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.*

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The distribution of photosynthetates, originating in leaves of different parts of the shoot of *Vitis vinifera* L. cv Cabernet Sauvignon at berry set, pea size, véraison and ripeness stages, was investigated.
Specific photosynthetic activity of the $^{14}CO_2$-treated leaves gradually decreased during the season. Photosynthetates were hoarded in the leaves at berry set, but were increasingly diverted to the bunches after that. The apical leaves displayed the highest photosynthesis. The leaves opposite and below the bunches accumulated very little photosynthetates, especially from véraison to ripeness. Redistribution of photosynthetates among the basal, middle and apical leaves was generally very restricted at all stages. Multidirectional distribution from the site of application of $^{14}CO_2$ occurred at berry set stage, while from pea size to ripeness photosynthetates were mainly translocated basipetally. Highest accumulation in the bunches occurred at véraison, while the basal leaves were primarily used to nourish the bunch.

Leaf photosynthesis depends upon demand for assimilates and is regulated by the source : sink relationship (Johnson, Weaver & Paige, 1982). Several investigators found that the distribution of photosynthetic products within the grapevine varies according to the different stages of growth and development (Hale & Weaver, 1962; Kriedemann, Kliewer & Harris, 1970; Quinlan & Weaver, 1970; Koblet & Perret, 1971; 1972; 1980; Koblet, 1975; 1977; 1984; Kriedemann, 1977; De la Harpe, 1984). However, these studies dealt mainly with autoradiographic techniques in which radioactivity was not quantitatively determined. The qualitative and quantitative contribution and distribution of $^{14}CO_2$ to the bunches and leaves of different physiological ages within the shoot in relation to leaf area, leaf age and developmental stage were not clearly defined.

It is generally accepted that the leaves of the grapevine start exporting their photosynthetates when 30% to 50% of their final size is reached (Hale & Weaver, 1962; Koblet, 1977; Yang & Hori, 1980). Young, rapidly expanding leaves are active sinks for photosynthetic products (Hale & Weaver, 1962; Leonard & Weaver according to Hale & Weaver, 1962; Currle according to Koblet, 1977; Koblet, 1977). From 50% to 75% of final size for the leaves of the main and lateral shoots, respectively, only an export of carbohydrates was found (Koblet, 1969). The age at which the leaf changes from a sink to a source may, however, differ among cultivars (Yang & Hori, 1980). According to Swanson & El-Shishiny (1959) and Koblet (1977) translocation of carbohydrates was mainly in the form of sucrose, while the speed of translocation was 27-30 cm/h (Koblet, 1969).

Although the roots are considered the most important sites of accumulation of carbohydrates as regards vine reserves (Winkler & Williams, 1945; Scholefield, Neales & May, 1978), the primary goal of the viticulturist is to divert carbohydrates to the grapes in order to obtain high quality. Sugar accumulation in the fruit can either be directed from photosynthesis or mobilized from stored carbohydrate reserves in the roots, canes and trunk (Mansfield & Howell, 1981). Because all the leaves on the shoot contribute to the source of reserve and recently produced carbohydrates, it is important to obtain a perspective about the specific contribution of leaves of different physiological ages to the reserve sinks, vegetative growth and the developing berry during the growth season. Such results can then be used to alter the vine's canopy to conditions more favourable to the production of high quality grapes. Translocation studies are therefore needed to obtain a perspective about the distribution pattern of photoassimilates that either directly or indirectly contribute to the quality of the grapes.

This investigation was done to determine the movement of photosynthetates, originating in leaves of different physiological ages within the shoot of Cabernet Sauvignon, at berry set, pea size, véraison and ripeness stages.

MATERIALS AND METHODS

Experimental vineyard

An eight year old *Vitis vinifera* L. cv Cabernet Sauvignon clone 4/R46 vineyard at 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

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1/30/1. Vines were planted (3,0 x 1,5 m spacing) on a Clovelly soil (MacVicar *et al.*, 1977) and trained onto a 1,5 m slanting trellis as described by Zeeman (1981). Vines used in the experiment were selected on the basis of 2,0–3,0 kg cane mass per vine. Bud loads of 10 buds per kg cane mass were applied. A 2% cyanamide (H_2NCN) solution was applied to the dormant buds approximately three weeks prior to the normal budding date. This treatment ensured an even bud break.

