Distribution of ^{14}C-Photosynthetate in the Shoot of *Vitis vinifera* L. cv Cabernet Sauvignon
II. The Effect of Partial Defoliation.*

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The effect of partial defoliation of *Vitis vinifera* L. cv Cabernet Sauvignon on the distribution of photosynthetates, originating in leaves in different positions on the shoot at berry set, pea size, véraison and ripeness stages, was investigated.
Partial defoliation (33% and 66%) resulted in a higher apparent photosynthetic effectivity for all the remaining leaves on the shoot. The pattern of distribution of photosynthetates would seem to stay the same between the defoliation treatments. The control vines were found to carry excess foliage. Optimal photosynthetic activity of all the leaves on the vine was therefore not reached.

In South Africa, vegetative growth of vines generally tends to be excessive, mainly because of high temperatures as well as irrigation practices during the growth season. According to Dry & Smart (1986) excessive vigour results from the use of planting material free of harmful viruses, advances in fertilization and irrigation technology and advances in pest and disease control. The concomitant increase in shoot growth and leaf area causes the canopy interior to become dense and to receive insufficient sunlight, which is detrimental to both grape and wine quality (Koblet, 1984; Smart, 1985; Smart *et al.,* 1985a; 1985b). Maximum photosynthesis requires a light intensity of ca. 400 W/m^2 (Kriedemann, 1977). Foliage management therefore becomes a major consideration for the viticulturist and a means must be found by which the full photosynthetic potential of the interior leaves can be exploited.

Many investigators have found that the photosynthetic efficiency of the leaves increases when the size of the photosynthetic source (leaf area) is decreased in relation to the size of the sinks (roots, trunk, shoots, fruits) (Buttrose, 1966; May, Shaulis & Antcliff, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson, Weaver & Paige, 1982). The contribution of leaves of various physiological ages to vegetative and reproductive growth in relation to leaf area at different developmental stages during the growth season must, however, be determined before any recommendations to reduce excess vegetative growth can be made.

This investigation was done to determine the effect of leaf area of Cabernet Sauvignon on the movement of photosynthetates, originating in leaves in different positions on the shoot, at berry set, pea size, véraison and ripeness stages.

MATERIALS AND METHODS

Experimental vineyard

Details of the experimental vineyard used as well as the methods for application and determination of radioactivity were given by Hunter & Visser (1988).

Experimental design

The experiment was laid out as a completely randomized 3 x 3 x 4 factorial design. The three factors were: defoliation treatments, applied to the whole vine (0%, 33%, 66%); application of $^{14}CO_2$ to three positions on one shoot per vine (apical, middle, basal); and developmental stages (berry set, pea size, véraison, ripeness). The defoliation treatments were initiated from approximately one month after budding, while the $^{14}CO_2$ treatments were applied at each of the four developmental stages. There were nine replications, comprising one-vine plots, for each of the 36 treatment combinations.

Defoliation treatments

Defoliation treatments consisted of removing the first leaf out of every three leaves (33%) and removing the first two leaves out of every three leaves (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 the initial defoliations were removed in the same manner as described above at approximately monthly intervals.

Statistical analyses

A standard VORI factorial statistical software package was used to test significant differences among treatment means. Log transformations, to compensate for heterogeneity of variance, were done on the raw data.

