Physiological Implications of Partial Defoliation of the Grapevine (*Vitis vinifera* L. cv. Cabernet Sauvignon)

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

J.J. Hunter

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ABSTRACT

The effect of partial defoliation as canopy management practice on metabolism and grape composition of the grapevine, *Vitis vinifera* L. cv. Cabernet Sauvignon, was investigated. The establishment of physiologically sound principles on how to overcome deleterious effects associated with vigorous and dense-canopy vines is emphasized. Experimental vines were defoliated 33 % and 66 % evenly over the whole canopy from different developmental stages in a field study. Effects on canopy microclimate, photosynthesis, photosynthate translocation, vegetative growth, reproductive growth, root development and distribution, as well as grape and wine quality, were determined. A method for the simultaneous extraction of sugars and organic acids from freeze-dried berries at different developmental stages is described.

Partial defoliation of vines improved canopy microclimate and photosynthetic efficiency of remaining leaves. Normal translocation and distribution patterns of photosynthates were apparently unaffected by partial defoliation. Translocation to and accumulation of photosynthetic products in the leaves and bunches of partially defoliated vines were, however, improved. Remaining leaves of partially defoliated vines were in comparison photosynthetically more active. Apart from a less favourable canopy microclimate, it seemed that the sink capacity of non-defoliated vines did not comply to the source capacity, inducing a reduced rate of photosynthesis.

Normal sigmoidal growth patterns of vines were not affected by partial defoliation as applied in this study. This is important for the longevity, healthiness and productivity of vines. Vegetative growth was differentially affected by partial defoliation. No compensatory leaf growth occurred in reaction to partial defoliation from different developmental stages. Main shoot length, however, decreased slightly. Lateral shoot length and number of laterals increased, whereas cane mass decreased when vines were partially defoliated, particularly the earlier and more severe the defoliation. Reproductive growth in terms of yield was deleteriously affected by 33 % defoliation prior to pea size and 66 % defoliation prior to véraison. Budding percentage was, however, improved by 33 % and 66 % defoliation, whereas bud fertility was only improved by 33 % defoliation. Partial defoliation changed the canopy microclimate to conditions favourable for pest and disease control and higher grape quality.

Subterranean growth was favourably affected by partial defoliation, particularly when applied from pea size stage. These changes included higher root densities, development of higher numbers of fine and medium diameter roots and occurrence of higher total root numbers in all soil layers. Generally, defoliations from pea size and véraison were more efficient regarding root development than defoliations from just after bud break and from berry set. Partially defoliated

vines reacted by forming new roots, creating a more efficient nutrient absorption capacity and utilization of soil and available water and that, together with higher photosynthetic activities of leaves, provided an efficient mechanism for continued high performance.

Grape quality was not affected markedly by partial defoliation. Total soluble solids in berries of defoliated vines were comparable to and even significantly higher than those of non-defoliated vines in some cases, in spite of much lower leaf areas. Generally, total titratable acidity of musts was also slightly higher for partially defoliated vines. Glucose and fructose concentrations in berries were unaffected by partial defoliation, while tartaric acid concentrations were slightly increased and malic acid concentrations slightly decreased. Partial defoliation generally increased the anthocyanin concentration of berry skins. These changes in grape composition suggest higher grape quality and seemed to result from improved light conditions in the canopy interior. Berry volume decreased with partial defoliation, which lowered the pulp:skin ratio. These berries are more desirable for quality wines. Regardless of severity or the developmental stage defoliation was commenced, wine cultivar character and overall wine quality were significantly improved.

Partial defoliation changed the general metabolism of vines, mainly in terms of more favourable source:sink ratios, resulting in more efficient photosynthesis, subterranean performance and canopy microclimate. In general, the results suggest that an even removal of 33 % of leaves opposite and below bunches during the period from flowering or berry set to pea size stage may be applied. It is further suggested that existing vigorous and dense-canopy vines be 33 % defoliated evenly on the lower half of the shoot (canopy) from pea size or véraison. This hypothesis proved effective in improving canopy microclimate, photosynthetic activity and yield, while vegetative growth was inhibited. Grape and wine quality were higher.

On the whole, partial defoliation as applied in this study, is recommended as canopy management practice in order to facilitate the abolishment of deleterious effects of excessive vegetative growth and canopy density on balanced metabolic activity, fruit and wine quantity and quality, as well as longevity and healthiness of grapevines.

UITTREKSEL

Die invloed van blaarverwydering as loofbestuurspraktyk op die metabolisme en druifsamestelling van die wingerdstok, *Vitis vinifera* L. cv. Cabernet Sauvignon, is ondersoek. Die vestiging van fisiologies-betroubare beginsels oor hoe nadelige effekte geassosieerd met geil en lower-verdigte wingerde uitgeskakel kan word, word beklemtoon. Proefstokke is in 'n veldondersoek 33 % en 66 % eweredig oor die hele lower vanaf verskillende ontwikkelingstadiums ontblaar. Effekte op lowermikroklimaat, fotosintese, translokasie van fotosintetiese produkte, vegetatiewe groei, reproduktiewe groei, wortelontwikkeling en verspreiding asook druif- en wynkwaliteit is bepaal. 'n Metode vir die gelyktydige ekstraksie van suikers en organiese sure uit gevriesdroogde korrels op verskillende groeistadiums is ontwikkel.

Blaarverwydering het lowermikroklimaat verbeter en fotosintetiese doeltreffendheid van oorblywende blare op die stok verhoog. Normale translokasie en verspreidingspatrone van produkte van fotosintese is skynbaar nie deur blaarverwydering beïnvloed nie. Translokasie na, en akkumulering van fotosintetiese produkte in die blare en druiwe van gedeeltelik ontblaarde stokke, is egter verbeter. Oorblywende blare van gedeeltelik ontblaarde stokke was fotosinteties meer aktief. Afgesien van 'n ongunstiger lowermikroklimaat, het die sinkkapasiteit van nie-ontblaarde stokke skynbaar ook nie teen die bronkapasiteit opgeweeg nie en is 'n verlaagde tempo van fotosintese verkry.

Normale sigmoïdale groeipatrone van die stokke is nie deur blaarverwydering beïnvloed nie. Dit is belangrik vir langlewendheid, gesondheid en produktiwiteit van stokke. Vegetatiewe groei is differensieel deur blaarverwydering beïnvloed. Geen kompenserende blaargroei het in reaksie op blaarverwydering vanaf verskillende ontwikkelingstadiums voorgekom nie. Hooflootlengte was egter effens korter. Sylootlengte en aantal sylote het toegeneem, terwyl lootmassa afgeneem het met blaarverwydering, veral hoe vroeër en strawwer dit toegepas is. Reproduktiewe groei in terme van opbrengs is nadelig beïnvloed deur 33 % ontblaring voor ertjiekorrelstadium en 66 % ontblaring voor die deurslaanstadium. Botpersentasie is egter deur blaarverwydering verbeter, terwyl oogvrugbaarheid slegs deur 33 % ontblaring verbeter is. Blaarverwydering het 'n gunstige lowermikroklimaat vir die beheer van plae en siektes en hoër druifkwaliteit geskep.

Ondergrondse groei is gunstig deur blaarverwydering beïnvloed, veral wanneer toegepas vanaf ertjiekorrelstadium. Hierdie veranderinge het ingesluit hoër worteldigtheid, ontwikkeling van groter hoeveelhede wortels met 'n fyn en medium deursnit en die voorkoms van 'n groter aantal totale wortels in alle grondlae. Blaarverwydering vanaf ertjiekorrel- en deurslaanstadia was in die

algemeen meer doeltreffend ten opsigte van wortelontwikkeling as blaarverwydering vanaf net na bot en vanaf korrelset. Gedeeltelik ontblaarde stokke het gereageer deur nuwe wortels te vorm, waardeur 'n meer doeltreffende vermoë tot voedingstofopname en benutting van grond en beskikbare water verkry is. Tesame met hoër fotosintetiese aktiwiteite van die blare is 'n doeltreffende meganisme vir aanhoudende hoë prestasie verkry.

Druifkwaliteit is nie aanmerklik deur blaarverwydering beïnvloed nie. Totale oplosbare stowwe in druiwe van gedeeltelik ontblaarde stokke was vergelykbaar en selfs betekenisvol hoër as dié van nie-ontblaarde stokke in sekere gevalle, ten spyte van die baie laer blaaroppervlakte. In die algemeen was die totale titreerbare suur in die mos van gedeeltelik ontblaarde stokke ook effens hoër. Glukose- en fruktosekonsentrasies in die druiwe is nie deur blaarverwydering beïnvloed nie. Die konsentrasie wynsteensuur is egter effens verhoog en die appelsuurkonsentrasie effens verlaag. Antosianienkonsentrasie van korreldoppe is in die algemeen deur blaarverwydering verhoog. Hierdie veranderinge in druifsamestelling dui op hoër druifkwaliteit en is skynbaar die resultaat van verbeterde ligtoestande in die binnekant van die lower. Korrelvolume het afgeneem met blaarverwydering. Dit het die pulp:dop verhouding verlaag. Sulke korrels is meer gewens vir bereiding van kwaliteitswyne. Wyn cultivarkarakter en totale wynkwaliteit is betekenisvol deur blaarverwydering verhoog, onafhanklik van die strafheid of ontwikkelingstadium waarvandaan blare verwyder is.

Blaarverwydering het die algemene metabolisme van die wingerdstok verander, hoofsaaklik ten opsigte van meer gunstige bron:sink-verhoudings en derhalwe meer doeltreffende fotosintese, ondergrondse groei en lowermikroklimaat. Die resultate dui in die algemeen daarop dat 'n eweredige blaarverwydering van 33 % regoor en onderkant die trosse tydens blomvorming of korrelset tot ertjiekorrelstadium toegepas kan word. Die resultate dui verder daarop dat 33 % van bestaande geil en lower-verdigte stokke se blare eweredig verwyder kan word op die onderste helfte van die loot (lower) vanaf ertjiekorrel- of deurslaanstadium. Hierdie hipotese was suksesvol in die verbetering van lowermikroklimaat, fotosintetiese aktiwiteit en oesmassa. Vegetatiewe groei is gestrem. Druif- en wynkwaliteit was hoër.

In die geheel kan blaarverwydering soos toegepas in hierdie ondersoek aanbeveel word as loofbestuurspraktyk ten einde die uitskakeling van nadelige effekte van oormatige vegetatiewe groei en lowerdigtheid op gebalanseerde metaboliese aktiwiteit, druif- en wynkwantiteit en kwaliteit, asook langlewendheid en gesondheid van wingerdstokke te bevorder.

LIST OF ABBREVIATIONS

A	=	Apical
Abs	=	Absorbance (with wavelength specified)
ADC	=	Analytical Development Company
B	=	Basal
°B	=	Degrees balling
BL	=	Bunch leaves (leaves opposite and below the bunches)
BU	=	Bunches
C_a	=	Chlorophyll *a*
C_b	=	Chlorophyll *b*
CS	=	Clone number code indication of the cultivar Cabernet Sauvignon
E_{max}	=	Maximum vapour pressure
GAE	=	Gallic acid equivalents
HPLC	=	High performance liquid chromatography
M	=	Middle
P_{fr}	=	Phytochrome far-red
P_r	=	Phytochrome red
PAL	=	Phenylalanine ammonia lyase
PFD	=	Photon flux density
Pn	=	Photosynthesis
r	=	Correlation coefficient
r_S	=	Stomatal resistance
RY	=	Clone number code indication of rootstock 99 Richter
T_r	=	Rate of transpiration
TSS	=	Total soluble sugars
TTA	=	Total titratable acidity
VORI	=	Viticultural and Oenological Research Institute

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CHAPTER I

1. General Introduction

Vigorous and excessive vegetative growth generally occurs in South African vineyards. This has resulted from generally improved viticultural practices such as soil management, vineyard establishment, vine training, cultivation, irrigation, fertilization and using of plant material free of harmful viruses. The favourable climate in South Africa also contributes to the development of vigorous growth.

Under conditions of excessive vegetative growth most photosynthetic products are canalised to shoot growth, while other parts such as the bunches, receive little nutrients for growth and development. An imbalance between vegetative and reproductive growth is therefore created in the vine. Moreover, the increase in shoot growth and leaf area as well as the appearance of too many lateral shoots, water shoots (infertile shoots) and the burst of basal (collar) buds also create conditions of density and shading in the canopy-interior. Bad pruning practices, such as the allocation of too many bearers (spurs) on a restricted cordon length, resulting in too closely spaced bearers, also favour a dense canopy. This condition is found to a certain extent for all trellising systems. Particularly the leaves in the canopy-interior that contribute to a large extent to fruit development and quality, as well as the fruits themselves, receive insufficient light for optimal functioning.

This condition can detrimentally affect yield (Smart *et al.*, 1990) and decrease budding and bud fertility (May, 1965; Shaulis *et al.*, 1966; Shaulis & May, 1971; Smart *et al.*, 1982; Archer & Swanepoel, 1987; Smart *et al.*, 1990). Concomitantly, inferior fruit composition may result, such as too low concentrations of sugar, tartaric acid and anthocyanins, and too high malic acid, potassium and nitrogen content and must pH (Smart, 1982; Smart *et al.*, 1985; Smart *et al.*, 1988; Smart *et al.*, 1990). The colour of grape skins may also develop inferiorly (Champagnol, 1977; Kliewer, 1970, 1977; Koblet, 1984, 1987). Furthermore, bunch rot is increased (Smart *et al.*, 1990), and pest and disease control is difficult and force the farmer to spend enormous amounts of money on chemical control annually. Most of these problems can be overcome by solid canopy management practices. Excessive vegetative growth of grapevines and canopy density have therefore become major concerns for the farmer and viticulturist.

It is generally accepted that total dry matter production is a function of how effectively a vine can utilize the soil and aerial environment. The quality of the harvest, on the other hand, may be

defined as its aptitude to yield a wine of merit and this is dependent on the composition of the numerous constituents of berries (Champagnol, 1977). Sink capacity and efficiency can, however, only be expressed fully when supply is sufficient to meet demand and environmental conditions are optimal for metabolic activity. Leaves have the greatest effect on constituents of grapes and should, consequently, be managed in such a way that their full potential is explored. Since the above comprise a complex system of diversion and balance, research regarding grapevine management is aimed at finding the perfect balance between root development, accumulation of reserves, canopy microclimate and optimal yield and quality. To facilitate this aim, different canopy management techniques (the altering of leaves, shoots and fruit in space) such as suckering, shoot positioning, tipping, topping, and leaf removal are applied to existing vigorous vineyards. More permanent remedies would include the changing of the rootstock-scion combination, trellising system, cordon development, interrow and intervine spacing, and fertilization and irrigation programmes. The focus of this study is, however, on the first-mentioned, i.e. what can be done to an existing vigorous vineyard? For this reason, partial defoliation as canopy management practice was investigated. Extensive research has already been conducted on various aspects of partial defoliation of grapevines. However, no complete study involving translocation of photosynthetic products, photosynthesis, microclimate, vegetative growth, reproductive growth, fruit and wine quality and subterranean performance has been done before. Furthermore, the methods, levels and time of defoliation differed greatly and divergent results were reported. Recommendations regarding how, when, how many and where leaves may be removed are lacking.

Against this background, an investigation on the effect of partial defoliation on the metabolism and grape composition of the vine was initiated. The aims of the study were : to set principles for the detection of vigorous vineyards and for the remedying of these vineyards on the short as well as long term; to improve the practice of canopy management by determining how, when, how many and where leaves may be removed; to facilitate the abolishment of deleterious effects of excessive vegetative growth; to improve yield, fruit composition and wine quality; and to restrict the excessive use of pest and disease controlling chemicals by improving canopy structure.

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CHAPTER II

Distribution of ^{14}C-Photosynthate in the Shoot of *Vitis vinifera* L. cv. Cabernet Sauvignon I. The Effect of Leaf Position and Developmental Stage of the Vine

Key words : *Vitis vinifera*, Leaf position, ^{14}C-Distribution, Developmental stages.

ABSTRACT

The distribution of photosynthates, orginating in leaves at different positions on 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 $^{14}C0_2$-treated leaves gradually decreased during the season. Photosynthates were hoarded in the leaves at berry set, but were increasingly diverted to the bunches from then on. Apical leaves displayed the highest photosynthesis. Leaves opposite and below bunches accumulated very little photosynthates, especially from véraison to ripeness. Redistribution of photosynthates among the basal, middle and apical leaves was generally very restricted at all stages. Multidirectional distribution from the site of application of $^{14}C0_2$ occurred at berry set stage, while from pea size to ripeness photosynthates were mainly translocated basipetally.

The highest accumulation in the bunches occurred at véraison, while the basal leaves were primarily used to nourish the bunch.

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1. INTRODUCTION

Leaf photosynthesis depends upon demand for assimilates and is regulated by a source:sink relationship (Johnson *et al.*, 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 *et al.*, 1970; Quinlan & Weaver, 1970; Koblet & Perret, 1971, 1972, 1982; Koblet, 1975, 1977, 1984; Kriedemann, 1977; De la Harpe, 1984). However, these studies mainly dealt with autoradiographic techniques during which radio-activity was only qualitatively determined. The qualitative and quantitative contribution and distribution of ^{14}C 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 leaves of the grapevine start exporting their photosynthates 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 (Leonard & Weaver according to Hale & Weaver, 1962; Currle according to Koblet, 1977). From 50 % to 75 % of the final size for leaves of main and lateral shoots, respectively, only export of carbohydrates was found (Koblet, 1969). The age at which the leaf changes from a sink to a source can, however, differ among cultivars (Yang & Hori, 1980). According to Swanson & El-Shishiny (1959) and Koblet (1977) translocation of carbohydrates is mainly in the form of sucrose, while the speed of translocation was 27-30 cm/h (Koblet, 1969).

Although roots are considered to be the most important site of carbohydrate accumulation as a reserve in vines (Winkler & Williams, 1945; Scholefield *et al.*, 1978), the primary goal of the viticulturist is to divert these carbohydrates to grapes to improve their quantity and 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 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 on the distribution pattern of photoassimilates that contribute directly or indirectly to grape quality.

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

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon, clone CS 46, vineyard at the experimental farm of the Viticultural and Oenological Research Institute near Stellenbosch in the Western Cape, was used. The grapevines were free of harmful viruses and stayed healthy for the rest of the study. The cultivar was grafted onto rootstock 99 Richter (*Vitis Berlandieri x Vitis rupestris*) clone RY 30. Vines were planted (3,0 x 1,5 m spacing) on a Glenrosa soil (Series 13, Kanonkop) (MacVicar & Soil Survey Staff, 1977) and trained onto a 1,5 m slanting trellis as described by Zeeman (1981). Vines used 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 to ensure 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 (full colour break) 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.

2.2 Experimental design

The experiment was laid out as a completely randomized 3 x 4 factorial design. The two factors were : application of $^{14}C0_2$ to three positions on one shoot per vine (apical, middle, basal) and developmental stages (berry set, pea size, véraison, ripeness). The $^{14}C0_2$ treatments were applied at each of the four developmental stages. Nine randomized replications, comprising one-vine plots, for each of the 12 treatment combinations, were used.

2.3 Application of labelled $C0_2$

Each main shoot to be treated with $^{14}C0_2$ 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. 2.1). Application of $^{14}C0_2$ was as follows : The entire basal, middle or apical part, including lateral shoots, was enclosed in a polyethylene bag. Labelled $C0_2$ was generated inside the polyethylene bag by addition of 1,85 MBq $NaH^{14}C0_3$ 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 $^{14}C0_2$ was allowed for 60 min., after which the polyethylene bag as well as the vial were removed. In all cases $^{14}C0_2$ application was done under maximum light intensity and at temperatures favourable for photosynthesis.

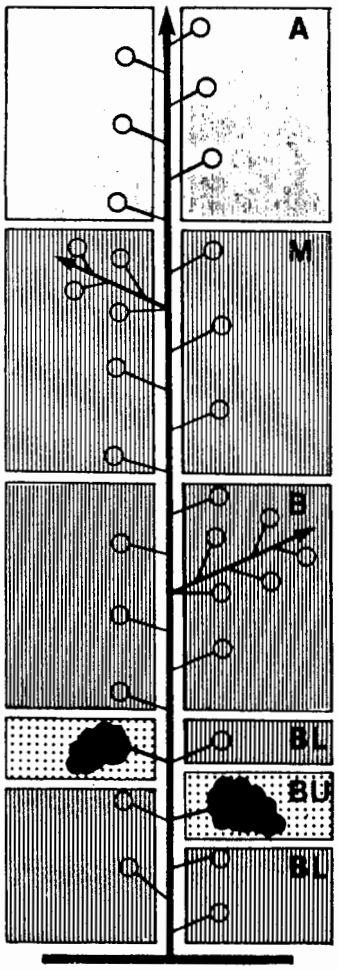

Fig. 2.1 The partitioning of a shoot into five parts, namely apical leaves (A), middle leaves (M), basal leaves (B), bunch leaves (BL) and bunches (BU).

2.4 Measurement of ^{14}C

Assimilation of $^{14}CO_2$ and translocation of labelled compounds were allowed for 24h after which the following five parts on the shoot were harvested separately : bunches, leaves opposite and below the bunches (hereafter called bunch leaves), basal leaves, middle

leaves and apical leaves (Fig. 2.1). The samples were sealed in polyethylene bags and stored in the dark at 5°C until required for further analyses.

Leaf areas were determined with a LI-COR LI 3000 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).

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 and 0,1 cm^3 $HClO_4$ for at least five days at 70°C in sealed vials. Ten cm^3 Instagel scintillation liquid (Beckman MP grade) was added and the mixture well shaken. The radio-activity was counted in a Packard Tri-carb 460 scintillation spectrophotometer. Quenching was automatically accounted for. The method used proved to be effective in digesting the plant material as well as oxidizing coloured pigments, especially chlorophyll.

2.5 Statistical analyses

A two-way analysis of variance (standard statistical software package of the VORI based on that of Snedecor & Cochran, 1980) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. The same program was used to perform log transformations, to compensate for heterogeneity of variance.

3. RESULTS AND DISCUSSION

3.1 Percentage activity

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

Treated part included : When ^{14}C-activity of a particular part to which label was applied is included in the calculations (Fig. 2.2), the overall impression is that translocation of radio-activity between different parts of the shoot did not progress very far after 24h, hence the high activity present in the treated part. However, it seems that ^{14}C was progressively translocated up to véraison, while at ripeness stage distribution was very restricted. Regardless of the site of application, the percentage activity in the leaves decreased from

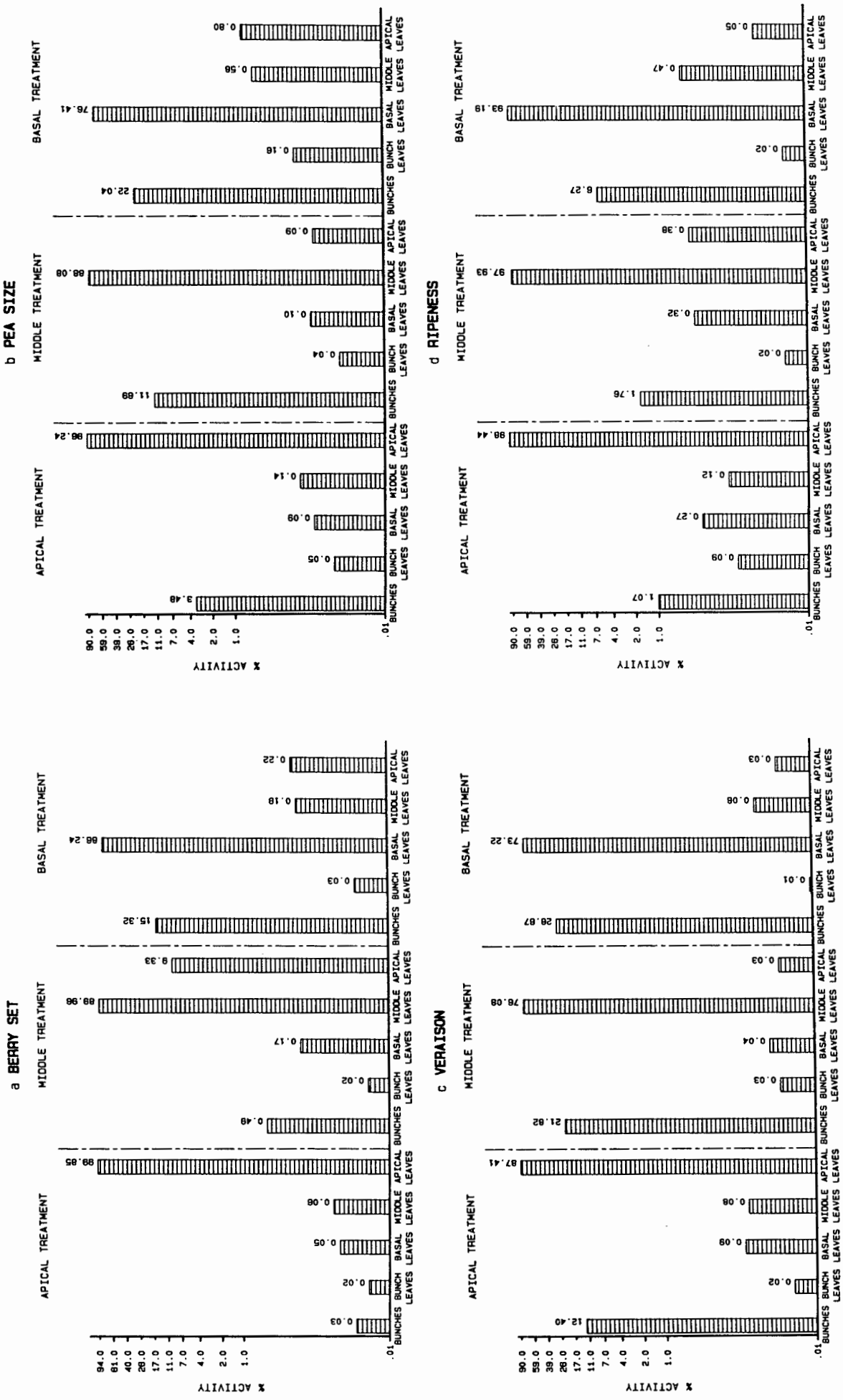

Fig. 2.2 The effect of leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as a percentage of total activity; treated part included. (Note log scale on y-axis).

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 demonstrated an 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 photosynthates were translocated (Fig. 2.2), resulting in a concomitant significantly higher specific activity in the bunches (Table 2.1). Although this could have resulted from the close site of application of $^{14}C0_2$, it emphasized 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 the leaves were situated into the canopy (Table 2.1). In contrast to this, the apical leaves mainly hoarded photosynthates for its 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. 2.3), the distribution pattern and site of accumulation of ^{14}C become more noticeable. It appeared as if translocation to the bunches was increasingly favoured up to véraison stage with a decline thereafter, irrespective of the position of application of $^{14}CO_2$. However, the lowest percentage activity in bunches 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 obviously were favoured at this stage. It appeared as if 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, bunch leaves generally demonstrated their incapability of acting as a strong sink.

TABLE 2.1 The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthate, 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^{e}	0,22^{e}	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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

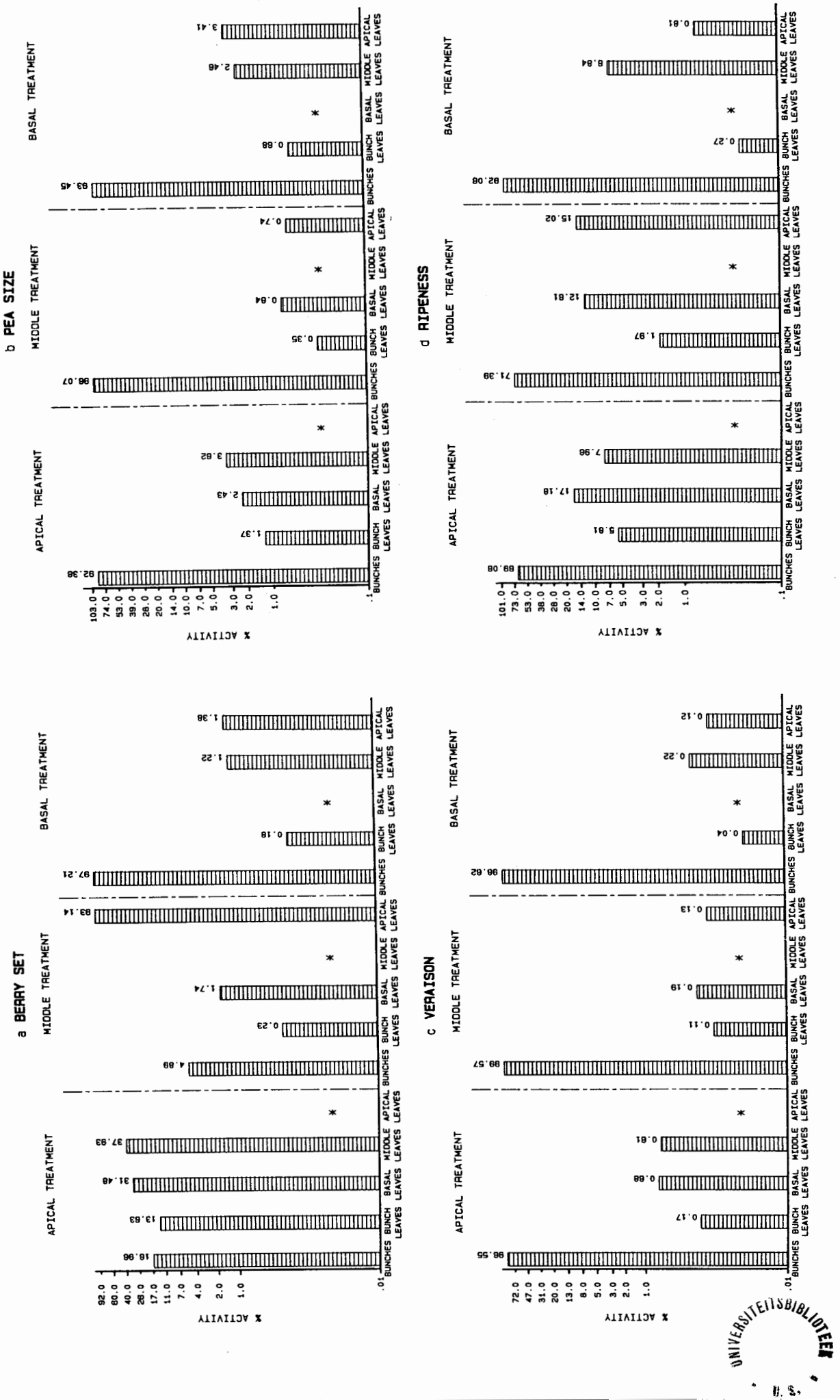

Fig. 2.3 The effect of leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as a percentage of total activity; treated part excluded(*). (Note log scale on y-axis).

3.2 Specific activity

Activity/dry mass : From the specific activity of the different plant parts (Fig. 2.4) it seemed that translocation from the part to which label was applied did not progress very far after 24h, especially in the case of the apical treatments. A significant gradual decrease in specific photosynthetic activity of the treated leaves during the season was evident (Table 2.1), verifying the findings of Pandey & Farmahan (1977). This led to a significant decrease in activity in the bunches. 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 2.2), they nevertheless displayed the highest photosynthetic activity (Fig. 2.4), probably because of a tendency to hoard assimilates as well as an inherent active metabolism.

TABLE 2.2 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

Where the middle and basal parts were treated, very low activity was found in apical leaves compared to leaves of treated parts. This is in contrast to the general conception that apical leaves are parasitic on the rest of the vine, because they are rapidly growing and therefore their photosynthetic activity is lower. However, a strong import of ^{14}C from the apical to the middle leaves was again found at berry set stage.

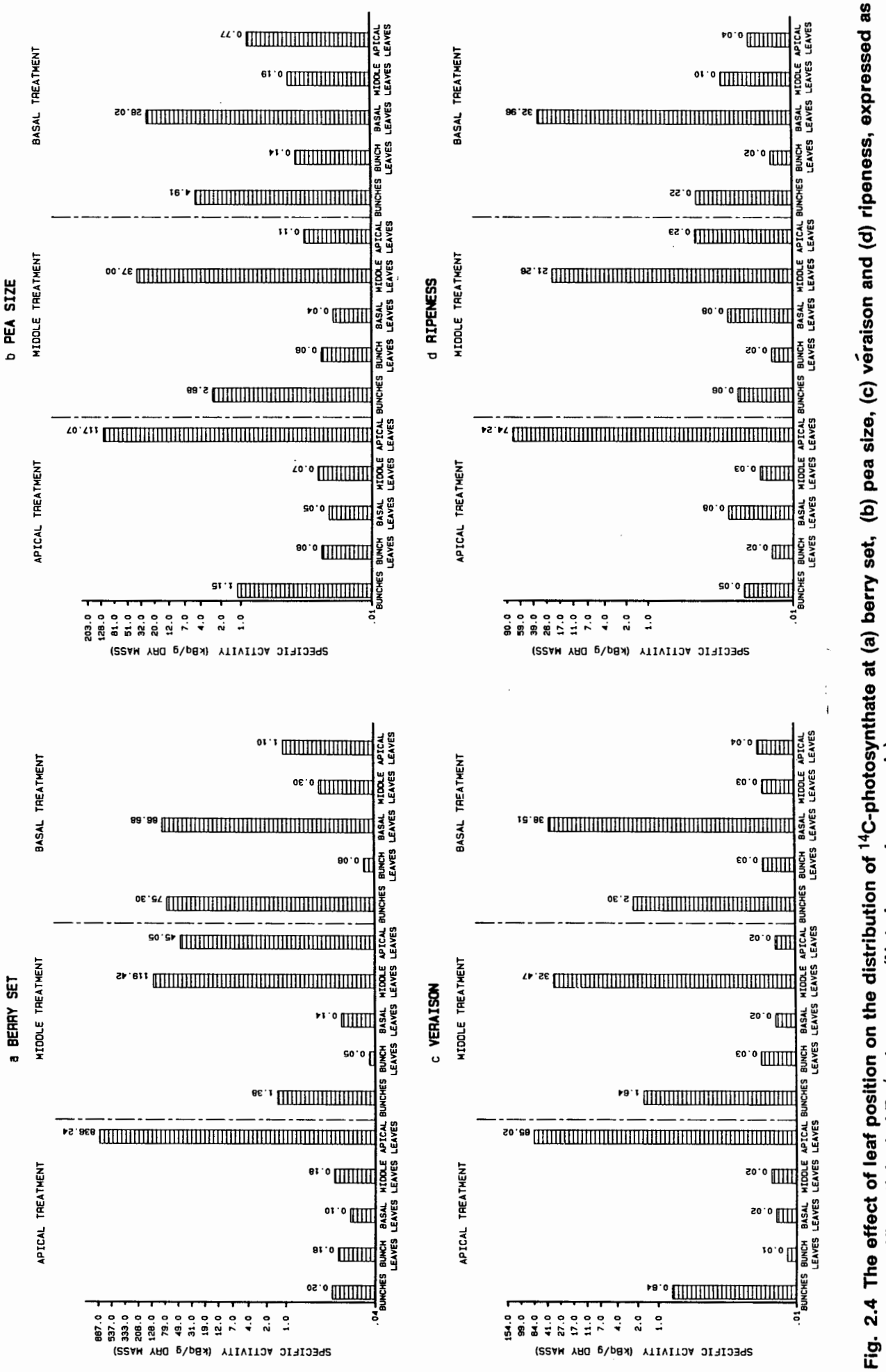

Fig. 2.4 The effect of leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as specific activity in kBq/g dry mass. (Note log scale on y-axis).

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 physiologically more active at berry set and pea size stages (Fig. 2.4). Senescence probably set in thereafter, as was evident from senescence, yellowing and abscission of leaves as found in the vineyard. Although distribution of photosynthates between leaves of different parts was generally negligible, middle leaves, and to a lesser extent basal leaves, translocated to the apical leaves at berry set stage.

Activity/leaf area : Although a general decline in specific photosynthesis was 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 2.3). The general decline is in agreement with the findings of Kriedemann (1977) and may partly be explained 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 increased senescence, as is evident from the decreasing moisture content (Table 2.4) 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 $C0_2$ assimilation.

Considering all criteria discussed, it seems that photosynthates 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, photosynthates 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 basal leaves mainly fed the bunches and to a limited extent distributed acropetally. At pea size apical, middle and basal leaves mainly translocated to the bunches. The same situation applies to véraison, whereas at ripeness the sink capacity of the bunches decreased, albeit still strong. At the latter stage photosynthates for growth and development of bunches were mainly obtained from basal leaves. These results verify those found by Hale & Weaver (1962) and Koblet (1977). The apical leaves were the biggest hoarders at all stages. Irrespective of the site of application, accumulation of ^{14}C in bunch leaves (those opposite and below the bunches) was very slight at all stages.

TABLE 2.3 The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthate, 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 2.4 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

4. CONCLUSIONS

A gradual decrease in specific photosynthetic activity of the leaves of 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 photosynthates to each other at all stages. Photosynthates were hoarded in the leaves at berry set, but were increasingly diverted to the bunches from there on. Although apical leaves displayed the highest photosynthesis, the only evidence of them acting as parasites on the rest of the shoot, as is generally believed, seemed to occur at berry set and to a lesser extent at ripeness. In general, the leaves opposite and below the bunches accumulated very low amounts of radio-activity and can readily be considered of lesser importance to the vine, especially from véraison to ripeness.

It seemed as if translocation was very much favoured during the first part of the growth season, i.e. up to véraison, 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 efficiency of basal leaves by an improved canopy management.

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

Percentage activity and specific activity seemed to be useful criteria to express results obtained in studies involving radio-active 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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CHAPTER III

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

Key words : *Vitis vinifera*, Defoliation, Leaf position, ^{14}C-Distribution, Developmental stages.

ABSTRACT

The effect of partial defoliation of *Vitis vinifera* L. cv. Cabernet Sauvignon on the distribution of photosynthates, originating in leaves at different positions on the shoot at berry set, pea size, véraison and ripeness stages, was investigated.

Partial defoliation (33 % and 66 %) resulted in higher apparent photosynthetic efficiency in all remaining leaves on the shoot. The pattern of distribution of photosynthates seemed to be the same between treatments. Control vines were found to carry excess foliage. Optimal photosynthetic activity of all the leaves was therefore not reached.

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1. INTRODUCTION

Vegetative growth of vines in South Africa generally tends to be excessive, mainly because of high temperatures as well as irrigation practices. 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 a dense interior receiving 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). Therefore, foliage management becomes a major consideration for the viticulturist aiming to exploit the full photosynthetic potential of interior leaves.

The photosynthetic efficiency of leaves increased when the size of the photosynthetic source (leaf area) was decreased in relation to the size of sinks (roots, trunk, shoots, fruits) (Buttrose, 1966; May *et al.*, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson *et al.*, 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 conducted to determine the effect of partial defoliation of Cabernet Sauvignon on the movement of photosynthates, originating in leaves at different positions on the shoot, at berry set, pea size, véraison and ripeness.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

Details of the experimental vineyard as well as the methods for application and determination of radio-activity, were given by Hunter & Visser (1988).

2.2 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.

2.3 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.

2.4 Statistical analyses

A three-way analysis of variance (standard statistical software package of the VORI) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. The same program was used to perform log transformations, to compensate for heterogeneity of variance.

3. RESULTS AND DISCUSSION

3.1 Percentage activity

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

Treated part included : From Fig. 3.1 it is evident that no major differences in translocation of labelled photosynthates occurred between defoliation treatments at any of the developmental stages. It seemed that translocation of ^{14}C did not progress very far after 24h for all defoliation treatments. Irrespective of leaf position, application of $^{14}CO_2$ at véraison nevertheless resulted in a prominent accumulation of photosynthetic products in bunches. Partial defoliation resulted in an increased translocation from the $^{14}CO_2$-treated part and a concomitant higher accumulation in bunches at véraison. The basal leaves strikingly contributed the most photosynthate to the bunches, regardless of degree of defoliation and developmental stage of the vine.

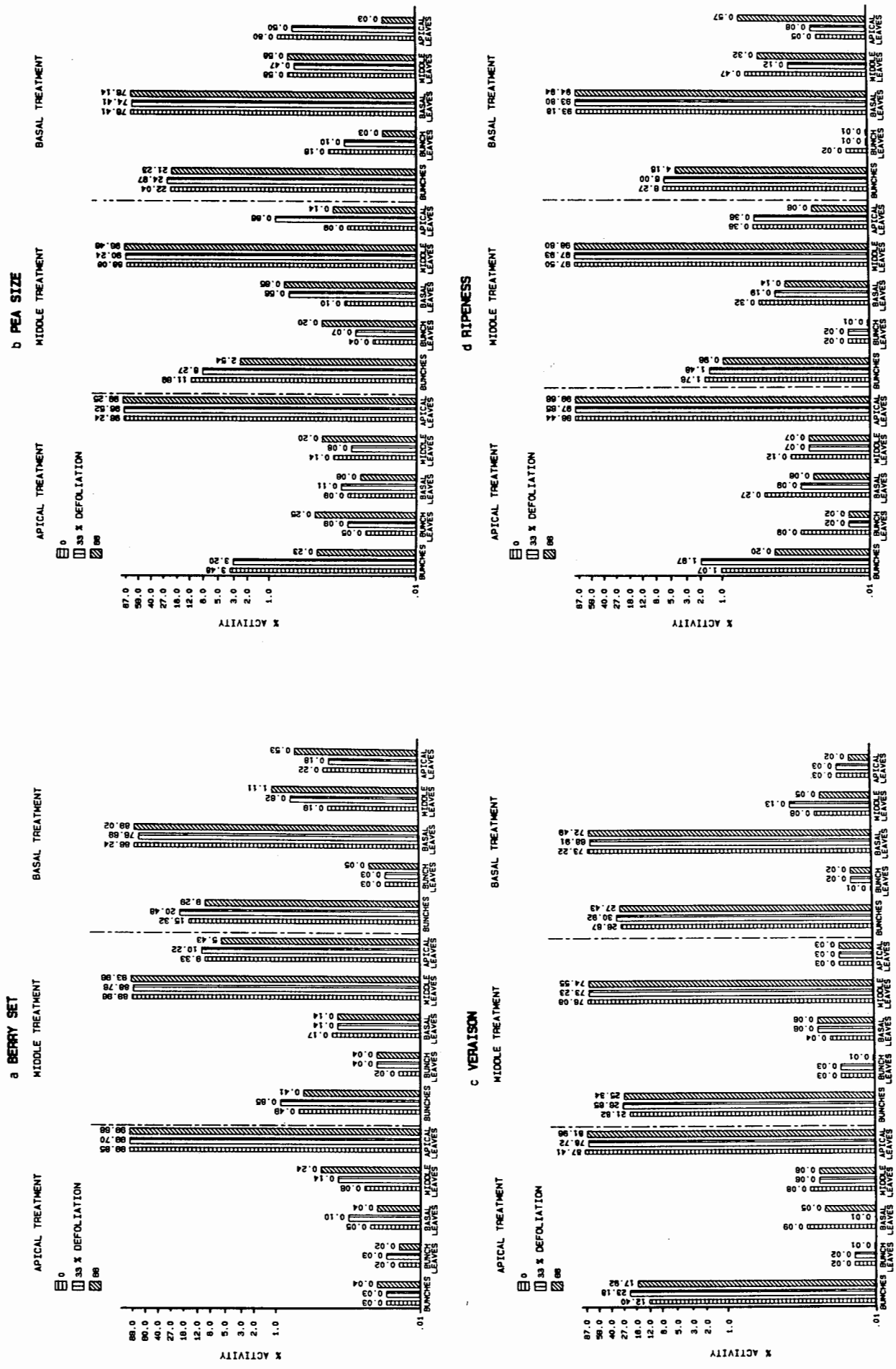

Fig. 3.1 The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as a percentage of total activity; treated part included. (Note log scale on y-axis).

Treated part excluded : By excluding the treated part, the distribution pattern and site of accumulation of ^{14}C became more pronounced (Fig. 3.2). No definite relationship between degree of defoliation and accumulation in either reproductive or vegetative organs existed.

3.2 Total activity

The effect of defoliation and developmental stage of the vine on the total ^{14}C-activity of each treated part, is depicted in Table 3.1. The approximate total activity per shoot, over all four developmental stages, for the 0 %, 33 % and 66 % defoliation treatments, amounted to 949, 846 and 801 kBq, respectively. Since no significant differences in the accumulation and distribution patterns between the defoliation treatments could be found (Figs. 3.1 & 3.2), the total ^{14}C-activities (Table 3.1) can be assume 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 non-defoliated vines (Table 3.2), it appeared 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 3.1). It would therefore appear as if the remaining leaves were able to adequately compensate for the loss of leaves and that partial defoliation may be safely applied in practice. Furthermore, the application of partial defoliation may be advantageous due to improved aeration of the canopy and increased light penetration. These advantages may be beneficial with regard to pest and disease control, fruit composition, accumulation of colouring compounds in the grapes, and fruitfulness of the basal buds in the following season.

A marked, although not significant, increase in photosynthetic activity was found for the apical leaves at ripeness. This possibly occurred to concentrate photosynthetic products for regrowth of shoot tips.