Rainfall was supplemented by sprinkler irrigation according to A pan evaporation figures on a weekly basis during the growth season. A crop factor of 0,3 was used.

Berry set was defined as that stage where the berry had a diameter of 3–4 mm, while the diameter of the berry at pea size was 8–10 mm. Véraison was defined as the appearance of the red colour and ripeness as 23–24°B.

Normal viticultural practices, namely suckering as well as pest and disease control, were applied during the growth season according to the standard program of the Viticultural and Oenological Research Institute.

Experimental design

The experiment was laid out as a completely randomized 3 x 4 factorial design. The two factors were : 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 $^{14}CO_2$ treatments were applied at each of the four developmental stages. There were nine randomized replications, comprising one-vine plots, for each of the 12 treatment combinations.

Application of labelled CO_2

Each main shoot that was to be treated with $^{14}CO_2$ was divided into three equal parts from just above the bunches, namely a basal (B), middle (M) and apical (A) part, according to number of leaves. The lower part of the shoot was further divided into the bunches (BU) and the leaves opposite and below the bunches (BL) and was not treated with $^{14}CO_2$ (Fig. 1). Application of $^{14}CO_2$ was as follows : The entire basal, middle or apical part, including lateral shoots, was enclosed in a polyethylene bag. Radioactivity ($^{14}CO_2$) was generated inside the polyethylene bag by addition of 1,85 MBq $NaH^{14}CO_3$ solution to 1 cm^3 20% (v/v) lactic acid in a 10 cm^3 vial, fixed to the stem of the main shoot. Fixation of $^{14}CO_2$ was allowed for 60 minutes, after which the polyethylene bag as well as the vial were removed. In all cases $^{14}CO_2$ application was done under maximum ambient light intensity and at temperatures favourable for photosynthesis.

Measurement of ^{14}C

Assimilation and translocation of the labelled CO_2 was allowed for 24h after which the following five parts on the shoot were harvested separately : the bunches, the leaves opposite and below the bunches (hereafter called bunch leaves), the basal leaves, the middle leaves and the apical leaves (Fig. 1). The samples were sealed in polyethylene bags stored in the dark at 5°C until required for further analyses.

Leaf areas were determined with a Li-cor LI3000 portable area meter and the leaves of each part subsequently dried for 48h at 80°C. Berries were frozen at -20°C prior to freeze-drying. The dry mass of each part was determined and the material individually ground (20 mesh).