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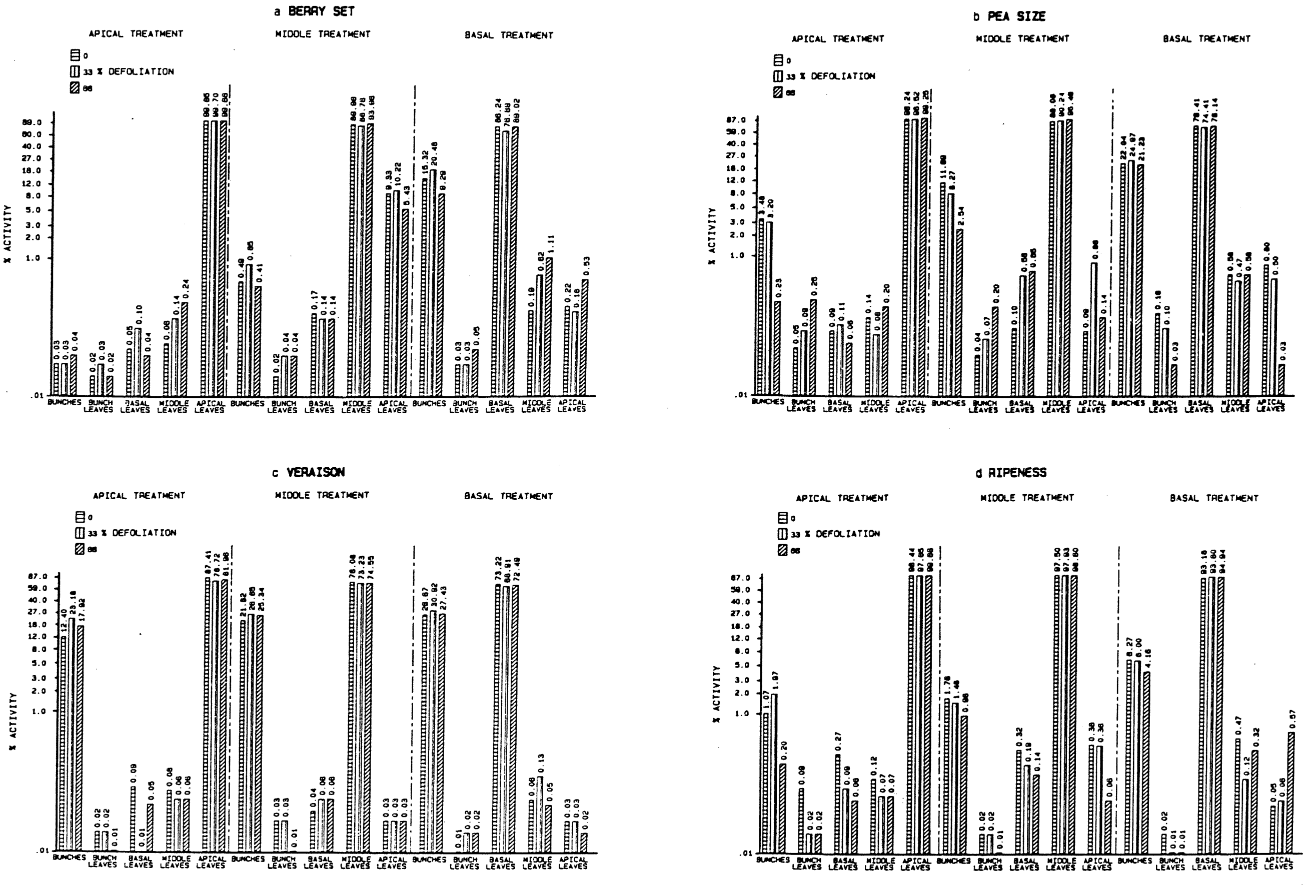

FIG. 1

The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthetate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness stage, expressed as a percentage of total activity – treated part included. (Note log scale on y-axis).

RESULTS AND DISCUSSION

Percentage activity

This was calculated as follows: Total ^{14}C-activity of the parts concerned was calculated on a mass basis and subsequently expressed as a percentage of the total activity of all the parts of the shoot.

Treated part included: From Fig. 1 it would seem that no major differences in the course of translocation of labelled photosynthetates occurred between defoliation treatments at any of the developmental stages. The impression is that translocation of radioactivity has not progressed very far after 24h for all defoliation treatments. Irrespective of leaf position, application of $^{14}CO_2$ at véraison stage nevertheless resulted in a prominent accumulation of photosynthetic products in the bunches. Partial defoliation resulted in an increased translocation from the $^{14}CO_2$-treated part and a concomitant higher accumulation in the bunches at véraison. The basal leaves strikingly contributed the most to the bunches, regardless of degree of defoliation and developmental stage of the vine.

Treated part excluded: By excluding the treated part, the distribution pattern and site of accumulation of ^{14}C become more pronounced (Fig. 2). No definite relationship between degree of defoliation and accumulation in either reproductive or vegetative organs exists.

