit**	**Lateral leaf area (cm^2)/g fruit**	**Main shoot leaf area & lateral shoot leaf area (cm^2)/g fruit**		
				L	**M**	**S**
No treatment		10.5a	14.1a	5.1a	12.4a	7.0a
Suckering & topping		7.5cde	10.9abc	4.8a	8.9bc	4.6b
Leaf removal (33%):	Berry set (bunch zone)	7.0de	12.6ab	4.4ab	10.4b	5.4ab
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower 1/2 of canopy)	6.5e	9.2cde	3.5b	7.5cd	4.4b
Lateral removal (all):	Berry set (bunch zone)	8.2bc	9.3bcd	3.9ab	8.7bcd	5.3ab
Lateral removal (all):	Berry set (bunch zone) Pea size (lower 1/2 of canopy)	7.9cd	6.6de	4.2ab	6.7d	4.0b
Lateral removal (all):	Berry set	8.1cd	5.9e	3.5b	7.4cd	3.4b
Lateral removal (all):	Pea size	9.4ab	5.9e	4.4ab	7.6cd	3.3b

L = Large leaves (> 70% of mature leaf size).
M = Medium leaves (30–70% of mature leaf size).
S = Small leaves (<30% of mature leaf size).

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

TABLE 11

Total leaf area per gram fresh fruit and main leaf area:lateral leaf area ratio as affected by different canopy management combinations.

Treatment		Total leaf area (cm^2)/g fruit	Main shoot leaf area:lateral shoot leaf area
No treatment (control)		24.6a	0.79cd
Suckering & topping		18.3bc	0.69cd
Leaf removal (33%):	Berry set (bunch zone)	20.1b	0.62d
Leaf removal (33%):	Berry set (bunch zone) Pea size (lower ½ of canopy)	15.3cd	0.73cd
Lateral removal (all):	Berry set (bunch zone)	18.2bc	0.89c
Lateral removal (all):	Berry set (bunch zone) Pea size (lower ½ of canopy)	14.9cd	1.27b
Lateral removal (all):	Berry set	12.7d	1.45ab
Lateral removal (all):	Pea size	15.3cd	1.61a

Values followed by the same letter within each column do not differ significantly ($p \leq 0.05$).

exposed to sunlight, cannot generally be accepted as a norm, but that the composition of this leaf area must be taken into account, because it plays a critical role in the efficient functioning of the canopy, the nourishing of the bunches and the realisation of the full potential of the vine in terms of yield and fruit quality. This confirms the conclusions reached by Koblet & Perret (1971), Koblet (1987, 1988) and Candolfi-Vasconcelos & Koblet (1990) and should be kept in mind whenever grapevine foliage is restructured towards a specific objective; naturally, foliage must be well exposed.

The ratio of main shoot leaf area to lateral shoot leaf area for the treatments with highest production was approximately 0.7 (Table 11). In practical terms, the best performance for the 1.5 m cordon vines under the conditions of this study was obtained with the following criteria, namely 18 – 19 shoots/vine, main shoot length of 1.4 – 1.5 m, 12 – 13 lateral shoots/main shoot with a length of 15 – 17 cm/lateral, and four leaf layers from side to side in the canopy. Lateral shoots must be positioned over the full height of the canopy.

General: Although the reason that the particular effects were obtained with the treatments in the study can be argued to a reasonable extent on a physiological basis, the question as to what triggered the various responses, particularly in the case of the lateral removal treatments, still remains. Clearly, a conclusive answer regarding the different substances which may be regulatory in terms of axillary bud growth is not available, e.g. any one or combination of hormones may be inhibitory or stimulatory through direct or indirect effects. According to Herold (1980), direct effects of all the hormones mentioned on photosynthesis are evident, and changes in activity of sinks (i.e. in this study mainly the developing bunch and growth of axillary buds) are also sometimes accompanied by increased or decreased synthesis of these hormones. The link between production of the hormone in sink tissue, translocation to the source and ensuing source response is, however, still an issue to be elucidated. In addition, the water and nutrient status of the sink and source as well as the prevailing microclimatic conditions have a great bearing on the distribution mechanisms in the grapevine.

CONCLUSIONS

Canopy composition perspectives are provided which contribute to the refinement of canopy criteria for high production standards. The results stress the presence of lateral shoots in the grapevine canopy and indicate that lateral shoots have a more important function that realised up till now. It is evident that the removal of lateral shoots cannot be recommended as part of a canopy management programme; significant additional compensatory growth is induced, impacting on the availability and distribution of energy in the canopy. Leaf removal is recommended instead. The results clearly showed that the presence of lateral shoots and correctly applied and timed canopy management (suckering, shoot positioning, topping and leaf removal) during the period just after budding to pea berry size will have a positive role in the attainment of maximum yield and grape quality. Sugar accumulation in bunches not only depends on the availability of sugar in the leaves, but also on microclimatic conditions conducive to sink strength.

It seems critical that more attention on a physiological basis be devoted to the understanding of the trigger mechanisms and communication between the different parts of the grapevine (as complicated by manipulation) in conjunction with merely stating reactions of the grapevine to the testing of hypotheses. This is critical for improving our knowledge and manipulation of events impacting on grape composition and eventual wine quality. Hormonal actions may have a firm bearing on compensatory growth and development in the grapevine in reaction to canopy manipulation, complicating many of the hitherto relatively simply explained observations of many investigations.

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