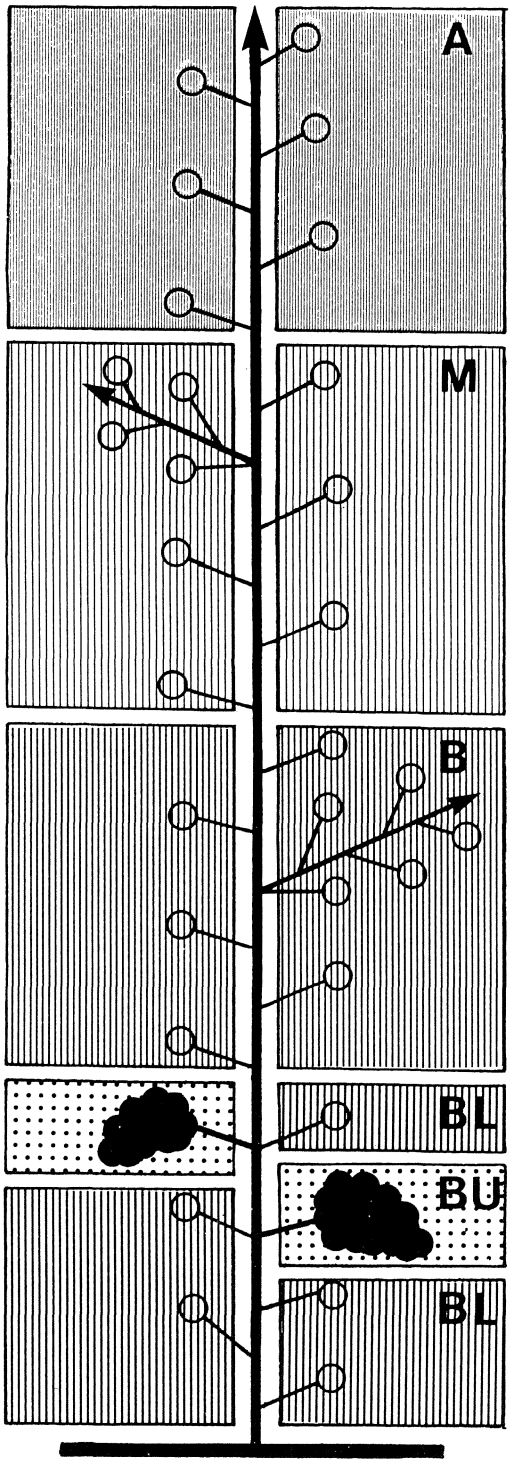

FIG. 1

The partitioning of the shoot into five parts, namely apical leaves (A), middle leaves (M), basal leaves (B), bunch leaves (BL) and bunches (BU).

For the determination of ^{14}C-activity in each part, 0,2 g of ground material was treated with 2 cm^3 30% H_2O_2 as well as 0,1 cm^3 $HClO_4$ for at least five days at 70°C. Ten cm^3 Instagel scintillation liquid (Beckman MP grade) was added and the mixture well shaken. The

radioactivity was counted in a Packard Tri-carb 460 scintillation spectrophotometer. Quenching was automatically accounted for. The method used was proven to be effective in digesting the plant material as well as oxidizing coloured pigments, especially chlorophyll. Interference of the chemicals with the counting of radioactivity was negligible.

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.

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: When the ^{14}C-activity of the particular part to which label was applied is included in the calculations (Fig. 2), the overall impression is that translocation of radioactivity between the different parts of the shoot has not progressed very far after 24h, hence the high activity present in the treated part. However, it seems that ^{14}C was progressively released up to véraison, while at ripeness stage distribution was very restricted. Regardless of the site of application, percentage activity in the leaves decreased from berry set to véraison, but increased thereafter. The almost total lack of translocation from the apical leaves at berry set is striking.

Except for the middle leaves at berry set, which exported 9% to the apical leaves, the apical, middle and basal leaves generally demonstrate their incapability in translocating to each other, while the very low accumulation in the bunch leaves at all stages is conspicuous. Evidently, the lower the position of the treated leaves on the shoot, the more photosynthetates were translocated (Fig. 2), resulting in a concomitant significantly higher specific activity in the bunches (Table 1). Although this could have resulted from the close site of application of $^{14}CO_2$, it emphasizes the importance of creating a suitable canopy microclimate for optimal photosynthetic activity of especially the basal leaves. The variable interior microclimate is also accentuated by the increase in the coefficient of variation the deeper into the canopy the leaves were situated (Table 1). In contrast to this, the apical leaves hoarded photosynthetates mainly for its own growth and development. This phenomenon occurred at all stages and is in agreement with the general conception that young, small leaves favour their own growth and development (Hale & Weaver, 1962; Kriedemann & Lenz, 1972; Koblet, 1977; Yang & Hori, 1980), while mature leaves nourish the fruits and add to the reserves (Hale & Weaver, 1962; Kriedemann *et al.*, 1970; Quinlan & Weaver, 1970; Koblet, 1977; Yang & Hori, 1980).

Treated part excluded : When the treated part is excluded from the calculations (Fig. 3), the distribution