Total activity

The effect of defoliation and developmental stage of the vine on the total ^{14}C-activity of each treated part, expressed in kBq, is depicted in Table 1. The approximate total activity per shoot, over all four developmental stages, for the 0%, 33% and 66% defoliation treatments, amounts to 949, 846 and 801 kBq, respectively. Because no significant differences in the accumulation and distribution patterns between the defoliation treatments could be found (Fig. 1 & 2), the total ^{14}C-activities (Table 1) can be assumed to provide an indication of the differences in total photosynthetic activity between the defoliation treatments. Considering the fact that the remaining leaf areas of the 33% and 66% defoliation treatments were considerably less (approximately 74% and 54%, respectively) than that of the 0% defoliation treatment (Table 2), it is clear that the remaining leaves of the partially defoliated vines were proportionally photosynthetically more active, especially those of the middle and basal parts of the shoot (Table 1). It would therefore seem that the remaining leaves of the partially defoliated vines were able to compensate adequately for the loss of leaves and that partial defoliation can be safely applied in practice. Furthermore, the application of partial defoliation can be advantageous due to an improved aeration of the canopy and an increased light penetration. These ad-

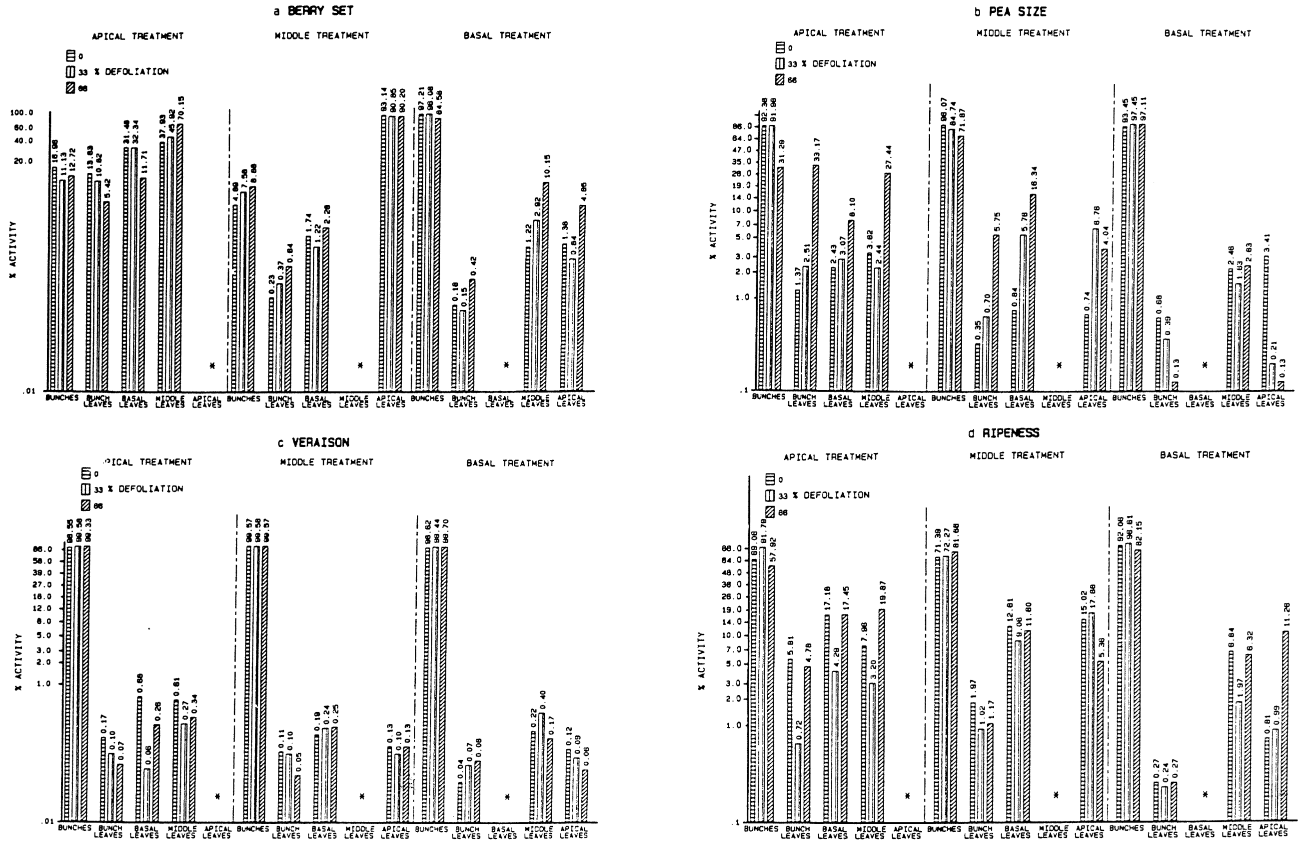

FIG. 2

The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthetate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness stage, expressed as a percentage of total activity – treated part (*) excluded. (Note log scale on y-axis).