3.3 Specific activity

Activity/dry mass : From the specific activity it is evident that the photosynthetic activity of all parts decreased during the growth season (Table 3.3). This probably resulted from an increased senescence as verified by the decreasing moisture content of the leaves (Table 3.4). 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 3.3) probably resulted from senescence of leaves as well as from berry growth. The efficiency of the leaves of all defoliation treatments decreased as they were

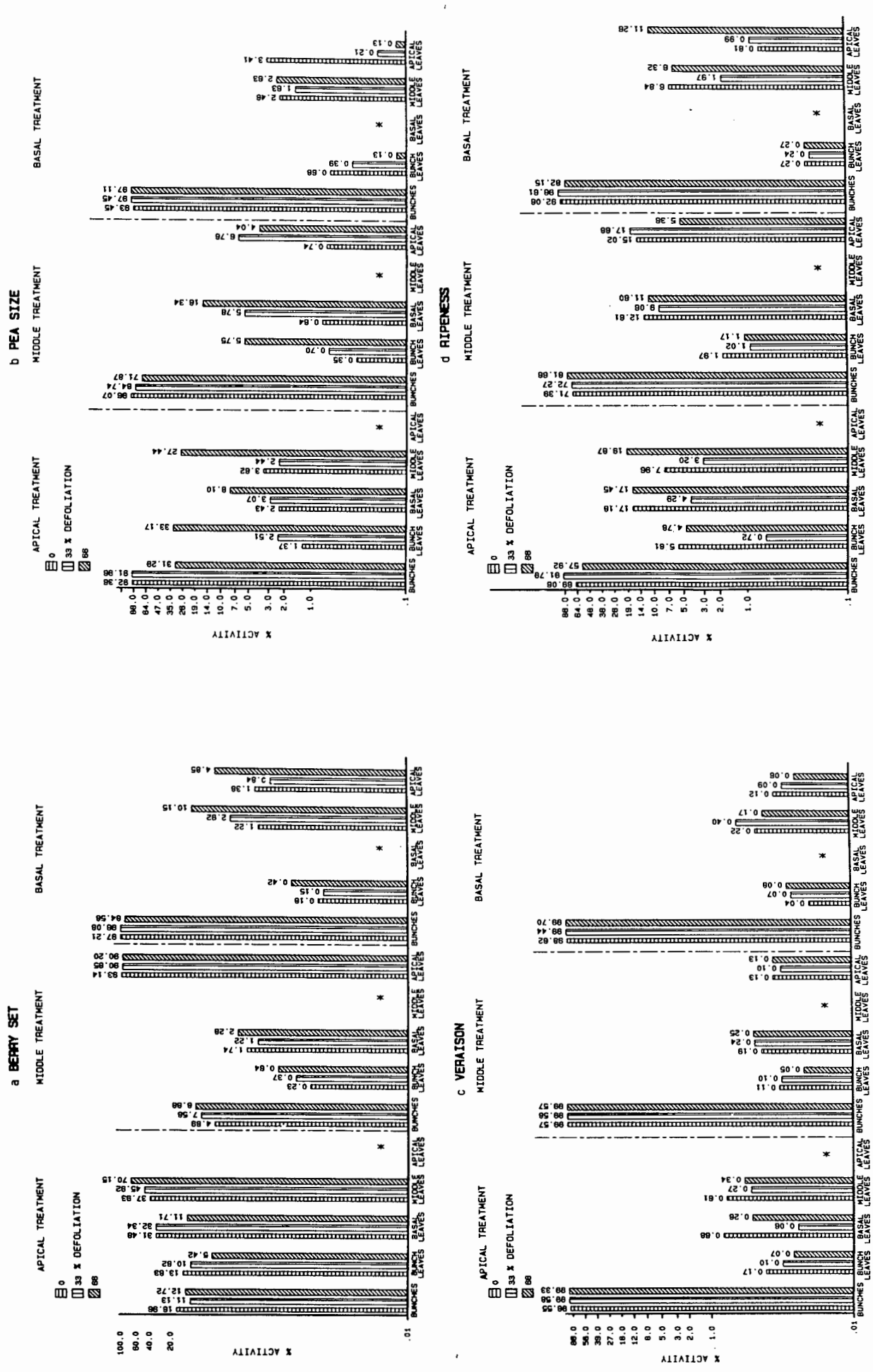

Fig. 3.2 The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as a percentage of total activity; treated part (*) excluded. (Note log scale on y-axis).

TABLE 3.1 The effect of defoliation and developmental stage of the vine on 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]		455,75[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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 3.2 The effect of defoliation and developmental stage of the vine on total area (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	309,13	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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 3.3 The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthate, 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	$0,19^{g}$	$3,80^{c}$	$73,41^{a}$	$25,80^{a}$	$0,12^{a}$	$0,09^{a}$	$0,10^{a}$	$0,10^{b}$	$0,12^{d}$	$0,17^{d}$	$109,97^{a}$	$36,76^{a}$	$0,24^{f}$	$204,24^{a}$	$1,23^{e}$	$68,57^{a}$	$991,67^{a}$	$64,19^{d}$	$1,62^{e}$	$352,49^{a}$
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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 3.4 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 3.5 The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthate, 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^{e}	1,44^{d}	20,68^{b}	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^{e}	52,54^{c}	0,16^{e}	17,59^{c}	273,14^{c}	11,35^{d}	0,49^{f}	94,99^{c}
33	0,64^{e}	2,89^{c}	18,14^{b}	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^{e}	89,48^{b}	0,17^{e}	29,92^{b}	344,69^{b}	17,22^{d}	0,28^{f}	122,73^{b}
66	0,48^{e}	1,61^{d}	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^{e}	95,33^{a}	0,85^{d}	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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

progressively situated deeper into the canopy, thus receiving less light (Table 3.5).

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. 3.3). Considering their significantly lower total leaf area (Table 3.2), it would therefore appear as if the full photosynthetic capacity of the leaves of control vines was not used (Table 3.1). 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; Johnson *et al.*, 1982). However, this finding may also be linked to that of Smart (1973) who found that the exposure of specific leaves to direct light may be of more importance than total light interception in determining yields of vigorous vines.

Activity/leaf area : This activity also verified the much higher photosynthetic activity of leaves of partially defoliated vines, generally increasing with degree of defoliation (Table 3.6). The higher photosynthetic activity of the leaves of 33 % and 66 % defoliated vines could have resulted from a decrease in source capacity, which caused the leaves to photosynthesize more effectively to supply in 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 exposure to sunlight could have made a larger contribution to leaves situated deeper in the canopy.

Regardless of the degree of defoliation, apical leaves demonstrated the highest photosynthetic efficiency (Table 3.6). Although a significant decrease in photosynthetic activity of the apical leaves was found up to véraison, it is again evident that activity significantly increased at ripeness (Table 3.7). In contrast to apical leaves, very low activity was generally detected in 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 control vines, as is evident from the higher mean radio-activity found for partially defoliated vines (Table 3.6). The much higher photosynthetic activity of partially defoliated vines suggested 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.

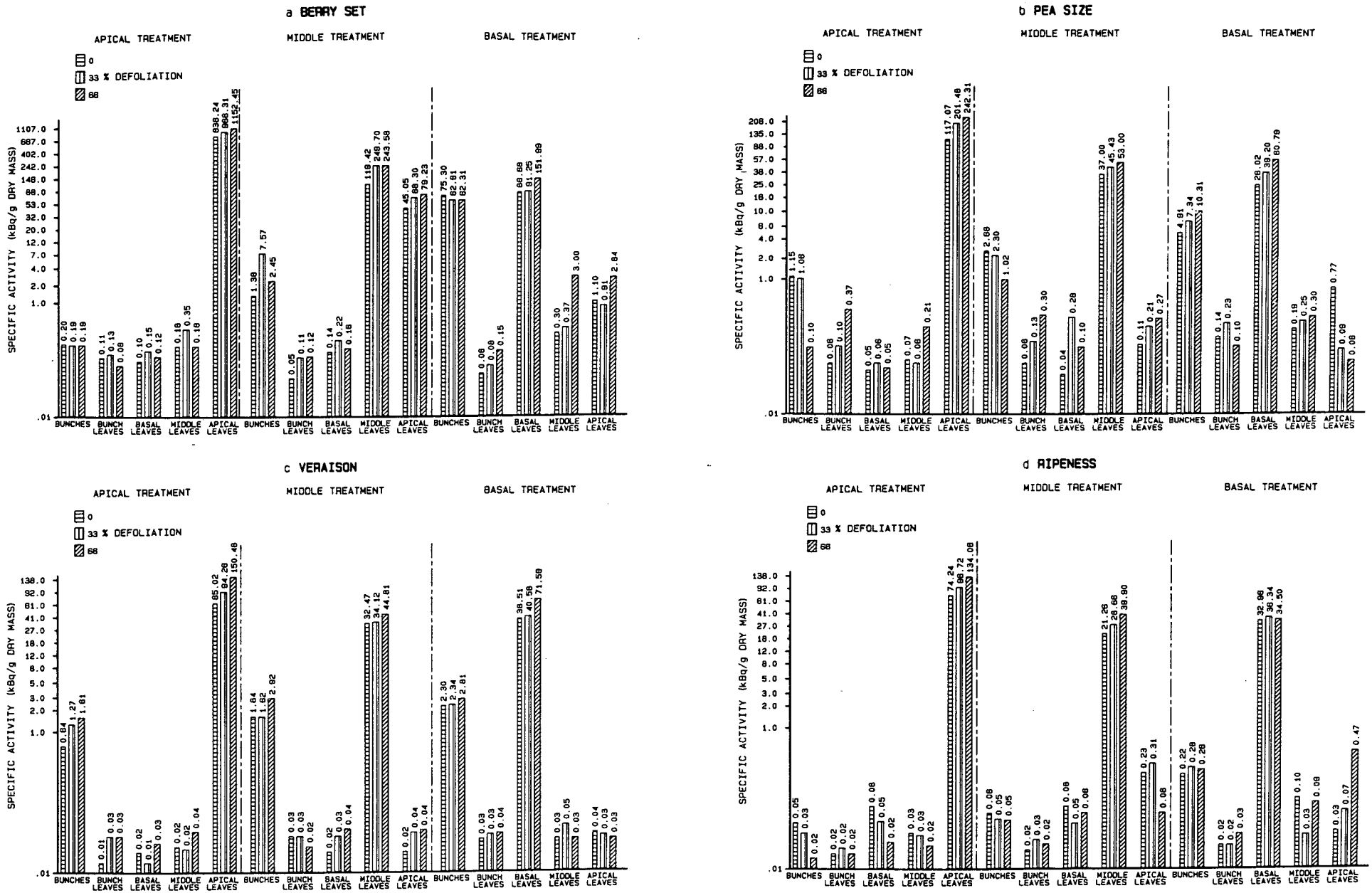

Fig. 3.3 The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthate at (a) berry set, (b) pea size, (c) véraison and (d) ripeness, expressed as specific activity in kBq/g dry mass. (Note log scale on y-axis).

TABLE 3.6 The effect of defoliation and leaf position on the distribution of ^{14}C-photosynthate, 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	$0,11^a$	$0,19^a$	$0,06^a$	$0,12^a$	$0,14^a$	$16,69^a$	$163,20^a$	$60,01^a$	$0,20^c$	$158,30^a$	$0,32^b$	$52,94^b$	$529,47^b$	$37,40^c$	$1,22^e$	$189,36^b$
33	$0,33^a$	$0,24^a$	$0,24^a$	$0,27^a$	$0,25^a$	$31,46^a$	$167,34^a$	$66,35^a$	$0,15^c$	$187,57^a$	$0,68^b$	$62,80^b$	$847,05^a$	$30,92^c$	$0,23^e$	$292,73^b$
66	$0,83^a$	$0,12^a$	$0,42^a$	$0,45^a$	$0,19^a$	$3,06^a$	$190,21^a$	$64,49^a$	$0,30^c$	$277,12^a$	$1,39^b$	$92,94^a$	$913,36^a$	$117,29^c$	$1,04^d$	$343,89^a$
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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 3.7 The effect of leaf position and developmental stage of the vine on the distribution of ^{14}C-photosynthate, 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

4. CONCLUSIONS

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

From these results it is proposed that non-defoliated vines carried excess foliage, which readily inhibited optimal photosynthetic activity of all the leaves on the vine. Accumulation of photosynthates in bunches was therefore reduced. It can be reasoned that the leaves opposite and below the bunches of such vines should be removed at véraison and that the shoots be positioned on the vine and trellis in such a way as to allow optimal exposure, especially of basal leaves, to sunlight. It also appeared that canopy density can be reduced by an even removal of up to 66 % leaves at véraison without deleteriously affecting yield. On the contrary, it would appear that yield may be increased as a result of defoliation. Defoliation would provide maximum photosynthesis of the remaining leaves as well as an optimum contribution of photosynthates to the bunches.

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CHAPTER IV

The Effect of Partial Defoliation, Leaf Position and Developmental Stage of the Vine on the Photosynthetic Activity of *Vitis vinifera* L. cv. Cabernet Sauvignon

Key words : *Vitis vinifera*, Defoliation, Leaf position, Photosynthesis, Stomatal resistance, Transpiration, Leaf microclimate, Developmental stages.

ABSTRACT

The effect of partial defoliation, leaf position and developmental stage of the vine on photosynthesis, stomatal resistance and transpiration of *Vitis vinifera* L. cv. Cabernet Sauvignon was investigated.

Partially defoliated vines displayed a higher rate of photosynthesis, generally increasing with degree of defoliation. The highest photosynthetic rates were found for apical leaves, while those of leaves opposite and below the bunches were restricted. The rate of photosynthesis generally declined as the season progressed.

The course of transpiration rate and stomatal resistance correlated with the rate of photosynthesis. However, transpiration and photosynthesis correlated poorly for apical leaves. In general, photon flux density and relative humidity at the leaf surface increased with an increase in defoliation percentage for all leaf positions. Leaf temperature was not significantly affected by partial defoliation.

The results suggested that excess vegetative growth was detrimental to interior-canopy microclimate as well as the photosynthetic rate of the entire vine. Partial defoliation seemed to provide a means to reduce some of the deleterious effects of vigorous growth.

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1. INTRODUCTION

Vegetative growth in South African vineyards tends to be excessively vigorous. This situation may result in poor canopy microclimate and eventually reduced grape quality (Smart, 1973, 1982, 1985; Koblet, 1977, 1984; Kliewer, 1982; Smart *et al.*, 1985a, 1985b) and productivity (Shaulis *et al.*, 1966; Smart *et al.*, 1982; Koblet, 1984).

Partial defoliation of Cabernet Sauvignon, in an attempt to reduce vegetative growth, stimulate metabolic activity and improve canopy microclimate, induced higher photosynthetic efficiency of remaining leaves and increases in assimilate supply to bunches (Hunter & Visser, 1988a, 1988b). The basal leaves, in particular, were found to be very important for fruit development during the entire growth season. Demand for assimilates, leaf age, and a suitable microclimate seemed to be of the utmost importance for maximum photosynthetic capacity. According to Kriedemann (1977), genetic factors primarily limit photosynthetic capacity by their effects on overall demand for photosynthates and partitioning of assimilates between vegetative and reproductive growth. The rate of photosynthesis and associated reactions, i.e. stomatal resistance and transpiration of grapevine leaves, are affected by light intensity (Kriedemann, 1968, 1977; Smart, 1974a; Kliewer, 1982; Koblet, 1984), intermittent light (Kriedemann, 1968; Koblet, 1984), temperature (Kriedemann, 1968, 1977; Alleweldt *et al.*, 1982; Koblet, 1984; Sepúlveda & Kliewer, 1986; Sepúlveda *et al.*, 1986), relative humidity (Sepúlveda & Kliewer, 1986), CO_2 and O_2 concentrations (Kriedemann *et al.*, 1968, 1977), leaf age (Kriedemann, 1968, 1977; Kriedemann *et al.*, 1970; Pandey & Farmahan, 1977; Alleweldt *et al.*, 1982; Koblet, 1984), moisture supply (Smart, 1974b; Hofäcker, 1976; Kriedemann, 1977; Alleweldt & Rühl, 1982), seasonal patterns and crop load (Kriedemann, 1977).

Apart from ^{14}C-translocation studies at different developmental stages (Hale & Weaver, 1962; Quinlan & Weaver, 1970; Koblet & Perret, 1971, 1972; Koblet, 1975, 1977; De La Harpe, 1984; Hunter & Visser, 1988a, 1988b), little research has been conducted on the rate of photosynthesis of grapevine leaves as affected by partial defoliation and developmental stage of the vine (Kriedemann, 1977; Pandey & Farmahan, 1977; Hofäcker, 1978). Consequently, this investigation deals with the effect of partial defoliation, leaf position and developmental stage of the vine on photosynthesis, stomatal resistance and transpiration of *Vitis vinifera* L. cv. Cabernet Sauvignon.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

Details of the experimental vineyard used were given by Hunter & Visser (1988a).

2.2 Experimental design

The experiment was laid out as a completely randomized 3 x 4 x 4 factorial design. The three factors were : defoliation treatments, applied to the whole vine (0 %, 33 %, 66 %); measurement of physiological and environmental factors at four positions on one shoot per vine (opposite and below the bunches; basal; middle; apical); and developmental stages (berry set, pea size, véraison, ripeness). The basal, middle and apical leaf positions were defined according to leaf number on the shoot. The measurements were performed at each of the four developmental stages. There were nine replications, comprising one vine per plot, for each of the 48 treatment combinations.

2.3 Defoliation treatments

The defoliation treatments were initiated from approximately one month after budding and 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.

2.4 Measurements

Rate of photosynthesis (mg $CO_2/dm^2/h$), stomatal resistance (s/cm), rate of transpiration (/ug $H_2O/cm^2/s$), photon flux density (PFD) (W/m^2), percentage relative humidity and leaf temperature (^oC), were measured using an ADC portable photosynthesis meter (The Analytical Development Co., England). The photosynthesis apparatus consisted of an infra-red CO_2 analyser, a data logger, a Parkinson broad leaf chamber (volume = 16 cm^3, area = 6,25 cm^2), and an air supply unit (length of sample tube = 4 m). Radiation was measured using a quantum sensor with filters providing response over 400 nm to 700 nm. The maximum vapour pressure (E_{max}) was taken as two. The air flow rate through the open system was adjusted to 300 cm^3/min. Measurements were carried out between

10:30 and 14:00 on the day scheduled. The maximum ambient temperatures for the days scheduled at berry set, pea size, véraison and ripeness were 27,4°C; 23,0°C; 23,5°C and 21,2°C, respectively.

2.5 Statistical analyses

A two-way analysis of variance (standard statistical software package of the VORI) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. Since no significant interactions between defoliation percentage and developmental stage of the vine were found for any of the leaf positions, only the main effects, i.e. defoliation percentage and developmental stage, were considered. The figures therefore depict either averages over stages or averages over defoliation treatments, while data over both factors were used to calculate the correlation coefficients. The same program was used to determine correlation coefficients.

3. RESULTS AND DISCUSSION

3.1 Rate of photosynthesis

The photosynthetic rates of Cabernet Sauvignon leaves, ranging from 2,64 mg $CO_2/dm^2/h$ to 14,09 mg $CO_2/dm^2/h$ (Figs. 4.1a & b), are comparable to those found for other cultivars (Kriedemann, 1968, 1977; Kriedemann & Lenz, 1972; Hofäcker, 1976, 1978; Marini & Marini, 1983; Tan & Buttery, 1986).

Partial defoliation (33 % and 66 %) stimulated the photosynthetic rate consistently, increasing with an increase in the degree of defoliation (Fig. 4.1a). This is in general agreement with the findings of Hodgkinson (1974), Kriedemann (1977), Hofäcker (1978) and Hunter & Visser (1988b). The apical leaves of all treatments displayed the highest rate of photosynthesis, supporting findings that young, actively growing leaves are largely photosynthetically self-sufficient (Kriedemann & Lenz, 1972; Hunter & Visser, 1988a). Evidently, the deeper the leaves were situated in the canopy, the more the rate of photosynthesis declined. Photosynthetic rates of the leaves opposite and below the bunches (bunch leaves) were very low, especially for control vines (0 % defoliation). This is also evident from Fig. 4.2. It seemed that the percentage photosynthetic rate of

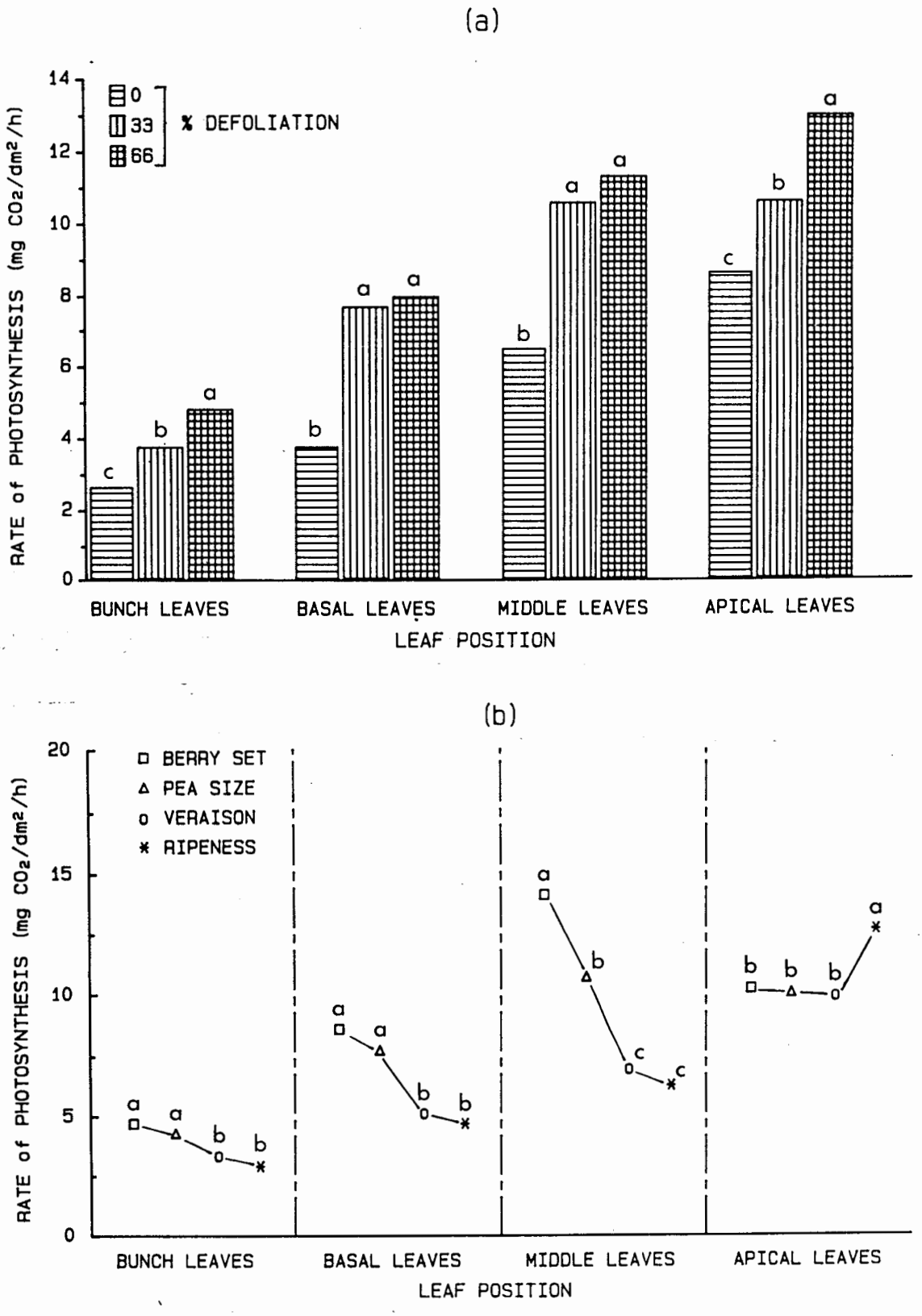

Fig. 4.1 a & b The effect of (a) defoliation, (b) developmental stage of the vine, and leaf position on the rate of photosynthesis of Cabernet Sauvignon leaves. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

basal and middle leaves of partially defoliated vines was higher than that of control vines, but noticeably lower than that of controls in the case of apical leaves. Comparatively, the photosynthetic contribution of bunch leaves was relatively low in all cases. This confirmed the conclusion by Hunter & Visser (1988a, 1988b) that leaves opposite and below the bunches did not substantially contribute photosynthates to bunches.

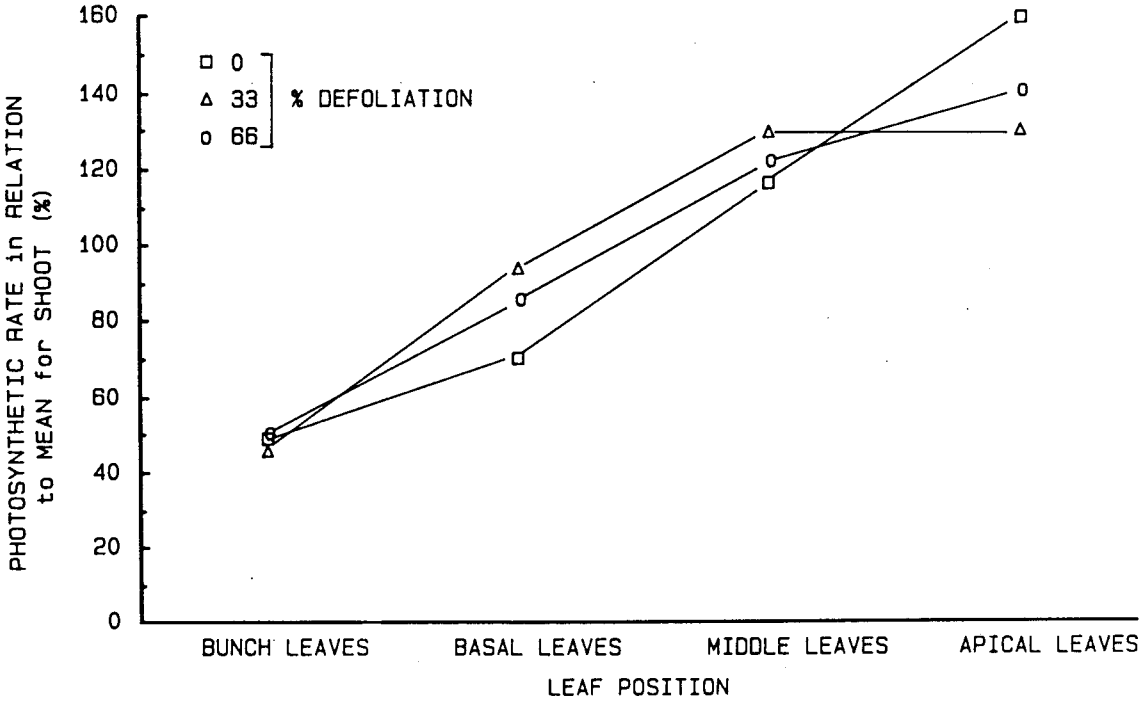

Fig. 4.2 The effect of defoliation on the percentage photosynthetic rate of leaves in different positions in relation to the mean photosynthetic rate of all the leaves on the shoot.

These results also support concepts and findings of other investigators that a dense canopy, receiving insufficient sunlight, is deleterious to the photosynthetic capacity of especially interior leaves (Shaulis *et al.*, 1966; Smart, 1973, 1974a, 1985; Kriedemann, 1977; Kliewer, 1982; Marini & Marini, 1983; Koblet, 1984). However, demand for assimilates from vegetative as well as reproductive sinks probably greatly increased with increasing degree of defoliation, causing leaves on the partially defoliated vines to photosynthesize more actively. This would substantiate the findings of Kriedemann & Lenz (1972), Hofäcker (1976, 1978) and Kriedemann (1977). According to Wareing *et al.* (1968) competition between leaves for mineral nutrients, and possibly also hormones such as cytokinins, originating in the roots, might also contribute to increased photosynthetic rates.

From Fig. 4.1b it is evident that the rate of photosynthesis of middle, basal and bunch leaves declined with time. Similar results were found by Kriedemann (1977) and Hunter & Visser (1988a, 1988b). Possible reasons for this phenomenon were given in the latter two papers, i.e. an increased senescence, an increase in sugar concentration, decreases in amino acids and organic acids and a decreased demand for assimilates from other sinks. The increase in photosynthetic rate of apical leaves at ripeness corresponded to that found by Hunter & Visser (1988a, 1988b).

3.2 Stomatal resistance

The stomatal resistance, varying from 1,24 s/cm to 6,18 s/cm, are presented in Figs. 4.3a & b. These results are comparable to those found for other cultivars (Hofäcker, 1976, 1978; Sepúlveda & Kliewer, 1986; Tan & Buttery, 1986; Van Zyl, 1986).

The lowest stomatal resistance was found in apical leaves (Fig. 4.3a). The values corresponded to values of 2 s/cm to 3 s/cm required for maximum rate of photosynthesis as was found by Kriedemann (1977) (Fig. 4.1a). Stomatal resistance of control vines in all cases was the highest, while it generally decreased with increasing defoliation. Similar results were obtained by Hofäcker (1978).

Although it seemed that stomatal resistance increased as the growth season progressed, peak resistances mostly occurred at véraison, followed by a decline (Fig. 4.3b).

3.3 Rate of transpiration

Transpiration rates, ranging from 2,82 /ug $H_2O/cm^2/s$ to 11,78 /ug $H_2O/cm^2/s$ (Figs. 4.4a & b) compared well with those found by Smart (1974b) for irrigated Shiraz vines. As for rate of photosynthesis (Fig. 4.1a), transpiration rates generally increased with an increase in partial defoliation (Fig. 4.4a). Transpiration generally decreased the deeper leaves were situated in the canopy. Similar results were reported by Fails *et al.* (1982).

A general decline in transpiration rate occurred as leaves aged with time (Fig. 4.4b). As for photosynthesis (Fig. 4.1b) and stomatal resistance (Fig. 4.3b), it seemed that no noticable change in transpiration occurred from véraison to ripeness, except for bunch leaves in which case it decreased significantly. These changes can probably be explained by a recommencement of vegetative growth at ripeness as suggested by Hunter & Visser (1988a, 1988b).

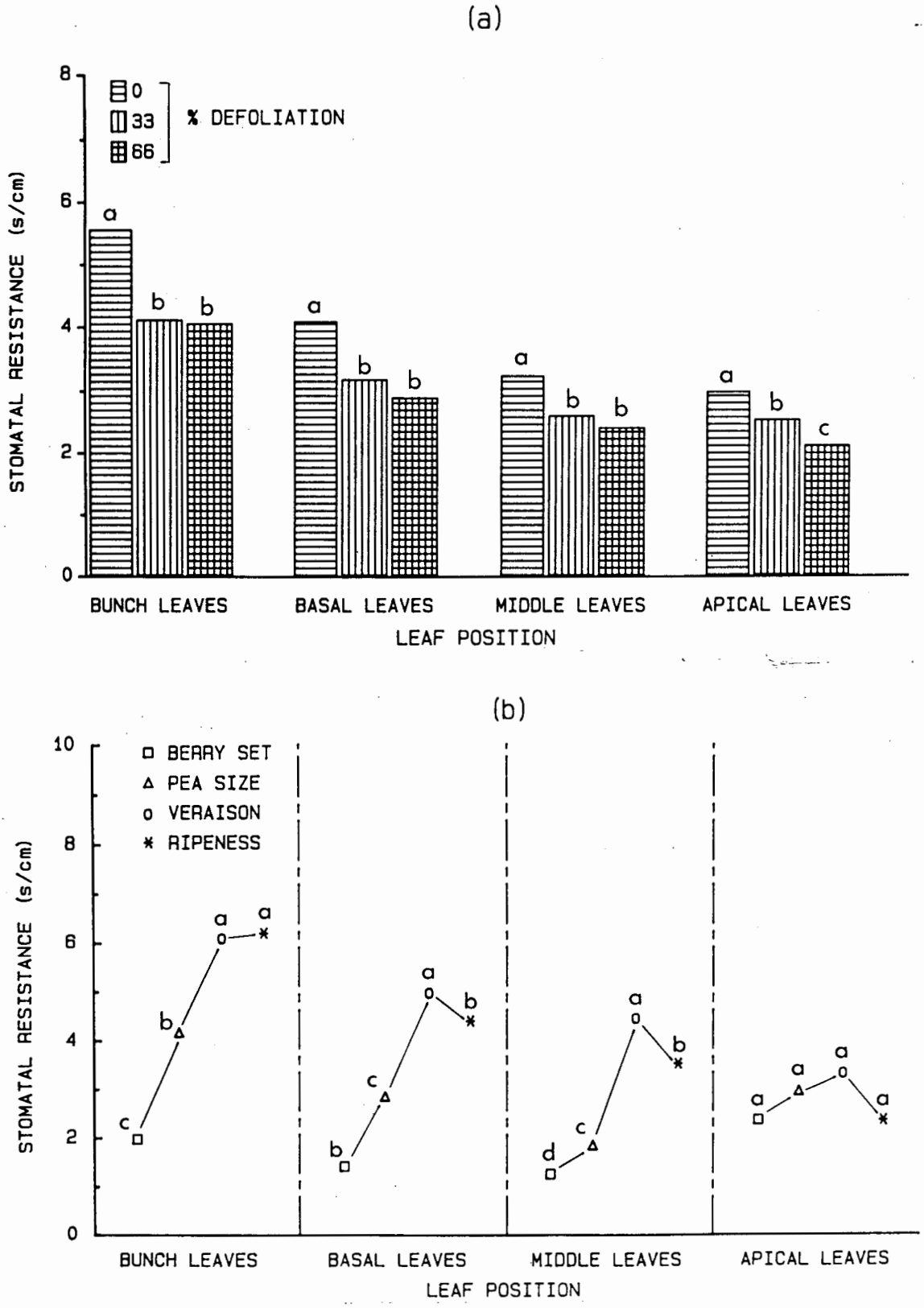

Fig. 4.3 a & b The effect of (a) defoliation, (b) developmental stage of the vine, and leaf position on the stomatal resistance of Cabernet Sauvignon leaves. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

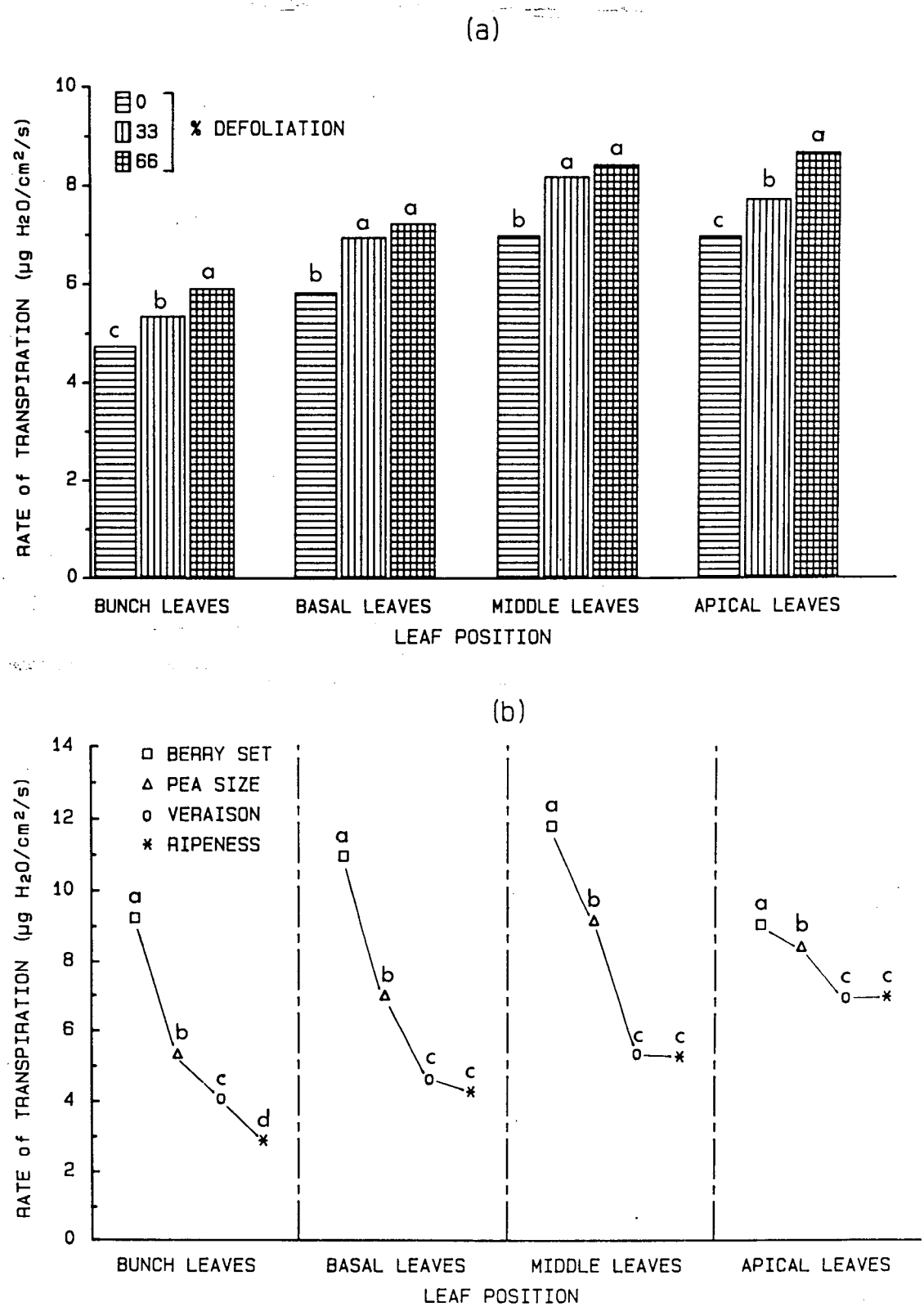

Fig. 4.4 a & b The effect of (a) defoliation, (b) developmental stage of the vine, and leaf position on the rate of transpiration of Cabernet Sauvignon leaves. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

3.4 Transpiration : photosynthesis ratio

It is evident that the ratio tended to decline with increasing degree of defoliation at all leaf positions (Fig. 4.5a). Although concomitant increases in both photosynthesis (Fig. 4.1a) and transpiration (Fig. 4.4a) were found, the transpiration:photosynthesis ratio implied that CO_2 was utilized more effectively with increasing degree of defoliation. These results confirmed the commonly observed more effective use of leaf area when the size of sources is reduced in relation to the size of sinks (Buttrose, 1966; May *et al.*, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson *et al.*, 1982). The ratio increased the deeper leaves were situated into the canopy, verifying the well-known inhibiting effect of shade on photosynthesis.

Carbon dioxide was more effectively assimilated at ripeness than at berry set for all leaves (Fig. 4.5b). It would therefore appear that although the capacity to assimilate CO_2 (Fig. 4.1b) as well as transpiration (Fig. 4.4b) declined and stomatal resistance increased (Fig. 4.3b), CO_2 exchange between the leaf interior and the atmosphere improved during leaf ageing. A better influx of CO_2 could be due to the more open structure of palisade and mesophyll tissues of mature or senescent foliage (Kriedemann *et al.*, 1970) and to decreases in selective membrane permeability of aged leaves (Sacher, 1957).

3.5 Photon flux density

The irradiance for apical leaves of non-defoliated vines corresponded to that needed for maximum photosynthetic rate of young grapevine leaves, while irradiance for middle and basal leaves were in accordance with the photosynthetic rates of old leaves (Kriedemann, 1977) (Figs. 4.6a & b). Evidently, sunlight penetration increased with increasing partial defoliation (Fig. 4.6a). Definite light saturation responses occurred with increasing defoliation from basal to apical leaf positions. The PFD levels for apical leaves did not differ significantly between treatments, though a slight increase occurred with an increasing degree of defoliation. According to Smart (1974a), the rate of photosynthesis depends on total light flux density onto leaf surfaces, which may be direct and/or diffused light, with the former the main determinant in sunny climates. Since light intensity for bunch leaves is greatly reduced, this might explain the low rate of photosynthesis found for bunch leaves (Figs. 4.1a & b).

Although the rate of photosynthesis of bunch and basal leaves of the different defoliation treatments (Fig. 4.1a) corresponded to the PFD patterns, the photosynthetic rate of middle leaves increased more than expected, while that of apical leaves increased significantly.

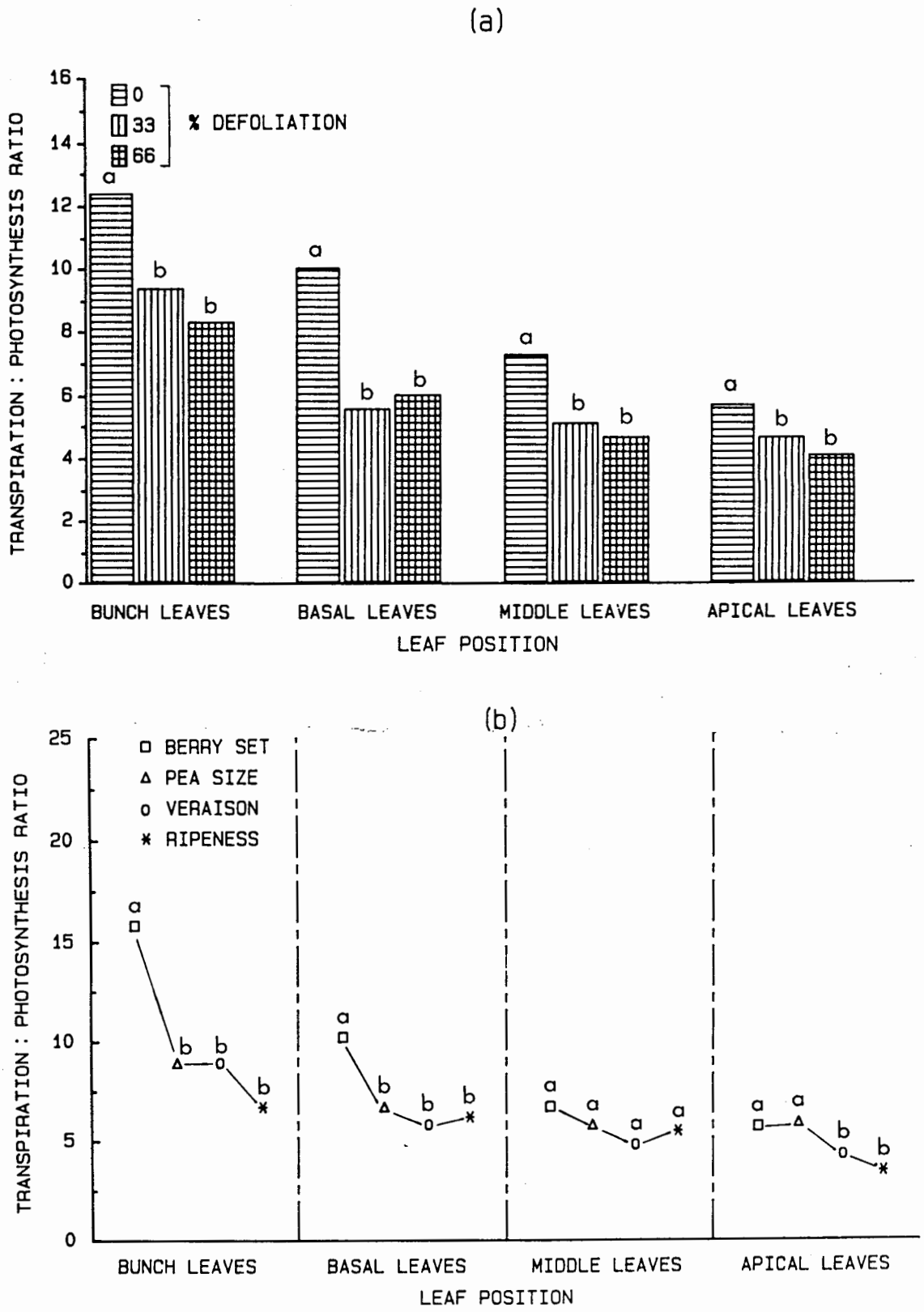

Fig. 4.5 a & b The effect of (a) defoliation, (b) developmental stage of the vine, and leaf position on the transpiration:photosynthesis ratio of Cabernet Sauvignon leaves. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

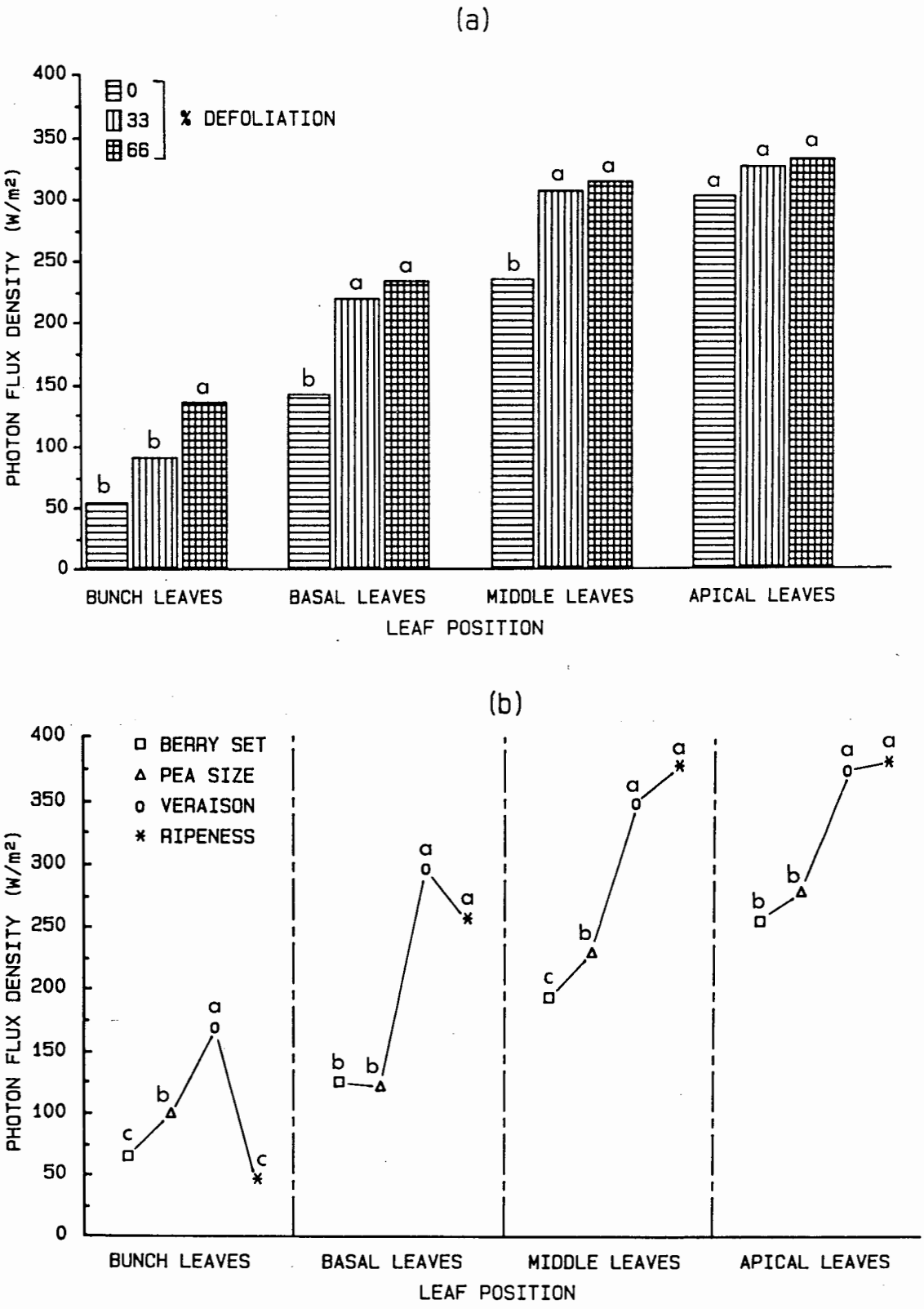

Fig. 4.6 a & b The effect of (a) defoliation and (b) developmental stage of the vine on the photon flux density in different leaf positions in the canopy of Cabernet Sauvignon. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

This suggests that the increase in photosynthetic rate of apical leaves did not solely result from an improved microclimate, but rather from internal control, as was already mentioned. This is also evident from Fig. 4.7, which shows the response of photosynthesis to increasing PFD levels at the different leaf positions.