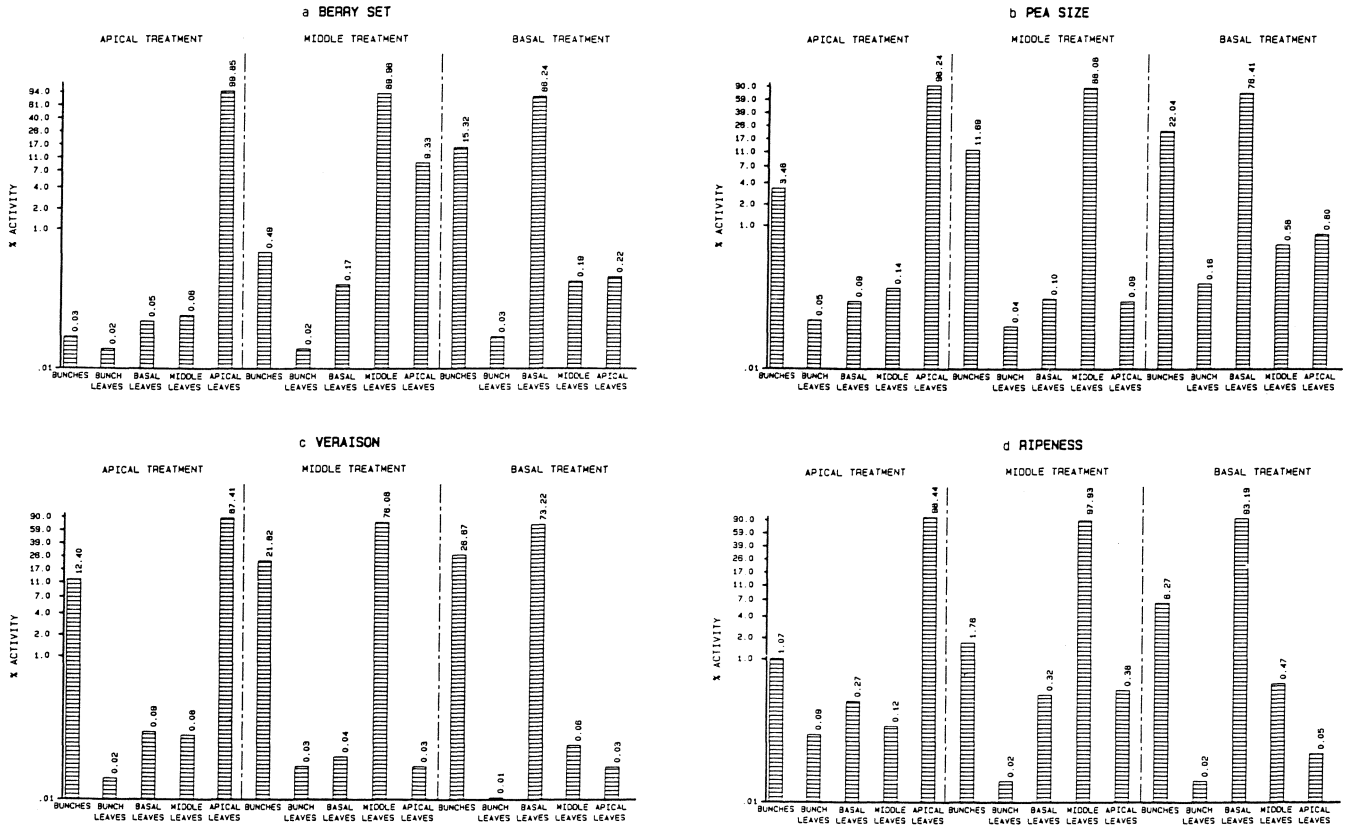

FIG. 2

The effect of 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).

TABLE 1

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	0,20^{e}	1,38^{d}	75,30^{a}	25,63^{a}	0,16^{a}	0,05^{b}	0,06^{b}	0,09^{a}	0,10^{d}	0,14^{d}	86,68^{a}	28,98^{a}	0,18^{d}	119,42^{a}	0,30^{d}	39,97^{a}	836,24^{a}	45,05^{d}	1,10^{e}	294,13^{a}
Pea size	1,15^{d}	2,69^{c}	4,91^{b}	2,92^{b}	0,06^{b}	0,06^{b}	0,14^{a}	0,09^{a}	0,05^{d}	0,04^{d}	26,02^{c}	8,70^{b}	0,07^{d}	37,00^{b}	0,19^{d}	12,42^{b}	117,07^{b}	0,11^{f}	0,77^{e}	39.32^{b}
Véraison	0.64^{d}	1.64^{c}	2.30^{c}	1,52^{c}	0,01^{c}	0,03^{c}	0,03^{c}	0.02^{b}	0,02^{d}	0,02^{d}	38.51^{b}	12,85^{b}	0.02^{d}	32,47^{b}	0,03^{d}	10.84^{b}	65.02^{c}	0,02^{f}	0,04^{f}	21,69^{c}
Ripeness	0,05^{e}	0.06^{c}	0.22^{c}	0,11^{d}	0,02^{c}	0,02^{c}	0,02^{c}	0.02^{b}	0,08^{d}	0,08^{d}	32,96^{b}	11,04^{b}	0,03^{d}	21,26^{c}	0,10^{d}	7,13^{c}	74,24^{c}	0,23^{f}	0,04^{f}	24.84^{c}
Mean	0.51^{c}	1,44^{b}	20.68^{a}		0,06	0,04	0,06		0,06^{b}	0,07^{b}	46.04^{a}		0.08^{b}	52,54^{a}	0,16^{b}		273,14^{a}	11,35^{b}	0,49^{c}	
CV(%)	29.29				78,18				19,10				17,32				13,12			