TABLE 1

The effect of defoliation and developmental stage on the total ^{14}C-activity of each treated part of the shoot, expressed in kBq.

Developmental stage	BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES				TOTAL ^{14}C/SHOOT		
	*0	*33	*66	Mean	0	33	66	Mean	0	33	66	Mean	0	33	66
Berry set	372,94	298,77	334,39	335,37[a]	374.21	457.77	441.70	424.56[a]	1035.16	777.50	701.51	838.05[a]	1782.31	1534.04	1477.60
Pea size	159,98	172,12	167,32	166,47[a]	190,82	186,92	174,70	184,15[a]	315,13	288,43	305,57	303.04[b]	665.93	647.47	647.59
Véraison	221,40	176,53	185,90	194,61[a]	229,75	205,65	174,75	203,38[a]	193,53	192,91	170,67	185,70[c]	644.68	575.09	531.32
Ripeness	224,16	191,16	147,98	187,77[a]	198,92	178,43	172,39	183,24[a]	279,16	260,28	225,50	254,98[c]	702.24	629.87	545.87
Mean	244,62[a]	209,65[a]	208,89[a]		248,42[a]	257,19[a]	240,88[a]		445,75[a]	379,78[a]	350,81[b]		948.79	846.62	800.60
CV(%)	28,81				28,63				8.93						

* Percentage defoliation
Values designated by the same symbol do not differ significantly (P≤0,05) for each plant part.

TABLE 2

The effect of defoliation and developmental stage of the vine on the total areas (cm^2) of leaves in different positions on the shoot.

Developmental stage	BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	*0	*33	*66	Mean	0	33	66	Mean	0	33	66	Mean	0	33	66	Mean
Berry set	408,27	392,13	300,92	367,11[a]	1021,73	787,96	569,35	793,01[b]	744,95	534,77	386,95	555,56[b]	191,68	166,57	102,95	153,73[c]
Pea size	426,37	236,65	244,42	302,48[b]	1220,22	988,74	570,86	926,61[a]	1170,13	870,46	640,82	893,81[a]	403,51	267,14	198,49	289,72[b]
Véraison	347,11	323,02	199,25	289,79[b]	1163,45	963,54	554,54	893,82[a]	1089,36	978,22	604,82	890,80[a]	448,94	315,00	236,73	333,55[a]
Ripeness	357,92	254,50	215,33	275,92[b]	1169,98	763,65	622,93	852,19[a]	1196,03	838,15	765,14	933,11[a]	423,01	309,31	263,32	331,82[a]
Mean	384,92[a]	301,58[b]	239,98[c]		1143,84[a]	875,98[b]	579,41[c]		1050,12[a]	805,40[b]	599,43[c]		366,79[a]	264,46[b]	200,37[c]	
CV(%)	10,16				6,13				5,87				5,73			

* Percentage defoliation
Values designated by the same symbol do not differ significantly (P≤0,05) for each plant part.

TABLE 3

The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthetate, expressed as specific activity in kBq/g dry mass.

Developmental stage	BUNCHES				BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean
Berry set	0,19^{g}	3,80^{c}	73,41^{a}	25,80^{a}	0,12^{a}	0,09^{a}	0,10^{a}	0,10^{b}	0,12^{d}	0,17^{d}	109,97^{a}	36,75^{a}	0,24^{f}	204,24^{a}	1,23^{e}	68,57^{a}	991,67^{a}	64,19^{d}	1,62^{e}	352,49^{a}
Pea size	0,77^{f}	2,00^{d}	7,52^{b}	3,43^{b}	0,18^{a}	0,16^{a}	0,16^{a}	0,17^{a}	0,05^{d}	0,14^{d}	48,67^{b}	16,29^{b}	0,11^{g}	45,15^{b}	0,25^{f}	15,17^{b}	186,96^{b}	0,20^{f}	0,31^{f}	62,49^{b}
Véraison	0,17^{e}	2,06^{d}	2,48^{c}	1,91^{c}	0,02^{a}	0,03^{a}	0,03^{a}	0,03^{c}	0,02^{d}	0,03^{d}	50,23^{b}	16,76^{b}	0,03^{g}	37,14^{c}	0,03^{g}	12,40^{c}	103,25^{c}	0,03^{g}	0,03^{g}	34,44^{c}
Ripeness	0,03^{h}	0,05^{h}	0,25^{g}	0,11^{d}	0,09^{a}	0,02^{a}	0,02^{a}	0,02^{c}	0,05^{d}	0,06^{d}	34,60^{c}	11,57^{c}	0,03^{g}	29,95^{d}	0,07^{g}	10,02^{c}	101,67^{c}	0,20^{f}	0,19^{f}	34,02^{c}
Mean	0,54^{c}	1,98^{b}	20,92^{a}		0,09^{a}	0,08^{a}	0,08^{a}		0,06^{b}	0,10^{b}	60,87^{a}		0,10^{c}	79,12^{a}	0,39^{b}		345,89^{a}	16,26^{b}	0,54^{c}	
CV(%)	27,82				115,60				17,73				18,05				12,80			