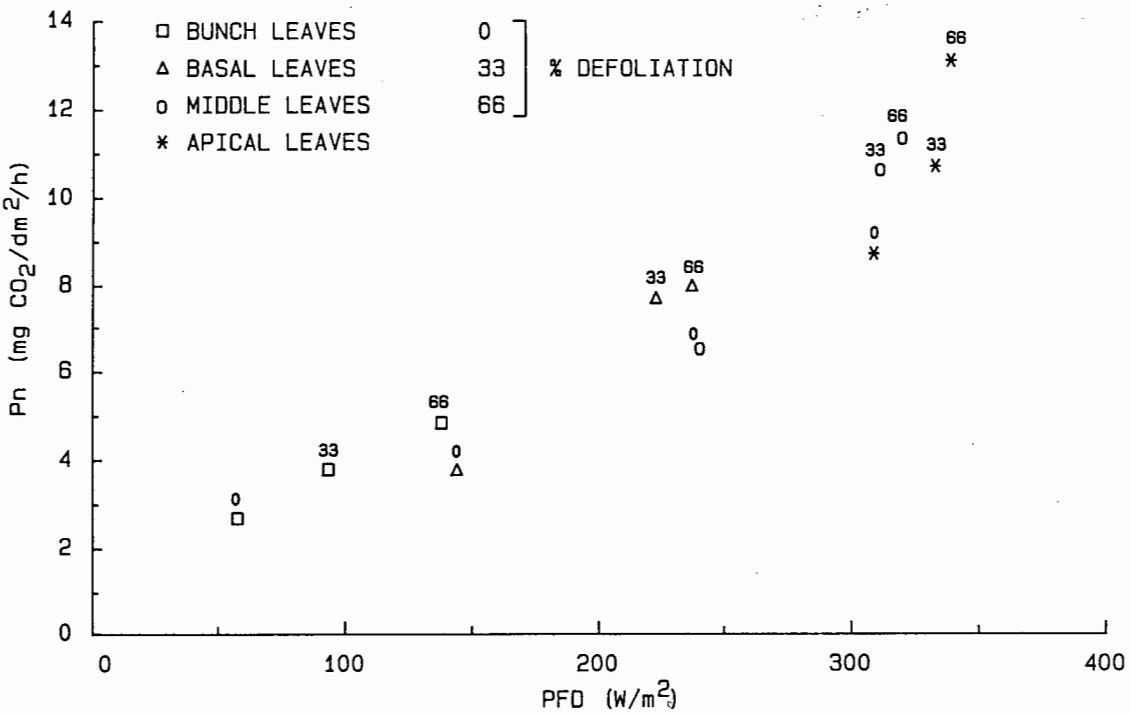

Fig. 4.7 The effect of defoliation and the response of photosynthesis (Pn) to increasing photon flux density (PFD) levels at different leaf positions.

Regarding the corresponding negative relationship between PFD and stomatal resistance (Fig. 4.3a), Raschke (1975) found that stomata responded to light indirectly by responding to the reduction in CO_2 concentration in mesophyll as well as in guard cells. Sheriff (1979) found that blue light was more effective than red light in causing stomatal opening or preventing stomatal closure. According to Smart *et al.* (1988) leaves in the centre of dense canopies receive light of low flux density in the photosynthetic waveband of 400 nm to 700 nm and are also relatively enriched in the near infra red waveband. This may explain the high stomatal resistance values of especially basal and bunch leaves of non-defoliated vines in contrast to that of partially defoliated vines.

The PFD for apical and middle leaves increased as the growth season progressed, while no definite tendency for basal and bunch leaves was found (Fig. 4.6b). The increase in

PFD at the former leaf positions possibly resulted from a more open canopy structure, created by the elongation and orientation of shoots on the trellising system (data not shown). The indefinite tendency found for basal and bunch leaves could be the result of overshadowing in the canopy-interior, creating irregular light conditions.

3.6 Percentage relative humidity

From Fig. 4.8a it is evident that the percentage relative humidity at leaf surfaces generally increased upon leaf removal. This probably resulted from the higher rate of transpiration (Fig. 4.4a), which also coincided with the general decline in humidity as the growth season progressed (Fig. 4.8b). The corresponding negative relationship between relative humidity and stomatal resistance (Figs. 4.3a & b) is in contrast to results obtained by Sepúlveda & Kliewer (1986) with Cardinal, Chardonnay and Chenin blanc vines. Although humidity was measured at the leaf surface, the decrease towards the center of the canopy is in contrast to the opinion of Smart (1985), namely that transpiration by leaves and perhaps fruits can cause humidity build-up in the center of a dense canopy.

3.7 Leaf temperature

No significant differences in leaf temperature between defoliation treatments were found. The higher transpiration rates found for the partial defoliation treatments (Fig. 4.4a) possibly exerted a stabilizing effect on leaf temperature, thereby preventing it from rising as would be expected. Leaf temperatures, which ranged from 24,7°C to 30,7°C during the growth season, exhibited a general decrease towards the end of the season (Fig. 4.9). The temperature regime during the investigation approximated that found for optimum photosynthesis (Kriedemann, 1977; Alleweldt *et al.*, 1982; Koblet, 1984).

3.8 Correlation coefficients

To determine the relationship between photosynthetic rate, stomatal resistance, and rate of transpiration, correlation coefficients were calculated (Table 4.1). Significant correlations between photosynthesis, transpiration and stomatal resistance were found for all leaf positions, except for apical leaves where the former two were poorly correlated. According to Raschke (1975) a lack of proportionality between CO_2 exchange and transpiration may result from the saturating effect of intercellular CO_2 concentration on assimilation. Tan & Buttery (1986) found a close relationship between the rate of photosynthesis and stomatal conductance over a range of light levels as well as

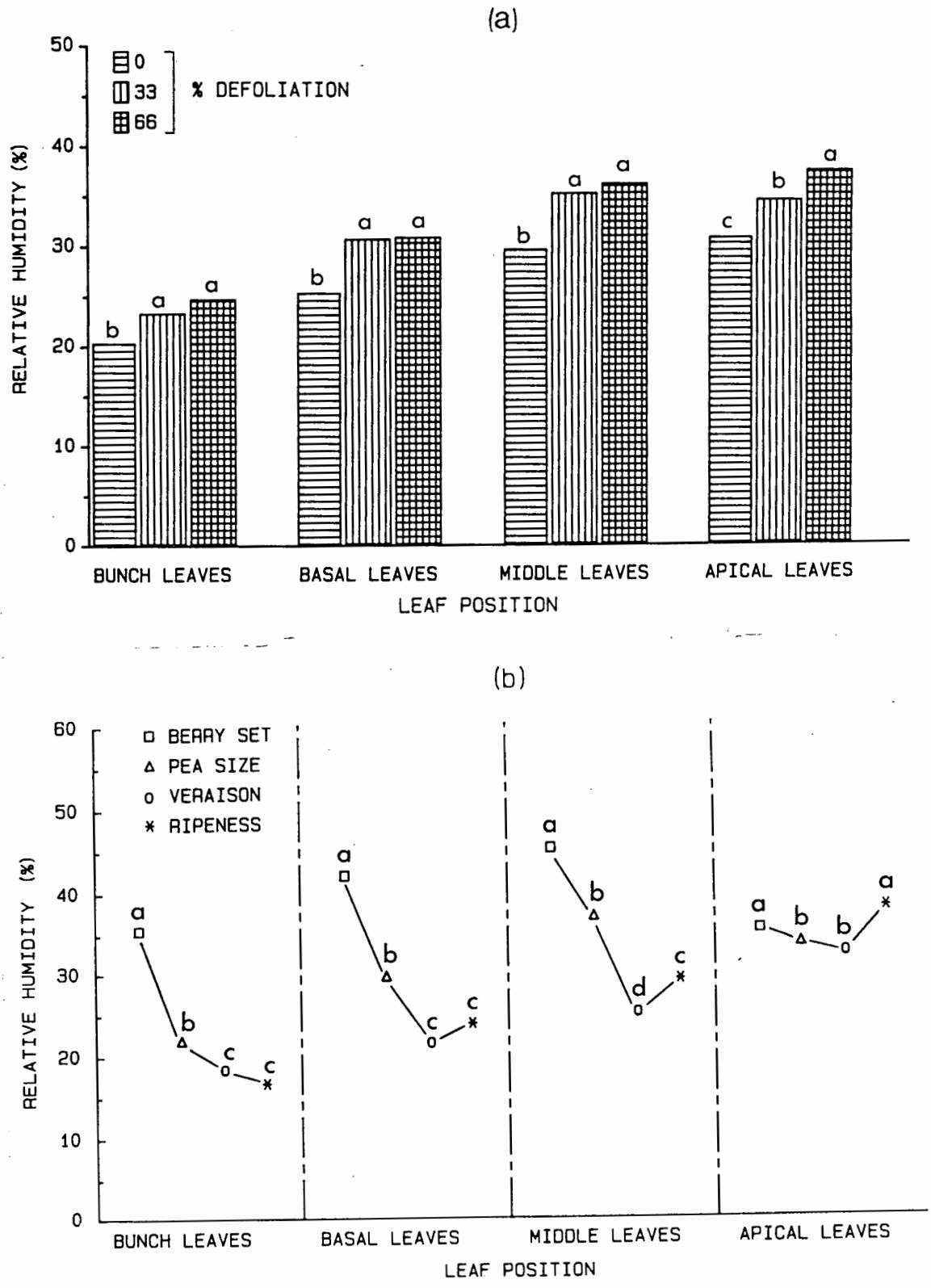

Fig. 4.8 a & b The effect of (a) defoliation, (b) developmental stage of the vine, and leaf position on the percentage relative humidity at the leaf surface of Cabernet Sauvignon. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

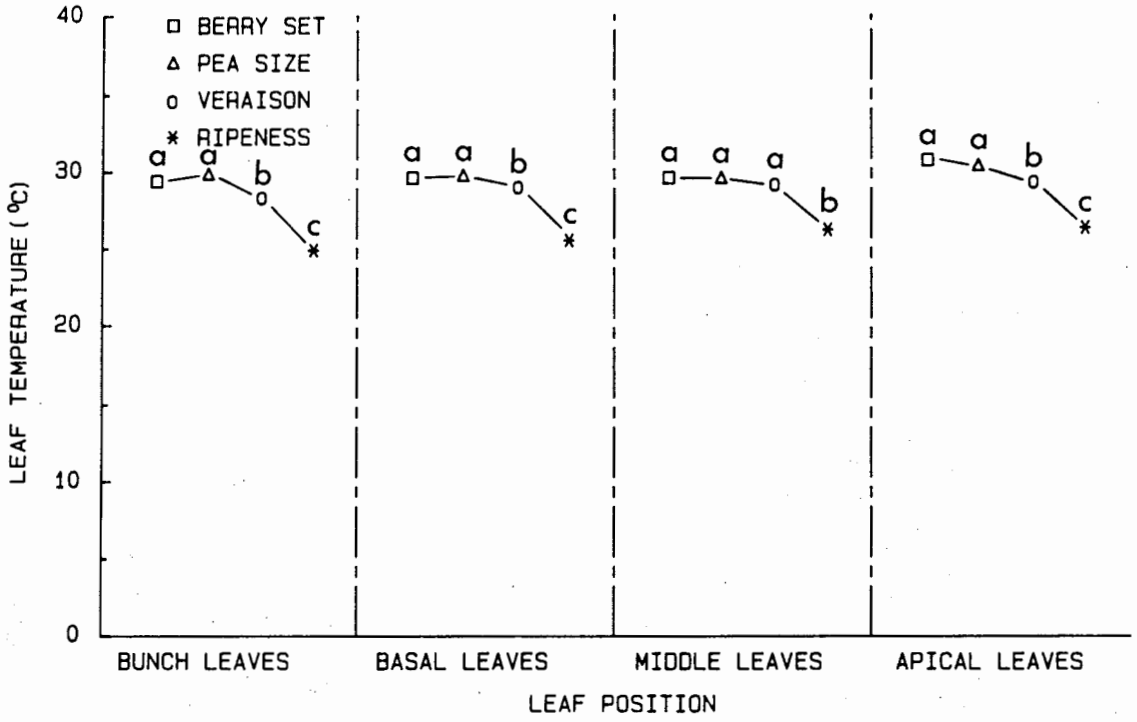

Fig. 4.9 The effect of developmental stage of the vine and leaf position on the temperature of Cabernet Sauvignon leaves. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each plant part.

TABLE 4.1 Correlation coefficients (r) between the different parameters measured at different leaf positions on the shoot

Independent variable	Bunch leaves		Basal leaves		Middle leaves		Apical leaves	
	r_s	T_r	r_s	T_r	r_s	T_r	r_s	T_r
Rate of photosynthesis	$-0,70^{*}$	$0,67^{*}$	$-0,68^{*}$	$0,73^{**}$	$-0,77^{**}$	$0,90^{**}$	$-0,84^{**}$	0,38
Stomatal resistance		$-0,93^{**}$		$-0,91^{**}$		$-0,92^{**}$		$-0,67^{*}$

r_s = Stomatal resistance
T_r = Rate of transpiration ($\mu g\ H_2O/cm^2/s$).
*** Significantly correlated at $p \leq 0,05$.**
**** Significantly correlated at $p \leq 0,01$.**

temperatures. Cowan (1972) also found stomatal oscillations to affect the ratios between CO_2 assimilation and transpiration, which may optimize the relationship between assimilation and growth. However, Downton *et al.* (1987), Farquhar & Sharkey (1982) and

Hodgkinson (1974) stated that stomatal movements only marginally limit the rate of CO_2 assimilation. Hodgkinson (1974) concluded that the resistance to CO_2 transfer between the intercellular spaces and fixation sites in chloroplasts exerted the greatest effect on photosynthetic rates. Although photosynthetic CO_2 assimilation was greatly dependent on stomatal conductance under natural, ambient CO_2 concentrations, Lange *et al.* (1986) also found an independence of stomatal conductance under saturating CO_2 partial pressures. The factors controlling non-stomatal limited CO_2 assimilation must, however, still be established (Lange *et al.*, 1985).

4. CONCLUSIONS

Photosynthetic rates of partially defoliated vines were higher than that of non-defoliated vines, generally increasing with degree of defoliation. Apart from the less favourable microclimate, the sink capacity of non-defoliated vines apparently did not comply to the source capacity. Therefore, feedback inhibition by assimilates and/or CO_2 at carboxylation sites in the mesophyll might also have occurred, inhibiting the rate of photosynthesis.

The apical leaves in all cases displayed the highest rate of photosynthesis, while leaves opposite and below bunches exhibited low photosynthetic rates, especially at véraison and ripeness. Photosynthetic contributions of leaves of all defoliation treatments decreased as they were progressively situated deeper into the canopy. Therefore, as often occurs, measurements of the photosynthetic activities of interior-canopy leaves alone can lead to an underestimation of photosynthetic capacity of the vine. More equally distributed photosynthetic rates in the canopies of partially defoliated vines were found, especially in regions above the bunches.

A general decline in the rate of photosynthesis occurred as the growth season progressed and leaves aged. It appeared that apical regrowth took place at ripeness.

Generally, tendencies of stomatal resistance and transpiration rate coincided with that found for photosynthetic rate. However, the latter two correlated poorly for apical leaves, suggesting that photosynthetic activity in that case was controlled internally rather than through stomatal behaviour. The transpiration:photosynthesis ratios suggest a more effective utilization of CO_2 by the partially defoliated vines.

Photon flux density and percentage relative humidity at the leaf surface increased upon partial defoliation, while leaf temperature showed no definite tendency. In general,

tendencies of photon flux density and relative humidity related well to photosynthesis, stomatal resistance and transpiration of leaves at all different leaf positions.

The results of this investigation suggest that excess vegetative growth is detrimental not only for interior-canopy microclimate, but also to the photosynthetic rate of the entire vine. Partial defoliation seems to be an appropriate means of reducing the deleterious effects of vigorous growth on some physiological parameters.

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CHAPTER V

The Effect of Partial Defoliation, Leaf Position and Developmental Stage of the Vine on Leaf Chlorophyll Concentration in Relation to Photosynthetic Activity and Light Intensity in the Canopy of *Vitis vinifera* L. cv. Cabernet Sauvignon

Key words : *Vitis vinifera*, Chlorophyll, Defoliation, Developmental stages, Leaf position, Light intensity, Photosynthesis.

ABSTRACT

The effect of partial defoliation and leaf position on leaf chlorophyll concentration in relation to photosynthetic activity and light intensity in the canopy of *Vitis vinifera* L. cv. Cabernet Sauvignon was investigated at berry set, pea size, véraison and ripeness stages.

Leaves of severely defoliated vines appeared to contain the highest chlorophyll concentration. In general, chlorophyll a decreased as leaves were situated progressively deeper into the canopy. Although photosynthetic activity and light intensity decreased concomitantly, no consistent relationship between chlorophyll concentration, light intensity and photosynthetic activity was found for the different leaf positions. Chlorophyll concentration can therefore not be regarded as a reliable index for photosynthetic activity of grapevine leaves. Photosynthetic activity and light intensity in the canopy was, however, still significantly increased by leaf removal.

The results indicated that excessive removal of metabolically active leaves must be avoided on the lower half of the canopy during early developmental stages of vines, and on apical parts of shoots from véraison to ripeness by for example severe topping during this period. To obtain leaves that photosynthesize optimally, the amount and time of leaf removal in the grapevine canopy must, therefore, be carefully planned.

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1. INTRODUCTION

Uncertainty exists whether an increase or decrease in chlorophyll concentration is associated with fluctuations in photosynthetic activity. Gabrielsen (1948) stated that the full effect of chlorophyll concentration can only be observed in weak light where photosynthesis is proportional to light intensity. According to Hesketh (1963), chlorophyll concentration was not critical in determining the differences in photosynthetic activity observed among species.

Although photosynthesis was not linearly related to chlorophyll concentration (Marini & Marini, 1983), higher chlorophyll concentrations and lower photosynthetic activities were found for interior-canopy leaves when compared to peripheral, sun-exposed peach (*Prunus persica*) leaves (Kappel & Flore, 1983; Marini & Marini, 1983). According to Sestak (1966), changes in the density and period of irradiation are the main factors opposing a linear relationship between chlorophyll content and photosynthetic rate.

Photosynthetic activity decreased in aged leaves, while chlorophyll concentration continued to increase (Kriedemann, 1968; Anderson & Brodbeck, 1988) or decreased only slightly (Sestak, 1966; Kriedemann *et al.*, 1970) with leaf age after full expansion. Fruiting had variable effects on photosynthesis (Schaffer *et al.*, 1986). According to Schaffer *et al.* (1986), chlorophyll concentration in old and young leaves of deblossomed strawberry (*Fragaria x ananassa* Duch.) plants was generally higher than in corresponding leaves of fruiting strawberry plants. Hofäcker (1978), however, reported increases in chlorophyll concentration as well as photosynthesis for bearing Riesling vines compared to vines bearing no grapes.

Reducing the size of the source relative to the sink, resulted in an increase in the photosynthetic efficiency of vine leaves (Buttrose, 1966; May *et al.*, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson *et al.*, 1982; Hunter & Visser, 1988b, 1988c). Hofäcker (1978) also found an increase in chlorophyll concentration in leaves of potted Riesling vines with increasing levels of defoliation. An increase in chlorophyll concentration was suggested as reason for the photosynthetic rejuvenation or inhibited leaf senescence induced by partial defoliation (Wareing *et al.*, 1968; Hodgkinson, 1974).

A grapevine canopy consists of leaves of different ages, which are subjected to variable light intensities during the entire growth season (Hunter & Visser, 1988c). According to Boardman (1977), a leaf's photosynthetic productivity is primarily governed by its position in the canopy. It would therefore be of interest to determine the changes in chlorophyll

concentration of the leaves as well as the relationship, if any, with the different photosynthetic activities observed by Hunter & Visser (1988c), especially with partial defoliation of the grapevine. The results may then be used to sensibly remove leaves making a lesser contribution to the photosynthetic capacity of the vine, thus altering the vine's canopy to conditions favourable for maximum photosynthesis of the remaining leaves as well as the production of high quality grapes. Therefore the effect was studied of partial defoliation on the chlorophyll concentration of Cabernet Sauvignon leaves, situated in different positions in the canopy, in relation to their photosynthetic activity and radiation exposure at berry set, pea size, véraison and ripeness.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon vineyard, clone CS 46, 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 RY 30. Vines were planted (3,0 x 1,5 m spacing) on a Glenrosa soil (Series 13, Kanonkop) (MacVicar *et al.*, 1977) and trained onto a 1,5 m slanting trellis as described by Zeeman (1981). Further details of the experimental vineyard used were given by Hunter & Visser (1988a).

2.2 Experimental design

The experiment was laid out as a completely randomized 3 x 4 x 4 factorial design. The three factors were : defoliation treatments, applied to the whole vine (0 %, 33 %, 66 %), leaves situated at four positions on one shoot per vine (opposite and below the bunches, basal, middle, apical), and developmental stages (berry set, pea size, véraison, ripeness). The basal, middle and apical leaf positions were defined according to leaf number on the shoot (Hunter & Visser, 1988a). Chlorophyll determinations as well as photosynthesis and photon flux density measurements (see below) were performed at each leaf position and developmental stage. There were nine replications, comprising one vine per plot, for each of the 48 treatment combinations.

2.3 Defoliation treatments

Different levels of defoliation were implemented from approximately one month after budding. The 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 as described above at approximately monthly intervals.

2.4 Measurements

Photosynthetic activity (mg $CO_2/dm^2/h$) and photon flux density (W/m^2) were determined as described by Hunter & Visser (1988c). Leaf areas were determined with a LI-COR 3000 portable area meter.

2.5 Chlorophyll determinations

A modified method of Mackinney (1941) was used for chlorophyll determinations. After determination of leaf area and leaf mass, a representative fresh leaf sample of 5 g was cut into pieces of 1 cm^2. The leaf material was added to 100 cm^3 80 % aqueous acetone containing 0,1 g $CaCO_3$ and macerated with a Kinematica Gmbh Ultra-Turrax macerator at room temperature for 60 s at 10 000 rpm. The homogenate was left to settle in the dark at 5 °C for 24 h, after which the sediment was completely discoloured.

The equations used for the determination of chlorophyll concentration were (Arnon, 1949):

Chlorophyll *a* (mg/dm^3) = 12,7 A_{663} - 2,69 A_{645}
Chlorophyll *b* (mg/dm^3) = 22,9 A_{645} - 4,68 A_{663}

2.6 Statistical analyses

A two-way analysis of variance (standard statistical software package of the VORI) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. The same program was used for log transformations, where applicable, and to determine correlation coefficients. Since no significant interactions between defoliation percentage and developmental stage of the vine were found for any of the leaf positions, only the main effects, namely defoliation percentage and developmental stage were considered. The figures therefore depict either averages over stages or averages over defoliation treatments, while data over both factors were used to calculate the correlation coefficients provided.

3. RESULTS AND DISCUSSION

3.1 Chlorophyll concentration

The severe defoliation treatment (66 %), albeit not significant, resulted in the highest chlorophyll *a* concentration (Fig. 5.1). An increase in chlorophyll concentration as a result of defoliation was also found by Hofäcker (1978) and suggests an inhibition of senescence of the remaining leaves. The chlorophyll *a* concentration tended to decrease as the leaves were progressively situated deeper into the canopy. At berry set and pea size the chlorophyll *a* as well as chlorophyll *b* concentrations were apparently the highest for basal and bunch leaves, while from véraison to ripeness middle and apical leaves had the highest chlorophyll concentration (Fig. 5.2). The higher chlorophyll concentration for the interior, recently matured leaves at the early developmental stages confirmed the findings of other investigators (Marini & Marini, 1983; Anderson & Brodbeck, 1988). Leaves which were progressively situated towards the periphery of the canopy reached maximum chlorophyll *a* and chlorophyll *b* concentrations later during the growth season. In bunch leaves the highest concentrations occurred at berry set, while in apical leaves maximum concentrations were only reached at ripeness. The variations in chlorophyll concentration observed for the different leaves during the growth season therefore primarily seem to reflect differences in leaf age.

3.2 Photosynthetic activity and light intensity

The photosynthetic activity (mg $CO_2/dm^2/h$) of leaves in relation to the photon flux density at different leaf positions is shown in Figs. 5.3 & 5.4. It is evident that photosynthetic activity generally increased upon partial defoliation (Fig. 5.3). This was fully discussed by Hunter & Visser (1988c). For the middle and apical leaves, photosynthetic activity increased more than expected with increasing light intensity, suggesting the probable involvement of a non - photochemical process(es) (Björkman & Holmgren, 1963; Wareing *et al.*, 1968; Hunter & Visser, 1988c). The photosynthetic activity as well as photon flux density declined as leaves were progressively situated deeper into the canopy (Fig. 5.3), confirming the well-known deleterious effects of interior-canopy shade as well as leaf age on photosynthetic response (Shaulis *et al.*, 1966; Smart, 1973, 1974, 1985; Kriedemann, 1977; Kliewer, 1982; Kappel & Flore, 1983; Marini & Marini, 1983; Koblet, 1984).

Except for bunch leaves and basal leaves at ripeness, the photon flux density increased as the growth season progressed (Fig. 5.4). The photosynthetic activity of the different leaves in general decreased with time. Possible reasons for the general decline in

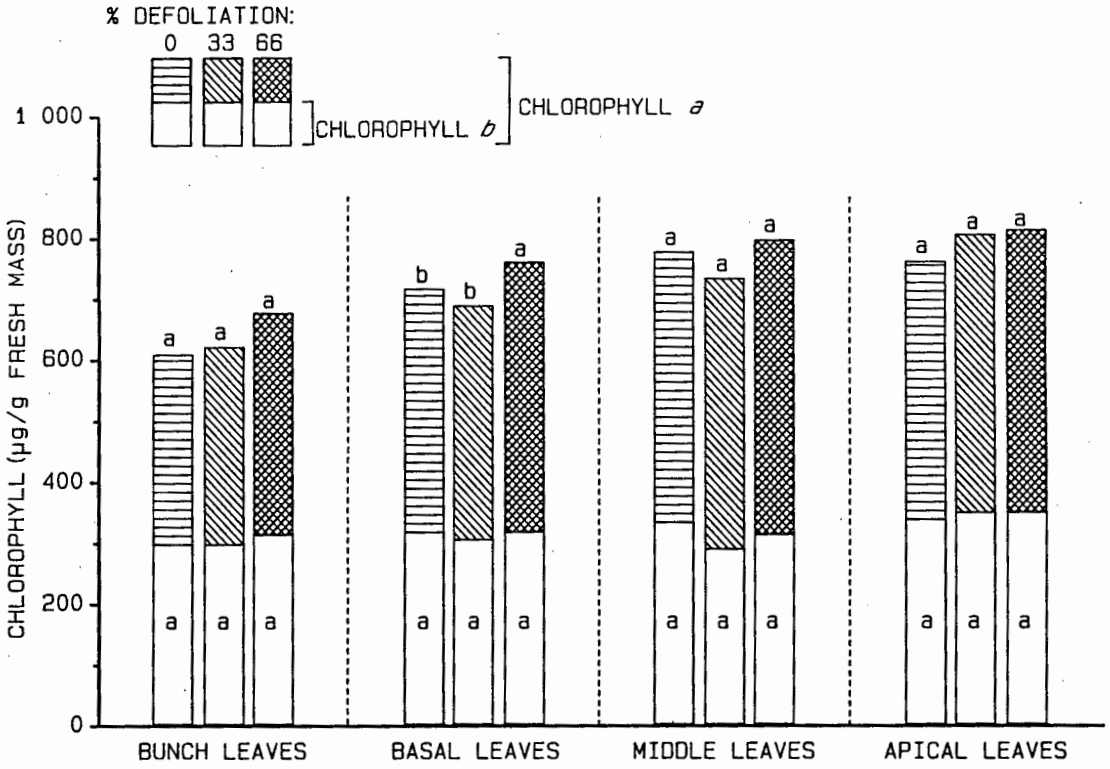

Fig. 5.1 The effect of defoliation on the chlorophyll *a* and *b* concentration of leaves in different positions on the shoot. Values represent the means over developmental stages. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

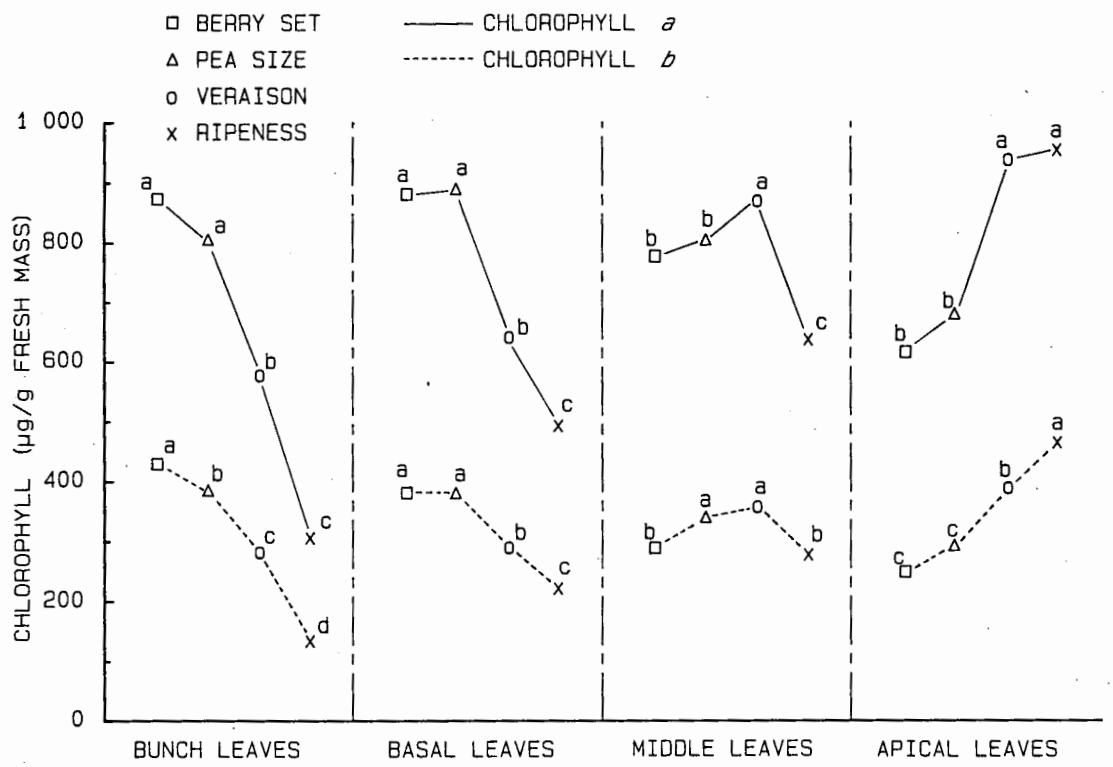

Fig. 5.2 The effect of developmental stage of the vine on the chlorophyll *a* and *b* concentration of leaves in different positions on the shoot. Values represent the means over defoliation treatments. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

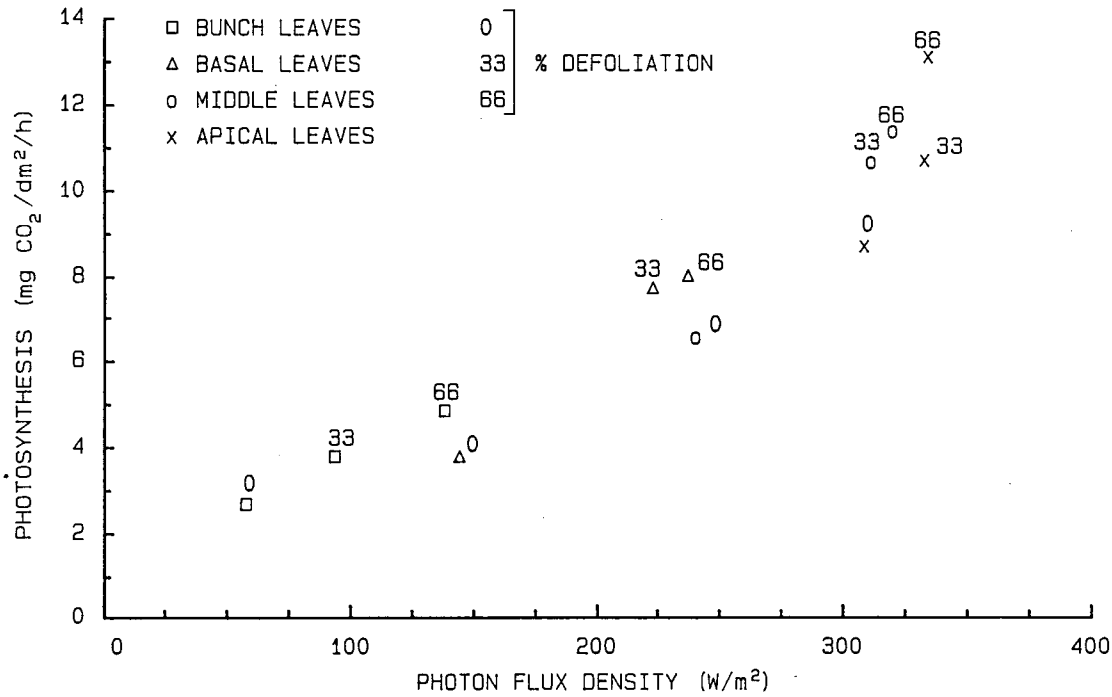

Fig. 5.3 The effect of photon flux density on photosynthesis of leaves in different positions on the shoot for different levels of defoliation.

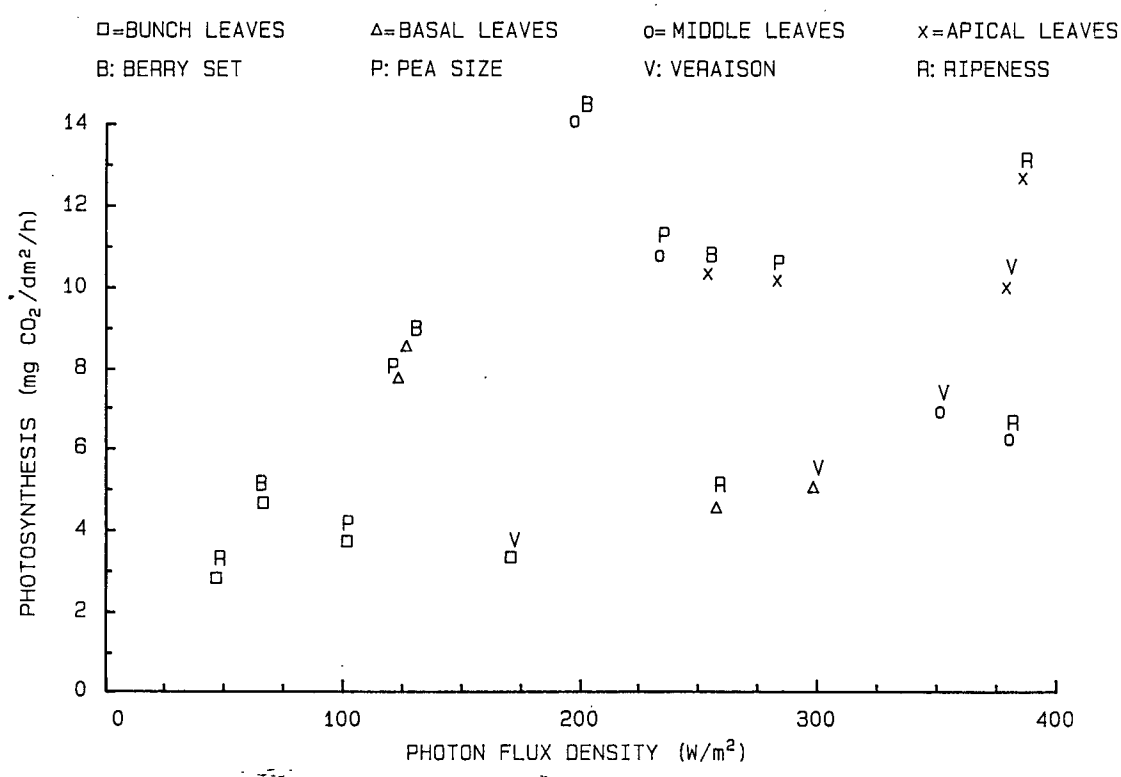

Fig. 5.4 The effect of photon flux density on photosynthesis of leaves in different positions on the shoot for different developmental stages of the vine.

photosynthetic activity could be the increase in total leaf area of the canopy during the season, resulting in a decreased specific photosynthetic activity of the leaves, an increase in leaf age, a change in chemical content, i.e. an increase in sugar and decreases in amino and organic acid concentrations (Kliewer & Nassar, 1966; Kriedemann *et al.*, 1970) and a decreased demand for assimilates because of a decrease in actively growing vegetative sinks and berry growth. The general increase in photon flux density could have resulted, amongst others, from lengthening of shoots on the slanting trellis as the growth season progressed, creating improved light conditions at especially the outer leaf positions. However, increasing senescence of vegetative growth on the vine could have been an overriding factor in the expression of the photosynthetic activity of the leaves.

3.3 Chlorophyll *a*:*b* ratio

The effect of defoliation and developmental stage of the vine on the chlorophyll *a*:*b* ratio of leaves in different positions on the shoot is shown in Table 5.1. Though not statistically significant, the chlorophyll *a*:*b* ratio increased in remaining leaves after partial defoliation. This was mainly due to a slight increase in chlorophyll *a* (Fig. 5.1). Since chlorophyll *a* is considered a more exact characteristic of photosynthetic activity (Sestak, 1966), this tendency towards a higher ratio might partly explain the higher photosynthetic activities of the remaining leaves of partially defoliated vines (Fig. 5.3). In general, the chlorophyll *a*:*b* ratio appeared to decline from middle to bunch leaves. This is in accordance with findings for leaves of plants grown in strong and weak light (Björkman & Holmgren, 1963), and also in agreement with the findings of Kriedemann (1968) for leaves of different ages. Although photosynthesis generally decreased during the growth season (Fig. 5.4), the chlorophyll *a*:*b* ratio, however, exhibited no definite tendency.

3.4 Assimilation number

The effect of defoliation and developmental stage on the assimilation number of different leaves is shown in Table 5.2. The assimilation number generally increased as a result of partial defoliation, which corresponded to the increase in photosynthetic activity (Fig. 5.3). This is in agreement with the findings of Hodgkinson (1974), Kriedemann (1977), Hofäcker (1978) and Hunter & Visser (1988b, 1988c). Compared to the small differences in chlorophyll concentration between non-defoliated and partially defoliated vines (Fig. 5.1), it is evident that chlorophyll concentration could not be the main reason for the increased photosynthetic activity of partially defoliated vines (Fig. 5.3). This substantiates the findings of Gabrielsen (1948), Kriedemann *et al.* (1970), Hofäcker (1976) and Schaffer *et al.* (1986) and implies that the light intercepting ability of vine leaves is not necessarily closely related to their CO_2 assimilating ability.

TABLE 5.1 The effect of defoliation and developmental stage of the vine on the chlorophyll *a:b* ratio 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	1,96	2,02	2,14	2,04 b	2,33	2,14	2,47	2,31 a	2,61	2,73	2,77	2,70 a	2,41	2,52	2,43	2,45 a
Pea size	2,09	2,07	2,10	2,09 b	2,25	2,37	2,42	2,34 a	2,15	2,44	2,52	2,37 b	2,37	2,17	2,43	2,33 a
Véraison	1,94	2,06	2,14	2,05 b	2,14	2,23	2,31	2,23 a	2,39	2,53	2,50	2,47 b	2,45	2,45	2,35	2,42 a
Ripeness	2,36	2,36	2,29	2,34 a	2,23	2,34	2,17	2,25 a	2,31	2,30	2,29	2,30 b	1,93	2,08	2,16	2,05 b
Mean	A 2,09	A 2,13	A 2,17		A 2,24	A 2,27	A 2,34		B 2,37	A 2,50	A 2,52		A 2,29	A 2,30	A 2,34	
Cv (%)	7,13				6,18				6,44				5,31			

* **Percentage defoliation.**

Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

TABLE 5.2 The effect of defoliation and developmental stage of the vine on the assimilation number (mg CO_2/mg chlorophyll/h) 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	1,20	2,07	2,75	2,01 b	2,16	4,39	4,43	3,66 a	4,02 c	9,54 a	6,83 b	6,80 a	4,66	5,92	7,69	6,09 a
Pea size	1,30	2,14	2,18	1,87 b	1,40	3,47	3,32	2,73 b	2,50 d	5,20 c	4,70 c	4,13 b	4,27	4,97	5,96	5,07 b
Véraison	1,62	1,97	2,17	1,92 b	1,78	2,89	2,63	2,43 b	2,19 d	2,66 d	2,51 d	2,45 c	3,48	3,42	4,13	3,68 c
Ripeness	2,50	3,33	3,80	3,21 a	2,08	3,33	3,33	2,91 b	2,08 d	3,20 d	3,34 d	2,87 c	3,76	4,34	4,89	4,33 c
Mean	1,66 B	2,38 A	2,73 A		1,86 B	3,52 A	3,43 A		2,70 C	5,15 A	4,34 B		4,04 B	4,66 B	5,67 A	
Cv (%)	37,47				18,40				18,71				15,77			

* **Percentage defoliation.**

Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

Hesketh (1963) stated that resistance to CO_2 diffusion should increase with increasing fresh mass or thickness and that the relation between photosynthesis and fresh mass per leaf area should therefore be negative. However, according to Table 5.3 leaves of the 66 % defoliated vines were in general heavier than those of non-defoliated vines. Hodgkinson (1974) found similar results and suggested that it was probably due to an increase in palisade cell size, which was evidently caused by an accumulation of starch grains in chloroplasts, or an increase in chloroplast population per cell. However, accumulation of starch in chloroplasts can cause reduced photosynthetic rates (Neales & Incoll, 1968; Wareing *et al.*, 1968). The latter probability is supported by the differences in chlorophyll concentration between the severely defoliated and non-defoliated vines in this study (Fig. 5.1).

Nevertheless, specific leaf mass apparently decreased from the middle leaves towards the inside of the canopy. This is in accordance with the effect of shading on specific leaf mass (Kappel & Flore, 1983) and also corresponds to the observed decreases in assimilation number (Table 5.2), light intensity and photosynthesis (Fig. 5.3) as well as chlorophyll *a*:*b* ratio (Table 5.1).

The assimilation number generally decreased up to véraison, but again increased towards ripeness for all leaf positions, albeit only significantly for bunch leaves (Table 5.2). The decrease in assimilation number corresponded to the decrease in photosynthesis (Fig. 5.4) as well as an apparent increase in specific leaf mass (Table 5.3). This confirms the findings of Kriedemann (1977) and Hunter & Visser (1988a, 1988b, 1988c). Nevertheless, except for apical leaves, the apparent increases in assimilation number found from véraison to ripeness do not relate to the corresponding photosynthetic activities (Fig. 5.4).

3.5 Total CO_2 assimilation rate

The effect of defoliation on the total CO_2 assimilation rate in relation to total leaf area and chlorophyll concentration of leaves in different positions on the shoot is presented in Table 5.4. The total remaining leaf areas as well as chlorophyll concentrations of apical, middle, basal and bunch leaves of 33 % and 66 % defoliated vines were significantly less than those of non-defoliated vines, generally decreasing with increasing defoliation. In spite of this, it is striking that the CO_2 assimilation rate of leaves of partially defoliated vines was still comparable to or even higher than that of control vines. From this it is evident that all leaves, especially the basal leaves of partially defoliated vines, were proportionally photosynthetically more active than those of non-defoliated vines. Therefore, the

TABLE 5.3 The effect of defoliation and developmental stage of the vine on the specific leaf mass (fresh mass per leaf area, mg/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	17,85	18,79	17,15	17,93 b	16,98	19,48	17,97	18,14 b	19,61	17,15	23,28	20,01 b	18,40	20,16	20,24	19,60 a
Pea size	21,24	17,57	22,31	20,37 a	20,71	23,35	22,24	22,10 a	22,73	23,49	23,69	23,31 a	20,14	20,42	20,69	20,42 a
Véraison	20,02	21,42	20,26	20,57 a	21,82	22,23	23,33	22,46 a	22,88	22,71	24,55	23,38 a	20,67	19,86	21,31	20,62 a
Ripeness	20,83	20,36	20,36	20,51 a	21,87	21,54	23,04	22,15 a	22,69	24,08	23,92	23,56 a	20,41	21,58	20,92	20,97 a
Mean	A 19,98	A 19,54	A 20,02		A 20,35	A 21,65	A 21,64		B 21,98	B 21,86	A 23,86		A 19,91	A 20,51	A 20,79	
Cv (%)	10,51				7,72				7,83				8,27			

* **Percentage defoliation.**

Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

TABLE 5.4 The effect of defoliation on the total CO_2 assimilation rate (A) (calculated on a total leaf area basis as mg CO_2/h), total leaf area (cm^2) and total chlorophyll concentration (mg) of leaves in different positions on the shoot

	Bunch leaves			Basal leaves			Middle leaves			Apical leaves		
	*0	*33	*66	*0	*33	*66	*0	*33	*66	*0	*33	*66
Leaf area	a 234,13	b 199,72	c 115,24	a 783,15	b 500,37	c 302,80	a 859,60	b 585,77	c 387,13	a 372,74	b 241,83	c 148,58
% of control	100,00	85,30	49,22	100,00	63,89	38,66	100,00	68,14	45,04	100,00	64,88	39,86
Chlorophyll	a 4,47	a 3,71	b 2,24	a 16,50	b 10,66	c 6,97	a 21,54	b 13,49	b 10,39	a 8,82	b 6,19	c 3,80
% of control	100,00	83,00	50,11	100,00	64,61	42,24	100,00	62,63	48,24	100,00	70,18	43,08
A	a 18,71	a 23,14	a 16,52	b 87,51	a 114,24	c 73,37	a 167,31	a 180,20	b 129,50	a 100,31	b 78,88	c 58,32
% of control	100,00	123,68	88,30	100,00	130,55	83,84	100,00	107,70	77,40	100,00	78,64	58,14
Cv (%) : Leaf area	20,06			15,71			15,88			15,30		
Chlorophyll	26,81			15,34			25,79			27,01		
A	9,00			4,76			4,70			4,92		

* Percentage defoliation.

Values designated by the same letter in a row do not differ significantly ($p \leq 0,05$) for each leaf position. Log transformations, to compensate for heterogeneity, were done on the raw A data.

remaining leaves compensated adequately for the loss of leaves provided that defoliation was not too severe (66 %). These results confirm those found when $^{14}CO_2$ was applied to the different leaves (Hunter & Visser, 1988b). The higher total CO_2 assimilation rate of partially defoliated vines is particularly important because of the substantial contribution of especially basal leaves to the developing berry during the entire growth season (Hunter & Visser, 1988b, 1988c). It is therefore of the utmost importance to create a suitable microclimate in the canopy-interior for maximum photosynthetic activity of especially the leaves on the lower half of the shoot.

There was no consistent relationship between chlorophyll concentration and photosynthetic activity of the leaves (Table 5.5). The significant correlations found for basal and bunch leaves probably suggest that a relationship exists between chlorophyll concentration and photosynthetic activity only for interior-canopy mature leaves exposed to lower light conditions. It seems likely that factors such as the source:sink relationship, competition between leaves for mineral nutrients and hormones, feedback inhibition of photosynthesis by end products and enzymes involved in carboxylation in chloroplasts as well as internal resistance to CO_2 diffusion between intercellular spaces and CO_2 fixing positions in the chloroplasts (Neales & Incoll, 1968; Wareing *et al.*, 1968), were probably more regulatory to photosynthetic activity than chlorophyll concentration and light intensity, although their involvement cannot be ignored.