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

pattern and site of accumulation of $^{14}CO_2$ become more noticeable. It would seem that translocation to the bunches was increasingly favoured up to véraison stage with a decline thereafter, irrespective of the position of application. However, the lowest percentage activity distributed to the bunch was found at berry set when vegetative growth was seemingly more pronounced. These results coincide with observations (data not shown) that vegetative growth as well as berry growth of these Cabernet Sauvignon vines virtually stop around véraison stage. The accumulation of sugars as well as precursors for anthocyanin-synthesis is obviously favoured at this stage. It would appear that diversion towards vegetative organs was resumed at ripeness, possibly to supplement the accumulation of reserves as well as regrowth of the shoot tips, while maximum levels of photosynthetic products are virtually reached in the berry. This is in agreement with results found by De la Harpe (1984). Although a noticeable contribution of the apical leaves to the bunch leaves at especially berry set was found, the bunch leaves generally demonstrated their incapability of acting as a strong sink.

Specific activity

Specific activity: From the specific activity (kBq/g dry mass) of the different plant parts (Fig. 4) the impression is again gained that translocation from the part to which label was applied has not progressed very far after 24h, especially in the case of the apical treatment. A significant gradual decrease in specific photosynthet-

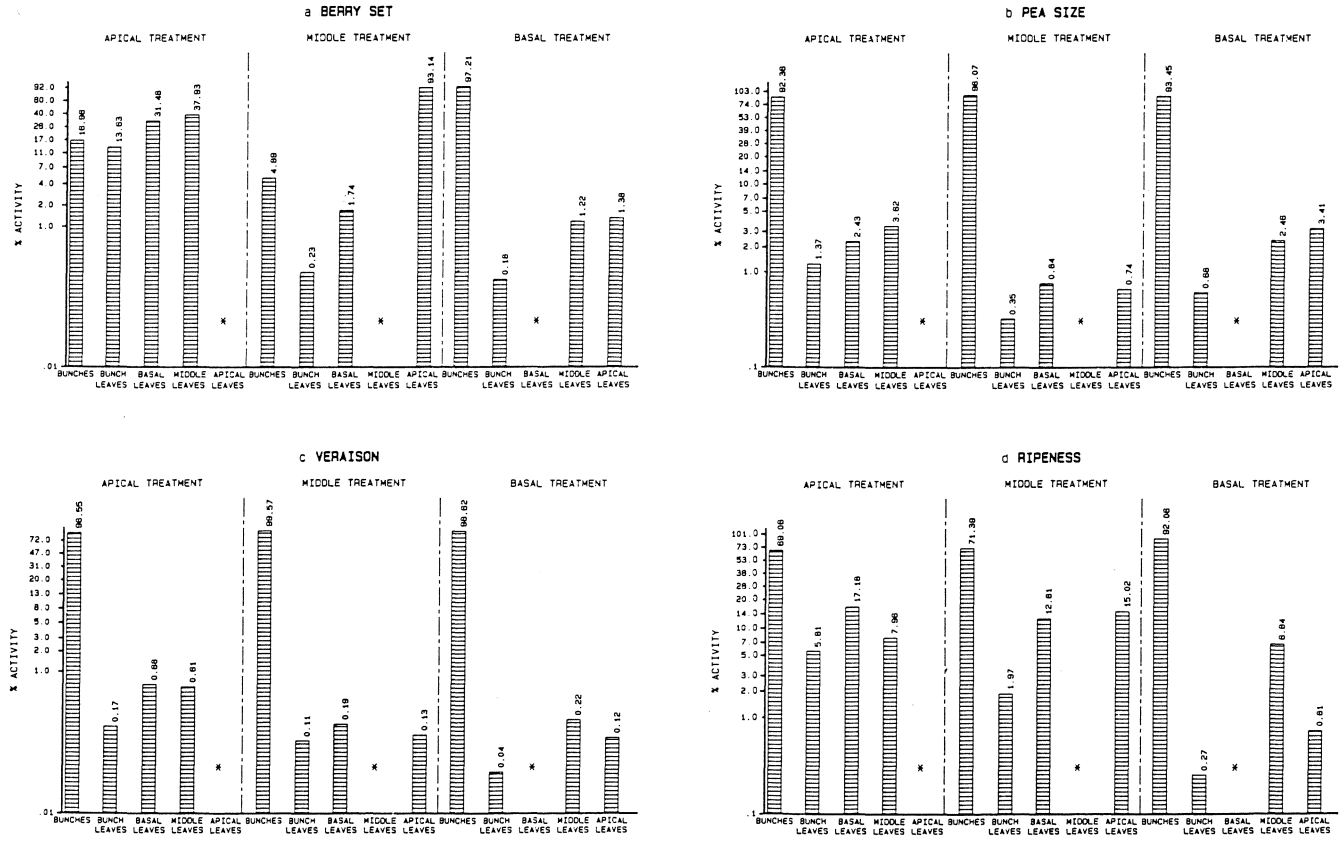

FIG. 3

The effect of 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).