Apical (A), Middle (M) and Basal (B) application of $^{14}CO_2$
Values designated by the same symbol do not differ significantly ($P \leq 0,05$) for each plant part.

TABLE 4

The effect of defoliation and developmental stage of the vine on the moisture content (%) of leaves in different positions on the shoot.

Developmental stage	BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	0*	*33	*66	Mean	0	33	66	Mean	0	33	66	Mean	0	33	66	Mean
Berry set	72,06	72,21	71,40	71,89^{a}	73,29	73,10	73,02	73,14^{a}	73,61	73,53	73,77	73,64^{a}	74,81	74,46	75,12	74,79^{a}
Pea size	68,33	67,16	67,78	67,76^{b}	70,23	70,18	70,80	70,40^{b}	70,32	70,70	71,27	70,76^{b}	71,89	72,58	73,30	72,59^{b}
Véraison	66,77	64,13	60,52	63,80^{c}	64,96	65,19	63,38	64,51^{c}	65,35	65,00	64,74	65,03^{c}	65,04	65,95	66,52	65,83^{c}
Ripeness	64,64	61,64	60,62	62,30^{d}	63,06	60,62	59,57	61,09^{d}	61,48	60,82	60,70	61,00^{d}	61,52	60,52	63,28	61,77^{d}
Mean	67,95^{a}	66,29^{b}	65,08^{c}		67,89^{a}	67,27^{b}	66,69^{c}		67,69^{a}	67,51^{a}	67,62^{a}		68,31^{b}	68,38^{b}	69,55^{a}	
CV(%)	1,05				0,79				0,94				1,02			

* Percentage defoliation
Values designated by the same symbol do not differ significantly ($P \leq 0,05$) for each plant part.

vantages may be beneficial with regard to pest and disease control, accumulation of colouring compounds in the grapes, and fruitfulness of the basal buds in the following season. The marked increase in photosynthetic activity of the apical leaves at ripeness stage possibly concentrated photosynthetic products for the regrowth of shoot tips.

Specific activity

Specific activity: From the specific activity (kBq/g dry mass) it is evident that the photosynthetic activity of all parts decreased during the growth season (Table 3). This probably resulted from an increased senescence as verified by the decreasing moisture content of the leaves (Table 4). In order to remain biochemically active, vine leaves need to maintain a high moisture content (Kriedemann, 1977). The concomitant decrease in specific activity in the bunches (Table 3) probably resulted from the former as well as berry growth. The effectivity of the leaves of all defoliation treatments decreased as they were progressively situated deeper into the canopy, thus receiving less light (Table 5).

The remaining leaves of the 33% and 66% defoliation treatments prominently demonstrated the highest photosynthetic efficiency, irrespective of leaf position, especially during the early developmental stages of the vine (Fig. 3). Considering their significantly lower total leaf area (Table 2), it seems that the full photosynthetic capacity of the leaves of the control vines was not used (also Table 1). This is in agreement with previous reports about the source : sink relationship (Buttrose, 1966; May *et al.*, 1969; Kliewer, 1970; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978: Scholefield, Neales & May, 1978; Johnson *et al.*, 1982). However, this finding may also be linked to that of Smart (1973), namely that the exposure of specific leaves to direct light may be of more importance than total light interception in determining yields of vigorous vines.

TABLE 5

The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthetate, expressed as specific activity in kBq/g dry mass.