TABLE 5.5 Correlation coefficients between rate of photosynthesis (mg $CO_2/dm^2/h$) and chlorophyll *a* and *b* concentration (/ug/g fresh mass)

Independent variable	Bunch leaves		Basal leaves		Middle leaves		Apical leaves	
	C_a	C_b	C_a	C_b	C_a	C_b	C_a	C_b
Rate of photosynthesis	0,64*	0,58*	0,63*	0,59*	0,13	-0,30	0,42	0,39

C_a = Chlorophyll *a*.
C_b = Chlorophyll *b*.

*** Significantly correlated at $p \leq 0,05$.**

4. CONCLUSIONS

The chlorophyll *a* concentration of leaves of severely defoliated vines (66 %) tended to be the highest. It also tended to decrease the deeper leaves were situated in the canopy. During the first part of the growth season (berry set and pea size stages), basal and bunch leaves had the highest chlorophyll *a* and chlorophyll *b* concentrations, while from véraison to ripeness the middle and apical leaves had the highest chlorophyll concentration. Partial defoliation increased the chlorophyll *a*:*b* ratio. Photosynthetic activity and light intensity in the canopy were significantly increased by partial defoliation.

Although changes in chlorophyll concentration corresponded to photosynthetic activity in certain cases, this relationship was not consistent. Therefore, chlorophyll concentration cannot be regarded as a reliable index for photosynthetic activity of grapevine leaves.

In spite of much lower total remaining leaf areas and chlorophyll concentrations of apical, middle, basal and bunch leaves of partially defoliated vines, total CO_2 assimilation rates were still comparable to or even higher than that of non-defoliated vines. Due to the significant stimulation of photosynthetic activity in especially the remaining basal leaves of partially defoliated vines, it is necessary to create an optimum microclimate in the canopy-interior for photosynthesis. However, the results propose that excessive removal of metabolically active leaves must be avoided on the lower half of the canopy during early developmental stages of the vine, and on apical parts of the shoots from véraison to ripeness by, for example, severe topping during this period.

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CHAPTER VI

The Effect of Partial Defoliation on Vegetative Growth of *Vitis vinifera* L. cv. Cabernet Sauvignon

Key words : *Vitis vinifera*, Vegetative growth, Defoliation.

ABSTRACT

The effect of partial defoliation of the whole canopy on vegetative growth of *Vitis vinifera* L. cv. Cabernet Sauvignon was investigated.

Vegetative growth of vines followed the well-known pattern for 0 %, 33 % and 66 % defoliation, i.e. an increase until véraison followed by a decline. Partial defoliation conducted from different developmental stages had no significant effect on leaf area and main shoot length at subsequent developmental stages. The earlier defoliation was applied, the more lateral shoot length and the number of lateral shoots increased, resulting in higher total shoot lengths but no significant differences in cane mass. Partial defoliation from véraison had no effect on lateral growth. Canopy density and relative humidity decreased, while sunlight penetration and windspeed increased in the canopy with partial defoliation. The improved canopy light environment facilitates improved photosynthetic efficiency of leaves as well as development and composition of grapes.

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1. INTRODUCTION

Vegetative growth of vines in South Africa tends to be excessive due to generally improved viticultural practices, such as soil management, fertilization, vineyard establishment, vine training, cultivation, and using of high quality propagation material. Moreover, the favourable climate in South Africa is also a contributing factor. Under conditions of excessive growth, shoot growth becomes a strong sink for products of photosynthesis, with other parts receiving little or no nutrients for growth and development (Hunter & Visser, 1988a, 1988b). The increase in shoot growth and leaf area, as well as the appearance of too many lateral shoots, water shoots and the outburst of basal buds may also create conditions of density and shading in the canopy interior. Bad pruning practices, such as the allocation of too many bearers on a restricted cordon length, resulting in too closely spaced bearers, also favour a dense canopy. This unfavourable condition is found to a certain extent for all trellising systems. Foliage management therefore becomes a major priority for the viticulturist in order to improve light conditions for photosynthesis of especially interior-canopy leaves, as well as for budding, bud fertility, fruit development and pest and disease control.

Extensive research has been done on the effect of defoliation on various parts of grapevines. Since the methods, levels and time of defoliation differed greatly, divergent results were obtained. Buttrose (1966) found that trunks of grapevines were least affected by defoliation, followed by shoots, berries and roots, while Kliewer & Fuller (1973) reported the opposite. Some investigators found reduced yields with partial defoliation (Coombe, 1959; May *et al.*, 1969; Kliewer & Antcliff, 1970; Sidahmed & Kliewer, 1980), while others failed to demonstrate any differences (Peterson & Smart, 1975; Bledsoe *et al.*, 1988; Koblet, 1988).

In general, 10-12 cm^2 leaf area is required to adequately ripen one gram of fruit in terms of soluble solid accumulation (Kliewer & Antcliff, 1970; Kliewer & Ough, 1970; Kliewer & Weaver, 1971). It is known that the photosynthetic efficiency of leaves increases when leaf area is reduced relative to the different sinks in the grapevine (Buttrose, 1966; May *et al.*, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson *et al.*, 1982; Hunter & Visser, 1988b, 1988c). Since the distribution of photosynthetic products is regulated by the so-called source:sink relationship (Johnson *et al.*, 1982), decreases in leaf area would cause changes in the availability of photosynthates for the different sinks. However, total dry matter production is a function of how effectively a vine can utilize the soil and aerial environment. Therefore, the size of a grapevine canopy does not necessarily determine the magnitude and quality of a harvest.

Although leaf removal, together with foliage management practices such as suckering, shoot positioning, tipping and topping, are existing practices, great uncertainty exists on how, when, where, and how many leaves must be removed. The effect of leaf removal on different vegetative parameters is also uncertain. Consequently, this investigation was carried out to determine the effect of different levels of defoliation, implemented continuously from different developmental stages of the vine, on the vegetative growth of *Vitis vinifera* L. cv. Cabernet Sauvignon.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon vineyard (clone CS 46), grafted onto rootstock 99 Richter (clone RY 30), situated at the Nietvoorbij experimental farm in the Western Cape was used. More detail was given by Hunter & Visser (1988a).

2.2 Experimental design

The experiment was laid out as a completely randomized design. Three defoliation levels were applied to the whole canopy, i.e. 0 % (control), 33 % and 66 %. The control consisted of four treatments, while the 33 % and 66 % defoliation levels consisted of 10 treatments each (Fig. 6.1). The defoliation treatments were implemented as follows: Four from approximately one month after bud break, three from berry set, two from pea size and one from véraison. Data were collected at different developmental stages as shown in Fig. 6.1. Nine replications, comprising one-vine plots, for each of the 24 treatments were used.

2.3 Defoliation treatments

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

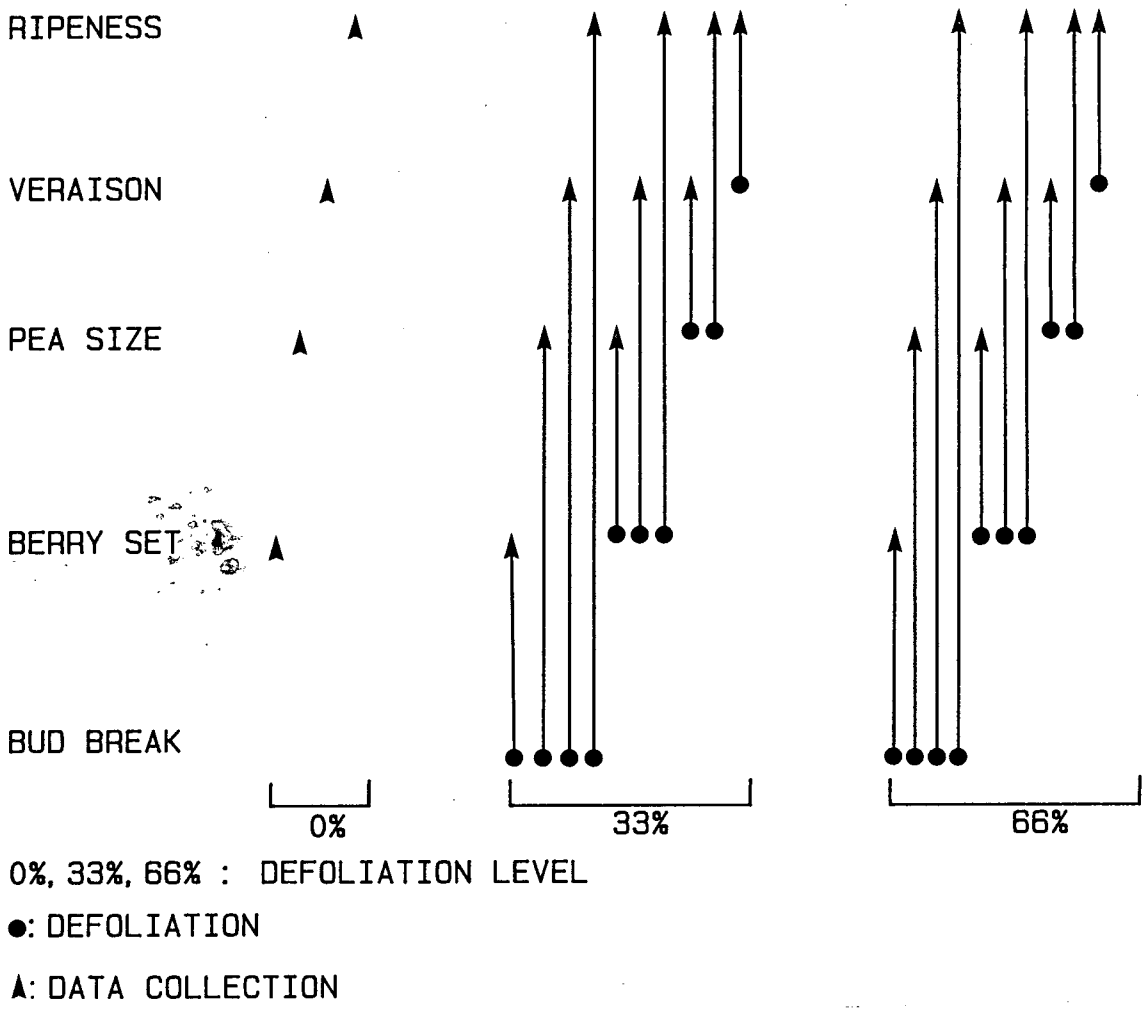

Fig. 6.1 Schematic representation of different stages of defoliation and sampling.

2.4 Measurements

Leaf area (cm^2), main shoot length (cm), lateral shoot length (cm), number of laterals, total shoot length (cm), cane mass (g), canopy density, relative humidity (%), windspeed (cm/s) and temperature (°C) were measured. Leaf area was determined with a LI-COR LI 3000 portable area meter. Canopy density was determined by means of an apparatus consisting of an adjustable frame and a thin steel rod [based on the point quadrat method described by Smart (1982)]. The rod was pushed horizontally through the canopy at five fixed distances just above the bunch zone over the whole cordon. Canopy density was expressed as number of leaves contacted. The percentage relative humidity in the canopy was measured with a Kane-May 8000 humidity meter, while the windspeed and temperature were determined with a Kane-May 4003 thermo-anemometer just above the bunch zone.

2.5 Statistical analyses

Depending on the parameter, a one-way analysis of variance or two-way analysis of variance (standard VORI statistical software packages) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. The experiment was conducted over three growth seasons. No interactions between growth seasons were found and the data therefore represent the overall means.

3. RESULTS AND DISCUSSION

3.1 Effect of defoliation

The effect of the 33 % and 66 % defoliation levels at berry set, pea size and véraison is depicted in Table 6.1. The criterium for the determination of percentage remaining leaf area was total leaf number. It is evident that for both treatments the percentage remaining leaf area per shoot (determined according to leaf area removed at the time of defoliation) was more than the theoretically expected value at each developmental stage. This is in agreement with the findings of Kliewer & Ough (1970) and Kliewer & Fuller (1973) with the cultivar Sultanina. At the higher defoliation level the percentage remaining leaf area increased compared to the expected remaining leaf area. This tendency can be attributed to the fact that the method of treatment was dependent on the removal of specific leaves instead of leaf area.

TABLE 6.1 The effect of time and severity of defoliation on the remaining leaf area per shoot at different developmental stages

Developmental stage	Defoliation (%)	Remaining leaf area (% of control)
Berry set	33	67,99 ± 2,81
	66	39,78 ± 2,65
Pea size	33	66,51 ± 1,12
	66	43,27 ± 5,82
Véraison	33	66,98 ± 4,08
	66	43,54 ± 10,81

A comparison between the average remaining leaf area per shoot calculated on the basis of leaves removed, and that calculated on the basis of leaves retained on the vine, is shown in Table 6.2. Differences between leaf area calculated on the basis of leaves removed from vines and that calculated on the basis of leaves retained was approximately 4 % for the 33 % defoliation and 5 % for the 66 % defoliation treatment. These differences could have resulted from increases in leaf areas of the remaining leaves following partial defoliation. Except for apical leaves, this was evident for the 66 % defoliation treatment, although not significant (Fig. 6.2). Leaf growth responses after defoliation was also found for lucerne (Hodgkinson, 1974). However, a possible increase in lateral shoot growth and/or number of laterals with partial defoliation could also have contributed to increased remaining leaf areas. Nevertheless, the two methods for determining remaining leaf areas seem comparable. It can therefore readily be assumed that the method used in partially defoliating the vines yielded reliable results during the entire growth season.

TABLE 6.2 Comparison between the average remaining leaf area per shoot, calculated on the basis of leaves removed (A) and on the basis of leaves retained (B) on the vine

Defoliation (%)	*Average remaining leaf area	
	A	**B
0	100,00	100,00
33	67,16	71,09
66	42,20	46,84

*** As percentage of controls.**
**** Average of leaf area measured at each developmental stage during the growth season.**

3.2 Leaf area

As expected, the 33 % and 66 % defoliation levels significantly reduced the leaf area per shoot over the growth season (Table 6.3). Partial defoliation improved the canopy light environment, as is evident from the shade patterns (Fig. 6.3) and densities of the canopies (Table 6.4). The 33 % defoliation level resulted in a more favourable situation, namely an even distribution of small sunflecks in the canopy, implying that sufficient sunlight penetrated the canopy for maximum light absorption by leaves. In contrast, the 66 % defoliation was too severe and resulted in a loss of potentially utilizable light energy. However, the leaf layer numbers of the 33 % as well as 66 % defoliation treatments approximated the optimum of three, as suggested by Smart (1985). Partial defoliation from

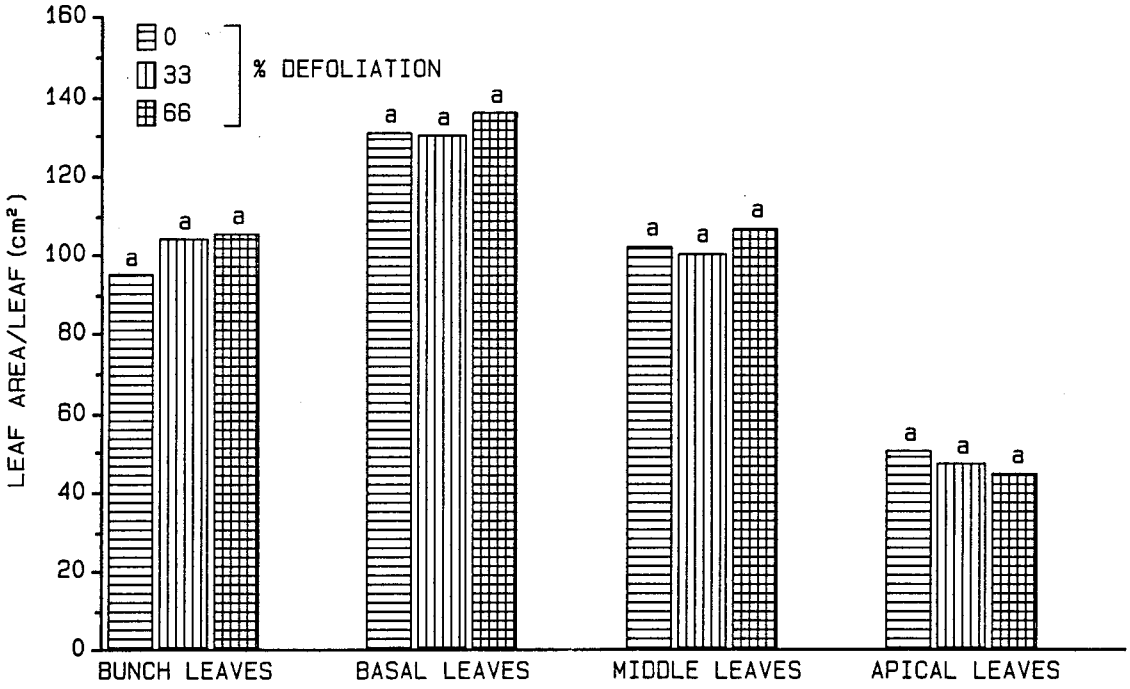

Fig. 6.2 The effect of defoliation on areas of leaves in different positions on the shoot. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

different developmental stages had no significant effect on leaf areas at subsequent developmental stages for each treatment.

In general, apparent increases in leaf area from bud break until véraison followed by a decline, occurred (Table 6.3). A similar growth pattern was found for the cultivar Cape Riesling (De la Harpe & Visser, 1985). The ostensible decrease in leaf area at ripeness likely resulted from leaf senescence. Partial defoliation also significantly reduced the water content of interiorly situated leaves (Table 6.5). Due to the gradual decline in water content as the season progressed (Table 6.5), elasticity of petioles probably decreased and therefore vulnerability of leaves to normal abscission and removal by wind increased. The decrease at ripeness seemed to be more pronounced for leaves of partially defoliated vines, probably as a result of less dense canopies. Therefore, the leaves were probably more affected by unfavourable climatic conditions. Chlorosis of interior-canopy leaves generally occurred in control vines. Although the specific fresh mass per leaf area tended to increase for the severe defoliation level (Fig. 6.4), the results confirmed those of Kliewer & Fuller (1973), who found no increases in leaf dry masses for 25 %, 50 % and 75 % defoliated Sultanina vines compared to non-defoliated vines.

TABLE 6.3 The effect of defoliation from different developmental stages of the vine on the total leaf area (cm^2) per shoot

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	2961^b	2641^b	1773^c
	Pea size	4010^a	3224^b	1982^c
	Véraison	4294^a	3166^b	2159^c
	Ripeness	4277^a	2987^b	1932^c
Berry set	Pea size	4010^a	2967^b	1933^c
	Véraison	4294^a	3362^b	2258^c
	Ripeness	4277^a	2954^b	1950^c
Pea size	Véraison	4294^a	3029^b	1767^c
	Ripeness	4277^a	2767^b	2033^c
Véraison	Ripeness	4277^a	2931^b	1780^c
Cv(%)		18,15		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

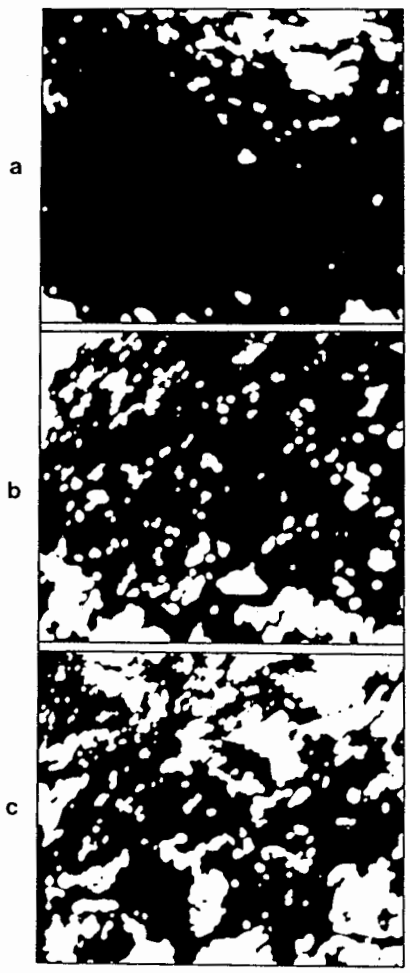

Fig. 6.3 Shade patterns of canopies of vines defoliated (a) 0 %, (b) 33 % and (c) 66 %.

TABLE 6.4 The effect of defoliation on canopy density over the growth season, expressed as number of contacts with leaves (number of leaf layers)

Defoliation (%)	Number of leaf layers
0	5,29[a]
33	3,71[b]
66	2,98[c]
Cv (%)	22,02

Values designated by the same letter do not differ significantly ($p \leq 0,05$).

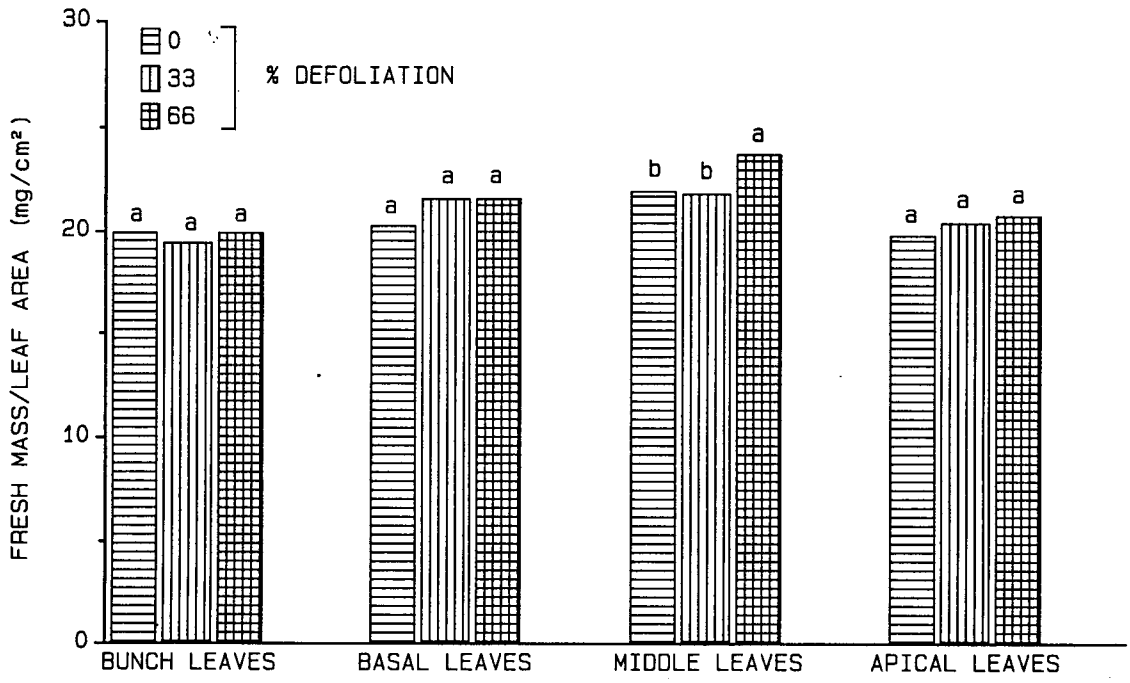

Fig. 6.4 The effect of defoliation on specific fresh mass per leaf area of leaves in different positions on the shoot. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each leaf position.

TABLE 6.5 The effect of defoliation and developmental stage of the vine on the water 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 letter do not differ significantly ($p \leq 0,05$) for each plant part.

3.3 Main shoot length

Though not significant, the mean main shoot length decreased as a result of defoliation (Table 6.6). This apparent decrease may facilitate the diversion of photosynthates to other parts of the vine. In contrast to the elongated internodes of interiorly-situated parts of shoots of control vines, the shoots of partially defoliated vines had shorter internodes, occurring from the basis of the shoot (data not shown). This was also found by Kliewer & Fuller (1973) and Fournioux & Bessis (1984). The improved light conditions found in canopies of partially defoliated vines (Hunter & Visser, 1988c), may have played a role in the shortening of internodes (Leopold & Kriedemann, 1975). According to Salisbury & Ross (1978) a major function of phytochrome (P) is to detect mutual shading and to modify growth accordingly. A higher ratio of P_{fr}:P_r in the interior of control vine canopies may have been responsible for longer internodes (Morgan *et al.*, 1985). Although the vines used in this study did not grow excessively vigorous, the apparent reduction in main shoot length with partial defoliation suggests that vigorous growth may be inhibited by leaf removal practices. Partial defoliation from different developmental stages had no significant effect on the main shoot length at subsequent developmental stages.

TABLE 6.6 The effect of defoliation from different developmental stages of the vine on the mean main shoot length (cm)

Development stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	116[b]	112[b]	109[b]
	Pea size	130[a]	132[a]	123[b]
	Véraison	145[a]	133[a]	138[a]
	Ripeness	143[a]	142[a]	137[a]
Berry set	Pea size	130[a]	119[b]	137[a]
	Véraison	145[a]	140[a]	141[a]
	Ripeness	143[a]	140[a]	144[a]
Pea size	Véraison	145[a]	138[a]	130[a]
	Ripeness	143[a]	143[a]	141[a]
Véraison	Ripeness	143[a]	144[a]	145[a]
Cv(%)		9,57		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

In general, the main shoot length increased until véraison and virtually ceased thereafter. This was also found by Zelleke & Kliewer (1979) and De la Harpe & Visser (1985) for the cultivars Cabernet Sauvignon and Cape Riesling, respectively.

3.4 Lateral shoot growth

Generally, lateral shoot length as well as the number of lateral shoots increased significantly when partial defoliation was implemented from bud break, berry set and pea size stages (Tables 6.7 & 6.8). Similar results were found for Perlette and Sultanina vines (Marangoni *et al.*, 1980). According to the latter investigators the uniformity of carbohydrate content in the rest of the shoots and the reasonably good growth occurring during the next season suggested that the vine benefitted from the production of new leaves during midseason. With earlier defoliation, larger increases of total lateral shoot length per shoot, as well as number of laterals per shoot, were obtained than with subsequent defoliations (Tables 6.7 & 6.8). The latter results were also found by Kliewer & Fuller (1973). However, no compensatory growth at subsequent developmental stages occurred for each defoliation treatment. The stimulation in lateral growth is possibly associated with a substance, produced by the leaves during early developmental stages, which inhibited lateral bud growth (Kliewer & Fuller, 1973). By removing leaves, the

TABLE 6.7 The effect of defoliation from different developmental stages of the vine on the total lateral shoot length (cm) per shoot

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	63^{d}	79^{c}	91^{b}
	Pea size	71^{c}	118^{a}	115^{a}
	Véraison	57^{d}	95^{b}	105^{a}
	Ripeness	60^{d}	82^{c}	92^{b}
Berry set	Pea size	71^{c}	86^{b}	100^{b}
	Véraison	57^{d}	80^{c}	92^{b}
	Ripeness	60^{d}	88^{b}	73^{c}
Pea size	Véraison	57^{d}	90^{b}	72^{c}
	Ripeness	60^{d}	58^{d}	82^{c}
Véraison	Ripeness	60^{d}	58^{d}	63^{d}
Cv(%)		24,82		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

TABLE 6.8 The effect of defoliation from different developmental stages of the vine on the number of lateral shoots per vine

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	102^{b}	143^{a}	150^{a}
	Pea size	97^{c}	139^{a}	134^{a}
	Véraison	58^{d}	85^{c}	119^{b}
	Ripeness	52^{d}	59^{d}	93^{c}
Berry set	Pea size	97^{c}	110^{b}	111^{b}
	Véraison	58^{d}	84^{c}	92^{c}
	Ripeness	52^{d}	64^{d}	70^{d}
Pea size	Véraison	58^{d}	84^{c}	85^{c}
	Ripeness	52^{d}	72^{d}	74^{d}
Véraison	Ripeness	52^{d}	58^{d}	57^{d}
Cv(%)		21,82		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

concentration of this substance is reduced. According to Leopold & Kriedemann (1975) the regulation of auxin formation may be involved in compensatory growth.

Apart from mobilizing vine reserves (Koblet & Perret, 1982), increased lateral growth (especially the number of lateral shoots) as well as the accompanied use of photosynthates probably inhibited the distribution of compounds contributing to the development and quality of grapes. According to Koblet (1984), the shoot tip alone used the photosynthates of one to six mature leaves. However, since maximum lateral shoot length was reached relatively early during the season (pea size stage), the competitive effects could have been neutralised by the availability of recently matured, active leaves with high photosynthetic activities from véraison to harvest. According to Johnson & Lakso (1985) newly formed leaves continued to increase in size after shoot growth had stopped. Lateral shoots carried 25 % to 50 % of the total leaf area on the vine (Schneider, 1985).

The potential to export photosynthates was attained when 30 % to 50 % of the final size of the leaves was reached (Hale & Weaver, 1962; Koblet, 1977; Yang & Hori, 1980). Young leaves produced more organic acids and mature leaves more sugar (Kriedemann, 1977). Provided that the microclimate is optimal, the presence of young leaves on lateral shoots

and the apical parts of carrier shoots during the period véraison to ripeness would therefore be important to ensure a balanced organic acid:sugar ratio in the fruit, especially in regions where a lack of acid in grapes is experienced. The leaves of lateral shoots without grapes exported their carbohydrates to bunches of main shoots (Koblet, 1969; Koblet & Perret, 1971). The practice of removing lateral shoots to improve canopy microclimate should therefore be done with great caution. According to Koblet (1987) the growth of lateral shoots and subsequent higher proportion of young leaves increased fruit quality.

Partial defoliation from véraison had no effect on lateral growth, probably because vegetative growth of the vine had already virtually ceased. This is in agreement with the results found for Sultanina vines (Kliewer & Fuller, 1973). Inhibition or abscence of lateral shoots may not only save food reserves, but would also be beneficial to pest and disease control, canopy microclimate and photosynthetic activity of all leaves on the vine.

TABLE 6.9 The effect of defoliation from different developmental stages of the vine on the mean total shoot length (main and lateral shoots) (cm)

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	178^{b}	191^{b}	201^{b}
	Pea size	201^{b}	250^{a}	238^{a}
	Véraison	203^{b}	228^{a}	243^{a}
	Ripeness	202^{b}	219^{a}	229^{a}
Berry set	Pea size	201^{b}	205^{b}	237^{a}
	Véraison	203^{b}	221^{a}	233^{a}
	Ripeness	202^{b}	212^{b}	217^{a}
Pea size	Véraison	203^{b}	226^{a}	203^{b}
	Ripeness	202^{b}	202^{b}	223^{a}
Véraison	Ripeness	202^{b}	203^{b}	209^{b}
Cv(%)		11,02		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

3.5 Total shoot length

As for leaf area (Table 6.3) and main shoot length (Table 6.6), the mean total shoot length followed the general pattern of rapid increase until véraison with a decline thereafter (Table 6.9). This tendency remained the same for all defoliation treatments. In general, partial defoliation significantly increased the total shoot length per bud. This increase may be ascribed to the increase in lateral growth (Tables 7 & 8). Although partial defoliation from earlier stages resulted in increases in lateral shoot growth with concomitant increases in leaf area and total shoot length, the method by which partial defoliation was applied in this study was still effective in improving light intensity at especially interior-canopy leaves, as well as the photosynthetic activity of all leaves on the shoot (Hunter & Visser, 1988c). Distribution of photosynthates was not affected (Hunter & Visser, 1988b).

Furthermore, it is evident from Table 6.10 that partial defoliation significantly increased windspeed, but decreased relative humidity in the canopy, while the canopy temperature was similar to that of control vines. Along with the less dense canopies of partially defoliated vines (Fig. 6.3, Table 6.4), the results imply that the incidence of diseases would be reduced and chemical control of diseases by spraying would benefit from the change in canopy microclimate as created by partial defoliation as was reported by Boniface & Dumartin (1977), Koblet (1987) and English *et al.* (1989).

TABLE 6.10 The effect of defoliation on windspeed, relative humidity and temperature in the grapevine canopy over the growth season

Defoliation (%)	Windspeed (cm/s)	Relative humidity (%)	Temperature (°C)
0	12,78^{c}	34,81^{a}	29,59^{a}
33	20,28^{b}	33,69^{b}	29,46^{a}
66	27,78^{a}	33,11^{b}	29,57^{a}
Cv (%)	27,67	5,51	4,55

Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

3.6 Cane mass

The earlier and more severe partial defoliation was applied, the more cane mass was reduced, albeit not significantly (Fig. 6.5). Except for the 33 % defoliation, carried out from pea size and véraison, cane mass per vine apparently also declined with defoliation. The apparent decrease in cane mass with long-term and severe defoliation could be due to a deprivation of vine reserves, differences in budding percentage as well as thinner shoots. According to Kliewer & Fuller (1973) cane mass does not seem to be a good indicator of reduced vine capacity as a result of defoliation, especially when applied at véraison or later.

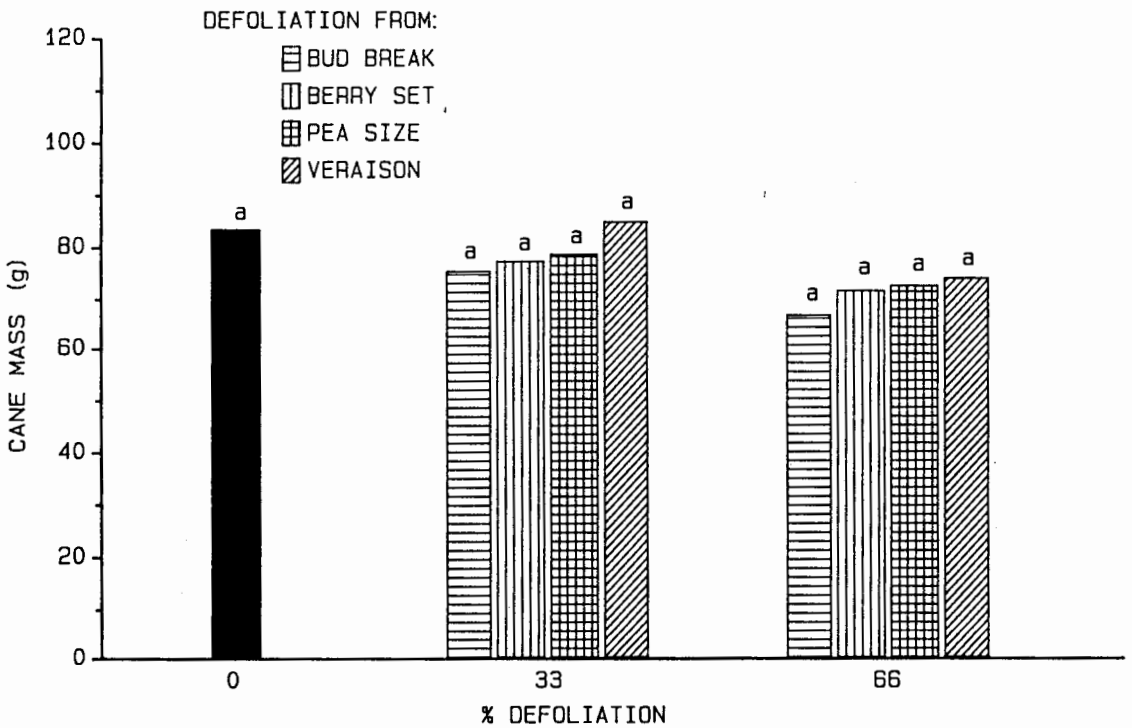

Fig. 6.5 The effect of defoliation, implemented from different developmental stages of the vine, on cane mass at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

4. CONCLUSIONS

Regardless of degree of defoliation, vegetative growth of vines generally increased until véraison with a decline thereafter. In spite of the severe defoliation, the normal sigmoidal growth pattern of vines was not affected. This is important for the general well-being and longevity of vines. This may have resulted mainly from the fact that leaves were removed evenly and not, as in some other studies, block-stripped or selectively.

Partial defoliation significantly reduced leaf area, but only slightly reduced main shoot length. The latter effect may have been more pronounced if the vines had grown more vigorously. However, partial defoliation from especially early in the growth season, significantly increased lateral shoot length, number of laterals and therefore total shoot length. In spite of this, light conditions in canopies of especially 33 % defoliated vines were still more favourable compared to non-defoliated vines. Grape composition would also benefit from the appearance of young and recently matured leaves in the canopy. The removal of lateral shoots at any stage should therefore be carried out with great care. Although cane mass was slightly reduced the earlier defoliation was applied, these reductions were not significant. Cane mass is therefore not a good indicator of changed vine capacity as a result of partial defoliation.

Due to the problem of excessive growth in South African vineyards, grapevine canopies can be dense or become very dense when the overall canopy structure is reduced by, for example, severe topping early during the growth season, or expanded by applying more bearers and/or extending the cordon vertically and/or horizontally. Grapevine canopy management practices should therefore be aimed at creating a canopy consisting of well-positioned leaves, favouring maximum interception of sunlight as well as maximum photosynthetic activity, without reducing quantity and quality of the grapes. Although the vines used in this study were not excessively vigorous, the results indicated that partial defoliation would facilitate in creating the required canopy. Recommendations in this regard can, however, only be made after studying the effect of partial defoliation on reproductive growth.

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CHAPTER VII

The Effect of Partial Defoliation on Reproductive Growth of *Vitis vinifera* L. cv. Cabernet Sauvignon

Key words : *Vitis vinifera*, Reproductive growth, Defoliation.

ABSTRACT

The effect of partial defoliation over the whole canopy on reproductive growth of *Vitis vinifera* L. cv. Cabernet Sauvignon was investigated.

The 33 % defoliation treatment prior to pea size and the 66 % defoliation treatment prior to véraison adversely affected fresh mass per berry and yield at harvest. The 33 % defoliation treatment from véraison increased fresh berry mass. Partial defoliation had no effect on berry water content. Dry matter started to accumulate rapidly from after pea size stage.

The fresh berry mass:cane mass ratio increased with partial defoliation from véraison. Leaf area/g fresh mass results indicated that control vines carried excess foliage which prevented their maximum photosynthetic activity.

Partial defoliation of the canopy improved budding percentage, generally increasing with increasing defoliation, while bud fertility was improved only by 33 % defoliation. In general, leaf removal from bud break and berry set was more effective in improving budding, while bud fertility was favoured by partial defoliation from bud break.

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1. INTRODUCTION

A clear definition of physiological balances in grapevines requires measurements relating to the capacity of the vine, a term which represents vegetative growth, crop yield and grape composition (Winkler *et al.*, 1974). The capacity of a grapevine is determined by its genetic potential for CO_2-assimilation (Kriedemann, 1977). Genetic information is used to direct increases in size (growth) and changes in form (development) (Weier *et al.*, 1974). According to Ho (1988) the potential sink strength is also determined genetically and can only be expressed fully when the supply is sufficient to meet the demand and the environmental conditions for the metabolic activity of the sink organ are optimal. However, research concerning canopy microclimate indicates leaf area, especially the percentage effective leaf surface, as a major factor determining the capacity of a grapevine (Koblet, 1984; Schneider, 1985; Smart, 1985; Smart *et al.*, 1985a; Smart, 1987).

The magnitude of a harvest is dependent, among others, on the proportion of assimilates diverted towards fruit development rather than vegetative growth (Kriedemann, 1977). Maggs (1964) stated that future crop plants may be expected to convert a greater proportion of their assimilates into economic end-products and less into mere plant machinery. This will lead to greater yield per plant and, due to reduced foliage, more plants per hectare. It is therefore necessary to minimise vegetative dominance without reducing assimilate supply to the fruit. Concomitantly, it is essential that an optimum canopy microclimate be created for maximum budding and bud fertility (May, 1965; Shaulis *et al.*, 1966; Shaulis & May, 1971; Smart *et al.*, 1982; Archer & Swanepoel, 1987) as well as grape quality (Smart, 1982; Smart *et al.*, 1985b; Kliewer & Bledsoe, 1987; Bledsoe *et al.*, 1988; Kliewer *et al.*, 1988; Koblet, 1988). Research regarding grapevine management is consequently aimed progressively at finding the perfect balance between accumulation of reserves, vegetative growth, canopy microclimate, and optimal fruit quantity and quality.

Due to excessive growth and canopy density problems generally occurring in South African vineyards, research concerning the manipulation of foliage is of special importance. This investigation was therefore conducted to determine the effect of different levels of defoliation, implemented from different developmental stages of the vine, on the reproductive growth of *Vitis vinifera* L. cv. Cabernet Sauvignon.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon vineyard (clone CS 46), situated at Nietvoorbij experimental farm in the Western Cape, was used (Hunter & Visser, 1988a).

2.2 Experimental design

The experiment was laid out as a completely randomized design as previously described by Hunter & Visser (1990).

2.3 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 as described above at approximately monthly intervals.

2.4 Measurements

Leaf area (cm^2), cane mass (g), fresh and dry berry mass (g), water content of the berries (%), budding percentage, bud fertility and light intensity ($\mu mol/m^2/s$) were measured. Budding percentage and bud fertility were determined at the end of the season following the season of treatment. Leaf area was determined with a LI-COR LI 3000 portable area meter. The bunches of five randomly selected shoots per vine were harvested and the fresh mass of the berries determined. Berries were frozen at -20°C prior to freeze-drying. Ambient light intensity between the vine rows as well as light intensity just above the cordon were determined with a LI-COR Line Quantum Sensor during late morning. Light intensity was expressed as percentage of the ambient light level.

The following equations were used to determine budding percentage and bud fertility per vine :

Budding percentage = Number of shoots/number of buds allocated during pruning x 100.

Bud fertility = Number of bunches/number of shoots originating from buds allocated during pruning.

2.5 Statistical analyses

Depending on the parameter, a one-way analysis of variance or two-way analysis of variance (standard VORI statistical software packages) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were carried out using a Scott-Knott analysis. The experiment was conducted over three growth seasons. No interactions between growth seasons were found and the data therefore represent the overall means.

3. RESULTS AND DISCUSSION

3.1 Fresh berry mass

The earlier and more severe partial defoliation was applied, the less fresh mass was produced at subsequent developmental stages compared to those of control vines (Table 7.1). This was also found by Kliewer (1970) for Sultanina vines. A decrease of hormones or hormone precursors, synthesized in leaves and involved in berry growth, was suggested by Kliewer (1970) as a possible reason for the decrease in berry mass. It is evident that 33 % defoliation prior to pea size and 66 % defoliation prior to véraison severely affected yield at harvest (Fig. 7.1). This is also evident from the fresh mass per berry (Table 7.2) and is in contrast to results of Bledsoe *et al.* (1988) who found no differences in crop mass and bunch mass due to either the timing or level of leaf removal. However, their experiments were conducted during a single growth season and the defoliation applied was not as severe as in the present investigation.

Koblet (1984) stated that an early removal of too many leaves will weaken the vine and may stop fruit development. Since the whole canopy was evenly defoliated during three growth seasons in this study, creating severe stress conditions, the decreases in yield of vines subjected to long-term defoliation may have resulted from the depletion of reserves. However, translocation patterns of photosynthate in shoots were not different and the total photosynthetic activity of especially 33 % defoliated vines was similar to or even higher than that of control vines (Hunter & Visser, 1988b, 1989), while increases in number and length of laterals (Hunter & Visser, 1990) were not enough to account for the decreased masses. According to Brown & Coombe (1985), accumulation is primarily controlled by phloem unloading in the berry, while Ho (1988) stated that the import of assimilate may be controlled by energy-dependent processes. Due to the drastic changes in microclimate, source:sink relationships and metabolic activity, it is possible that changes in enzyme

TABLE 7.1 The effect of defoliation from different developmental stages of the vine on the fresh berry mass (g) per shoot

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	18^{h}	18^{h}	15^{h}
	Pea size	67^{g}	82^{f}	56^{g}
	Véraison	174^{d}	151^{e}	96^{f}
	Ripeness	247^{a}	215^{c}	134^{e}
Berry set	Pea size	67^{g}	82^{f}	81^{f}
	Véraison	174^{d}	155^{e}	133^{e}
	Ripeness	247^{a}	206^{c}	163^{d}
Pea size	Véraison	174^{d}	180^{d}	150^{e}
	Ripeness	247^{a}	228^{b}	195^{c}
Véraison	Ripeness	247^{a}	256^{a}	234^{b}
Cv (%)		16,21		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

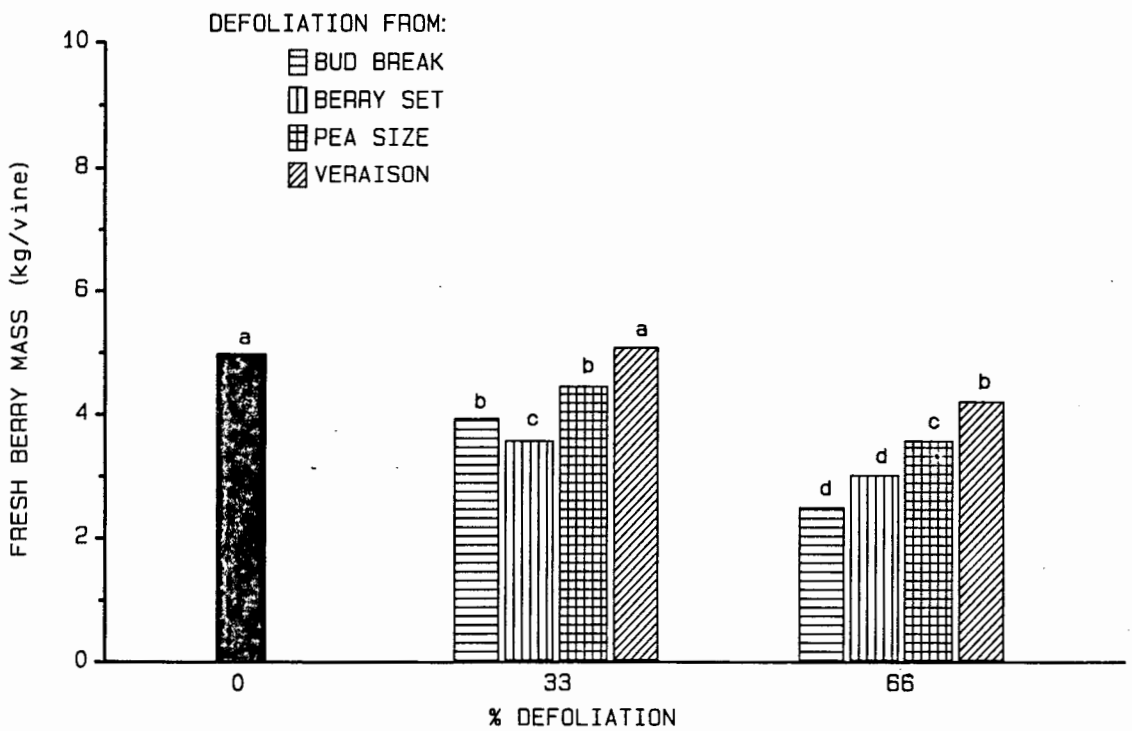

Fig. 7.1 The effect of defoliation, implemented from different developmental stages of the vine, on the fresh berry mass at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

TABLE 7.2 The effect of defoliation from different developmental stages of the vine on the fresh mass (g) per berry at ripeness

Developmental stage defoliation commenced	Defoliation (%)		
	0	33	66
Bud break	1,20 [b]	1,18 [b]	1,11 [b]
Berry set	1,20 [b]	1,18 [b]	1,08 [b]
Pea size	1,20 [b]	1,32 [a]	1,17 [b]
Véraison	1,20 [b]	1,26 [a]	1,30 [a]
Cv (%)	8,26		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

activity in leaves and/or grapes also played important roles in the control of accumulation in berries. Furthermore, partial exposure of berries to direct sunlight may also have contributed to the lower fresh berry mass (Kliewer, 1970). Crippen & Morrison (1986) found that shaded berries were significantly heavier than sun-exposed berries, attributing it to a higher water content of the former.