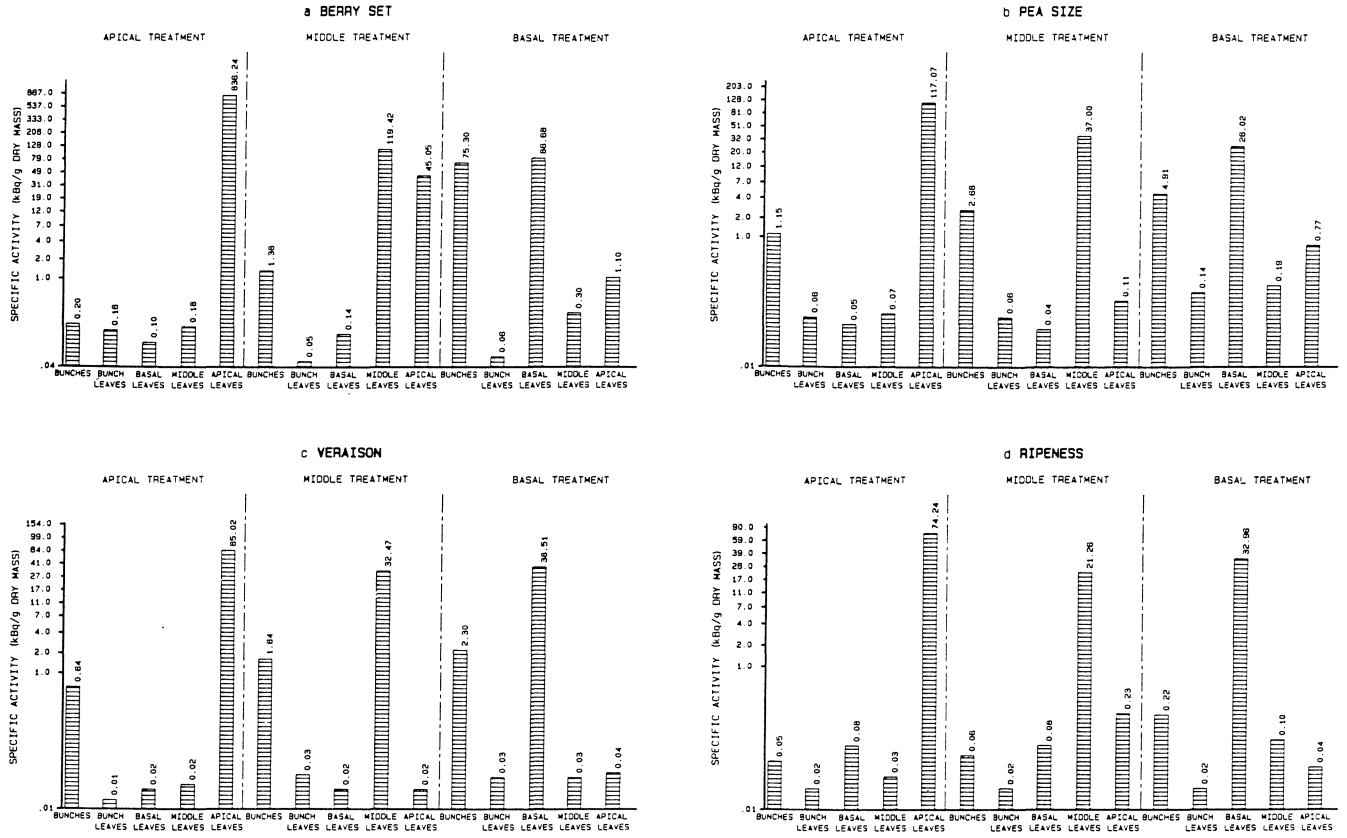

FIG. 4

The effect of 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).

ic activity of the treated leaves during the season is evident (Table 1), verifying the findings of Pandey & Farmahan (1977). As a result activity in the bunches also decreased significantly. However, the latter could also be a consequence of berry growth.

Although the apical leaves were immature and their total leaf areas only approximated 33% of that of the middle and basal leaves (Table 2), they nevertheless displayed the highest photosynthetic activity (Fig. 4), probably because of a tendency to hoard assimilates as well as an inherent active metabolism.

When the middle and basal parts were treated, very low activity was found in the apical leaves compared to that in the leaves of the treated parts. This is in contrast to the findings of other investigators that the apical leaves are parasitic on the rest of the vine (Hale & Weaver, 1962; Koblet, 1977), because they are rapidly growing and therefore their photosynthetic activity would be lower (Kriedemann, 1968; Kriedemann *et al.*, 1970). However, strong import of ^{14}C from the apical to the middle leaves was again found at berry set stage.

Even though the poor sink capacity of the bunch leaves is evident from the very low accumulation of ^{14}C, it appears as if these leaves were more physiologically active at berry set and pea size stages (Fig. 4). Senescence set in thereafter, as was evident from senescence, yellowing and abscission observed in the vineyard. Although distribution of photosynthetates between leaves of the different parts was generally negligible, the middle leaves, and to a lesser extent the basal leaves, translocated to the apical leaves at berry set stage.