Defoliation (%)	BUNCHES				BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean
0	0,51^{a}	1,44^{a}	20,68^{a}	7,55^{b}	0,06^{a}	0,04^{a}	0,06^{a}	0,05^{b}	0,06^{d}	0,07^{d}	46,04^{c}	15,39^{c}	0,08^{c}	52,54^{b}	0,16^{c}	17,59^{c}	273,14^{c}	11,35^{d}	0,49^{f}	94,99^{c}
33	0,64^{a}	2,89^{a}	18,14^{a}	7,22^{a}	0,07^{a}	0,07^{a}	0,09^{a}	0,08^{b}	0,07^{d}	0,14^{d}	51,84^{b}	17,35^{b}	0,12^{c}	89,48^{a}	0,17^{c}	29,92^{b}	334,69^{b}	17,22^{d}	0,28^{f}	122,73^{b}
66	0,48^{a}	1,61^{a}	23,92^{a}	8,67^{a}	0,13^{a}	0,12^{a}	0,08^{a}	0,11^{a}	0,05^{d}	0,09^{d}	84,72^{a}	28,29^{a}	0,11^{c}	95,33^{a}	0,85^{c}	32,10^{a}	419,82^{a}	19,90^{d}	0,85^{e}	146,86^{a}
CV (%)	27,82				115,60				17,73				18,05				12,80			

Apical (A), Middle (M) and Basal (B) application of $^{14}CO_2$
Values designated by the same symbol do not differ significantly ($P \leq 0,05$) for each plant part.