Partial defoliation (33 %) from véraison resulted in an apparent higher fresh berry mass. Apart from higher photosynthetic activities of remaining leaves, as induced by partial defoliation (Buttrose, 1966; May *et al.*, 1969; Kliewer & Antcliff, 1970; Kriedemann, 1977; Hofäcker, 1978; Johnson *et al.*, 1982; Hunter & Visser, 1988b, 1988c), another possible explanation for increased berry mass may be an enhancement of mobilization of carbohydrate reserves in woody tissues available for accumulation in fruits (Kliewer, 1970). However, partial defoliation had no apparent effect on the amount of photosynthates added to the reserve pool (Hunter & Visser, 1988b). Due to changes in the canopy microclimate of partially defoliated vines, light composition could have also played a major role in morphological and physiological activity, especially the expression of enzyme activity.

Nevertheless, the improved canopy microclimate due to leaf removal (Hunter & Visser, 1988c, 1990) may also have dramatic effects on grape composition, such as an increased sugar concentration and a decrease in malate, pH and potassium content, as well as an increase in wine colour (Smart, 1982; Smart *et al.*, 1985b; Kliewer & Bledsoe, 1987; Bledsoe *et al.*, 1988; Kliewer *et al.*, 1988; Koblet, 1988).

3.2 Dry berry mass

Dry mass increased slightly up to pea size, whereafter accumulation of solutes increased rapidly until harvest (Table 7.3). In general, it seemed that later leaf removals led to smaller effects on dry mass production. It is therefore clear that maintaining enough leaf area to nourish the rapidly dividing cells of young berries are critical for obtaining high yields at harvest. These results are in agreement with the findings of other investigators, i.e. that removal of the photosynthetic source during the early stages of berry development resulted in lower yields (Coombe, 1959; Kliewer, 1970; Kliewer & Ough, 1970; Kliewer & Fuller, 1973; Sidahmed & Kliewer, 1980).

TABLE 7.3 The effect of defoliation from different developmental stages of the vine on the dry berry mass (g) per shoot

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	2^{i}	2^{i}	2^{i}
	Pea size	6^{h}	8^{h}	5^{h}
	Véraison	37^{e}	34^{e}	21^{g}
	Ripeness	69^{a}	57^{b}	37^{e}
Berry set	Pea size	6^{h}	8^{h}	6^{h}
	Véraison	37^{e}	32^{e}	28^{f}
	Ripeness	69^{a}	58^{b}	45^{d}
Pea size	Véraison	37^{e}	35^{e}	28^{f}
	Ripeness	69^{a}	59^{b}	51^{c}
Véraison	Ripeness	69^{a}	69^{a}	61^{b}
Cv (%)		18,65		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

3.3 Water content

The water status of berries of defoliated vines were almost similar (Table 7.4). It is therefore evident that the improved light conditions in the canopy (Hunter & Visser, 1990) had no effect on the water content of berries. This is in contrast to the findings of Crippen & Morrison (1986). This finding is very important because of the well-known effect of water in the regulation of solute concentration in the berry (Coombe, 1987). The mean berry

water content over defoliation treatments were 90 %, 90 %, 80 % and 72 % at berry set, pea size, véraison and ripeness, respectively. It was evident that the components of dry matter only started to accumulate rapidly from after pea size until harvest. According to Coombe *et al.* (1987) this principally constitutes glucose and fructose.

TABLE 7.4 The effect of defoliation from different developmental stages of the vine on the water content (%) of the berries

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)		
		0	33	66
Bud break	Berry set	90[b]	90[b]	89[b]
	Pea size	90[b]	90[b]	90[b]
	Véraison	80[c]	78[d]	79[d]
	Ripeness	72[f]	72[f]	71[f]
Berry set	Pea size	90[b]	90[b]	91[a]
	Véraison	80[c]	80[c]	79[d]
	Ripeness	72[f]	71[f]	72[f]
Pea size	Véraison	80[c]	80[c]	80[c]
	Ripeness	72[f]	73[e]	73[e]
Véraison	Ripeness	72[f]	73[e]	72[e]
Cv (%)		1,16		

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

3.4 Fresh mass:cane mass ratio

Except for defoliation from bud break, no significant differences between the fresh mass at ripeness:cane mass ratio of the non-defoliated and 33 % defoliated vines were found (Fig. 7.2). Defoliation prior to berry set (33 %) and prior to véraison (66 %) led to the most marked reductions in fresh mass:cane mass ratios. However, when implemented from véraison, the ratio apparently increased compared to control vines.

3.5 Leaf area/fresh mass and fresh mass/leaf area

Generally, the later and more severe the defoliation, the more the leaf area per gram fresh mass was reduced compared to that of control vines (Table 7.5). The larger leaf areas with early defoliation mainly resulted from the still low berry masses at the early stages. The

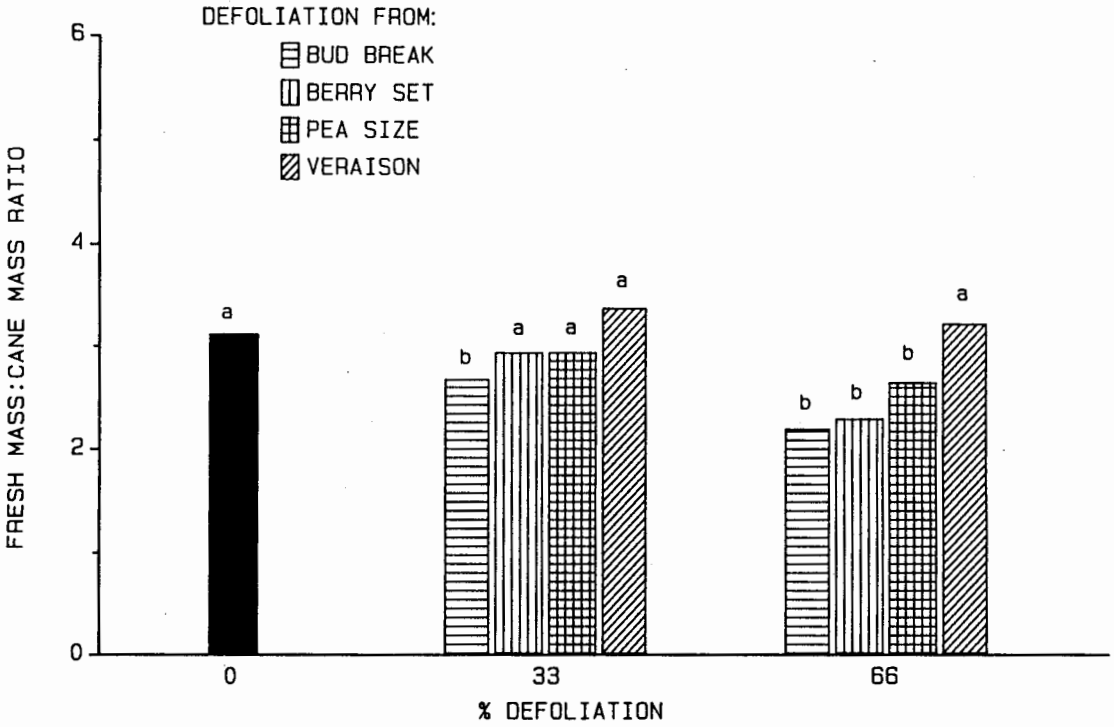

Fig. 7.2 The effect of defoliation, implemented from different developmental stages of the vine, on the fresh mass:cane mass ratio. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

TABLE 7.5 The effect of defoliation from different developmental stages of the vine on the leaf area (cm^2) per fresh berry mass (g) and fresh berry mass (mg) per leaf area (cm^2)

Developmental stage defoliation commenced	Developmental stage measured	Defoliation (%)					
		0		33		66	
		cm^2/g	mg/cm^2	cm^2/g	mg/cm^2	cm^2/g	mg/cm^2
Bud break	Berry set	176^a	6^h	177^a	7^h	134^b	9^h
	Pea size	62^c	17^h	42^d	27^g	37^d	30^g
	Véraison	27^e	41^f	23^e	48^f	24^e	46^f
	Ripeness	18^e	60^e	15^e	79^c	15^e	73^d
Berry set	Pea size	62^c	17^h	37^d	29^g	25^e	44^f
	Véraison	27^e	41^f	23^e	49^f	18^e	61^e
	Ripeness	18^e	60^e	15^e	73^d	12^e	86^c
Pea size	Véraison	27^e	41^f	18^e	62^e	12^e	89^c
	Ripeness	18^e	60^e	12^e	90^c	11^e	111^b
Véraison	Ripeness	18^e	60^e	12^e	90^c	8^e	134^a
Cv (%) : cm^2/g		35,12					
mg/cm^2		21,57					

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

stimulation in lateral growth and accompanied leaf area (Hunter & Visser, 1990) could also have contributed to larger leaf areas. Considering the 10 cm^2 to 12 cm^2 leaf area generally required to ripen one gram of fruit (Winkler, 1930; Kliewer, 1970; Kliewer & Antcliff, 1970; Kliewer & Ough, 1970; Kliewer & Weaver, 1971; Archer & Beukes, 1983; Jooste, 1983), it is evident that the control vines carried excess foliage. The fresh berry mass per leaf area clearly showed that the metabolism and photosynthesis of remaining leaves of partially defoliated vines were more effective, having the ability to support much higher berry masses throughout the growth season (Table 7.5). It is therefore of utmost importance to create a microclimate and physiological condition that will allow optimal photosynthetic activity of all grapevine leaves. This will prevent them from functioning below their maximum efficiency.

3.6 Budding percentage and bud fertility

Partial defoliation of canopies improved budding percentage, which generally increased with increased defoliation (Fig. 7.3). Leaf removal from bud break and berry set was generally more effective in improving budding. Though not significantly, bud fertility was improved by 33 % defoliation as well as 66 % defoliation from bud break (Fig. 7.4). According to May (1965), shading may reduce the import of assimilates into the bud and therefore contributes to a reduced fruitfulness. Smart *et al.* (1982) suggested that the leaf subtending the bud may be the principal source of photosynthates for the bud. Although light intensity at the basal parts of the shoots was improved (Table 7.6), 66 % defoliation was probably too severe, especially regarding the availability of nutrients for the initiation and differentiation of inflorescence primordia. This was also evident from the lower yields (Fig. 7.1) as well as the lesser total photosynthetic activity of 66 % defoliated vines compared to those of control vines (Hunter & Visser, 1988b, 1989). According to Shaulis & May (1971), yield of grapevines is determined by, amongst others, the growth of buds and their inflorescence primordia as well as accumulation of photosynthates in the season preceding harvest.

Bud fertility was favoured by partial defoliation from bud break. This coincided with the period for the formation of inflorescence primordia and their initiation and differentiation (Swanepoel & Archer, 1988). It is therefore evident that the exposure of basal buds to higher light intensities during this period only, exerted an effect on the fruitfulness of the buds. Smart *et al.* (1982) found a positive relationship between the radiation microclimate of the leaf subtending a bud and the productivity of the shoot from that bud in the following growth season. The correlation was also the highest with an improved microclimate in the pre-flowering period. The duration of exposure, as well as the quality (specific wavelengths) of light, may also have been important (Morgan *et al.*, 1985; Archer &

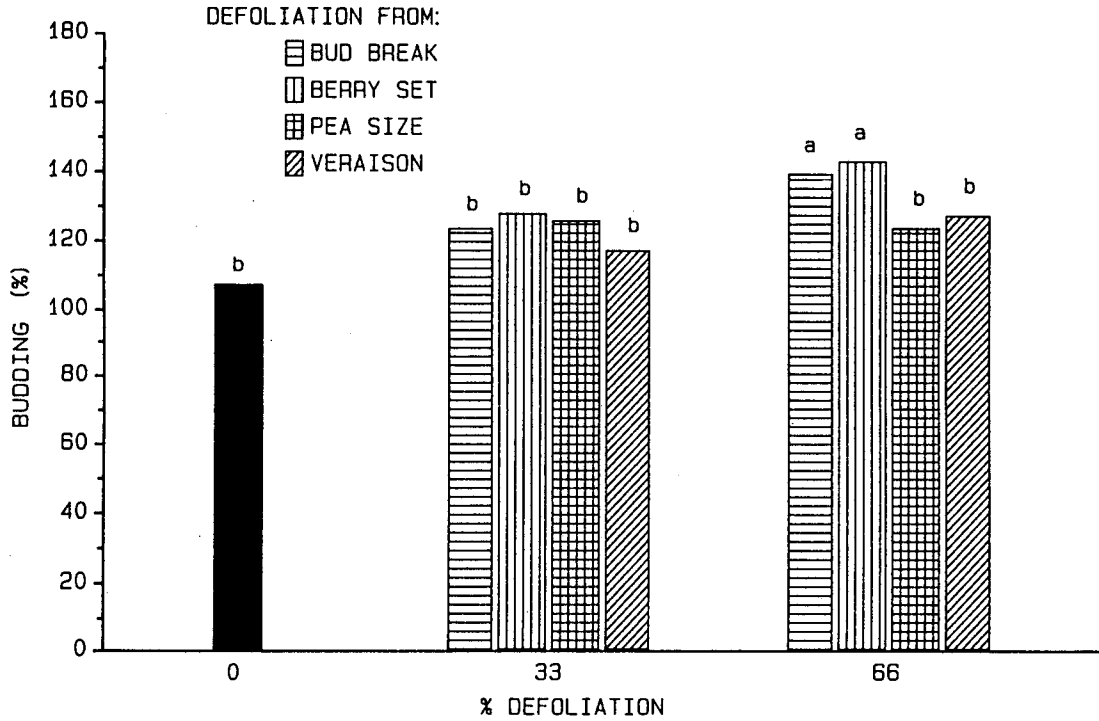

Fig. 7.3 **The effect of defoliation, implemented from different developmental stages of the vine, on budding percentage. Values designated by the same letter do not differ significantly ($p \leq 0,05$).**

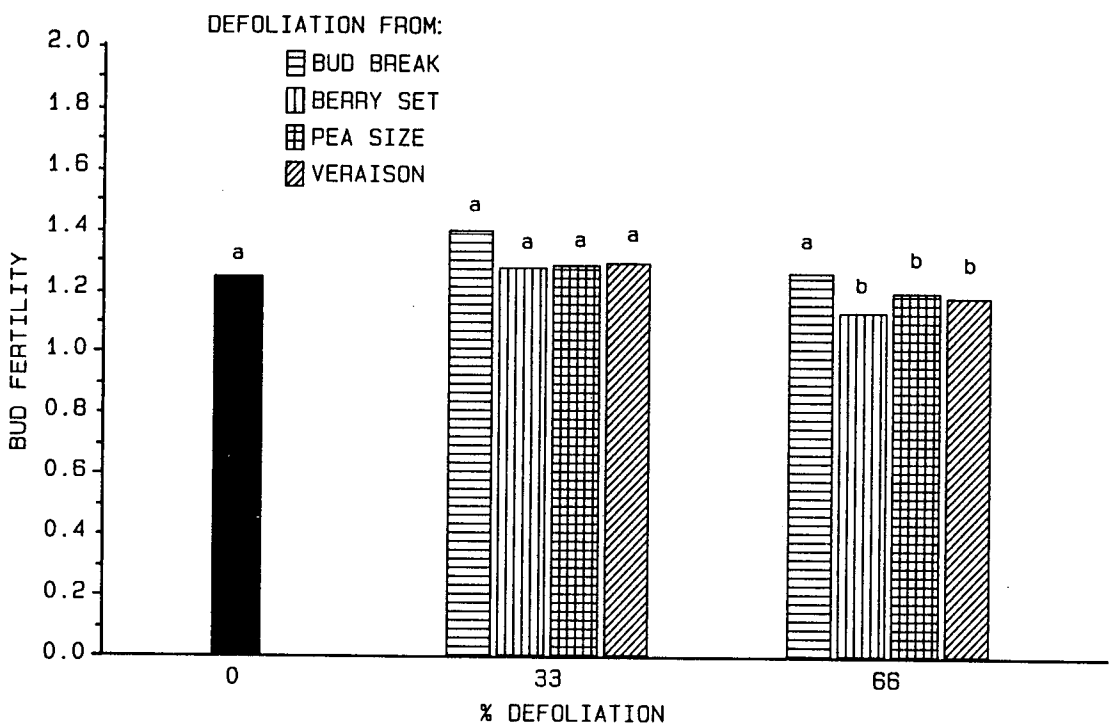

Fig. 7.4 **The effect of defoliation, implemented from different developmental stages of the vine, on bud fertility. Values designated by the same letter do not differ significantly ($p \leq 0,05$).**

TABLE 7.6 The effect of defoliation and developmental stage of the vine on the canopy light intensity, expressed as percentage of ambient light intensity

Developmental stage	Defoliation (%)			Mean
	0	33	66	
Berry set	7,65	10,84	21,35	13,28[c]
Pea size	11,60	21,74	25,45	19,60[b]
Véraison	14,02	27,67	36,45	26,05[a]
Ripeness	24,33	26,56	38,34	29,74[a]
Mean	14,40[c]	21,70[b]	30,40[a]	
Cv (%)	46,87			

Values designated by the same letter do not differ significantly ($p \leq 0,05$).
Data represent the means over three growth seasons.

Swanepoel, 1987). May (1965), however, found that the effect of shading on fruitfulness was not related to light quality, but rather total reduced light intensity. Nevertheless, the results of this study indicated that no direct relationship existed between fruitfulness of buds and yield per vine. This may partly be attributed to the decrease in cane mass for especially the long-term severe defoliations (Hunter & Visser, 1990), resulting in lower bud loads per vine and, consequently, lower yields per vine over three growth seasons. It is possible that the high budding percentage further deprived the already severely stressed vines of essential nutrients and reserves, possibly resulting in the apparently reduced shoot lengths and cane masses reported by Hunter & Visser (1990). Nevertheless, budding percentage was seemingly directly affected by the improved light intensity resulting from partial defoliation (Table 7.6), albeit only when implemented from bud break and berry set.

4. CONCLUSIONS

The 33 % defoliation treatment prior to pea size and 66 % defoliation prior to véraison adversely affected fresh mass per berry and yield at harvest, while 33 % defoliation from véraison increased fresh berry mass compared to that of non-defoliated vines. When applied from véraison, partial defoliation increased the fresh berry mass:cane mass ratio.

The leaf area/fresh mass and fresh mass/leaf area results implied that non-defoliated vines carried excess foliage, preventing maximum metabolism and photosynthetic activity, but that remaining leaves of partially defoliated vines were able to support substantially higher berry masses throughout the growth season. Furthermore, partial defoliation improved budding, especially when applied from bud break and berry set. Bud fertility was only improved by 33 % defoliation, which was more favourable when applied from bud break.

It is clear that early removal of highly active, newly matured leaves will deprive the vine of essential nutrients with a deleterious effect on its longevity and healthiness. The even defoliation over the whole grapevine canopy applied in this study was, however, too severe and is not recommended as a canopy management practice. It is, however, essential that leaves of the grapevine be maximally exploited to the benefit of vegetative as well as reproductive growth during the growth season. The present results, together with previous results, suggest that an even removal of 33 % of leaves opposite and below bunches during the period from flowering or berry set to pea size, may be applied. The results further suggest that an even partial defoliation of 33 % from as early as pea size may be safely applied in practice on the lower half of the grapevine canopy. This will not only facilitate the prevention of potentially deleterious effects of excessive vegetative growth and a dense canopy-interior, but improve canopy microclimate and stimulate metabolic activity and contribution of photosynthates to the developing berry.

An improved canopy microclimate, securing maximum photosynthetic activity of leaves as well as fruit development, before pea size should be obtained by other canopy management practices such as suckering, shoot positioning, tipping and topping. If necessary at all, topping must preferably be carried out before pea size to leave enough time for leaves on sprouting lateral shoots to become active and contribute to the berry during the period véraison to ripeness. Due to the multidirectional translocation in the shoot, which is still evident before pea size, it is expected that the effect on fruit development would be more dramatic. Topping during the period pea size or véraison to ripeness must be avoided because of the importance of young and recently matured, active leaves on the upper half of the shoot in terms of photosynthesis, the accumulation of reserves and translocation of photosynthetic products to the grapes. Photosynthetic products are mainly translocated to bunches during this period. Except in cases of excessive growth, shoots should only be tipped if active growth continues. To prevent the canopy from becoming too dense when topping prior to pea size was carried out, leaf removal is a necessity during the period pea size to ripeness.

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CHAPTER VIII

The Effect of Partial Defoliation on the Root System of *Vitis vinifera* L. cv. Cabernet Sauvignon Grafted onto Rootstock 99 Richter

Key words : *Vitis vinifera*, Defoliation, Root system, Field conditions.

ABSTRACT

The effect of partial defoliation (33 %) over the whole canopy from different developmental stages of the vine on the development and distribution of roots of *Vitis vinifera* L. cv. Cabernet Sauvignon was investigated under field conditions.

Partial defoliation significantly stimulated root density, increasing the later during the growth season defoliation was commenced. Yield and cane mass of partially defoliated vines coincided with root densities. This relationship was not clear for non-defoliated vines. Root development in fine to medium diameter classes was increased by partial defoliation. However, the development of thick roots was apparently decreased. Partial defoliation from pea size seemed to create the most effective root system. Early defoliation (from bud break and berry set) reduced root development compared to later defoliations (from pea size and véraison).

Partially defoliated vines had higher total root numbers in all soil layers, although differences were not significant. Regardless of treatments, roots were mainly located in 0 to 800 mm soil layers, with deeper layers containing much less roots. Higher root densities and generally larger numbers of particularly fine roots in all soil layers for partially defoliated vines suggested a more efficient nutrient absorption capacity and utilization of soil for these vines. It was evident that partially defoliated vines responded to the loss in leaf area by forming new roots, providing prolonged vine performance.

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1. INTRODUCTION

Excessive vegetative growth of grapevines is commonly observed in South Africa. Canopy management practices are, therefore, of particular interest to viticulturists to improve canopy microclimate, decrease source:sink ratios and increase physiological reactions, particularly those dependent on light energy, e.g. photosynthetic and enzyme activities.

In an endeavour to reduce deleterious effects of excessive vegetative growth, many studies have focused on partial defoliation (May *et al.*, 1969; Kliewer, 1970; Peterson & Smart, 1975; Kliewer & Bledsoe, 1987; Koblet, 1987; Williams *et al.*, 1987; Bledsoe *et al.*, 1988). However, they mainly dealt with above-ground performance, whereas effects on the root system were ignored. Vegetative growth and yield were adversely affected when partial defoliation was imposed from early developmental stages (bud break and berry set), whereas defoliation from later stages (pea size and véraison) had no effect on, or even increased yields (Hunter & Visser, 1990a, 1990b). Partial defoliation improved canopy microclimate and photosynthetic activity significantly and increased total photosynthetic activity to values similar to or even higher than those of non-defoliated vines (Hunter & Visser, 1988a, 1988b, 1989). In spite of this, the possibility still exists that mobilization of reserves could have played an important role in performances of partially defoliated vines (Kliewer, 1970; Hunter *et al.*, 1990). Mansfield & Howell (1981) found that sugar accumulation in the fruit can be derived directly from photosynthesis or mobilized from stored carbohydrate reserves in roots, canes and trunks. Kliewer & Antcliff (1970) found that up to 40 % of the total sugar in fruits of grapevines may come from storage parts (roots, trunk, arms, canes).

A positive relationship between subterranean and aerial growth was found for grapevines (Van Zyl & Van Huyssteen, 1980; Saayman, 1982; Archer *et al.*, 1988; Swanepoel & Southey, 1989). Root density and number of fine roots made a significant contribution to yield (Swanepoel & Southey, 1989). Comprehensive studies on the effect of partial defoliation on root growth of grapevines were conducted with rooted cuttings grown in pots (Buttrose, 1966; Kliewer & Fuller, 1973). Scholefield *et al.* (1978) studied the effect of defoliation at harvest on carbohydrate reserves in roots of field-grown Sultana vines. However, the effect of long-term partial defoliation from different developmental stages of the vine on root development and distribution under field conditions, has as yet not been studied.

Wareing *et al.* (1968) found that partial removal of *Zea mays* roots prevented the increase in photosynthetic rate in response to partial defoliation. This was attributed to a reduced demand for photosynthates and a reduction in the supply of cytokinins by roots to leaves. Therefore, if the root system is reduced by long-term severe defoliation, the stimulatory effect of partial defoliation on photosynthesis may be lost with time. Since Buttrose (1966) reported that the roots of grapevines were the most affected by partial defoliation, the effect of severe partial defoliation (as applied annually during canopy management practices) on root systems must be taken into account. Consequently, the effect was determined of partial defoliation from different developmental stages of the vine on root development and distribution of *Vitis vinifera* L. cv. Cabernet Sauvignon.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon (clone CS 46) vineyard, grafted onto rootstock 99 Richter (clone RY 30), situated at Nietvoorbij experimental farm near Stellenbosch in the Western Cape, was used. Vines were planted (3,0 x 1,5 m spacing) on a Glenrosa soil (Series 13, Kanonkop) (MacVicar *et al.*, 1977) and trained onto a 1,5 m slanting trellis as described by Zeeman (1981). Rainfall was supplemented by sprinkler irrigation according to A pan evaporation figures on a weekly basis.

2.2 Experimental design

The experiment was laid out as a completely randomized design, comprising a control treatment (0 % defoliation) and 33 % defoliation treatments implemented from four developmental stages : Approximately one month after bud break, berry set, pea size and véraison. These defoliations were applied over the whole vine during four consecutive growth seasons. Three uniform, healthy vines (replications) per treatment were randomly selected.

2.3 Defoliation treatments

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

2.4 Soil characteristics

The soil was double delved in two directions to a depth of 800 mm prior to planting of the vines. Chemical characteristics, clay, silt and sand contents, bulk density and water content were determined according to standard VORI methods in four soil layers, i.e. 0-300 mm; 300-600 mm; 600-900 mm and 900-1200 mm. The occurrence of important soil-borne pests, i.e. phylloxera, margarodes and nematodes was determined according to methods described by De Klerk (1970, 1978) and Loubser (1985).

2.5 Root study

A profile wall method proposed by Böhm (1979) was used to plot the roots. A trench of approximately 1,4 m deep was dug parallel to the vine row and 300 mm from the vine trunk. After careful exposure of roots a 200 mm x 200 mm grid system, 1,2 m high and 1,6 m wide was set up against the profile wall. Roots were plotted in five root diameter classes, i.e. < 0,5 mm; 0,5-2 mm; 2-5 mm; 5-10 mm and > 10 mm (Southey & Archer, 1988).

2.6 Statistical analyses

A one-way analysis of variance (standard VORI statistical software package) was performed on the raw data, comprising five treatments and three replications. Statistical analyses for the determination of significant differences between treatment means were carried out using Scott-Knott and Students t-LSD tests.

3. RESULTS AND DISCUSSION

3.1 Soil characteristics

Physical and chemical characteristics of the soil are shown in Table 8.1. Except for coarse silt, clay and silt contents of the soil increased with depth, while the sand content decreased. Although soil pH was lower than the recommended (Conradie, 1983), 99 Richter is tolerant to soil acidity and root growth would, therefore, not have been impeded. Soil pH, resistance and P, K and Ca contents decreased, whereas Mg and water content increased with increasing depth. Bulk density was unaffected by soil depth.

TABLE 8.1 Analytical data of the Glenrosa soil (Series 13, Kanonkop) at Nietvoorbij, Stellenbosch

Depth (mm)	Clay (%)	Fine silt (%)	Coarse silt (%)	Fine Silt & clay (%)	Coarse sand (%)	Medium sand (%)	Fine sand (%)	Very fine sand (%)	Total sand (%)	pH (KCl)	Resistance (ohm)	P (mg/kg)	K (mg/kg)	Exchangeable cation (me %)		Water (%)	Bulk density (g/cm^3)
														Ca	Mg		
0 - 300	15,86	14,18	9,79	30,04	8,46	11,39	23,22	17,63	60,70	4,8	1600	10,25	55,00	1,67	0,79	4,30	1,57
300 - 600	20,36	16,10	9,32	36,46	7,14	10,36	20,88	15,53	53,92	4,6	1388	2,20	29,80	1,01	1,00	6,68	1,63
600 - 900	23,71	18,44	8,06	42,16	6,69	9,60	18,40	13,68	48,38	4,5	1270	0,69	10,00	0,72	1,33	8,21	1,59
900 - 1200	-	-	-	-	-	-	-	-	-	4,4	954	1,10	5,50	0,28	1,75	10,56	1,61

Low numbers of phylloxera were present, while margarodes were absent. However, rootstock 99 Richter is resistant to phylloxera (Loubser *et al.*, 1987). Low numbers of less important nematode species were present and therefore any pronounced effect on the root system was unlikely. Since vines appeared perfectly healthy, the presence of phytophthora cinnamomi was unlikely (J.H.S. Ferreira - personal communication, 1989).

3.2 Root density

Root density was significantly stimulated by partial defoliation, increasing the later defoliation was commenced (Fig. 8.1). This suggests a more effective utilization of soil and water by partially defoliated vines. Yield and cane mass following partial defoliation coincided with root densities, decreasing with less dense root distributions (Fig. 8.2). This is in agreement with findings of Swanepoel & Southey (1989) for various rootstocks. Therefore, considering yield and cane mass of partially defoliated vines in comparison to those of non-defoliated vines, higher root densities were to be expected for the latter vines. However, it is possible that stress conditions as created by the severe reduction in source size of partially defoliated vines, induced a closer relationship between aerial and subterranean growth. It is also possible that excessive vegetative growth, particularly with leaves functioning below their photosynthetic capacity, as was found by Hunter & Visser (1988a, 1988b, 1989), may have masked the sensitivity of the root system to above-ground performance. On the other hand, with all plant parts functioning at maximum levels, tolerance to changes is lower, resulting in higher sensitivities and therefore closer relationships between parts.

3.3 Root size

Partial defoliation stimulated the development of roots of fine to medium diameter (< 0,5 to 5 mm) (Fig. 8.3). However, an apparent decrease in thick root development occurred. This was also evident from the root distribution examples (Figs. 8.4 & 8.5). Partial defoliation from early developmental stages (bud break, berry set) reduced root development compared to later defoliations. The increase in development of thin roots implies a more efficient utilization of soil and available water, whereas the decrease in development of thick roots may have impeded the regenerative ability (Van Zyl & Van Huyssteen, 1986) and carbohydrate storage potential of the root system. Buttrose (1966) and Kliewer & Fuller (1973) found that total root dry mass of respectively Muscat of Alexandria and Thompson Seedless pot-grown grapevines was severely affected by reductions in leaf area. Considering effects on the development of thick roots, these findings might not be different to those of the former workers, albeit total root mass was not determined. However, the effectiveness of root systems may be misrepresented if only dry mass is taken into account.

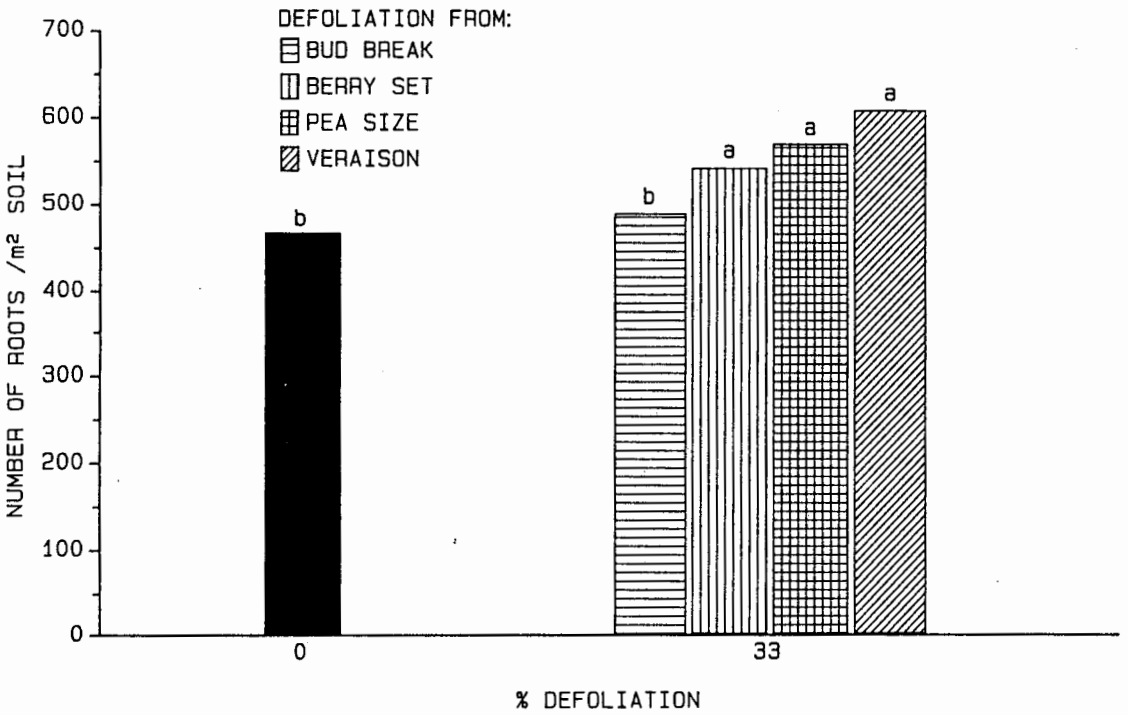

Fig. 8.1 **The effect of defoliation from different developmental stages of the vine on root density. Values designated by the same letter do not differ significantly ($p \leq 0,05$).**

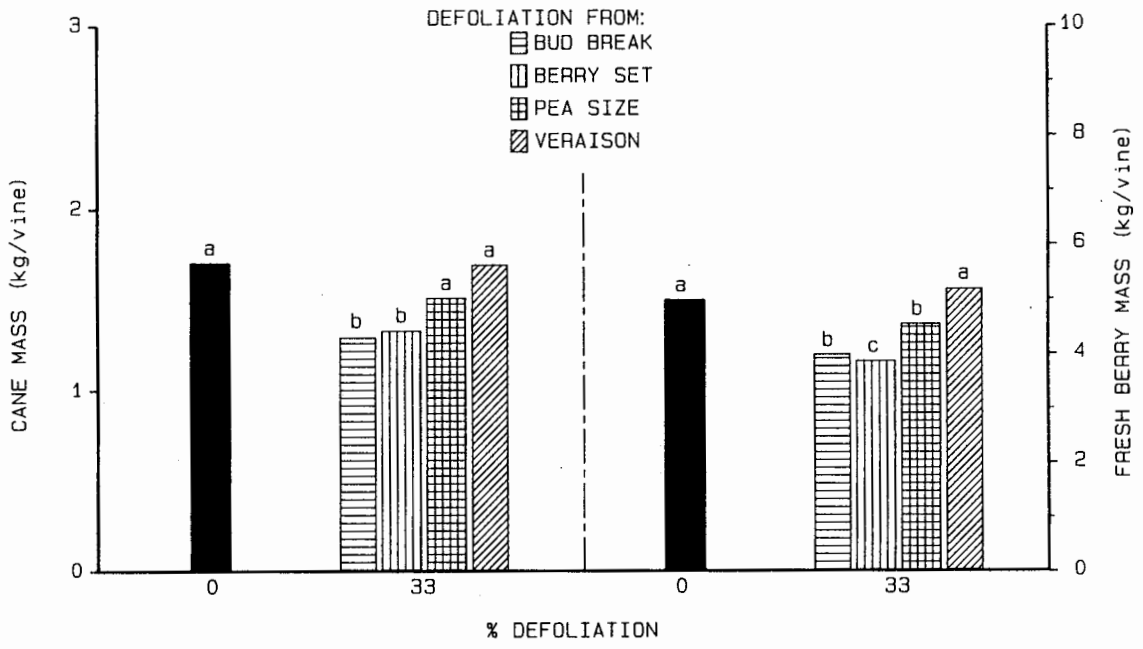

Fig. 8.2 **The effect of defoliation from different developmental stages of the vine on cane mass and fresh berry mass. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.**

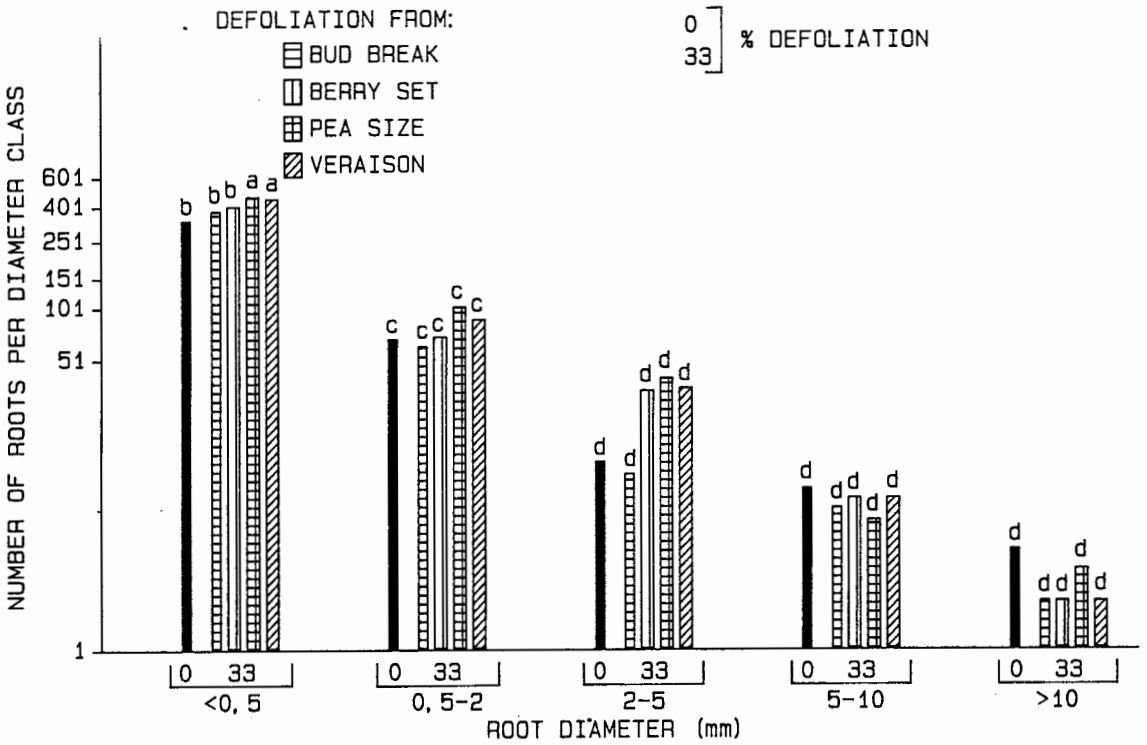

Fig. 8.3 **The effect of defoliation from different developmental stages of the vine on the number of roots per diameter class. Values designated by the same letter do not differ significantly ($p \leq 0,05$) (Note log scale on y-axis).**

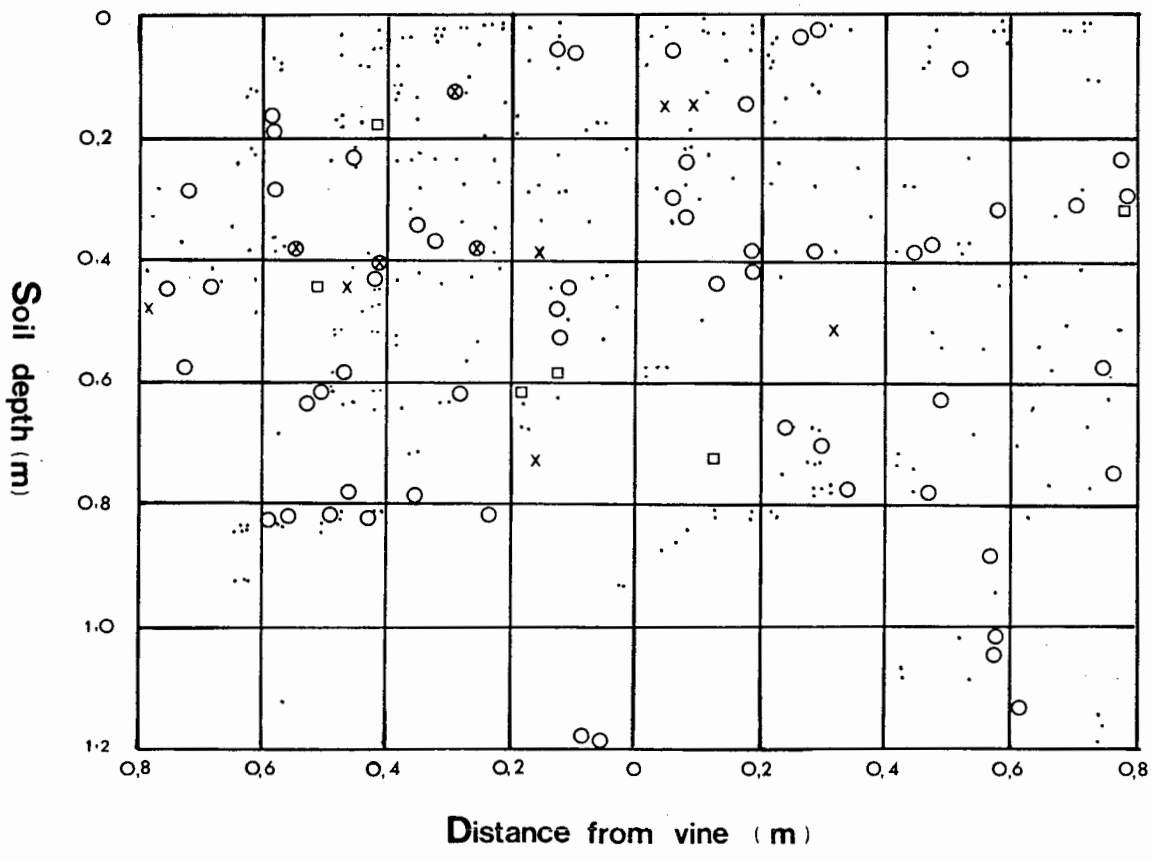

Fig. 8.4 **Root distribution of non-defoliated vines. · < 0,5 mm, ○ = 0,5-2 mm, X = 2-5 mm, □ = 5-10 mm, ⊗ > 10 mm.**

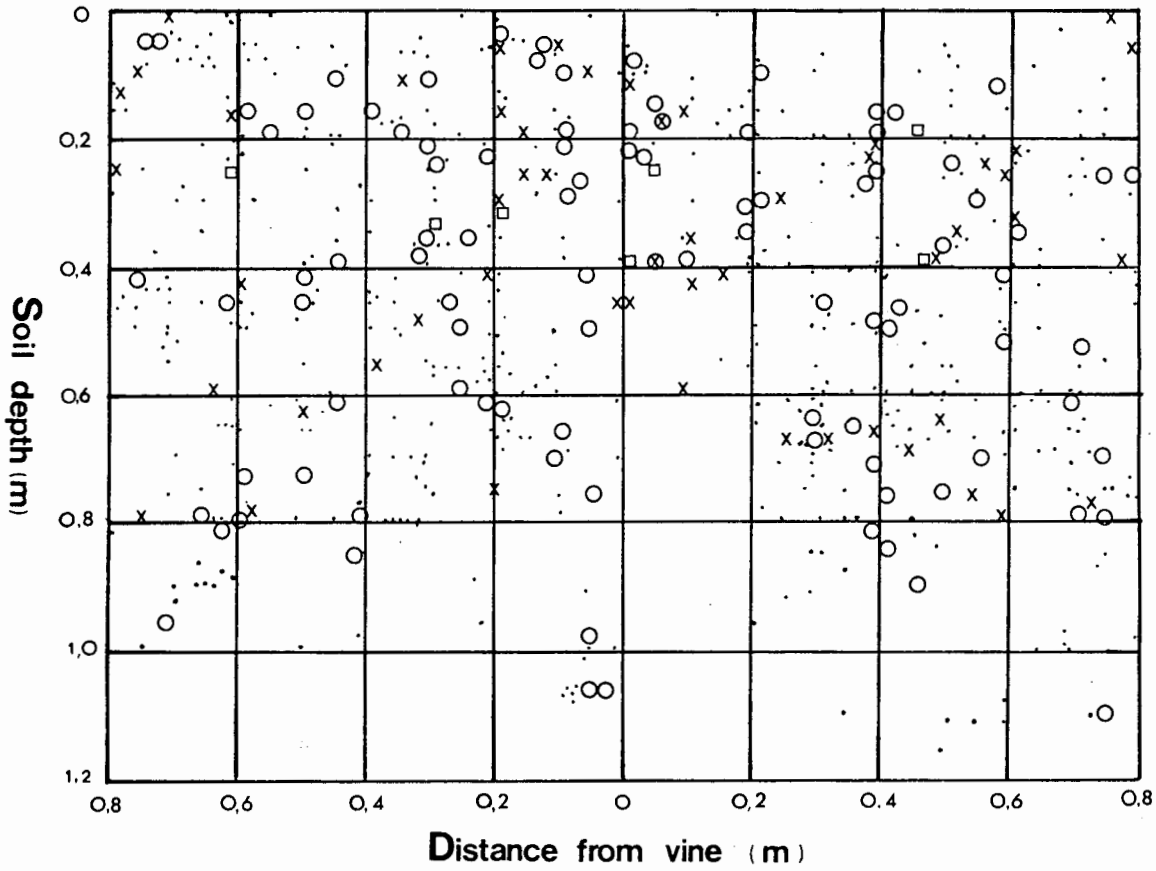

Fig. 8.5 Root distribution of 33 % defoliated vines. · < 0,5 mm, ○ = 0,5-2 mm, X = 2-5 mm, □ = 5-10 mm, ⊗ > 10 mm.

Given the lower source:sink ratios of partially defoliated vines, their root activity probably also increased. According to Maggs (1964) the root system had practically unlimited capacity to vary its own growth rate by initiating new roots according to different growing conditions, in order to maintain homeostatic mechanisms in the plant. Since fine and thin roots have higher absorptive abilities than thick roots, this was probably one of the main factors contributing to the good performances of partially defoliated vines in spite of the severity of defoliation. It therefore appeared that partially defoliated vines responded to the loss of leaves by forming new roots, creating a more efficient root system. Therefore, though reserves may have been used to support vegetative and reproductive growth of these vines during the growth season, the depletion thereof was seemingly efficiently neutralized. Although partial defoliation was conducted during four consecutive growth seasons, it is possible that long-term severe partial defoliation may deplete vines to such an extent that the development of thick roots and, consequently, fine roots, is restricted. This may result in a deterioration of vines in the long run.