Activity/leaf area ($Bqx10^2/cm^2$): Although a general decline in specific photosynthesis was again noticeable as the growth season progressed, a marked increase in photosynthetic activity of the apical leaves from véraison to ripeness occurred, possibly to supplement regrowth of the shoot tips (Table 3). The general decline is in agreement with the findings of Kriedemann (1977) and may be explained partly by the increase in total leaf area of the canopy during the season, which could then result in a decrease in specific photosynthetic activity of the leaves. An increasing senescence, as is evident from

TABLE 2

Total areas (cm^2) of leaves in different positions on the shoot at different developmental stages of the vine.

Developmental stage	BUNCH LEAVES	BASAL LEAVES	MIDDLE LEAVES	APICAL LEAVES
Berry set	408,27[a]	1021,73[a]	744,95[b]	191,68[b]
Pea size	426,37[a]	1220,22[a]	1170,13[a]	403,51[a]
Véraison	347,11[a]	1163,45[a]	1089,36[a]	448,94[a]
Ripeness	357,92[a]	1169,98[a]	1196,03[a]	423,01[a]
Mean	384,92	1143,84	1050,12	366,79
CV(%)	9,08	6,71	7,06	5,65

Values designated by the same symbol do not differ significantly ($P \leq 0,05$) 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 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	0,04[a]	0,05[a]	0,07[a]	0,05[a]	0,08[b]	0,07[b]	318,08[a]	106,08[a]	0,28[a]	193,81[a]	0,79[a]	64,96[a]	975,60[a]	148,93[b]	4,63[c]	376,39[a]
Pea size	0,35[a]	0,54[a]	0,05[a]	0,32[a]	0,26[b]	0,15[b]	207,09[a]	69,17[a]	0,35[a]	238,77[a]	0,14[a]	79,75[a]	361,50[b]	0,34[c]	0,13[c]	120,65[b]
Véraison	0,04[a]	0,08[a]	0,08[a]	0,06[a]	0,06[b]	0,03[b]	127,38[a]	42,49[a]	0,03[a]	134,10[a]	0,06[a]	44,73[a]	261,70[b]	0,06[c]	0,09[c]	87,28[b]
Ripeness	0,02[a]	0,07[a]	0,04[a]	0,05[a]	0,15[b]	66,53[b]	0,27[b]	22,31[b]	0,15[a]	66,53[a]	0,27[a]	22,31[a]	519,07[b]	0,26[c]	0,05[c]	173,13[b]
Mean	0,11[a]	0,19[a]	0,06[a]		0,14[b]	16,69[b]	163,20[a]		0,20[b]	158,30[a]	0,32[b]		529,47[a]	37,40[b]	1,22[c]	
CV(%)	154,10				73,38				62,69				47,99			