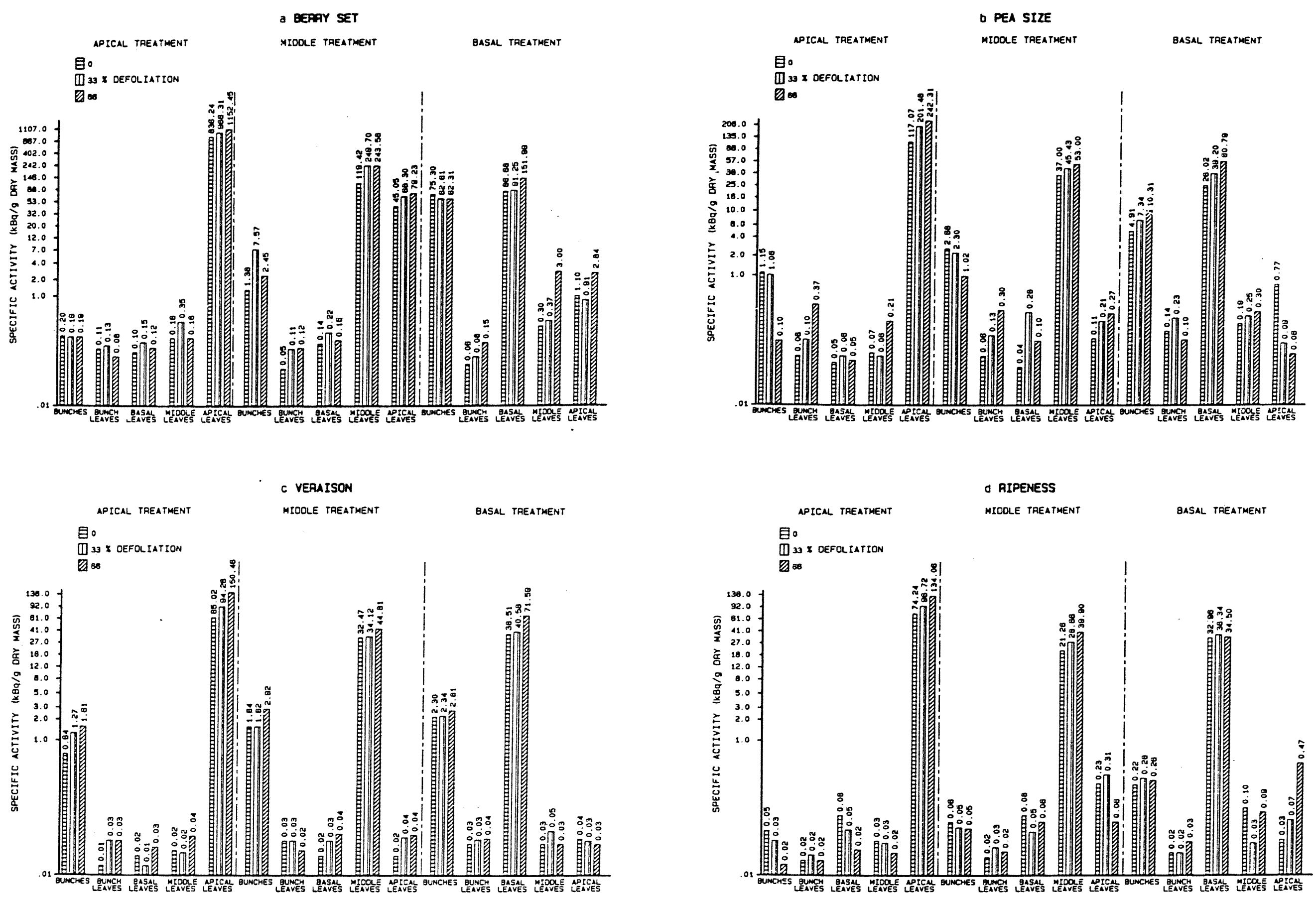

FIG. 3

The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthetate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness stage, expressed as specific activity in kBq/g dry mass. (Note log scale on y-axis).

Activity/leaf area (Bqx10^2/cm^2): This activity again verifies the much higher photosynthetic activity of the leaves of the partially defoliated vines, generally increasing with degree of defoliation (Table 6). The higher photosynthetic activity of the leaves of the 33% and 66% defoliation treatments could have resulted from a decrease in source capacity, which caused the leaves to photosynthesize more effectively to supply the needs of the vine and/or from a more efficient penetration of sunlight. However, assuming that the apical leaves received the same quanta sunlight and still showed marked differences between defoliation treatments, it can readily be accepted that the differences in photosynthetic capacity mainly resulted from the former. It must, however, be stressed that sunlight exposure could have made a larger contribution for the leaves situated deeper into the canopy.

Regardless of degree of defoliation, the apical leaves demonstrated the highest photosynthetic efficiency (Table 6). Although a significant decrease in photosynthesis of the apical leaves was observed up to véraison stage, it is again evident that activity significantly increased at ripeness (Table 7). In contrast to the apical leaves, very low activity was generally detected in the bunch leaves, verifying their poor capacity as sinks. This was possibly due to senescence as well as insufficient penetration of sunlight, especially in the case of the control vines, as is evident from the higher mean

TABLE 6

The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthetate, expressed as specific activity in Bqx10^2/cm^2 leaf area.

Defoliation (%)	BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean
0	0,11^a	0,19^a	0,06^a	0,12^a	0,14^a	16,69^a	163,20^a	60,01^a	0,20^c	158,30^a	0,32^b	52,94^b	529,47^b	37,40^c	1,22^c	189,36^b
33	0,33^a	0,24^a	0,24^a	0,27^a	0,25^a	31,46^a	167,34^a	66,35^a	0,15^c	187,57^a	0,68^b	62,80^b	847,05^a	30,92^c	0,23^c	292,73^b
66	0,83^a	0,12^a	0,42^a	0,45^a	0,19^a	3,06^a	190,21^a	64,49^a	0,30^c	227,12^a	1,39^b	92,94^a	913,36^a	117,29^c	1,04^d	343,89^a
CV(%)	64,99				45,24				24,84				17,15			

Apical (A), Middle (M) and Basal (B) application of $^{14}CO_2$
Values designated by the same symbol do not differ significantly ($P \leq 0,05$) for each plant part.

TABLE 7

The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthetate, expressed as specific activity in $Bqx10^2/cm^2$ leaf area.