3.4 Root distribution

The available horizontal soil volume was colonized completely by vines of all treatments, as is evident from the root distribution patterns (Figs. 8.4 & 8.5). Therefore, only the vertical distribution of roots is discussed.

Generally, partially defoliated vines demonstrated higher total root numbers in all soil layers, although the differences were not significant (Fig. 8.6). The distribution of fine roots followed the same pattern (Fig. 8.7). Roots of both partially and non-defoliated vines were mainly located in 0 to 800 mm zones, whereas deeper layers contained considerably less roots. This was also demonstrated by the root distribution patterns (Figs. 8.4 & 8.5). High root numbers in the top layer (0-200 mm) probably resulted from regular irrigation. Nevertheless, the distribution pattern is in agreement with findings of Van Zyl (1984), Loubser & Meyer (1986) and Swanepoel & Southey (1989). Considering the generally larger amounts of fine roots in particular, in all soil layers for partially defoliated vines, it is evident that their nutrient absorption capacity and therefore utilization of soil, was more efficient.

4. CONCLUSIONS

Partial defoliation stimulated root density, increasing with later defoliations. Root densities of partially defoliated vines followed a similar pattern to that of yield and cane mass. A similar relationship could, however, not be found for non-defoliated vines. It is therefore possible that excessive vegetative growth, particularly leaf area, impeded this relationship.

Partial defoliation stimulated the development of roots in the fine to medium diameter classes, but failed to do so for thick roots. On the contrary, the development of thick roots tended to decrease. Considering all root sizes, it would appear that 33 % defoliation from pea size created the most effective root system. Defoliation from just after bud break and from berry set reduced root development, compared to later defoliations, suggesting that long-term severe defoliation may cause deterioration of the root system and reduced vine performance. Annual severe defoliation from these stages is therefore not recommended. As fine to medium roots are mainly responsible for uptake of nutrients, it is evident that the mere determination of total root mass, as often occurs, may misrepresent the effectiveness of root systems.

Although not significant, partially defoliated vines generally had higher total root numbers in every soil layer. The preferential root zone of all vines was 0 to 800 mm. The higher numbers of fine roots for particularly partially defoliated vines suggest an increased nutrient absorption capacity and therefore a more efficient utilization of soil. It therefore seemed that partially defoliated vines compensated for the loss of leaf area by forming new roots. Together with the higher photosynthetic activities of leaves, as previously found, this provided an efficient mechanism for continued high performance.

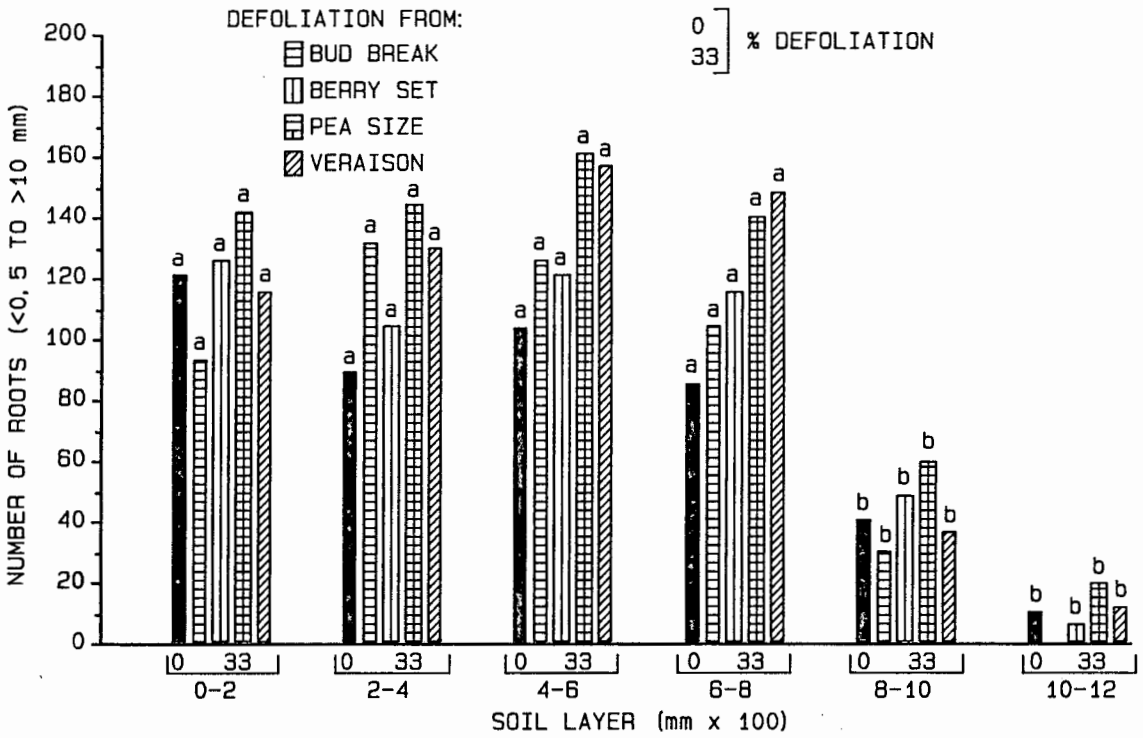

Fig. 8.6 **The effect of defoliation from different developmental stages of the vine on the number of roots in different soil layers. Values designated by the same letter do not differ significantly ($p \leq 0,05$).**

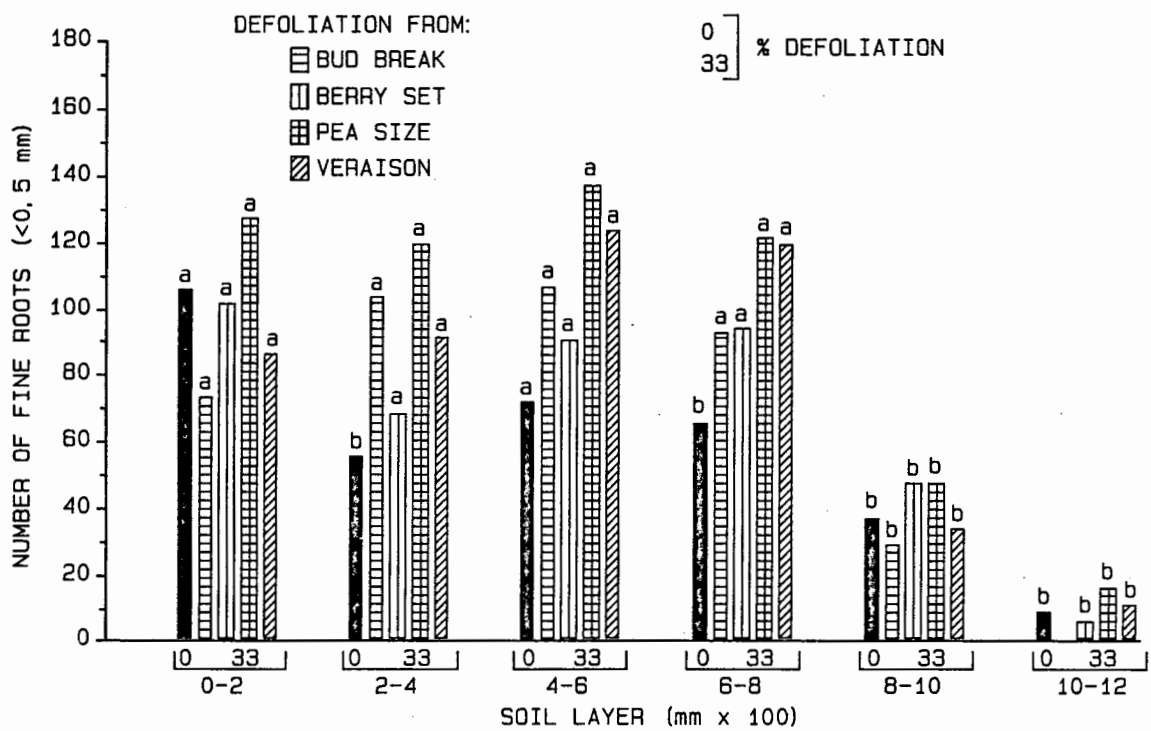

Fig. 8.7 **The effect of defoliation from different developmental stages of the vine on the number of fine roots in different soil layers. Values designated by the same letter do not differ significantly ($p \leq 0,05$).**

The reflection of the above-ground performance of partially defoliated vines in subterranean growth, supported findings that above-ground and subterranean growth are closely related. Since partial defoliation stimulated metabolic activity of the whole vine, it seemed that this relationship was more pronounced for these vines, suggesting a higher sensitivity to management practices. Severe canopy management practices and even annual canopy management practices must therefore be carried out with great care and awareness of potential dangers of mismanagement. This would ensure longevity and continued high productivity of vines.

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CHAPTER IX

Extraction and Determination of Sugars and Organic Acids by High Performance Liquid Chromatography

Key words : *Vitis vinifera*, Grapes, Sugars, Organic acids, HPLC.

ABSTRACT

A comparison of different extraction procedures for determination of sugars and organic acids in grapes is described.

Reliable recoveries during simultaneous extraction of sugars and organic acids were obtained. The procedure comprised extraction of freeze-dried berries with deionised water for 60 min. at room temperature, sample:solvent ratios of 1 g dry mass/50 cm^3 water up to véraison and 1 g dry mass/12,5 cm^3 water at ripeness, followed by adsorption on 2 cm^3 anion exchange resin. Good resolution and reproducibility were obtained during HPLC analyses. The mean recovery percentages of glucose, fructose, tartaric acid and malic acid were 105,10; 106,08; 99,33 %; and 99,00 %, respectively. To prevent deterioration of grapes and interconversions between compounds, the grapes should be freeze-dried and analysed as soon as possible.

SUBMITTED FOR PUBLICATION

Am. J. Enol. Vitic. (1990)

1. INTRODUCTION

Tartaric and malic acid are commonly found as major organic acids in grapes, while citric and other acids are present in smaller quantities (Kliewer, 1966; Ruffner, 1982a, 1982b). Glucose and fructose are the major sugars (Kliewer, 1966), while sucrose and other sugars occur in small quantities.

Grape samples are often frozen and stored for extended periods to facilitate analyses of sugars and acids at a more convenient time. Takeda *et al.* (1983) found no changes in percent soluble solids, percent titratable acidity, individual sugars and individual organic acids during storage of Muscadine grapes at 20°C, 4,5°C and 0°C for 24 days. However, according to Spayd *et al.* (1987) freezing of Chardonnay, Chenin blanc and White Riesling grapes at -12°C for 12-16h resulted in a significant decrease in percentage acidity and an increase in pH of the must and wine, while sugar concentration was not affected. Suresh *et al.* (1981) also found slightly lower acidity and higher pH of the must and wine from grapes stored at -10°C for one month. According to Amerine & Ough (1974) tartrates precipitate during frozen storage of grapes. The ideal situation would therefore be to store grape samples in a compact, easy to handle, non-perishable form. A convenient way to achieve this would be to freeze-dry the grapes, thus preventing the interaction of cell contents and ensuring long term storage capability. The samples may then be analysed at any convenient time.

In spite of this, freeze-drying of grapes prior to analyses and the extraction of sugars and acids at different developmental stages have seldom been done. Philip & Kuykendall (1973) freeze-dried berries in a study on the changes in °Balling, tartaric and malic acids during Thompson Seedless berry development. Saito & Kasai (1978) freeze-dried berries while studying the fate of ^{14}C-labelled substrates fed into Delaware grapes. Freeze-dried berries were extracted with water in the first case, while in the latter case 80 % ethanol, H_2O, hot H_2O, and a hot EDTA solution were used successively. A method development for each developmental stage is, however, lacking.

Some investigators extracted fresh grapes with water (Johnson & Nagel, l976; Mattick, 1983; Takeda *et al.*, l983), while others used various ethanol concentrations, mostly higher than 70 % (Hardy, 1967; Saito & Kasai, 1968; Hawker *et al.*, 1976; Niimi & Torikata 1978; Selvaraj *et al.*, 1978). These extractions were mostly done at room temperature. In this study preliminary results, however, indicated that high ethanol concentrations were not effective for the extraction of sugars and acids, especially tartaric acid, from freeze-dried

berries. Saito & Kasai (1968) found that most of the tartaric acid in grapes occurs in the salt form and is therefore insoluble in 80 % ethanol.

High performance liquid chromatography (HPLC) procedures are used for both separate or simultaneous determination of most sugars (Takeda *et al.*, 1983; Pfeiffer & Radler, 1985; Sepúlveda & Kliewer, 1986) and organic acids (Takeda *et al.*, 1983; McCord *et al.*, 1984; Mentasti *et al.*, 1985; Pfeiffer & Radler, 1985; Frayne, 1986; Polo *et al.*, 1986; Schneider *et al.*, 1987). The speed, sensitivity and selective resolution of these techniques (Dwyer & Brown, 1987) render them very useful for the analyses of sugars and organic acids in grape musts and wines. Except for filtration during sample preparation, some investigators analysed samples on HPLC columns without prior separation of compounds of different ionic character (Takeda *et al.*, 1983; Pfeiffer & Radler, 1985; Frayne, 1986; Schneider *et al.*, 1987) and therefore ran the risk of column contamination and interference by impurities. Others made effective use of ion exchange resins to separate must and wine samples into neutral and acidic fractions before application to analytical columns (McCord *et al.*, 1984; Polo *et al.*, 1986; Sepúlveda & Kliewer, 1986). The high cost of analytical columns necessitates a thorough cleaning of samples prior to analyses and the use of specific columns for sugar and acid analyses.

The purpose of this investigation was to develop an easy and reliable procedure for the preparation, extraction and quantitative determination of sugars and organic acids in grapes at different developmental stages of the vine.

2. MATERIALS AND METHODS

2.1 Plant material

Grapes (*Vitis vinifera* L. cv. Cabernet Sauvignon) were harvested at four developmental stages, namely at berry set, pea size, véraison and ripeness [see Hunter & Visser (1988) for details of berry sizes and maturity level]. Véraison in this study refers to full colour break, which is later than physiological véraison, i.e. maximum acid concentration and the start of sugar accumulation. All analyses were done on freeze-dried berries. For the comparison of storage methods a composite sample of berries were divided into three lots. One lot was analysed immediately after harvest, the second frozen at -20°C for one month, and the third frozen at -20°C just prior to freeze-drying with a Chriss freeze-drying unit.

Freeze-dried berries were ground in a Sorvall Omni-mixer and stored at room temperature until required for analyses. Dry, full ripe berries, which were inclined to stickiness because of their high sugar content, were stored in a desiccator containing silica gel. Representative samples from a composite sample at each developmental stage were used for the determination of sugars and organic acids.

2.2 Ion exchange chromatography

An intermediate base anion exchange resin, Bio-Rex 5 (Bio-Rad Laboratories), in the chloride form, was used. The wet mesh designation was 200-325 and the total capacity 2,8 meq/cm^3 resin bed. The resin was hydrated prior to usage.

A 30 cm long 10 cm^3 burette was stoppered with glass wool just above the tap and filled with either 2 cm^3 or 3 cm^3 resin. The packed column was washed with approximately five bed volumes deionised water. Water was deionised by distillation and passing through Elgacan (Elga Ltd) and Norganic (Millipore Co) filtering cartridges. Prior to sample application the water was drained to just above the resin bed.

2.3 Standard solutions

Two external standard solutions were prepared in water. One contained 10 g/dm^3 each of sucrose, glucose and fructose, while the other contained 1 g/dm^3 oxalic acid, 2 g/dm^3 citric, tartaric, malic, succinic, lactic and acetic acid and 0,04 g/dm^3 fumaric acid. Both solutions were membrane filtered (0,45 μm) and stored at -4°C.

2.4 Extraction procedure

Fresh berries were macerated (no water added) at room temperature by means of an IKA Ultra-Turrax macerator (model T25) operating at 20 500 rpm for 60 s. The extraction of freeze-dried, ground berries was performed at room temperature by means of a shaker (New Brunswick Scientific Co) operating at 250 rpm for 60 min. Soluble sugars and organic acids were simultaneously extracted with either deionised water or different ethanol/water mixtures. The solvent volumes used per 1 g dried material were : 12,5; 25; 50 cm^3 and 75 cm^3. The ethanol/water (v/v) mixtures used were 5, 10, 20, 30, 50, 70 % and 80 %. Recovery percentages were determined by combining equal volumes of double strength sugar and acid standard solutions and using the resultant solution to extract sugars and acids from the dry samples.

2.5 Sample preparation

After extraction (freeze-dried berries) or maceration (fresh and frozen berries), the samples were immediately vacuum-filtered through 0,45 /um membranes (Millipore Co). A 5 cm^3 aliquot was pipetted onto the Bio-Rex 5 resin bed and allowed to run through freely, followed by deionised water to a final volume of 25 cm^3. This eluate contained the soluble sugars, while the organic acids were retained on the column. The organic acids were desorbed from the resin with 5 cm^3 10 % (v/v) H_2SO_4, followed by deionised water to a final volume of 25 cm^3. Phenolic and lipophilic compounds were removed from both eluates by gentle forcing through Sep-pak C_{18} cartridges (Millipore Co) using a syringe. The cartridges were activated with 5 cm^3 methanol followed by 5 cm^3 deionised water prior to use. The neutral and acidic fractions were stored at -4°C until used.

2.6 High performance liquid chromatography

Sugars and organic acids were analysed using a Varian 5000 liquid chromatograph equipped with a 10 /ul injection loop.

For sugar analysis the chromatograph was equipped with a Waters R401 differential refractometer and 100 mV Varian model 9176 recorder. A Sugar-Pak I column (300 X 6,5 mm) in Ca^{++} form (Waters Associates) was used. The column was operated at 85°C and the samples eluted with deionised water containing 15 mg/dm^3 CaEDTA. The mobile phase was freshly prepared immediately before use. The flow rate was 0,5 cm^3/min. and eluted compounds were detected at an attenuation of 8.

For organic acid analysis the chromatograph was equipped with a Varian UV-50 detector and 10 mV Varian model 9176 recorder. An Aminex HPX-87H^+ organic acid column (300 X 7,8 mm) with a cation H^+ micro-guard column cartridge (40 X 4,6 mm) (Bio-Rad Laboratories) was used. The column was operated at 65°C and the samples eluted with 0,0089 M H_3PO_4 at a flow rate of 0,5 cm^3/min. The same mobile phase was not used for more than 2 days. Eluted compounds were detected at 210 nm (band width = 8 nm; absorbance range = 0,2).

Both mobile phases were filtered through 0,22 /um membranes (Millipore Co) and degassed in a Bransonic 321 ultrasonic water bath prior to use.

A Vista 401 chromatography data system was used to integrate peak areas according to the external standard solution calibrations.

2.7 Enzymatic analyses

Glucose, fructose and malic acid were enzymatically analysed using the methods of Boehringer Mannheim GmbH (1980).

2.8 Calculations

Results obtained with the freeze-dried grapes represent the mean of at least three separate extractions, each extract being analyzed two or three times. However, the comparisons between the sugar and acid contents of the fresh, frozen and dried berries represent the mean of nine separate extractions. The results obtained by the enzymatic methods represent the mean of five separate extractions and determinations for each developmental stage. The recovery percentages of the HPLC results were calculated using the following formula :

$(A - B)/C \times 100,$

where A = concentration of sample + standard solution,
B = concentration of sample only, and
C = concentration of standard solution.

2.9 Statistical analyses

Depending on the parameter, a one-way analysis of variance or two-way analysis of variance (standard VORI statistical software packages) was performed on the raw data. Statistical analyses for the determination of significant differences between treatment means were conducted using a Scott-Knott analysis.

3. RESULTS AND DISCUSSION

3.1 Standard solution analysis

Typical chromatograms of two standard solutions containing three sugars and eight organic acids respectively, are depicted in Figs. 9.1 and 9.2. A good resolution was obtained for both analyses. The sugars eluted from the column in less than 12 min. and organic acids in less than 18 min.

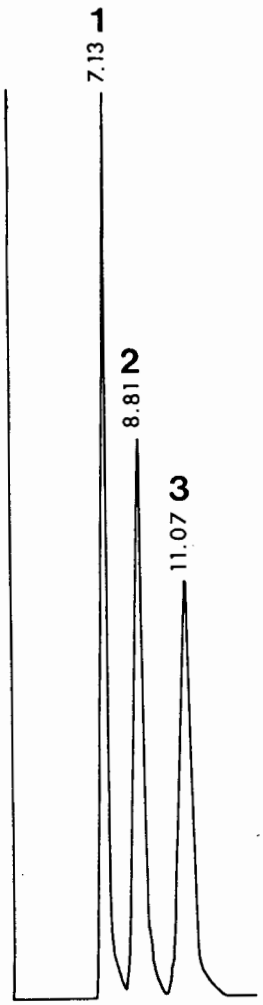

Fig 9.1 Chromatogram of a standard sugar solution (1 = sucrose; 2 = glucose; 3 = fructose). Retention times are given in minutes at each peak.

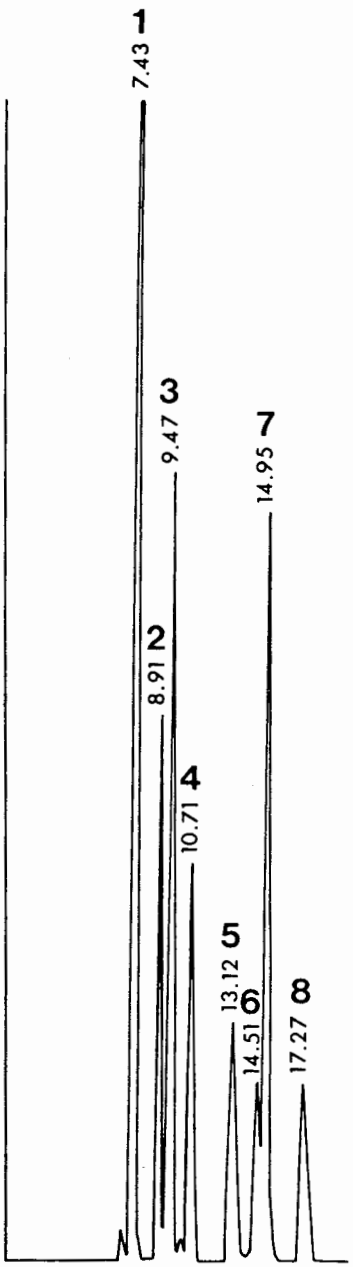

Fig 9.2 Chromatogram of a standard organic acid solution (1 = oxalic acid; 2 = citric acid; 3 = tartaric acid; 4 = malic acid; 5 = succinic acid; 6 = lactic acid; 7 = fumaric acid; 8 = acetic acid). Retention times are given in minutes at each peak.

3.2 Sample analysis

Figure 9.3 illustrates typical chromatograms of sugars from freeze-dried grape samples at véraison and at ripeness. No glucose and fructose were found in the berries at berry set and pea size stages. Figure 9.4 represents typical chromatograms of organic acids from freeze-dried grape samples at berry set, pea size, véraison and ripeness stages. Tartaric

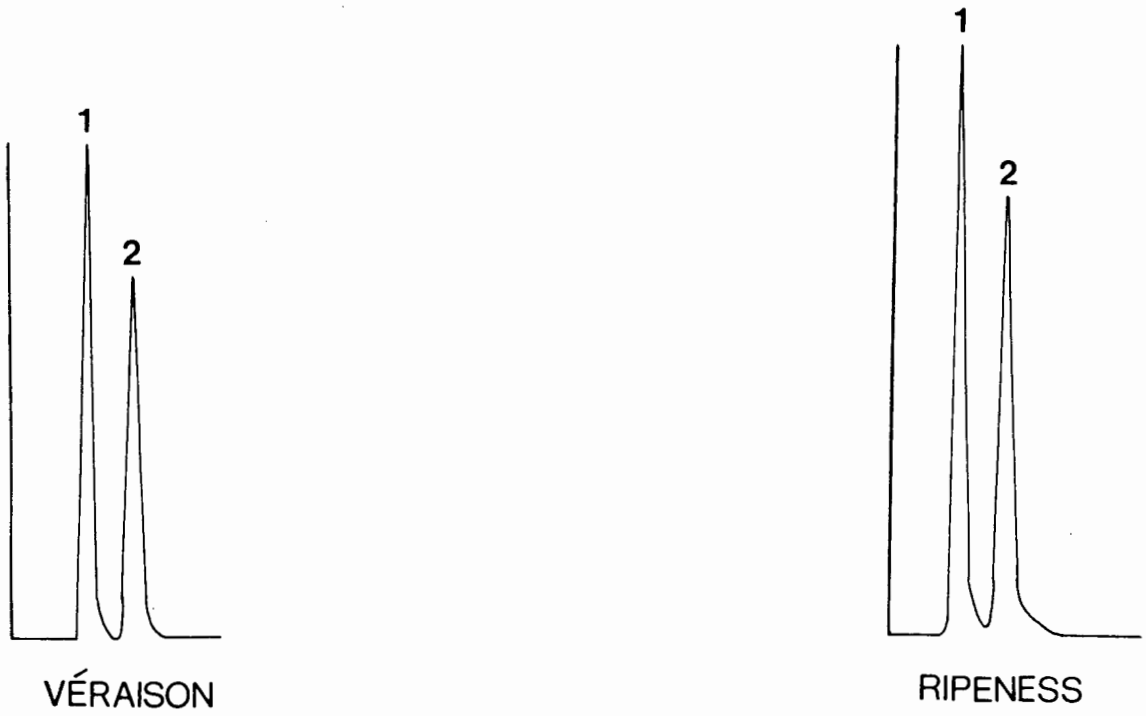

Fig 9.3 **Chromatograms of sugars in freeze-dried grape samples at véraison and at ripeness (1 = glucose; 2 = fructose).**

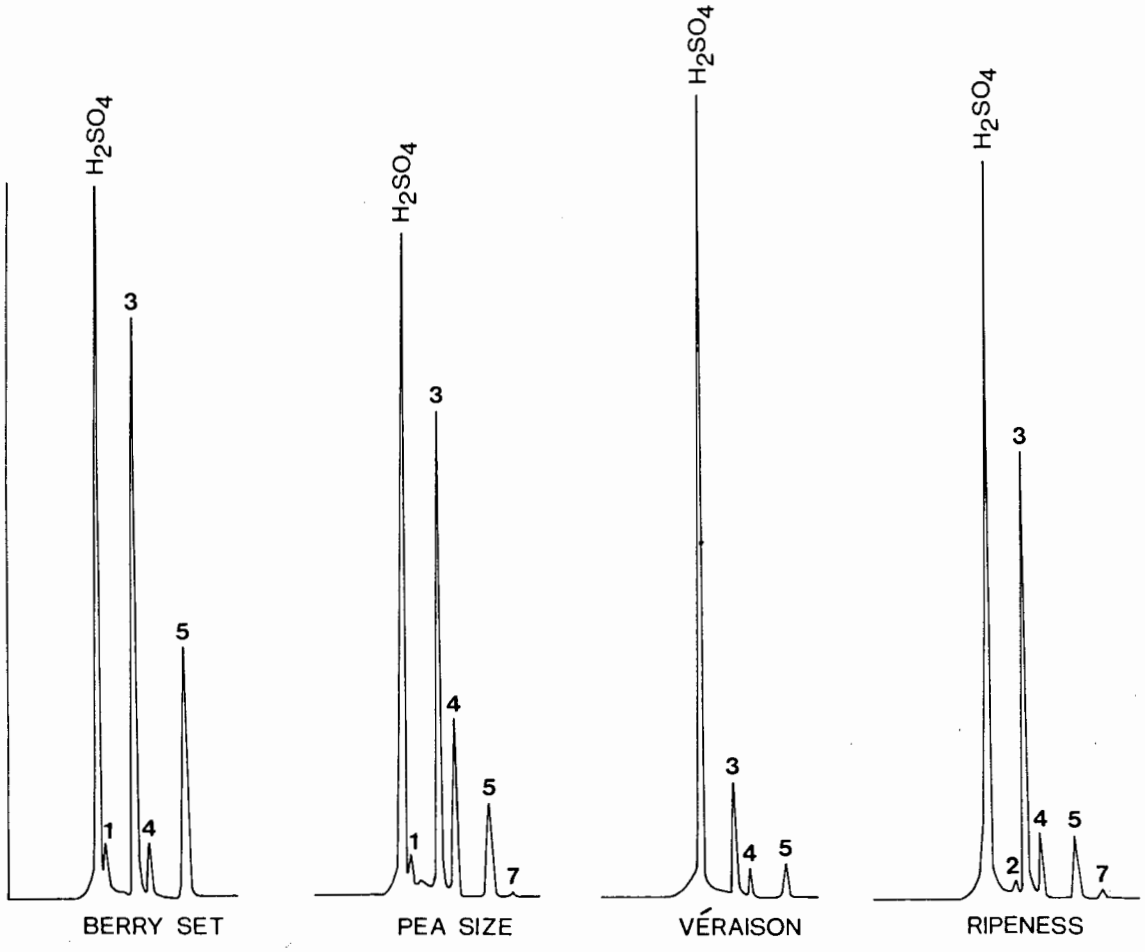

Fig 9.4 **Chromatograms of organic acids in freeze-dried grape samples at different developmental stages (1 = oxalic acid; 2 = citric acid; 3 = tartaric acid; 4 = malic acid; 5 = succinic acid/shikimic acid; 7 = fumaric acid).**

and malic acids were the major acids, while oxalic, citric, fumaric and acetic acid occurred either irregularly or only in trace amounts. Since succinic acid was present in much higher concentrations than that reported by Amerine & Ough (1974), co-elution with another compound, possibly shikimic acid (Frayne, 1986; Schneider *et al.*, 1987), might have occurred. This was confirmed during an analysis of shikimic acid, which revealed very strong absorption and probably masked the succinic acid peak.

3.3 Extraction period

Preliminary investigations proved extraction periods of 15, 30 or 60 min. as equally effective for the extraction of organic acids up to pea size stage. However, the 60 min. extraction was approximately 7 % more effective than the 30 min. extraction from véraison to ripeness. A subsequent 30 min. extraction of the same residue provided less than 4 % of the acid concentration found with the first 30 or 60 min. extraction. A 30 min. or 60 min. extraction period was equally effective for the recovery of sugars at either of the developmental stages. A 15 min. extraction period resulted in obtaining approximately 11 % less glucose and 6 % less fructose.

3.4 Effect of extracting solvent

Though low ethanol concentrations (up to 20 %) were equally effective than deionised water for the extraction of glucose and fructose over both developmental stages, high ethanol concentrations significantly decreased extractability (Table 9.1). Tartaric acid recovery was conspicuously decreased by high ethanol concentrations, while malic acid recovery was apparently not affected (Table 9.2). Samples were therefore extracted with water in subsequent experiments.

Due to differences in methods used, maturity, cultivar and region, it was difficult to compare these results with those of other investigators. The glucose and fructose concentrations were, however, comparable to those found by Kliewer (1967a) with enzymatic and colorimetric procedures as well as to those found by Frayne (1986) using HPLC. The tartaric and malic acid concentrations at ripeness were within the maximum levels reported by Amerine & Ough (1974) as well as comparable to results obtained by HPLC and enzymatic studies (Schneider *et al.*, 1987).

3.5 Effect of solvent:sample ratio

The effect of solvent:sample ratio (cm^3 H_2O/g dry berry mass) on the extraction of sugars and organic acids at different developmental stages is shown in Tables 9.3 and 9.4.

TABLE 9.1 The effect of ethanol in the solvent mixture on the extraction of glucose and fructose from freeze-dried berries at different developmental stages (mg/g dry mass)

Developmental stage	*Ethanol concentration (%)							
	0	5	10	20	30	50	70	80
	GLUCOSE							
Véraison	362,00^{a}	344,00^{a}	357,50^{a}	362,50^{a}	312,50^{a}	315,00^{a}	289,00^{a}	298,50^{a}
Ripeness	415,50^{a}	392,50^{a}	422,00^{a}	402,50^{a}	374,50^{a}	363,50^{a}	332,50^{a}	320,00^{a}
Mean	388,75^{A}	368,25^{A}	389,75^{A}	382,50^{A}	343,50^{B}	339,25^{B}	310,75^{C}	309,25^{C}
Cv (%)	4,94							
	FRUCTOSE							
Véraison	295,00^{a}	304,50^{a}	326,00^{a}	332,00^{a}	280,00^{a}	299,00^{a}	270,50^{a}	247,50^{a}
Ripeness	411,00^{a}	384,50^{a}	411,00^{a}	375,00^{a}	341,00^{a}	345,50^{a}	332,50^{a}	273,50^{a}
Mean	353,00^{A}	344,50^{A}	368,50^{A}	353,50^{A}	310,50^{B}	322,25^{B}	301,50^{B}	260,50^{C}
Cv (%)	6,87							

***1 g dry mass/50 cm^3 solution. Extraction period : 60 min.**
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each sugar.

Regarding the sugars, it is evident that concentrations over both developmental stages increased significantly with increased solvent:sample ratio (Table 9.3). The glucose concentration was higher than that of fructose at véraison, whereas the opposite tendency prevailed at ripeness. These results are in accordance with those found for different species and cultivars (Amerine, 1956; Kliewer, 1966, 1967a, 1967b).

Except for the lower recoveries for tartaric acid at berry set and pea size stages and malic acid at pea size stage in the case of the lowest solvent:sample ratio (12,5 cm^3), the organic acids were unaffected by higher solvent:sample ratios (Table 9.4). The lower concentrations obtained at the early stages probably resulted from the very high acid

TABLE 9.2 The effect of ethanol in the solvent mixture on the extraction of tartaric and malic acid from freeze-dried berries at different developmental stages (mg/g dry mass)

Developmental stage	*Ethanol concentration (%)							
	0	5	10	20	30	50	70	80
	TARTARIC ACID							
Berry set	157,00^{a}	156,50^{a}	154,50^{a}	151,50^{a}	126,00^{c}	65,50^{f}	68,50^{f}	57,00^{g}
Pea size	130,00^{c}	140,50^{b}	140,00^{b}	123,50^{c}	114,50^{d}	74,00^{e}	50,00^{g}	52,00^{g}
Véraison	38,50^{h}	36,50^{h}	36,00^{h}	36,50^{h}	33,00^{h}	14,50^{j}	1,00^{k}	1,00^{k}
Ripeness	27,00^{i}	30,00^{i}	28,00^{i}	24,50^{i}	23,50^{i}	14,50^{j}	3,00^{k}	2,00^{k}
Mean	88,13^{A}	90,88^{A}	89,63^{A}	84,00^{B}	74,25^{C}	42,13^{D}	30,63^{E}	28,00^{E}
Cv (%)	4,49							
	MALIC ACID							
Berry set	27,00^{d}	25,00^{d}	26,00^{d}	27,00^{d}	25,50^{d}	24,50^{d}	27,00^{d}	24,00^{d}
Pea size	111,50^{b}	115,00^{a}	117,00^{a}	104,00^{c}	108,00^{b}	102,50^{c}	98,50^{c}	111,00^{b}
Véraison	22,50^{d}	22,00^{d}	22,50^{d}	21,50^{d}	22,50^{d}	22,00^{d}	21,50^{d}	20,00^{d}
Ripeness	8,50^{e}	5,00^{e}	8,50^{e}	7,00^{e}	8,00^{e}	6,50^{e}	4,50^{e}	7,50^{e}
Mean	42,38^{A}	41,75^{A}	43,50^{A}	39,88^{B}	41,00^{A}	38,88^{B}	37,88^{B}	40,63^{A}
Cv (%)	6,77							

***1 g dry mass/50 cm^{3} solution. Extraction period : 60 min.**
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each acid.

TABLE 9.3 The effect of solvent:sample ratio on the extraction of glucose and fructose from freeze-dried berries at different developmental stages (mg/g dry mass)

Developmental stage	*Solvent:sample ratio (cm^3 H_2O/g dry mass)			
	12,5	25	50	75
	GLUCOSE			
Véraison	267,50[a]	283,00[a]	291,50[a]	302,50[a]
Ripeness	331,50[a]	335,50[a]	351,50[a]	366,00[a]
Mean	299,50[C]	309,25[C]	321,50[B]	334,25[A]
Cv (%)	2,17			
	FRUCTOSE			
Véraison	245,50[a]	264,00[a]	268,00[a]	298,50[a]
Ripeness	337,00[a]	341,00[a]	371,00[a]	371,00[a]
Mean	291,25[B]	302,50[B]	319,50[A]	334,75[A]
Cv (%)	3,19			

***Extraction period : 60 min.**
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each sugar.

concentrations in the berry. A sample:solvent ratio of 1g/50 cm^3 was therefore used up to véraison because a better resolution of the acids was found with this ratio. Although the sugar concentrations were slightly higher with the higher solvent:sample ratios (Table 9.4), the resolution of the acids at ripeness was improved with a lower solvent:sample ratio. A solvent:sample ratio of 1 g/12,5 cm^3 was therefore used for this stage.

Levels of tartaric acid decreased from berry set to pea size, whereas the reverse was true for malic acid. Both acids, however, reached their highest concentration during the rapid growth phase of the berry, which is in accordance with the results of Johnson & Nagel (1976).

TABLE 9.4 The effect of solvent:sample ratio on the extraction of specific organic acids from freeze-dried berries at different developmental stages (mg/g dry mass)

Developmental stage	*Solvent:sample ratio (cm^3 H_2O/g dry mass)				Mean
	12,5	25	50	75	
	TARTARIC ACID				
Berry set	134,50^{b}	153,50^{a}	158,00^{a}	153,50^{a}	149,88^{A}
Pea size	116,00^{c}	127,50^{b}	130,00^{b}	130,00^{b}	125,88^{B}
Véraison	36,00^{d}	36,00^{d}	35,00^{d}	35,50^{d}	35,63^{C}
Ripeness	27,50^{e}	29,50^{e}	29,00^{e}	28,50^{e}	28,63^{D}
Mean	78,50^{B}	86,63^{A}	88,00^{A}	86,88^{A}	
Cv (%)	4,05				
	MALIC ACID				
Berry set	28,00^{c}	28,00^{c}	28,50^{c}	26,00^{c}	27,63^{B}
Pea size	78,00^{b}	107,00^{a}	111,50^{a}	109,00^{a}	101,38^{A}
Véraison	21,50^{d}	21,50^{d}	21,00^{d}	21,50^{d}	$^{+}$21,38^{C}
Ripeness	9,00^{e}	9,00^{e}	8,50^{e}	7,50^{e}	8,50^{D}
Mean	34,13^{B}	41,38^{A}	42,38^{A}	41,00^{A}	
Cv (%)	4,73				

***Extraction period : 60 min.**

$^{+}$Malic acid should be the highest at this stage. Véraison is, however, taken as full colour break in South Africa, which is passed physiological véraison.

Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each acid.

The highest total concentration occurred at pea size. The malic acid concentration declined rapidly from véraison to ripeness, while tartaric acid decreased only slightly, eventually resulting in the concentration of the latter being more than three times that of malic acid. This is in agreement with the findings of Amerine (1956), Kliewer (1971) and Van Zyl (1984).

3.6 Effect of anion exchange resin

From Table 9.5 it is evident that the concentration of tartaric and malic acid were not significantly affected when using 2 or 3 cm^3 of resin. Two cm^3 of resin was adequate for adsorbing even the large amounts of organic acids at berry set and pea size stage. No acids were detected in neutral fractions and it was found that recovery of sugars from this fraction was unaffected by the amount of resin used (data not shown). Because of this, as well as reduced preparation time and cost per sample, 2 cm^3 resin was used in subsequent analyses.

TABLE 9.5 The effect of quantity of anion exchange resin on the concentration of organic acids obtained from freeze-dried berries at different developmental stages (mg/g dry mass)

Developmental stage	*Solvent:sample ratio (cm^3 H_2O/g dry mass)	Tartaric acid		Malic acid	
		2 cm^3	3 cm^3	2 cm^3	3 cm^3
Berry set	50	148,50[a]	153,00[a]	26,00[a]	25,50[a]
Pea size	50	121,50[a]	120,50[a]	90,00[a]	88,00[a]
Véraison	50	29,50[a]	36,50[a]	16,50[a]	18,00[a]
Ripeness	12,5	29,50[a]	28,00[a]	8,50[a]	8,00[a]
Mean		82,25[A]	84,50[A]	35,25[A]	34,88[A]
Cv (%)		4,13		6,68	

***Extraction period : 60 min.**
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each acid.

Although the use of anion exchange resin improved resolution (Fig. 9.5), analyses of sugars and acids prior to or after separation on the resin gave similar results. By using the HPLC method for acid-analysis, fructose could also be fully recovered when analysed prior to separation on the anion exchange resin (Fig. 9.5). However, the use of ion exchange resins to clean samples prior to analyses on analytical columns (McCord *et al.*, 1984), as well as the use of specific columns for sugar and acid analyses, can be strongly recommended to ensure a longer column life.

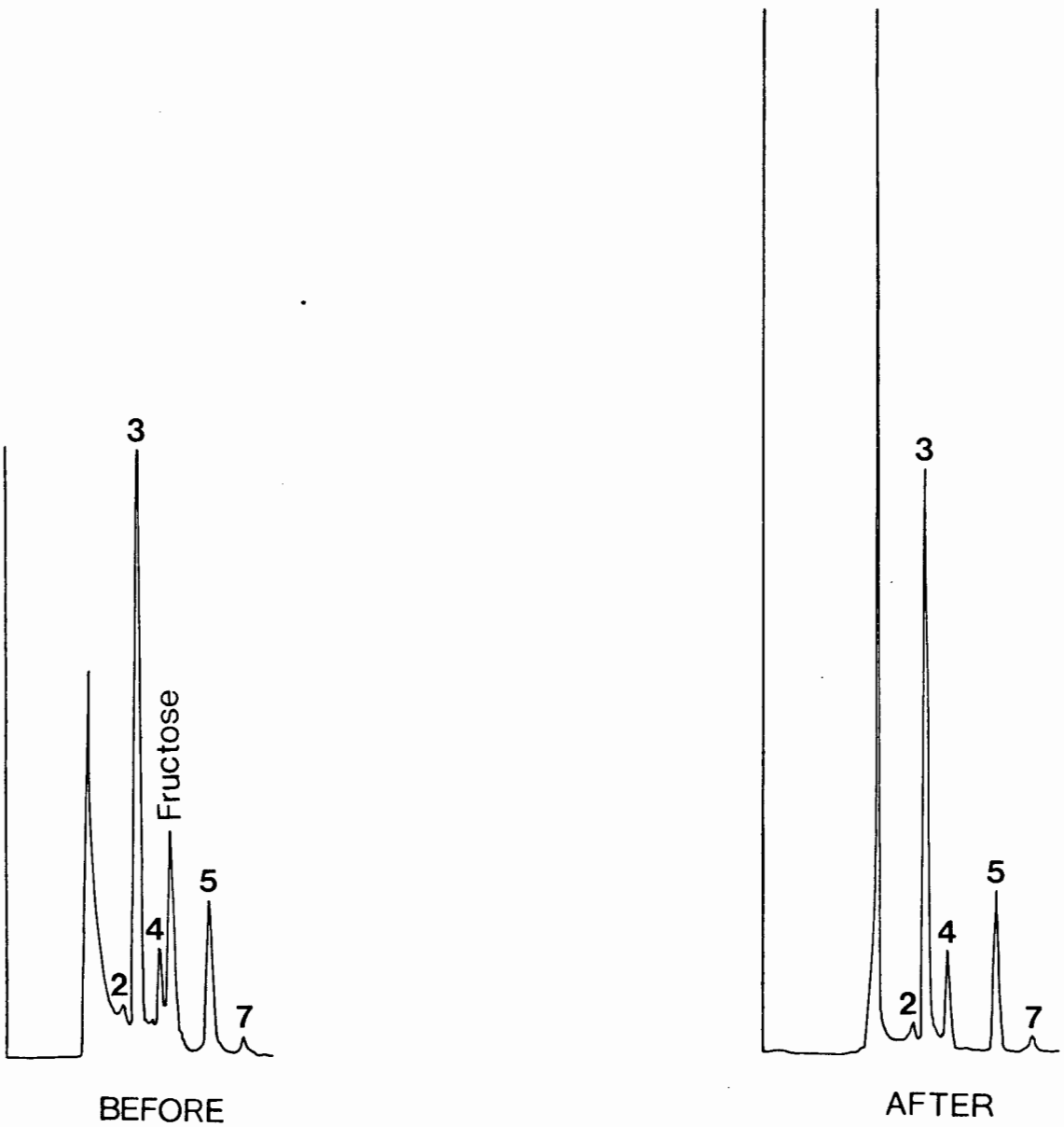

Fig 9.5 The effect of the anion exchange resin on the resolution of organic acids extracted from a freeze-dried grape sample at ripeness. Analyses were performed before and after separation on the anion resin (2 = citric acid; 3 = tartaric acid; 4 = malic acid; 5 = succinic acid/shikimic acid; 7 = fumaric acid).

3.7 Recovery percentages

The recovery percentages of the sugars and organic acids at different developmental stages are shown in Table 9.6. The mean recovery percentages of glucose and fructose and tartaric and malic acid were 105,10; 106,08; 99,33 % and 99,00 %, respectively.

3.8 Comparison of fresh, frozen and dry berry extraction

A comparison between glucose, fructose, malic acid and tartaric acid concentrations obtained during extraction from fresh, frozen and freeze-dried berries at ripeness, is depicted in Table 9.7. The glucose and fructose concentrations obtained during extraction of dried berries were significantly lower than that extracted from fresh berries, whereas the tartaric acid concentration was significantly higher. No differences in malic acid concentration were found between dried and fresh berries. The decreased sugar concentration found in freeze-dried berries probably resulted from the fact that enzymes may have remained active during freeze-drying, leading to possible interconversions (sugars ⇄ starch) (Smith, 1981). The decreased tartaric acid concentration found in fresh berries was probably due to the fact that not all of the tartrate dissolved when berries were crushed, because some tartrate salts, particularly potassium-bi-tartrate, are not completely soluble (Iland, 1987). According to Iland (1984) only about 55 % of the tartrate in the pulp is dissolved in the juice when berries are crushed. After storage of fresh berries for approximately one month at -20°C, the frozen berries had a glucose and fructose concentration of 20 % and 21 % respectively, lower than that obtained from fresh berries. Tartaric acid was reduced by 53 % and malic acid by 17 %. The deterioration of grapes during frozen storage can be attributed to natural breakdown and disruption of membrane structure. This may cause mixing of cell contents, resulting in oxidation, polimerization and precipitation of compounds. Precipitation of tartaric acid during freezing may probably be the main reason for the sharp decrease in its concentration. Long-term freezing of fresh grapes at -20°C prior to analyses is therefore not recommended.

3.9 Method of analysis

The HPLC results compared to those obtained by enzymatic methods are shown in Table 9.8. Although significantly higher in certain cases, the HPLC results were comparable to the enzymatic results, especially at ripeness.