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.

the decreasing moisture content (Table 4) and corresponding change in chemical content, e.g. an increase in sugar and decreases in amino and organic acid concentrations (Kliewer & Nassar, 1966; Kriedemann *et al.*, 1970), could also contribute to a change in metabolic rate. Concomitantly, demand for assimilates could have decreased because of a decrease in actively growing vegetative sinks as well as in berry growth. According to Kriedemann (1977) old leaves showed a reduction in both efficiency and capacity which was associated with a substantial increase in internal resistance to CO_2 assimilation.

TABLE 4

Moisture content (%) of leaves in different positions on the shoot at different developmental stages of the vine.

Developmental stage	BUNCH LEAVES	BASAL LEAVES	MIDDLE LEAVES	APICAL LEAVES
Berry set	72,06[a]	73,29[a]	73,61[a]	74,81[a]
Pea size	68,33[b]	70,23[b]	70,32[b]	71,89[b]
Véraison	66,77[c]	64,96[c]	65,35[c]	65,04[c]
Ripeness	64,64[d]	63,06[d]	61,48[d]	61,52[d]
Mean	67,95	67,89	67,69	68,31
CV(%)	0,98	0,79	1,00	0,99

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

Considering all criteria discussed, it would seem that photosynthetates of the apical, middle and basal leaves were gradually released during the season reaching a peak at véraison, but decreasing thereafter. Although distribution from the apical leaves was very restricted at berry set stage, photosynthetates were evenly distributed in the shoot. At this stage the middle leaves translocated acropetally to the apical leaves as well as basipetally to the bunches, while the basal leaves mainly fed the bunches and to a limited extent distributed acropetally. At pea size the apical, middle and basal leaves translocated mainly to the bunches. The same situation applies for véraison stage, whilst at ripeness the sink capacity of the bunches decreased, albeit still strong. At the latter stage photosynthetates for growth and development of the bunches were mainly obtained from the basal leaves. These results verify those found by Hale & Weaver (1962) and Koblet (1977). Irrespective of the site of application, accumulation of ^{14}C in the bunch leaves (those opposite and below the bunches) was very slight at all stages.

CONCLUSIONS

A gradual decrease in specific photosynthetic activity of the leaves of these Cabernet Sauvignon vines occurred during the season. The efficiency of leaves decreased as they were progressively situated deeper into the canopy. In general, the basal, middle and apical leaves contributed very little photosynthetates to each other at all stages. Photosynthetates were hoarded in the leaves at berry set, but were increasingly diverted to the bunches after that. Although the apical leaves displayed the highest photosynthesis, the only evidence of them acting as parasites on the rest of the shoot, as is generally believed, would seem to occur at berry set and to a lesser extent at ripeness stage. In general, the leaves opposite and below the bunches accumulated very low amounts of radioactivity and can readily be considered of lesser importance to the vine, especially from véraison to ripeness stage.

It would seem that translocation was very much favoured during the first part of the growth season, i.e. up to véraison stage, while the basal leaves played a very important role in the nourishing of the bunch at all stages. The results therefore clearly established the importance of increasing the photosynthetic effectivity of the basal leaves by an improved canopy management.

Multidirectional distribution of photosynthetates occurred at berry set stage. From pea size to ripeness stage translocation was mainly basipetal. However, it would seem that distribution to vegetative sinks was resumed during the latter stage, resulting in a decreased accumulation in the bunches.

Percentage activity and specific activity seem to be useful criteria to express results obtained in studies involving radioactive material. As regards specific activity, activity/leaf area is considered a more realistic criterium than activity/dry mass in a study which involves photosynthesis, leaf position, leaf size, physiological age and light exposure.

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