Developmental stage	BUNCH LEAVES				BASAL LEAVES				MIDDLE LEAVES				APICAL LEAVES			
	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean	A	M	B	Mean
Berry set	0,20^{b}	0,13^{b}	0,10^{b}	0,14^{b}	0,43^{c}	0,25^{c}	332,51^{a}	111,06^{a}	0,39^{d}	381,80^{a}	2,68^{c}	128,29^{a}	1076,33^{a}	246,46^{c}	2,63^{d}	441,81^{a}
Pea size	1,32^{a}	0,41^{a}	0,26^{a}	0,66^{a}	0,18^{c}	0,76^{c}	139,49^{b}	46,81^{b}	0,29^{e}	256,32^{b}	0,30^{e}	85,64^{b}	693,59^{b}	0,62^{e}	0,11^{e}	231,44^{b}
Véraison	0,12^{b}	0,08^{b}	0,52^{b}	0,24^{b}	0,04^{d}	0,17^{c}	222,22^{b}	74,14^{b}	0,07^{f}	125,43^{b}	0,08^{f}	41,86^{c}	599,72^{b}	0,10^{f}	0,11^{f}	199,98^{c}
Ripeness	0,05^{b}	0,10^{b}	0,07^{b}	0,08^{b}	0,12^{d}	67,10^{c}	0,12^{d}	22,45^{c}	0,12^{f}	67,10^{b}	0,12^{f}	22,45^{c}	683,52^{b}	0,30^{e}	0,46^{e}	228,09^{b}
Mean	0,42^{a}	0,18^{a}	0,24^{a}		0,19^{c}	17,07^{b}	173,58^{a}		0,22^{c}	207,66^{a}	0,80^{b}		763,29^{a}	61,87^{b}	0,83^{c}	
CV(%)	64,99				45,24				24,84				17,15			

Apical (A), Middle (M) and Basal (B) application of $^{14}CO_2$

Values designated by the same symbol do not differ significantly ($P \leq 0,05$) for each plant part.

radioactivity found in the partially defoliated vines (Table 6). The very much higher photosynthetic activity of the partially defoliated vines suggests that reserves would still be sufficiently provided for growth and development during the next season. This is important for the general well being and continued productivity of the vine.

CONCLUSIONS

The partial defoliation treatments proved to be successful in increasing the photosynthetic effectivity of all the remaining leaves on the shoot. The translocation and distribution of photosynthetates apparently did not differ between the defoliation treatments. That probably resulted from the even distribution of the remaining leaves of the partially defoliated vines. The locations of sinks on the shoot were therefore unaffected by the partial defoliation. However, increases in the amount and growth of lateral shoots might have created additional and/or emphasized existing sinks.

From the results obtained it is proposed that the control vines carried excess foliage, which readily inhibited optimal photosynthetic activity of all the leaves on the vine. As a result accumulation of photosynthetates in the bunches was reduced. It can be argued that the leaves opposite and below the bunches of such vines be removed at véraison stage and that the shoots be positioned on the vine and trellis in such a way as to allow optimal exposure, especially of the basal leaves, to sunlight. It would also seem that canopy density may be reduced by an even removal of up to 66% leaves at véraison stage without deleteriously affecting yield. On the contrary, it would appear that yield may be increased as a result of defoliation. Partial defoliation would provide maximum photosynthesis of the remaining leaves as well as optimum contribution of photosynthetates to the bunches.

LITERATURE CITED

BUTTROSE, M.S., 1966. The effect of reducing leaf area on the growth of roots, stems and berries of Gordo grapevines. *Vitis* **5,** 455–464.

DRY, P. & SMART, R., 1986. So your vineyard is too vigorous: What now? *Aust. Grapegrower and Winemaker* **1,** 11.

HOFÄCKER, W., 1978. Investigations on the photosynthesis of vines. Influence of defoliation, topping, girdling and removal of grapes. *Vitis* **17,** 10–22.

HUNTER, J.J. & VISSER, J.H., 1988. 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,** 3–9.

JOHNSON, J.O., WEAVER, R.J. & PAIGE, D.F., 1982. Differences in the mobilization of assimilates of *Vitis vinifera* L. grapevines as influenced by an increased source strength. *Am. J. Enol. Vitic.* **33,** 207–213.

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. & 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.

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. Oregan State University, Oregon, pp. 139–157.

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

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.

SCHOLEFIELD, P.B., NEALES, T.F. & MAY, P., 1978. Carbon balance of the Sultana vine (*Vitis vinifera* L.) and the effects of autumn defoliation by harvest-pruning. *Aus. J. Plant Physiol.* **5,** 561–570.

SMART, R.E., 1973. Sunlight interception by vineyards. *Am. J. Enol. Vitic.* **24,** 141–147.

SMART, R.E., 1985. Principles of grapevine canopy microclimate manipulation with implications for yield and quality. A review. *Am. J. Enol. Vitic.* **36,** 230–239.

SMART, R.E., ROBINSON, J.B., DUE, G.R. & BRIEN, C.J., 1985a. Canopy microclimate modification for the cultivar Shiraz. I. Definition of canopy microclimate. *Vitis* **24,** 17–31.

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