TABLE 9.6 Recovery percentages of sugars and organic acids from freeze-dried berries at different developmental stages

Developmental stage	*Solvent:sample ratio (cm^3 H_2O/g dry mass)	Sugar		Organic acid	
		Glucose	Fructose	Tartaric	Malic
Berry set	50	N.D.	N.D.	100,48 ± 5,97	102,75 ± 1,36
Pea size	50	N.D	N.D.	104,71 ± 3,73	97,84 ± 1,38
Véraison	50	102,05 ± 7,00	101,15 ± 9,12	102,11 ± 3,69	100,42 ± 2,81
Ripeness	12,5	108,15 ± 1,63	111,00 ± 2,78	90,01 ± 5,66	95,00 ± 2,08
Mean		105,10	106,08	99,33	99,00

***Anion exchange resin quantity: 2 cm^3; Extraction period : 60 min.**
N.D. = Not detected.

TABLE 9.7. Comparison between sugar and organic acid concentrations (mg/g dry mass) obtained by HPLC after extraction of fresh, frozen and freeze-dried berries at ripeness stage

Berry condition	Glucose	Fructose	Tartaric acid	Malic acid
Fresh	380,89^{a}	386,33^{a}	23,22^{b}	8,56^{a}
Frozen	318,67^{b}	318,67^{b}	11,00^{c}	7,11^{b}
Freeze-dried	327,56^{b}	327,56^{b}	26,67^{a}	8,30^{a}
Cv(%)	9,91	9,62	7,98	11,70

Values designated by the same letter within columns do not differ significantly ($p \leq 0,05$).

TABLE 9.8 Comparison between glucose, fructose and malic acid concentrations obtained by HPLC methods and those obtained by enzymatic methods, expressed in mg/g dry berry mass

Developmental stage	Sugar/organic acid					
	Glucose		Fructose		Malic acid	
	HPLC	Enzym.	HPLC	Enzym.	HPLC	Enzym.
Berry set	N.D.	N.D.	N.D.	N.D.	55,80^{c}	48,00^{d}
Pea size	N.D.	N.D.	N.D.	N.D.	135,80^{a}	131,80^{b}
Véraison	323,40^{a}	310,40^{a}	302,20^{c}	261,60^{d}	23,40^{e}	18,20^{f}
Ripeness	327,78^{a}	324,80^{a}	331,88^{a}	320,40^{b}	8,30^{g}	5,70^{h}
Mean	325,59^{A}	317,60^{A}	317,04^{A}	291,00^{B}	55,83^{A}	50,93^{B}
Cv (%)	5,63		3,12		4,66	

Extraction concentration: 1 g dry mass/50 cm^{3} water.
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each solute.
N.D. = Not detected.

4. CONCLUSIONS

Glucose and fructose were only found in berries at véraison and ripeness stages. Tartaric and malic acids were the predominant acids and were found at all developmental stages. The highest total acid concentration occurred at pea size. The malic acid concentration declined rapidly from véraison to ripeness, while tartaric acid decreased only slightly.

In general, a 60 min. extraction period was found to be effective for the simultaneous extraction of sugars and acids from freeze-dried berries. High ethanol concentrations decreased extractability, whereas deionised water proved to be effective in extracting sugars and acids. Sample:solvent ratios of 1 g dry mass/50 cm^3 water up to véraison and 1 g dry mass/12,5 cm^3 water at ripeness were found to be the most suitable. An anion exchange resin quantity of 2 cm^3 was found to be adequate in adsorbing even the high amounts of organic acid at berry set and pea size, thus reducing preparation time and cost per sample as opposed to 3 cm^3 resin. Although the resin did not increase the sugar or acid concentrations, it improved resolution and can be strongly recommended to clean samples prior to analyses on analytical columns. The use of specific columns for sugar and acid analyses also ensure a longer column life.

Along with the high reproducibility of the HPLC methods described, the extraction procedure allow fast, easy and reliable monitoring of soluble solids in grapes during the growth season. To prevent deterioration of grapes and interconversions among compounds, the period of freezing prior to freeze-drying as well as the drying time should be kept as short as possible. The use of liquid nitrogen, in stead of freezing at -20°C, to fast-freeze fresh material prior to freeze-drying would be an alternative in this regard. It is also essential that the grapes be thoroughly freeze-dried and that dryness be maintained during storage. Freeze-dried tissue should still be analysed as soon as possible.

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CHAPTER X

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

Key words : *Vitis vinifera*, Defoliation, Grapes, Sugars, Acids, pH.

ABSTRACT

The effect was studied of partial defoliation (33 % and 66 %) on sugar and acid accumulation and pH in grapes of *Vitis vinifera* L. cv. Cabernet Sauvignon.

Though total soluble sugar (TSS) in grapes of partially defoliated vines was significantly higher than that of non-defoliated vines in some cases, no significant differences were generally found. No significant differences in total titratable acidity (TTA) were found between treatments. The timing of defoliation had no effect on TSS in grapes, whereas TTA tended to be higher the earlier partial defoliation was commenced. In general, 33 % and 66 % defoliated vines respectively produced approximately 33 % and 200 % more TSS and TTA in the fruit per cm^2 leaf area than non-defoliated vines.

No significant differences between defoliation treatments were found on a per gram dry berry mass or per berry basis for glucose and fructose or tartaric and malic acid. However, 66 % defoliated vines had significantly less soluble solids in berries per shoot, which was probably caused by a lower total berry mass per shoot. Although no significant differences in sugar composition could be found between defoliation treatments, tartaric acid levels tended to be higher and malic acid levels lower as a result of partial defoliation. Partial defoliation had no effect on accumulation patterns of sugars and acids. Glucose dominated in berries at véraison, with fructose dominating at ripeness. The highest total tartaric and malic acid concentrations occurred at pea size. Malic acid content decreased rapidly from véraison, whereas the decrease in tartaric acid was not pronounced. Must pH was not affected by partial defoliation.

The results implied that the general metabolism of vines was favourably changed by partial defoliation, mainly in terms of a more favourable source:sink ratio, more efficient photosynthesis and improved canopy microclimate.

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S. Afr. J. Enol. Vitic. (1991)

1. INTRODUCTION

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

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

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

photosystems I and II (Woodrow & Berry, 1988). Light conditions in the canopy would therefore greatly affect accumulation of photosynthates in sinks.

Partial defoliation, in an endeavour to favourably alter grape composition, has already been widely applied. Different methods, levels and time of defoliation, however, led to divergent results. Some investigators found that partial defoliation increased total soluble solids and reduced titratable acidity, malic acid, pH and potassium levels in fruit (Wolf *et al.*, 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). However, others either failed to demonstrate any significant effects on grape composition (Koblet, 1987; Williams *et al.*, 1987) or even found a reduction in total soluble solids (May *et al.*, 1969; Kliewer, 1970; Kliewer & Antcliff, 1970; Sidahmed & Kliewer, 1980). The timing of leaf removal had no significant effect on fruit composition (Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). Sugar concentration was, however, slightly higher following early defoliation, as opposed to later defoliation (Koblet, 1987; Kliewer *et al.*, 1988).

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

This study deals with effects of partial defoliation on grape composition in general, the time at which defoliation should be applied for optimal accumulation in bunches and interrelationships between source size/activity and sink size/activity. The effect of partial defoliation on sugar and acid accumulation and pH in *Vitis vinifera* L. cv. Cabernet Sauvignon grapes was studied.

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight-year-old *Vitis vinifera* L. cv. Cabernet Sauvignon, clone CS 46, vineyard, situated 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 RY 30. Vines were planted (3,0 x 1,5 m spacing) on a Glenrosa (Kanonkop series 13) soil (MacVicar *et al.*, 1977) and trained onto a 1,5 m slanting trellis as described by Zeeman (1981). Further details of the experimental vineyard were given by Hunter & Visser (1988a).

2.2 Experimental design

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

2.3 Defoliation treatments

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

2.4 Analyses

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

2.5 Statistical analyses

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

3. RESULTS AND DISCUSSION

3.1 TSS and TTA

Although TSS in berries of partially defoliated vines was significantly higher than that of non-defoliated vines in some cases, no significant differences were generally found (Fig. 10.1). Koblet (1987) and Kliewer *et al.* (1988) found that sugar concentration slightly increased with early defoliation. That was not found in this study. Kliewer & Bledsoe (1987) also found that timing of leaf removal had no effect on sugar accumulation. Due to the severe defoliation applied in this study, the high sugar concentrations found is of special importance. Many investigators found that partial defoliation increased total soluble solids in berries (Wolf *et al.*, 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). Many explanations for this have been given, such as a remobilization of stored carbohydrates, an increase in photosynthetic activity of remaining leaves, an improvement in light microclimate of remaining leaves and an increased sink strength (Kliewer & Antcliff, 1970; Kliewer & Bledsoe, 1987). Furthermore, changes in the red:far-red radiation ratio in the canopy and therefore phytochrome stimulated responses on certain enzymes involved in maturation processes (Kliewer & Bledsoe, 1987), a change in the pattern of assimilate movement, and increased fruit temperatures (Bledsoe *et al.*, 1988) were also suggested. Kliewer & Lider (1970), Klenert (1975) and Brown & Coombe (1985) also found decreases in accumulation of sugars under shaded conditions.

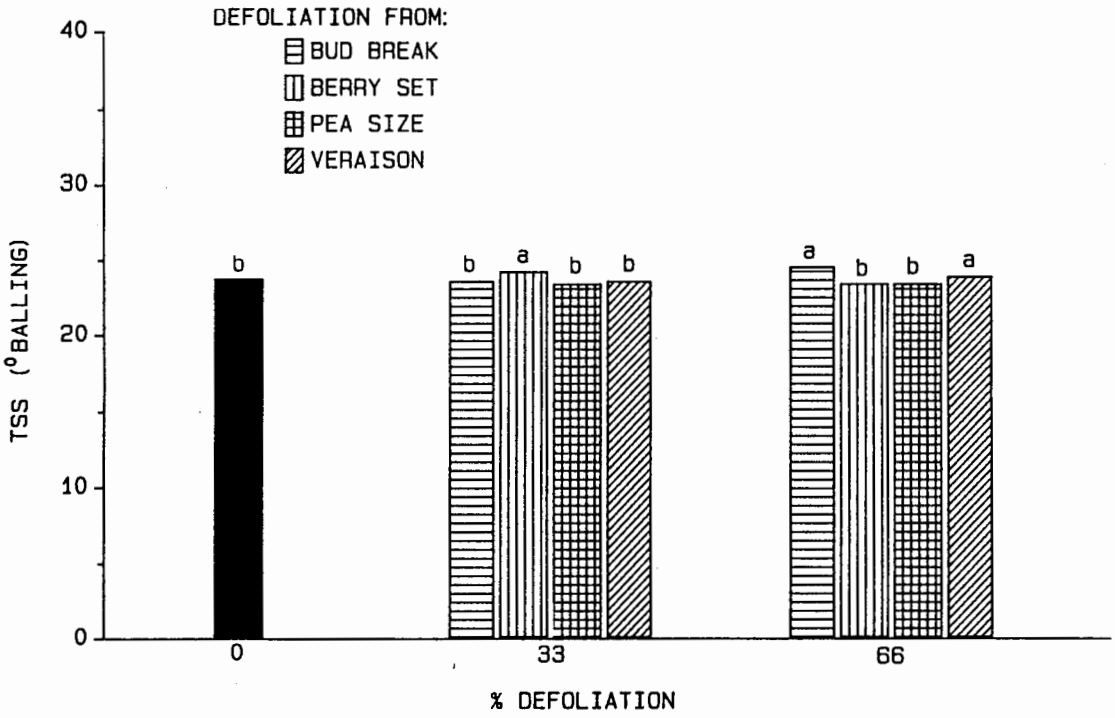

Fig. 10.1 The effect of defoliation from different developmental stages of the vine on total soluble sugars (TSS) in berries at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

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

No significant differences in TTA in berries were generally found (Fig. 10.2). However, except for defoliation from véraison, TTA in grapes of partially defoliated vines was seemingly slightly higher. This is in contrast to findings of Kliewer & Lider (1970) that shaded conditions increased TTA as well as to other investigators that partial defoliation reduced TTA (Wolf *et al.*, 1986; Kliewer & Bledsoe, 1987; Kliewer *et al.*, 1988). The apparently higher TTA found in grapes of partially defoliated vines in the present study can be ascribed to the increase in lateral shoot growth reported by Hunter & Visser (1990a), which resulted in an increase in the number of young and newly matured leaves in the canopy. However, the relationship, if any, between amount of TTA in grapes and the presence of young leaves must still be established. The higher TTA in grapes found with earlier defoliation may also suggest that ripening was delayed. Furthermore, since light intensity in the canopy was significantly increased by partial defoliation (Hunter & Visser,

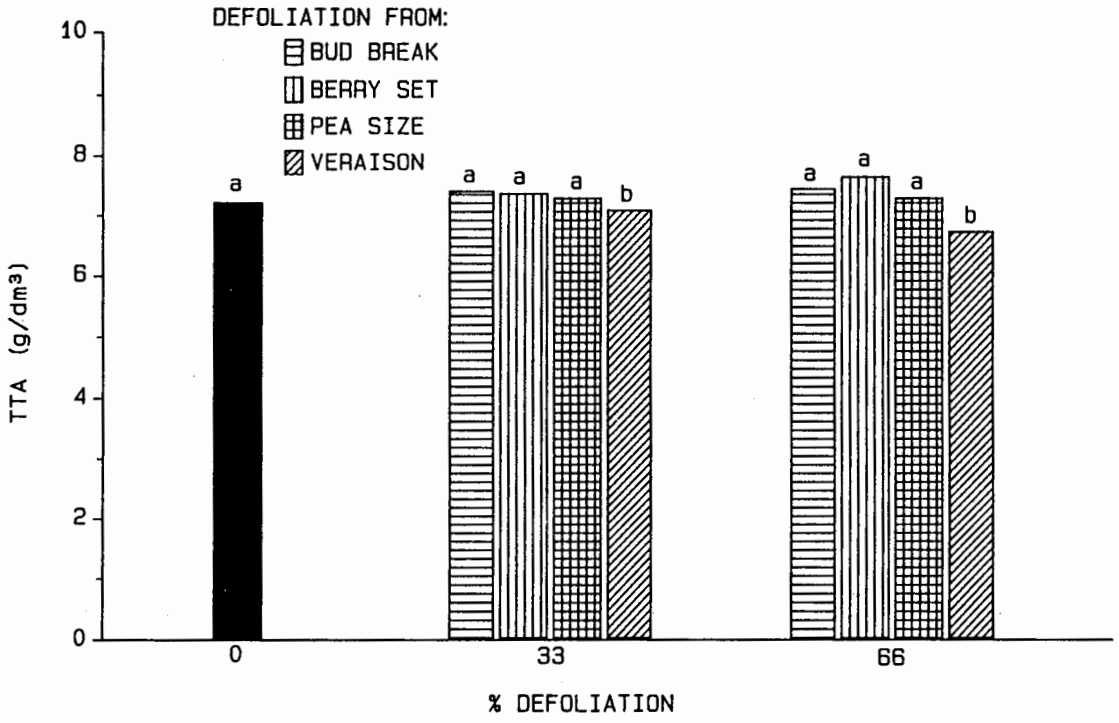

Fig. 10.2 The effect of defoliation from different developmental stages of the vine on total titratable acidity (TTA) in berries at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

1988c), photosynthetic activity of these leaves would also have increased. According to Kriedemann (1977) these leaves produce more organic acids in relation to sugars. Koblet (1987) suggested that a higher proportion of young leaves on lateral shoots would increase grape quality.

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

3.2 TSS and TTA/cm^2 leaf area.

Vines maintained at 33 % and 66 % defoliation during the entire growth season, respectively produced approximately one third and two times more TSS and TTA in the berries/cm^2 leaf area, compared to control vines (Fig. 10.3). Leaf areas of the treated vines were given by Hunter & Visser (1990a) and data on reproductive growth by Hunter & Visser (1990b). Similar results were found by Kliewer (1970). Leaves of partially defoliated vines were therefore metabolically stimulated by partial defoliation, resulting in more efficient photosynthesis. Furthermore, since the size of sinks were not altered, but only the size of sources, demand for photosynthetic products from sinks was increased,

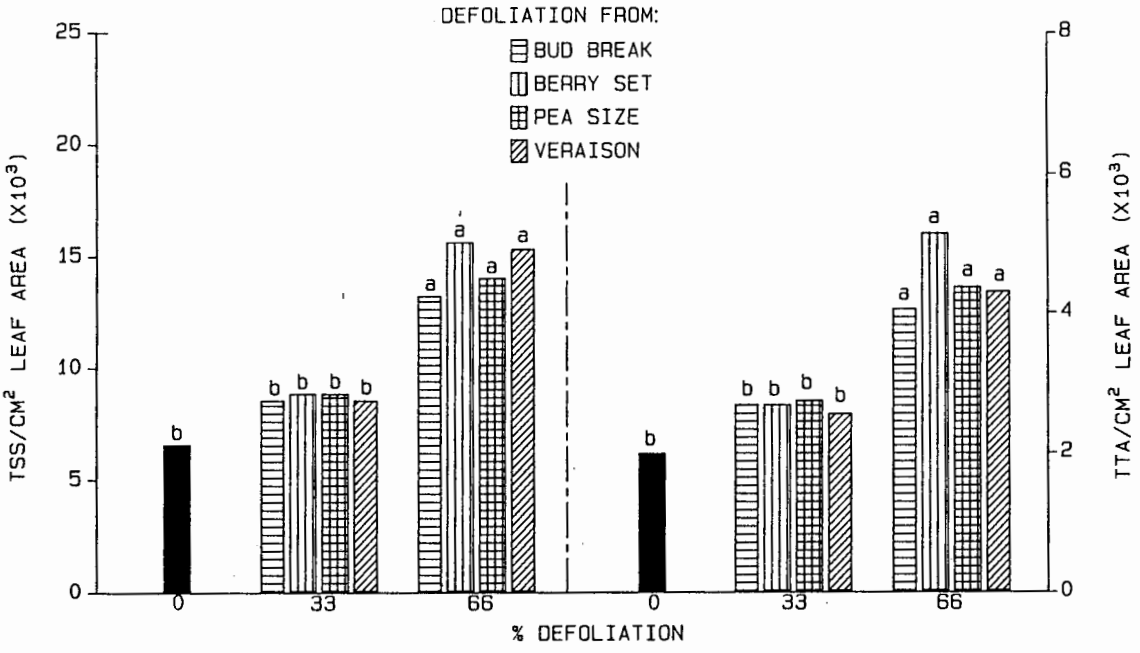

Fig. 10.3 The effect of defoliation from different developmental stages of the vine on TSS and TTA per cm^2 leaf area in berries at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

resulting in an increased photosynthetic activity. The latter was found by Hunter & Visser (1988b, 1988c, 1989). However, because of the improved sink microclimate (Hunter & Visser, 1990b), sink activity could also have increased, affecting accumulation in bunches. According to Brown & Coombe (1985), the major limitation to accumulation of photosynthetic products in grapes might be unloading from the phloem into vascular bundles. However, Ho (1988) stated that there was no evidence that rates of import were limited mainly by rates of unloading; the potential sink strength is rather determined genetically and can be expressed fully when supply of assimilate is sufficient to meet the demand and environmental conditions for metabolic activity of sink organs are optimal.

The data (Fig. 10.3) are, however, not indicative of photosynthetic products being used for respiration and vegetative growth as well as those translocated to and from storage parts of the vine, such as the roots, trunk, arms and canes. Kliewer & Antcliff (1970) found that as much as 40 % of the total sugar in fruits of grapevines may come from storage parts. A remobilization of stored carbohydrates could have contributed to accumulation in grapes of vines defoliated from just after bud break in particular. Nevertheless, as vegetative growth was not strikingly affected by partial defoliation (Hunter & Visser, 1990a), the results demonstrated a more efficient use of aerial parts of these vines. This confirms the findings of Hunter & Visser (1988b, 1988c, 1989).

3.3 Specific sugars

No significant differences on a mg/g dry berry mass or mg/berry basis between partially defoliated and non-defoliated vines were found for either glucose or fructose at véraison or ripeness. Mean glucose concentrations amounted to 317 and 340 mg/g dry mass and mean fructose concentrations to 303 and 349 mg/g dry mass at véraison and ripeness, respectively. Glucose dominated in berries at véraison, while fructose dominated at ripeness. These results verify those found for various species and cultivars (Amerine, 1956; Kliewer, 1966, 1967a, 1967b). However, 66 % defoliation treatments generally had significantly less glucose and fructose on a g/shoot basis than 33 % defoliated and non-defoliated vines (Fig. 10.4). Since no significant differences were found on a concentration or per berry basis, these differences mainly reflected lower total berry mass per shoot for especially vines defoliated early during the season. The latter was fully discussed by Hunter & Visser (1990a).

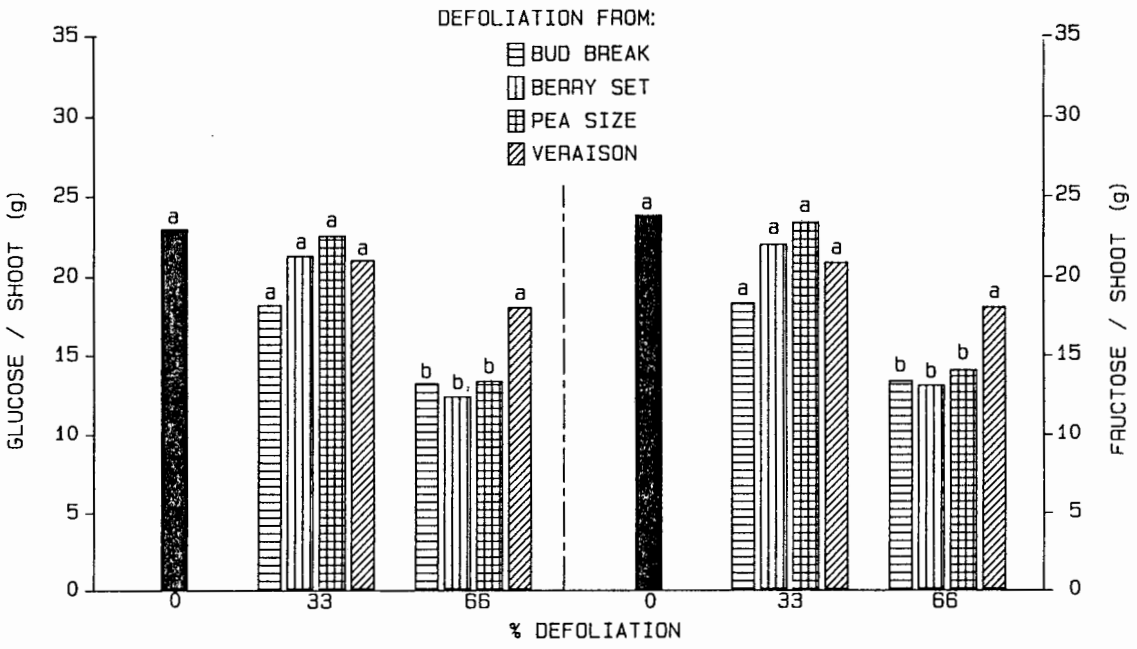

Fig. 10.4 The effect of defoliation from different developmental stages of the vine on glucose and fructose contents per shoot in berries at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each sugar.

3.4 Specific acids

It seemed that defoliation from early developmental stages (bud break and berry set) significantly affected tartaric and malic acid concentrations prior to véraison in some cases (Table 10.1) . No significant differences between defoliation treatments were, however,

found at véraison and ripeness. Partially defoliated vines therefore compensated adequately, probably as a result of increased photosynthetic activity (Hunter & Visser, 1988b, 1988c, 1989). Although no significant differences in tartaric or malic acid were generally found between partially defoliated and non-defoliated vines, it seemed that grapes of the former apparently had higher tartaric acid and lower malic acid concentrations. According to Philip & Kuykendall (1973) this suggests higher grape quality. The acidity balance was therefore apparently changed favourably by partial defoliation. Since only the ratio between tartaric and malic acid was changed, this might explain why no significant differences in TTA were found (Fig. 10.2). A decrease in malic acid concentration with partial defoliation was found by Wolf *et al.* (1986), Kliewer & Bledsoe (1987) and Kliewer *et al.* (1988).

TABLE 10.1 The effect of defoliation from different developmental stages of the vine on tartaric acid and malic acid concentration in the berry, expressed in mg/g dry mass

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

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

Partial defoliation had no effect on the pattern of acid accumulation in berries. Irrespective of defoliation or time of defoliation, the highest tartaric and malic acid concentrations were reached during the rapid growth phases (berry set and pea size) of berries. This is in accordance with that found by Johnson & Nagel (1976). The highest total acid concentration occurred at pea size. Although malic acid concentrations declined rapidly from véraison to ripeness, the decrease in tartaric acid concentration was not pronounced and eventually resulted in a concentration approximately four times that of malic acid. This verifies findings of Amerine (1956), Kliewer *et al.* (1967), Kliewer (1971) and Van Zyl (1984). Since tartaric acid concentrations are usually higher than that of malic acid during ripening, Kliewer (1964) suggested that tartaric acid is metabolized very slowly, either due to the lack of an active metabolizing enzyme system during this period or because of enzyme inhibition. However, Saito & Kasai (1968) stated that accumulation of tartaric acid during ripening is due to its conversion to an insoluble salt, which is barely affected by enzymes. According to Johnson & Nagel (1976), Coombe (1987), and Iland (1987) the small decline in tartaric acid concentration during ripening is the result of dilution, while the decline in malic acid concentration resulted from water uptake and metabolic reactions, causing malic acid to decrease in absolute amounts in the berry. Ruffner (1982) stated that malic acid is very much involved in sugar metabolism through processes of glycolysis and gluconeogenesis. According to Selvaraj *et al.* (1978) the decrease in total acidity during ripening might be due to oxidation of acids or preferential utilization of organic acids during respiration.

Though no significant differences for either of the acids on a per berry basis were found between partially defoliated and non-defoliated vines, berries of 66 % defoliated vines had significantly less tartaric and malic acid contents on a per shoot basis (Fig. 10.5). As for sugar content per shoot (Fig. 10.4), these results also primarily reflect differences in total berry mass between partially defoliated and non-defoliated vines.

3.5 pH

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

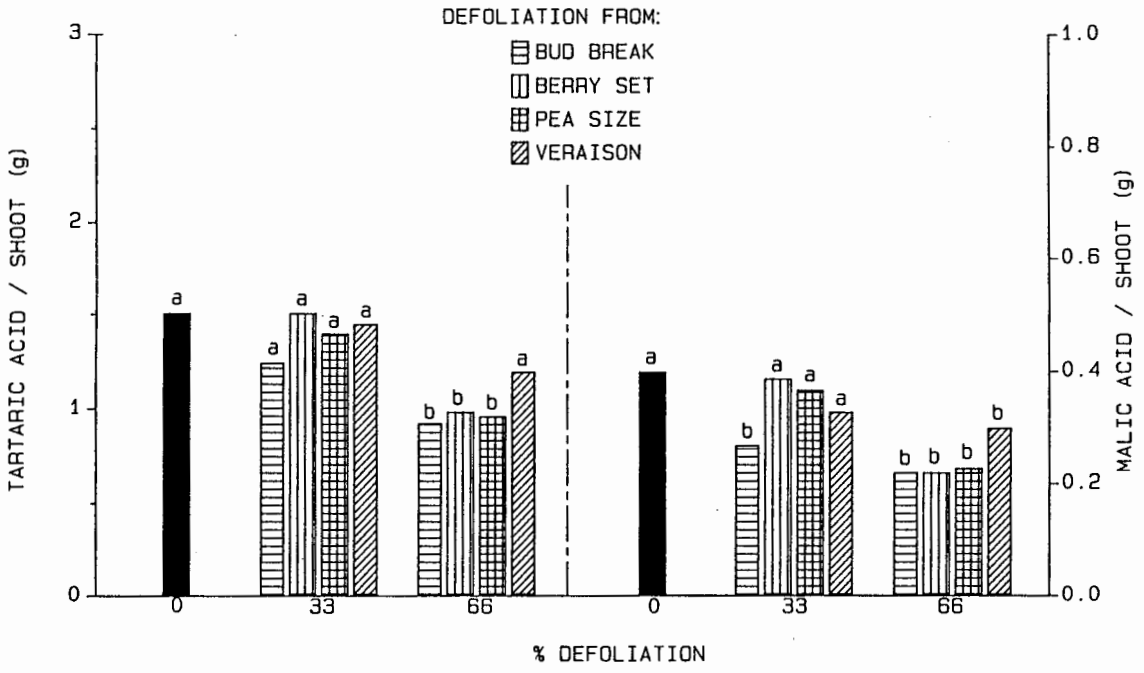

Fig. 10.5 The effect of defoliation from different developmental stages of the vine on tartaric acid and malic acid contents per shoot in berries at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each organic acid.

3.6 General

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

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

The results confirm the general conception that an optimal canopy microclimate is a necessity in the cultivation of wine grapes. This can only be beneficial to the general metabolic activity of vines and contribute to establishing the capacity of vines and finding

the perfect balance between vegetative and reproductive growth and accumulation of reserves. From the results it is evident that 66 % defoliation over the whole canopy of grapevines is too severe regarding the total accumulation of important sugars and organic acids in bunches. Nevertheless, it seems that partial defoliation can safely be applied in practice provided that defoliation is not too severe (66 %).

4. CONCLUSIONS

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

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

Partial defoliation did not change the accumulation pattern of sugars and acids during the growth season. The highest tartaric and malic acid concentrations occurred during rapid growth phases of berries, while the highest total concentrations were reached at pea size. Malic acid decreased rapidly from véraison to ripeness, while the decrease in tartaric acid

was not pronounced. No significant differences in must pH were found between partially defoliated and non-defoliated vines.

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

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CHAPTER XI

The Effect of Partial Defoliation on Quality Characteristics of *Vitis vinifera* L. cv. Cabernet Sauvignon Grapes II. Skin Colour, Skin Sugar and Wine Quality

Key words : *Vitis vinifera*, Defoliation, Grape skin, Anthocyanins, Sugar, Wine quality.

ABSTRACT

The effect was studied of partial defoliation (33 % and 66 %) on grape skin colour and sugar content as well as on wine quality of *Vitis vinifera* L. cv. Cabernet Sauvignon.

Anthocyanin concentrations tended to be higher following partial defoliation and tended to increase the later defoliation was applied, resulting in the highest concentration with defoliation from véraison. The anthocyanin content per berry was significantly higher for vines defoliated from véraison. Sugar levels in berry skins seemed to be associated with anthocyanin concentration. The phenolic content per berry was unaffected by partial defoliation.

Berry volume generally decreased with defoliation. Berry volume of partially defoliated vines increased the later defoliation was commenced. These berries are more desirable for quality wines. Wine quality was significantly improved by partial defoliation, regardless the severity or developmental stage defoliation was commenced.

The effect of defoliation on wine quality should be judged in conjunction with results on sugar and acid content of berries and must pH. It was evident that partial defoliation had no marked effect on berry composition and volume. However, it greatly improved wine quality and partial defoliation is therefore recommended as an invaluable canopy management practice.

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Am. J. Enol. Vitic. (1990)

1. INTRODUCTION

Vigorous growth and dense canopies are common features of South African grapevines. It is known that these conditions are detrimental to grape quality in general and may particularly lead to inferior colour development in skins of red grapes under warm and cool climates (Kliewer, 1970, 1977; Champagnol, 1977; Koblet, 1984, 1987). Vines of high vigour and/or having shaded canopies produced wines of low colour density, total anthocyanin and phenol content as well as reduced proportions of ionized anthocyanins (Smart, 1982; Smart *et al.*, 1985).

According to Singleton (1982) and Somers & Pocock (1986), phenols and their derivatives in grapes are the most important group of compounds distinguishing wines of different types and qualities. Extractability of these compounds are therefore of the utmost importance during vinification. The phenolic compounds of red grapes are essentially composed of anthocyanins and tannins (Ribéreau-Gayon & Glories, 1982). Five anthocyanidins occur in most *Vitis* species, namely cyanidin, peonidin, delphinidin, petunidin and malvidin (Hrazdina & Moskowitz, 1982). *Vitis vinifera* contains only anthocyanidin-3-monoglucosides of which malvidin-3-monoglucoside is the most prominent (Wulf & Nagel, 1978; Singleton, 1982). In most grape cultivars, anthocyanins are limited to vacuoles of about six cell-diameters below the epidermis (Hrazdina & Moskowitz, 1982).

Chemical and physical barriers exert large effects on colour expression in grape skins as well as on finished wines. Some factors recognized as being responsible for variation in skin pigment content are : skin sugar content (Pirie & Mullins, 1976, 1977, 1980; Pirie, 1979; Wicks & Kliewer, 1983), phenylalanine ammonia-lyase activity (Hrazdina *et al.*, 1984; Raubelakis-Angelakis & Kliewer, 1986), must pH (Smart *et al.*, 1985), vacuolar pH (Moskowitz & Hrazdina, 1981), light and temperature during ripening (Kliewer, 1970, 1977; Champagnol, 1977; Pirie, 1979; Wicks & Kliewer, 1983), plant growth regulators (Wicks & Kliewer, 1983), genetic effects (Pirie, 1979) and berry size (Champagnol, 1977; Pirie, 1979; Cirami *et al.*, 1985; Somers & Pocock, 1986).

Partial defoliation as canopy management practice has already been widely used by viticulturists in search of higher grape quality (Hunter *et al.*, 1990). However, although some investigators reported improvements in grape colouration with leaf removal (Koblet, 1987, 1988; Marquis *et al.*, 1989), no specific and extensive study on the effect of partial defoliation on pigment accumulation in the grape skin has been done.

This study was conducted to determine the effect of partial defoliation from different developmental stages on grape skin pigmentation in relation to skin sugar content and berry volume. It also reports on wine quality as affected by partial defoliation. The effect of partial defoliation on sugars, acids and must pH was investigated in a previous study (Hunter *et al.*, 1990).

2. MATERIALS AND METHODS

2.1 Experimental vineyard

An eight year old *Vitis vinifera* L. cv. Cabernet Sauvignon, clone CS 46, vineyard, situated at the experimental farm of the Viticultural and Oenological Research Institute near Stellenbosch, was used. Further details of the experimental vineyard were given by Hunter & Visser (1988a).

2.2 Experimental design

The experiment was laid out as a completely randomized design. Three defoliation levels were applied to the whole canopy, i.e. 0; 33 % and 66 %. The 0 % defoliation treatment consisted of one treatment, while 33 % and 66 % defoliation levels consisted of four treatments each. Defoliation treatments were implemented as follows : From approximately one month after bud break, from berry set, from pea size and from véraison. Analyses were carried out at ripeness only. Skin analyses consisted of eight replications, whereas determinations of berry size and mass were conducted on nine replications, comprising one-vine plots, for each of the nine treatments. Skin sugar analyses were only performed on control vines and those partially defoliated from approximately one month after bud break.

2.3 Defoliation treatments

The defoliation treatments were carried out as described by Hunter *et al.* (1990).

2.4 Grape skin analyses

Bunches were harvested and stored at -20°C until required. All berries were sampled and a random sample of hundred berries removed for further analyses. The volume of berries was determined and the skins separated from pulps by gentle squeezing between thumb

and forefinger. Any pulp adhering to skins was removed. Skins were then rinsed in distilled water, blotted dry and their fresh mass determined. Skins were frozen at -20°C just prior to freeze-drying with a Chriss freeze-drying unit. Dried skins were weighed, ground in a Sorvall Omni-mixer and stored at room temperature.

A modified method of Pirie & Mullins (1976) were used for the determination of phenolic compounds in grape skins. One gram of freeze-dried skin material was extracted in 30 cm^3 methanolic 0,1 % HCl solution (pH 3,5) at room temperature using a Janke & Kunkel horizontal shaker (model HS 500) operating at 250 rpm for 15 min. After centrifugation at 27 138 g for 15 min., the supernatant was decanted and the process repeated twice. Supernatants were combined and acidified to pH 1,0 using 1 M HCl. The solution was then made up to 100 cm^3 with extraction solvent (pH 1,0) and left in the dark at room temperature for approximately 1h. After proper dilution, absorbancies of total anthocyanins and total phenolics were determined at 520 nm and 280 nm respectively, with a Varian UV/VIS spectrophotometer (model 2200) using 10 mm quartz cells. Anthocyanins were expressed as mg of a mixture of acylated and non-acylated anthocyanins ($E^{10\ mm}_{1\ \%}$ = 500) according to Somers & Evans (1977). Total phenolics were expressed as gallic acid equivalents (GAE) using a gallic acid standard curve prepared from gallic acid in extraction solvent (pH 1,0). Both anthocyanin and phenolic contents were expressed as concentrations (mg/g skin dry mass) and as total amount per berry skin (mg/berry).

Glucose and fructose contents of skins were determined according to methods described by Hunter *et al.* (1990). Results were expressed as mg/g skin dry mass.

2.5 Wine quality

Wines from different treatments were made according to standard VORI oenological techniques. Wines were sensorially evaluated by a panel of 10 judges for cultivar character and overall quality on a nine point scale. The scores of each judge were expressed as a percentage of the maximum score.

2.6 Statistical analyses

Statistical analyses were conducted as previously described (Hunter *et al.*, 1990).

3. RESULTS AND DISCUSSION

3.1 Anthocyanin concentration

Regardless of defoliation percentage or commencement of defoliation, no significant differences in anthocyanin concentrations of berry skins were found at ripeness (Fig. 11.1). However, except for defoliation from just after bud break, it seemed that the later defoliation was commenced, the higher the anthocyanin concentration, resulting in the highest concentrations with defoliation from véraison. This stimulation in pigment accumulation is in accordance with the finding of Somers (1976), i.e. that the highest anthocyanin content occurred from 20 to 30 days after véraison and then decreased with further ripening. Véraison in this study was later than physiological véraison and therefore the time of defoliation coincided with this peak accumulation.

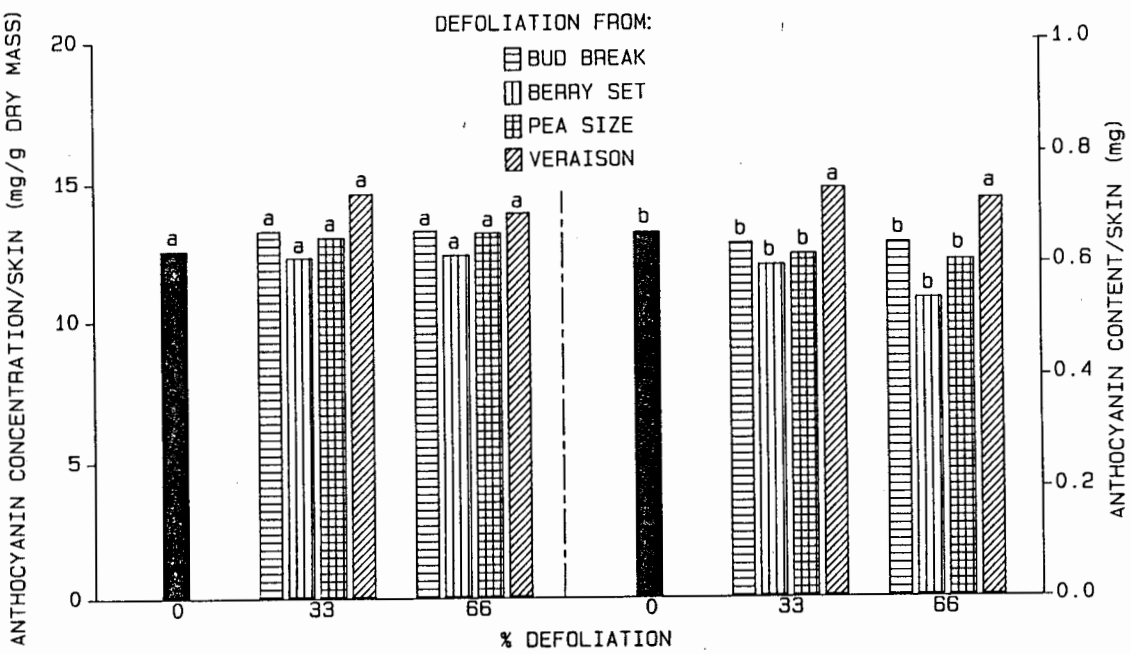

Fig. 11.1 The effect of partial defoliation from different developmental stages of the vine on the anthocyanin concentration and anthocyanin content per berry skin at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

Although leaves were already senescing, they were still photosynthetically stimulated by partial defoliation to values higher than those of control vines (Hunter & Visser, 1988b, 1988c). The highest accumulation of photosynthates in bunches occurred at véraison and was the highest for partially defoliated vines (Hunter & Visser, 1988b). The higher specific pigment accumulation with defoliation during ripening could therefore have resulted from an increased availability of precursors derived from a higher photosynthetic activity and a

stimulation in enzyme activity, especially phenylalanine ammonia-lyase (PAL). This enzyme is normally the key enzyme in the shikimic acid pathway that channels phenylalanine away from protein synthesis towards that of flavonoids and anthocyanins (Hrazdina *et al.*, 1984; Roubelakis-Angelakis & Kliewer, 1986). Because light is indispensable for PAL-activity, it has a major effect on anthocyanin biosynthesis and accumulation (Roubelakis-Angelakis & Kliewer, 1986). Improved light conditions in the interior-canopy and bunch zone, as attained with partial defoliation (Hunter & Visser, 1988c, 1990a, 1990b) may therefore have played a major role in obtaining higher pigmentation of the grape skin.

Although Weaver & McCune (1960) stated that exposure of berries to light from the period berry shatter to the beginning of colouration was probably unnecessary for pigment formation, partial defoliation from pea size slightly increased pigmentation at ripeness, compared to non-defoliated vines. The reason why partial defoliation applied from bud break was apparently more effective than when applied from berry set and pea size, is not clear. It may be related to the significantly lower berry dry mass found with defoliation from this stage (Hunter & Visser, 1990b). It seems that a direct relationship exists between dry mass per berry skin (Fig. 11.2) and anthocyanin concentration for the defoliation treatments, i.e. skins with the lowest dry mass have the lowest anthocyanin concentration. It can therefore be assumed that lower anthocyanin concentrations in berry skins of non-defoliated vines, having the highest dry mass per skin, exclusively resulted from inferior light conditions in the canopy interior.

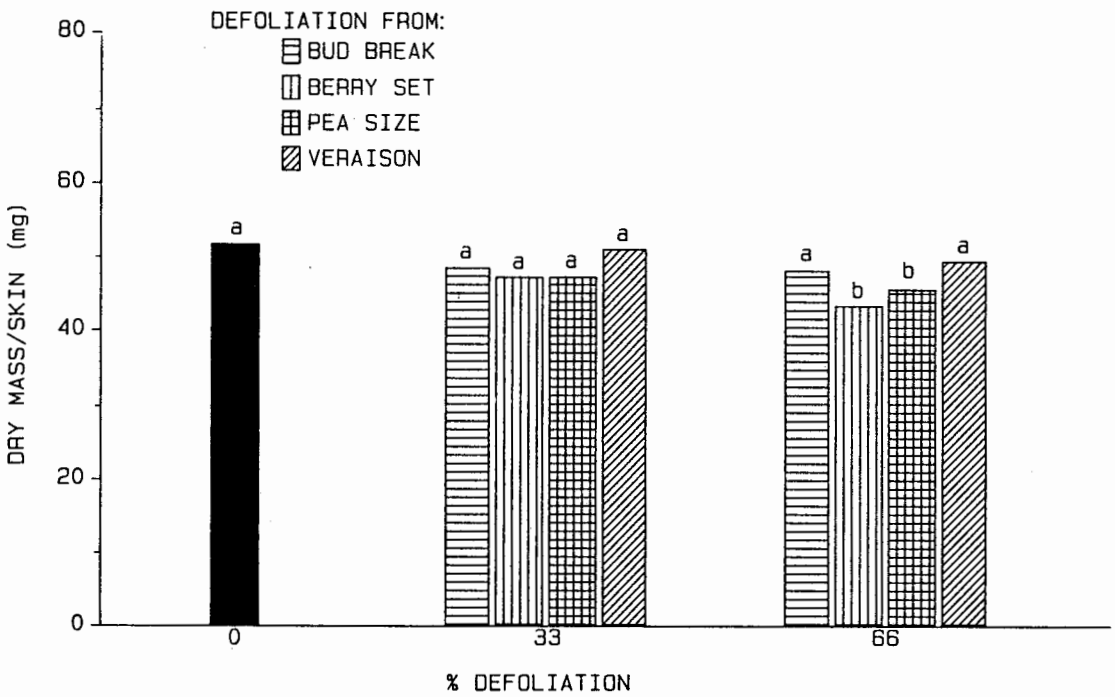

Fig. 11.2 The effect of partial defoliation from different developmental stages of the vine on the dry mass per berry skin at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

3.2 Total anthocyanin

Except for partial defoliation from véraison, the anthocyanin content per berry was slightly higher for non-defoliated vines, compared to that of partially defoliated vines (Fig. 11.1). These differences were, however, not significant. Apart from defoliations from véraison, in which case both anthocyanin contents and skin dry masses were high, slightly higher anthocyanin contents for non-defoliated vines solely resulted from higher skin dry masses (Fig. 11.2).

3.3 Phenolics

The concentration and total amount of phenolics per berry skin were unaffected by partial defoliation. The mean phenolic concentration was 18,25 mg GAE/g skin dry mass and the mean content per berry skin 0,88 mg GAE.

3.4 Berry volume

Generally, it seemed that berry volume decreased with increasing defoliation, resulting in a significant decrease for 66 % defoliation treatments, compared to that of control vines (Fig. 11.3). Furthermore, berry volume seemed to increase the later defoliation was commenced during the growth season. The same tendency was found for fresh berry

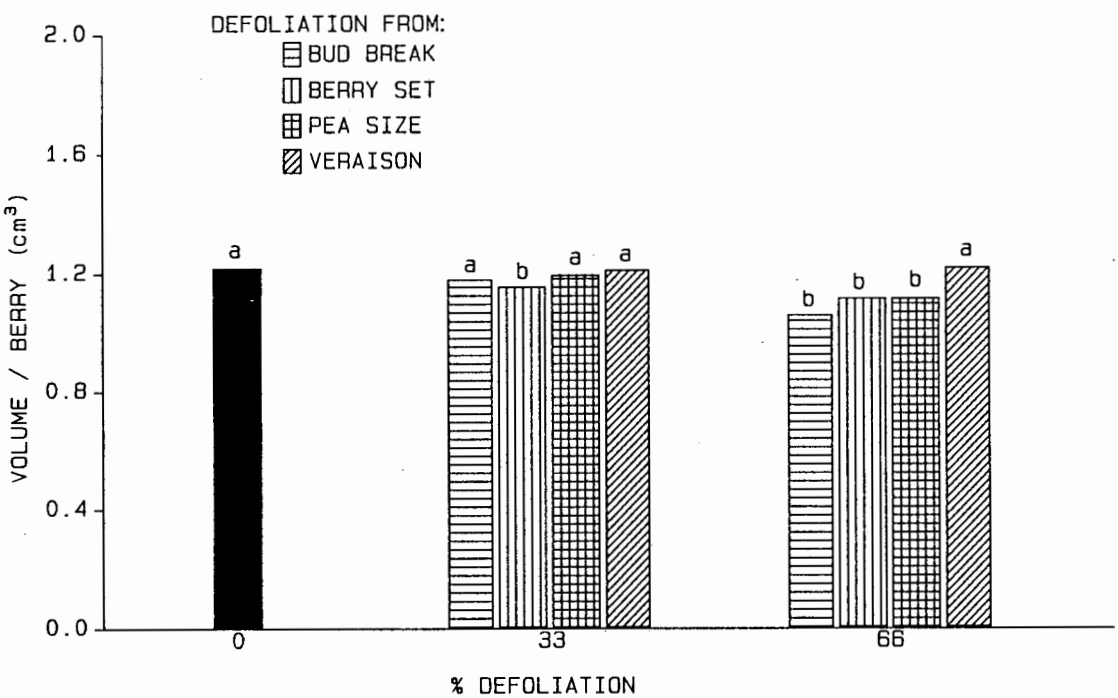

Fig. 11.3 The effect of partial defoliation from different developmental stages of the vine on berry volume at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$).

mass (Hunter & Visser, 1990b). Although small differences in berry volume between non-defoliated and 33 % defoliated vines were found, Somers & Pocock (1986) found that small differences in berry size can lead to surprisingly large variations in pulp:skin ratios. According to them a large berry size is an undesirable feature in relation to potential red wine quality. The pulp:skin ratio is of ultimate importance in determining concentrations of phenolic extractives attained during red vinification and is a determining factor in quality (Champagnol, 1977; Pirie, 1979; Cirami *et al.*, 1985; Somers & Pocock, 1986). Wine grapes should therefore be small and deeply pigmented.

3.5 Skin sugar

The concentrations of glucose and fructose were significantly lower in the grapes of non-defoliated vines than in those of partially defoliated vines (Fig. 11.4). A similar tendency was found for anthocyanin concentration (Fig. 11.1). Pirie (1979) and Pirie & Mullins (1976, 1980) found that endogenous sugars act as a trigger for accumulation of anthocyanin and other phenolic compounds. The sugar content of whole berries revealed no clear relationship with anthocyanin and total phenolics (Pirie & Mullins, 1977; Pirie, 1979), but a closer positive correlation between sugar levels in skin discs and levels of anthocyanin and total phenolics was found during ripening (Pirie & Mullins, 1977). However, no canopy manipulation was conducted on these vines. Applying light and/or

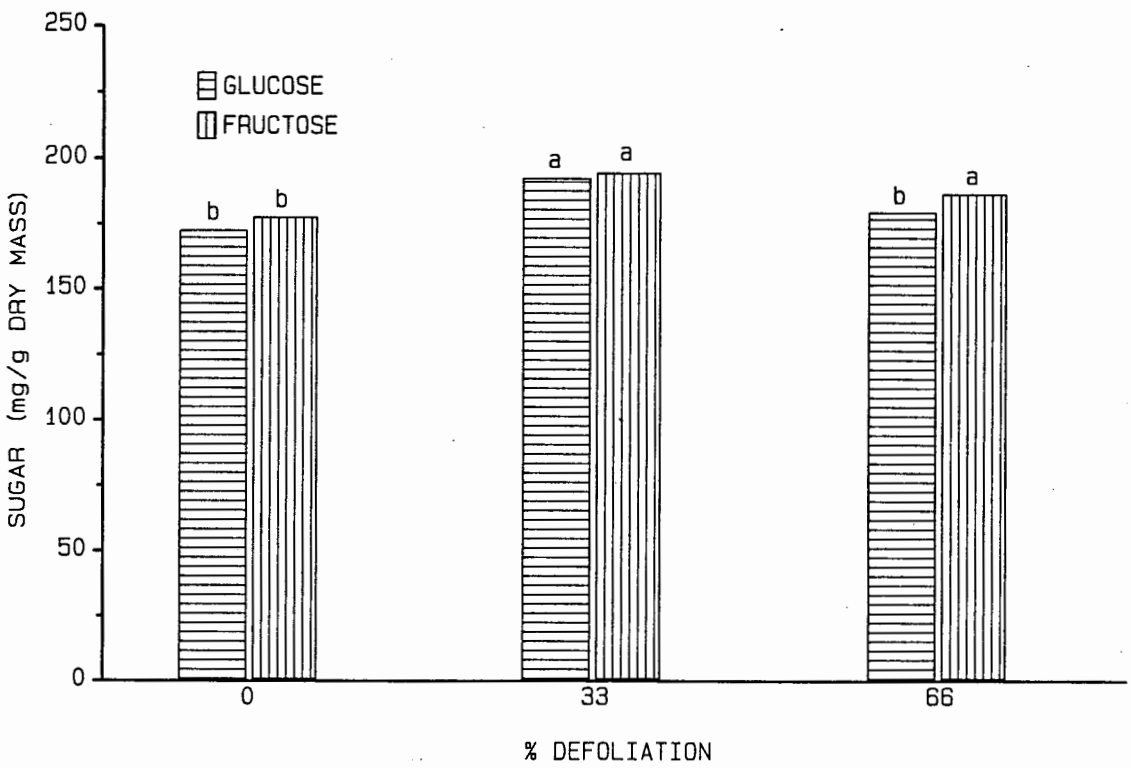

Fig. 11.4 The effect of partial defoliation from bud break on the concentration of glucose and fructose in berry skins at ripeness. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

ethephon, Wicks & Kliewer (1983) found that anthocyanin and total phenolic levels can change without any significant change in skin carbohydrate. They stated that the actual rate of accumulation of pigment in skins is more directly determined by environmental factors such as light, temperature and hormone levels. The low sugar and anthocyanin concentrations found for non-defoliated vines in relation to those of partially defoliated vines, imply that inferior microclimatical conditions existed in canopies of the former. This could have impeded optimum sink activity and thus anthocyanin biosynthesis, resulting in a decrease in sugar translocation to skins.

3.6 Wine quality

In general, wines made from grapes of partially defoliated vines were scored significantly higher for cultivar character and overall wine quality than those of non-defoliated vines (Fig. 11.5). Therefore, although no striking differences in fruit composition between non-defoliated and partially defoliated vines were found, wine quality was greatly affected. From this it can be deduced that all factors measured in this as well as in a previous study (Hunter *et al.*, 1990) should be considered when grapes are evaluated for their potential oenological value. Furthermore, it is clear that partial defoliation is beneficial to berry metabolism and should be considered an invaluable canopy management practice. These results are in agreement with findings of Smart (1982), Smart *et al.* (1985) and Smart *et al.* (1988), i.e. that an inferior canopy microclimate caused by excessive vegetative growth is detrimental to wine quality.

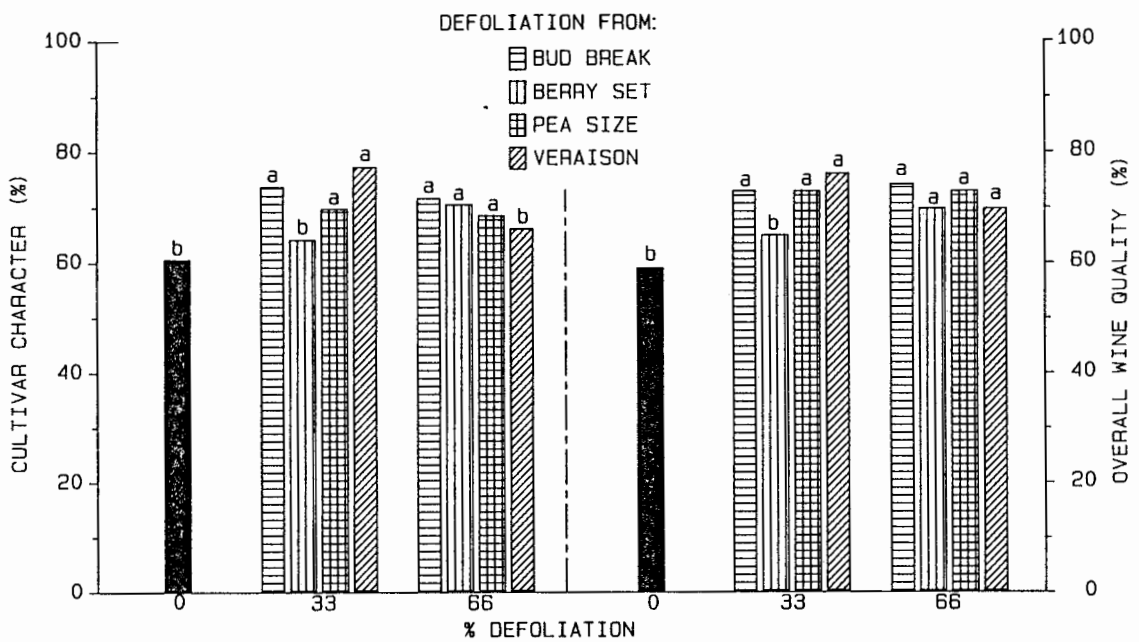

Fig. 11.5 The effect of partial defoliation from different developmental stages of the vine on wine quality, expressed as percentage of maximum score. Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

4. CONCLUSIONS

Although a general increase in skin anthocyanin concentration occurred following partial defoliation, this was not significant. Anthocyanin concentration apparently increased the later defoliation was applied, resulting in the highest concentration with defoliation from véraison. The ostensible higher anthocyanin concentration in berry skins of partially defoliated vines probably resulted mainly from improved light microclimates in their canopies. The higher anthocyanin concentrations were also associated with higher sugar levels in berry skins. Except for a significantly higher anthocyanin content per berry following partial defoliation from véraison, anthocyanin content per berry was slightly higher for non-defoliated vines, albeit not significant. This solely resulted from higher skin masses. No differences in either phenolic concentration or total phenolic content in berry skins were found between treatments.

Berry volume generally decreased with defoliation and increased the later defoliation was commenced. Though these differences were relatively small, it may greatly affect pulp:skin ratios and therefore the extractability of phenolic compounds during vinification. Small and deeply pigmented berries are desired for high quality wines.

Although berry colour and volume were not markedly affected and phenolic content was unaffected by partial defoliation, a significantly higher wine quality was found. These results should be judged considering previous results regarding sugars, acids and must pH. Considering all criteria discussed, it is evident that partial defoliation had no marked effect on fruit composition and volume. It, however, greatly improved wine quality and is therefore considered an invaluable canopy management practice.

It is evident from this and previous studies that the improved canopy microclimate and more balanced source:sink ratio created by partial defoliation, affect vegetative and reproductive growth as well as fruit composition. In the majority of cases, this effect was favourable to grapevine metabolism. However, the method used to partially defoliate vines is not practically and economically feasible. It is therefore recommended that existing vigorous and dense-canopy vines be 33 % defoliated evenly on the lower half of the shoot (canopy) from pea size stage. This would ensure an optimal canopy microclimate in which both vegetative and reproductive organs can function and develop to full potential.

However, viticulturists are striving to create vines with balanced vegetative and reproductive growth rates, resulting in an optimal canopy microclimate and vines capable of a maximum production of high quality grapes. This essentially means vines with less

vegetative growth terminating at véraison, resulting in maximum exposure of all leaves in the canopy without losses in light energy. The above as well as previous results showed that 66 % defoliation of the canopy, albeit favourable to some parameters, was too severe regarding vegetative and reproductive growth as well as fruit composition. The 33 % defoliated vines, however, demonstrated high metabolic activity and increased performance. It can therefore be reasoned that if the same principles of canopy microclimate and leaf exposure as well as source:sink ratio can be realized when a larger leaf area is created on the vine by, for example, longer cordon lengths per root volume, much higher production as well as improved grape and wine quality would materialize.

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CHAPTER XII

Excessive Vegetative Growth and Canopy Density : A Physiological-Practical Approach by Means of Partial Defoliation

Review and Recommendations

Partial defoliation as canopy management practice for grapevines has already been widely investigated in an endeavour to favourably alter canopy structure, fruit composition as well as pest and disease control. Different methods, levels and time of defoliation, however, led to divergent results. These studies mainly dealt with selective or block removal of leaves and therefore the possibility existed of disturbing the normal translocation pattern within shoots and the whole vine. As a result the longevity and healthiness of vines might have been affected detrimentally. Recommendations concerning how, when, where and how many leaves may be removed and the consequences thereof were frequently omitted.

In the present study *Vitis vinifera* L. cv. Cabernet Sauvignon was defoliated 33 % and 66 % evenly over the whole canopy and from different developmental stages, i.e. approximately one month after budding, berry set, pea size, and véraison. Effects on microclimate, photosynthesis, photosynthate translocation, vegetative growth, reproductive growth, root development and distribution, as well as quality characteristics, were determined.

Physiologically sound principles for use in planning of canopy management strategies in practice were established. Partial defoliation of 33 % significantly improved the canopy light environment without a loss in potentially utilizable light energy (Fig. 12.1). Defoliation had no effect on patterns of photosynthate distribution within shoots (Fig. 12.2). Basal leaves (above the bunches) were the most important regarding bunch feeding, and they therefore need to receive enough light for optimum photosynthesis. Light intensity, photosynthetic activity, translocation to and the accumulation of photosynthetic products in leaves and bunches were increased in vines with less leaves. Photosynthetic activity of leaves decreased as the growth season progressed and decreased the deeper into the canopy the leaves were situated (Fig. 12.3). Specific photosynthesis of partially defoliated vines was much higher than that of non-defoliated vines. Total photosynthesis of recently matured, middle leaves was the highest and that of old matured bunch leaves the lowest at all developmental stages. Photosynthesis was especially stimulated

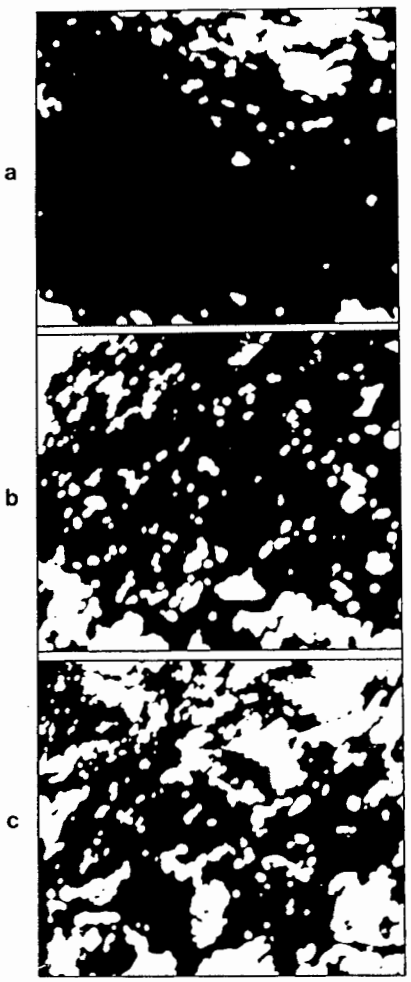

Fig. 12.1 Shade patterns of canopies of (a) non-defoliated (0 %) and (b) and (c) partially defoliated (33 % and 66 %) vines.

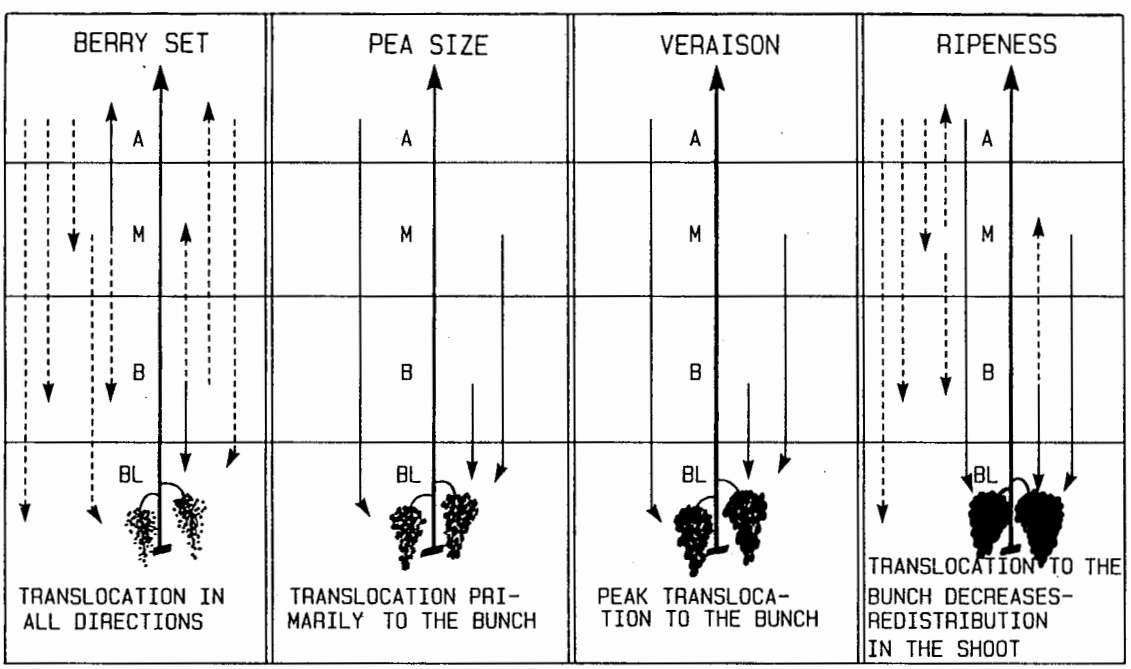

Fig. 12.2 A schematic representation of translocation of photosynthetic products at different developmental stages of the vine. A, M, B, BL = apical, middle, basal and bunch leaves, respectively.

	BERRY SET			PEA SIZE			VERAISON			RIPENESS		
	* 0	* 33	* 66	* 0	* 33	* 66	* 0	* 33	* 66	* 0	* 33	* 66
APICAL	8 *44*	10 *41*	13 *33*	7 *74*	10 *66*	13 *55*	9 *123*	9 *82*	12 *64*	10 *149*	14 *129*	14 *83*
MIDDLE	9 *197*	17 *264*	17 *175*	7 *198*	12 *205*	13 *159*	6 *163*	7 *142*	8 *90*	4 *104*	7 *122*	8 *102*
BASAL	4 *92*	11 *182*	11 *114*	4 *96*	10 *122*	10 *78*	4 *99*	5 *90*	6 *55*	3 *67*	5 *68*	5 *46*
BUNCH LEAVES	3 *25*	5 *32*	7 *24*	3 *23*	4 *30*	6 *19*	2 *13*	4 *26*	4 *12*	2 *11*	3 *11*	3 *13*
TOTAL PHOTOSYNTHESIS	24 *358*	43 *519*	48 *346*	21 *391*	36 *423*	42 *311*	21 *398*	25 *340*	30 *221*	19 *331*	29 *330*	30 *244*

* % DEFOLIATION

Fig. 12.3 The effect of defoliation on the photosynthetic activity (mg $CO_2/dm^2/h$) (arabic numbers) and total photosynthesis (mg CO_2/h) (italic numbers) of leaves in different positions on the shoot at different developmental stages of the vine.

by defoliation until pea size, which stressed the necessity of creating a well-exposed canopy during this period in order to realize the full potential of the vines. It also emphasized the fact that foliage be stimulated photosynthetically during the second part of the growth season to increase photosynthate contribution to bunches.

Photosynthetic activity generally increased with an increase in chlorophyll concentration. As leaves were progressively situated towards the periphery of the canopy, maximum chlorophyll *a* and *b* concentrations were reached later during the growth season. According to these results excessive removal of metabolically active leaves on the lower half of the canopy should be avoided during early developmental stages of vines (until pea size) and on the apical parts from véraison to ripeness. In spite of much lower total remaining leaf areas and chlorophyll contents of partially defoliated vines, total CO_2 assimilation rates were still comparable to or even higher in relation to that of non-defoliated vines. In particular, basal leaves of partially defoliated vines were proportionally photosynthetically more active. Remaining leaves of partially defoliated

vines therefore compensated adequately for the loss of leaves, provided that defoliation was not too severe (66 %).

In spite of the severity of defoliation from different developmental stages, no compensatory leaf growth at subsequent developmental stages was found. Main shoot length decreased slightly, while lateral shoot length and number of laterals increased significantly with defoliation - increasing also with severity of defoliation and the earlier during the season defoliation was implemented. To prevent the canopy from becoming denser later in the season, severe leaf removal early in the season must therefore be avoided. Cane mass was reduced the earlier and more severe partial defoliation was applied. Except for 33 % defoliation carried out from pea size and véraison, cane mass per vine also declined with defoliation.

Yield at harvest seemed to be severely affected by 33 % defoliation prior to pea size and 66 % defoliation prior to véraison. The fresh mass:cane mass ratio was increased with defoliation from véraison. Considering the 10-12 cm^2 leaf area generally required to ripen one gram of fruit, it was evident that control vines carried excess foliage and that defoliation from pea size and véraison fell in this category.

Partial defoliation of the canopy improved budding percentage, the latter generally increasing with increasing defoliation. Defoliations from bud break and berry set were generally the most effective. Bud fertility was only improved by 33 % defoliation and was favoured by partial defoliation from bud break. This coincided with the period for the formation, induction and differentiation of inflorescence primordia. Light intensity and windspeed in the canopy increased with partial defoliation, while relative humidity decreased and temperature remained unchanged. The number of leaf layers decreased. These conditions are beneficial to pest and disease control and to the development of healthy and higher quality grapes.

Root densities of 33 % defoliated vines were significantly stimulated by partial defoliation and increased the later defoliation was commenced. This suggests a more efficient utilization of soil and water by partially defoliated vines. Yield and cane mass following 33 % defoliation coincided with root densities, decreasing with less dense root distribution. Partial defoliation stimulated the development of fine to medium diameter roots, but not of thick roots. Since increases in the development of thin roots imply a more efficient utilization of soil and available water, whereas decreases in the development of thick roots may have impeded the regenerative and carbohydrate storage ability of the root system, the effectiveness of root systems may be misrepresented if only total dry mass is determined. Generally, defoliation from early developmental stages (bud break, berry set) reduced root development compared to later defoliations (pea size, véraison). Since peak root activity occurs just after bud break, at bloom

and just after harvest, these early defoliations apparently affected root activity. Severe reductions in leaf area during this period should therefore be avoided. Generally, partially defoliated vines demonstrated higher total root numbers in all soil layers. Roots were preferentially located in the 0-800 mm zone. The generally larger amounts of particularly fine roots in all soil layers for 33 % defoliated vines, implied a more efficient nutrient absorption capacity and utilization of soil and available water.

Considering all root sizes, it appeared that 33 % defoliation from pea size created the most effective root system. Partially defoliated vines probably responded to the loss of leaves by forming new roots. In conjunction with the higher photosynthetic activities mentioned earlier, this may provide an efficient mechanism for continued high performance.

Total soluble solids in berries of partially defoliated vines were significantly higher than that of non-defoliated vines in some cases. The timing of defoliation had no effect on sugar accumulation. Except for defoliation from véraison, total titratable acidity in grapes of partially defoliated vines was slightly higher than that of non-defoliated vines. Acid accumulation was decreased the later defoliation was commenced. The 33 % and 66 % defoliated vines respectively produced approximately one third and twice as much TSS and TTA in the berries per cm^2 leaf area compared to control vines. No differences in glucose and fructose concentrations could be found between partially defoliated and non-defoliated vines on a mg/g dry mass or mg/berry basis. However, glucose and fructose/shoot were significantly less for 66 % defoliated vines. Tartaric acid concentrations were slightly higher and malic acid concentrations slightly lower with partial defoliation on a mg/g dry mass basis. This suggested higher grape quality. The pattern of acid accumulation in the berry during the growth season was unaffected by partial defoliation. Lower sugar and organic acid levels per shoot mainly reflected lower total berry mass per shoot.

Except for defoliation from berry set, anthocyanin concentrations were increased by defoliation. Apart from defoliation from bud break, anthocyanin concentrations were increased the later defoliation was commenced. The lower pigmentation of berries of non-defoliated vines probably resulted exclusively from inferior light conditions in the canopy interior. Glucose and fructose concentrations in grape skins of partially defoliated vines were higher, coinciding with anthocyanin concentrations. It may be reasoned that the inferior microclimate in the canopies of control vines impeded optimum sink activity and thus anthocyanin biosynthesis, resulting in decreases in sugar translocation to the skins. Generally, berry volume decreased with increasing defoliations and tended to increase the later defoliation was commenced. Since large berry size is an undesirable feature for red wine quality, this result is quite important, as reflected by the fact that wines made from grapes of partially defoliated vines were scored significantly

higher for cultivar character and overall wine quality, in spite of the small differences in fruit composition.

From the results it is evident that partial defoliation as applied in this study changed the general metabolism of vines, mainly in terms of more favourable source:sink ratios, resulting in more efficient photosynthesis, subterranean performance and canopy microclimate. This was beneficial for the production of grapes needed for quality wine. In the majority of cases the metabolism of grapevines was favoured, particularly with 33 % defoliation from pea size and véraison. The results, however, suggested that an even removal of 33 % of leaves opposite and below bunches during the period from flowering or berry set to pea size can be applied. The results further suggested that existing vigorous and dense-canopy vines be defoliated 33 % evenly on the lower half of the shoot (canopy) from pea size or véraison stage. This would ensure an optimal canopy microclimate in which both vegetative and reproductive organs can function and develop to full potential. This method is also practically and economically feasible.

This hypothesis was tested for two consecutive years on the basis of certain important parameters, i.e. canopy score, light intensity at the cordon, photosynthetic activity (middle and basal leaves) at ripeness, yield and cane mass, TSS, TTA and pH of the must, wine colour, cultivar character and overall wine quality. All measurements were conducted as already described in previous chapters. Except for canopy scores, light intensities and photosynthetic activities, means over the two years are presented.

Percentage canopy gaps, fruit exposure and number of leaf layers of partially defoliated vines were in accordance with that needed for the production of higher quality grapes (Table 12.1). Light intensity in the canopy-interior was greatly improved by partial defoliation (Fig. 12.4) and contributed to the higher photosynthetic activities of middle and basal leaves (Fig. 12.5). These higher photosynthetic activities were manifested in yields of partially defoliated vines (Fig. 12.6). Although these vines had approximately 25-30 % less leaf area per gram fresh mass (Fig. 12.6), they gave similar yields with defoliation from pea size and 11 % higher yields with defoliation from véraison. Cane masses of partially defoliated vines were lower, vines defoliated from pea size having the lowest cane mass (Fig. 12.7). This may be related to the improved light environment in the canopies and probably resulted from shorter and/or thinner shoots. It is evident that vegetative growth was inhibited by partial defoliation.

Except for higher TTA with defoliation from véraison, no significant differences in TSS, TTA and pH of grape musts were found between partially defoliated and non-defoliated vines (Table 12.2). However, anthocyanin content, as indicated by Abs $_{530}$-values, was increased by 9 % and 19 %, colour density (Abs $_{420 + 530}$) by 8 % and 17 % and phenolic content (Abs $_{280}$) by 12 % and

TABLE 12.1 The effect of defoliation from different developmental stages of the vine on **canopy scores at ripeness

Developmental stage defoliation commenced	Canopy parameters																Total	
	Canopy gaps		Leaf size		Leaf colour		Canopy density (mean leaf layer number)		Fruit exposure		Shoot length		Lateral growth		Growing tips			
	*0	*33	0	33	0	33	0	33	0	33	0	33	0	33	0	33	0	33
Pea size	3	8	8	9	6	6	2	6	4	8	5	4,5	8	8,5	10	10	46	60
Véraison	3	9	8	8	6	6	2	5	4	9	5	4	8	9	10	10	46	60

Explanation of scores

Canopy parameter	Control treatment	Defoliation treatment
Canopy gaps	10-20 %	50 %
Leaf size	Average	Average
Leaf colour	Leaves yellowish green, healthy	Leaves yellowish green, healthy
Canopy density	More than 2 leaf layers	About 2 leaf layers
Fruit exposure	30 %	50 %
Shoot length	10-12 nodes	10-12 nodes
Lateral growth	limited	limited
Growing tips	5 % or less	5 % or less

*** Defoliation percentage.**
**** Means of 5 vines scored by 3 judges.**

19 % for wines made from vines partially defoliated from pea size and véraison, respectively (Table 12.3). Similarly, cultivar character (typicity) of wines was more pronounced (5 % and 12 %), whereas overall wine quality was improved by 4 % and 10 % (Fig. 12.8).

From the above it appears that the applied partial defoliations were successful in inhibiting vegetative growth, whereas metabolic activity of leaves and fruit was stimulated by *inter alia* an improved light environment in the canopy. Vines were therefore able to support similar or even higher yields with no detrimental effect on grape quality and a significant improvement in wine quality. It is evident that partial defoliation can be applied, not only to the benefit of both

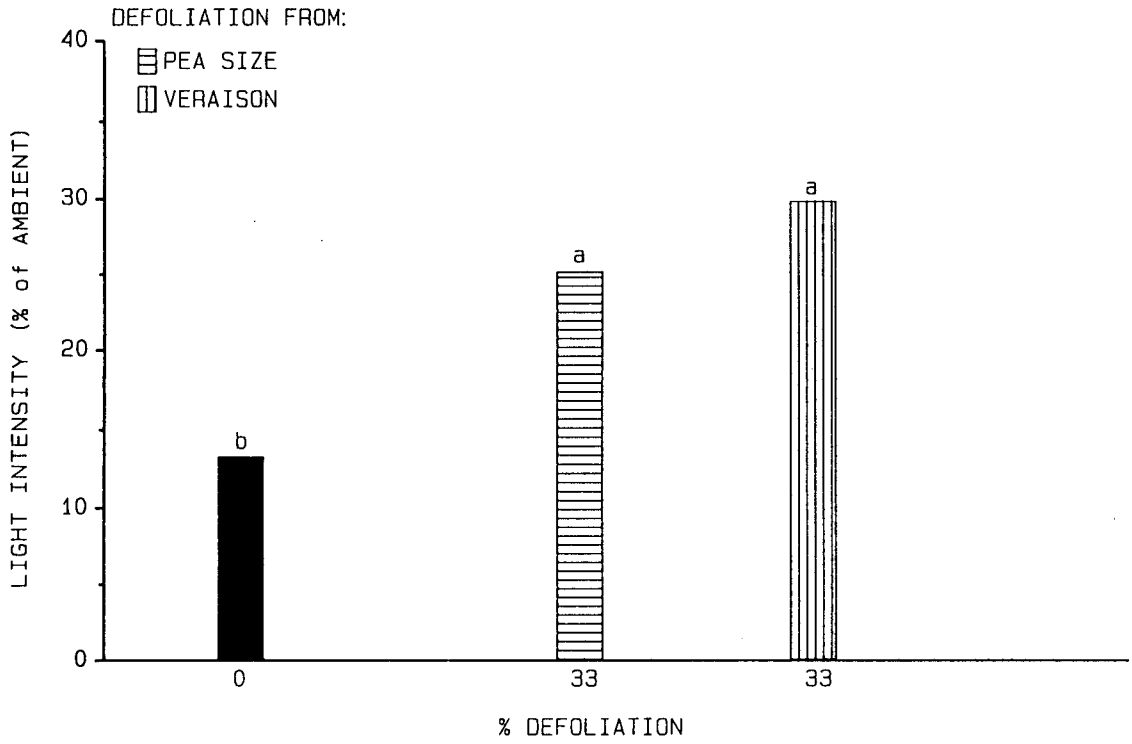

Fig. 12.4 The effect of defoliation from different developmental stages of the vine on light intensity at the cordon.

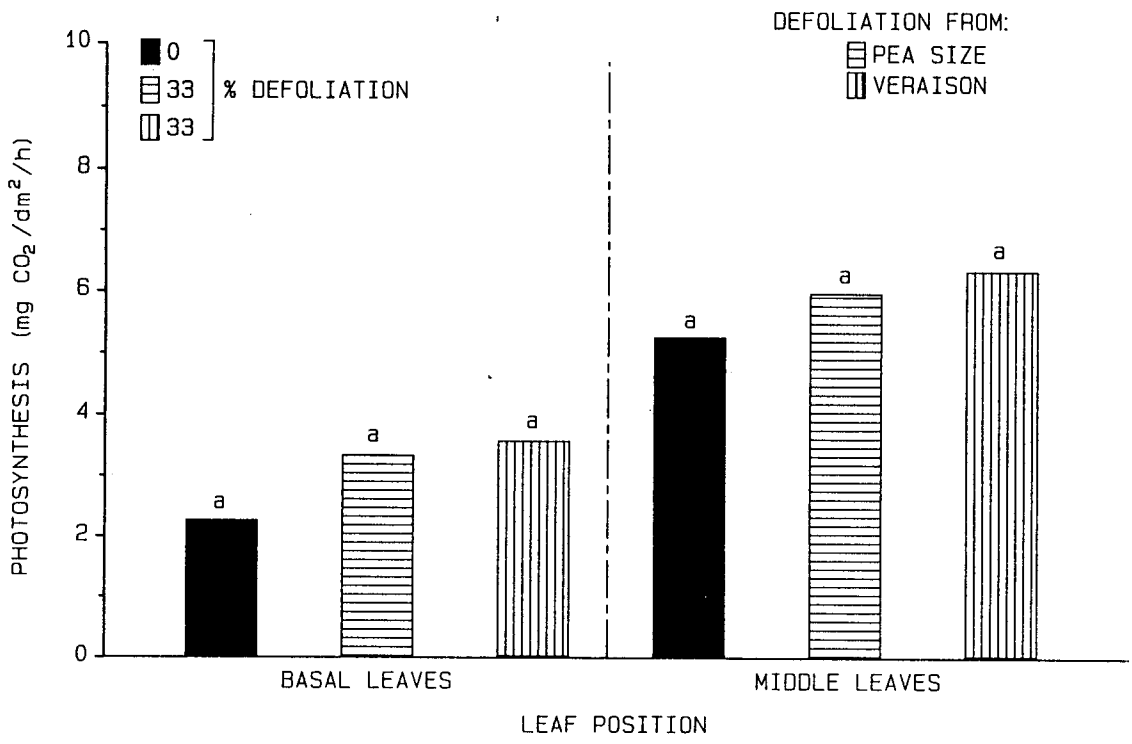

Fig. 12.5 The effect of defoliation from different developmental stages of the vine on photosynthetic activities of basal and middle leaves at ripeness.

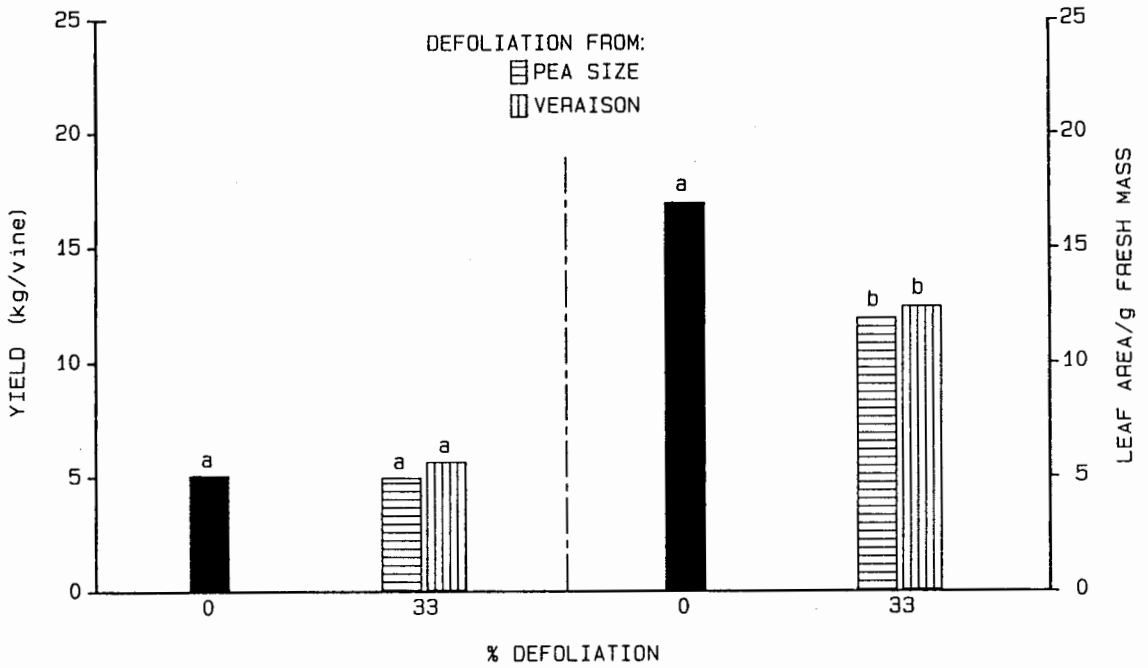

Fig. 12.6 The effect of defoliation from different developmental stages of the vine on yield and leaf area per gram fresh mass at ripeness.

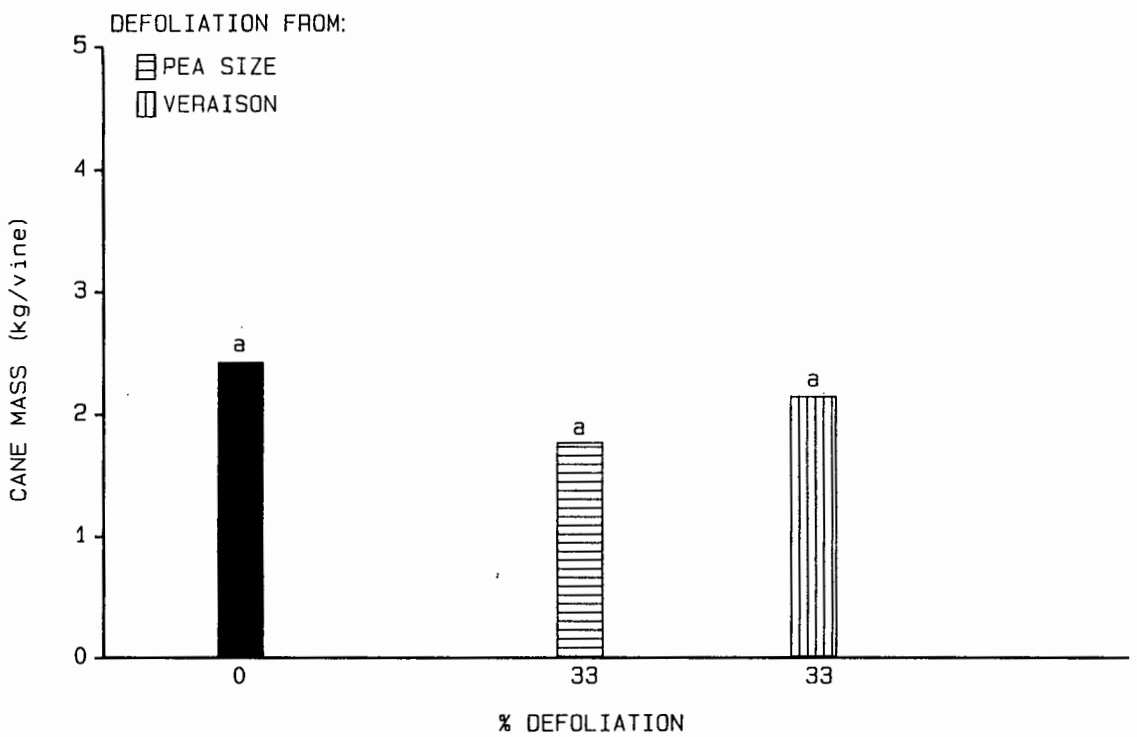

Fig. 12.7 The effect of defoliation from different developmental stages of the vine on cane mass.

TABLE 12.2 The effect of defoliation from different developmental stages of the vine on total soluble solids (TSS), total titratable acidity (TTA) and pH of the must at ripeness

Developmental stage defoliation commenced	TSS		TTA		pH	
	*0	*33	*0	*33	*0	*33
Pea size	25,00[a]	24,77[a]	7,63[b]	7,75[b]	3,10[a]	3,09[a]
Véraison	25,00[a]	24,71[a]	7,63[b]	8,35[a]	3,10[a]	3,08[a]

*** Percentage defoliation.**
Values designated by the same letter do not differ significantly ($p \leq 0,05$) for each parameter.

TABLE 12.3 The effect of defoliation from different developmental stages of the vine on wine colour (absorbance units)

Developmental stage defoliation commenced	Abs 530		Abs 420 + 530		Abs 280	
	*0	*33	*0	*33	*0	*33
Pea size	0,73	0,80	1,31	1,42	5,91	6,61
Véraison	0,73	0,87	1,31	1,53	5,91	7,01

*** Percentage defoliation.**
Abs = Absorbance.

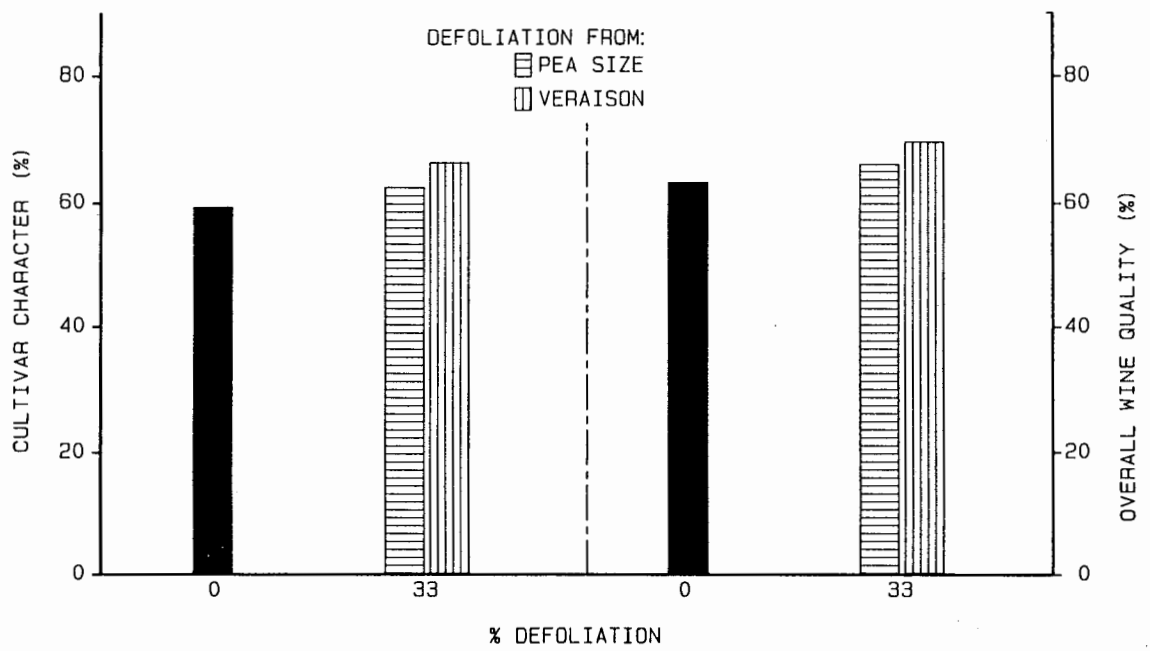

Fig. 12.8 The effect of defoliation from different developmental stages on wine cultivar character (scored by 17 judges) and overall wine quality (scored by 22 judges).

vegetative and reproductive growth of the vine, but also to improve pest and disease control, grape production and wine quality.

An improved canopy microclimate to secure maximum photosynthetic activity of leaves as well as fruit development before pea size should be obtained by other canopy management practices such as suckering, shoot positioning, tipping and topping. If necessary at all, topping must preferably be carried out before pea size to leave enough time for leaves on sprouting lateral shoots to become active and contribute to the berries during the period véraison to ripeness. Due to multidirectional translocation in the shoot, which was still evident before pea size, it is expected that the effect on fruit development would be more dramatic. Topping during the period pea size or véraison to ripeness must be avoided because of the importance of young and recently matured, active leaves on the upper half of the shoot in terms of photosynthesis, the accumulation of reserves and translocation of photosynthetic products to the grapes. Except in cases of excessive growth, shoots should only be tipped if active growth continues. To prevent the canopy from becoming too dense when topping prior to pea size was carried out, leaf removal is a necessity during the period pea size to ripeness. These recommendations are summarised schematically in Fig. 12.9.

Viticulturists are, however, striving to create vines with balanced vegetative and reproductive growth rates, resulting in an optimal canopy microclimate and vines capable of a maximum production of high quality grapes. This essentially means vines with less vegetative growth terminating at véraison, resulting in maximum exposure of all leaves in the canopy without losses in light energy. The study showed that 66 % defoliation of the canopy, albeit favourable to some parameters, was too severe regarding vegetative and reproductive growth as well as fruit composition. The 33 % defoliated vines, however, demonstrated high metabolic activity and increased performance. It may therefore be reasoned that if the same principles of canopy microclimate and leaf exposure as well as source:sink ratios can be realized by creating a larger leaf area on the vine by, for example, longer cordon lengths per root volume, much higher production as well as improved grape and wine quality would materialize.

CANOPY MANAGEMENT PRACTICES	BUDDING	SHOOTS 30 cm	FLOWERING	BERRY SET	PEA SIZE	VÉRAISON	RIPENESS
SUCKERING	———	———					
SHOOT POSITIONING		———	———	———	———	———	———
TIPPING			———	———		= = = = =	= = = = =
TOPPING			(1)	———	———		
DEFOLIATION		(2)	———	———	———	———	———
				(3)	———	———	———

——— : **Time of application.**

= = = = = : **When vigorous vegetative growth still occurs.**

(1) : **Number of times will depend on growth - preferably not more than three times.**

(2) & (3) : **Two levels of defoliation : (2) = opposite and below bunches, (3) = lower half of shoot (canopy). Follow (2) when canopy is not too dense and (2) and (3) when canopy is very vigorous and dense (and also when topping prior to pea size was carried out).**

Fig. 12.9 Schematic representation of the application of canopy management practices.

CHAPTER XIII

General Summary

Due to the occurrence of excessive vegetative growth and canopy density in South African vineyards, the effect of partial defoliation as canopy management practice on the metabolism and grape composition of the vine was investigated. The study was conducted on *Vitis vinifera* L. cv. Cabernet Sauvignon (clone CS 46), grafted onto rootstock 99 Richter (clone RY 30). Vines were spaced 3,0 x 1,5 m on a Glenrosa soil (Series 13, Kanonkop) and trained onto a 1,5 m slanting trellis. The treatments comprised a control (0 % defoliation) as well as 33 % and 66 % defoliation carried out evenly over the whole canopy. These defoliations were commenced from different developmental stages, i.e. approximately one month after budding; berry set; pea size and véraison. Vines were continuously defoliated at approximately monthly intervals. Analyses and measurements were conducted at subsequent developmental stages. Effects on microclimate, photosynthesis, photosynthate translocation, vegetative growth, reproductive growth, root development and distribution and quality characteristics were determined. Extraction procedures for the determination of sugars and organic acids in freeze-dried berries by high pressure liquid chromatography have also been developed.

Partial defoliation significantly improved canopy microclimate, photosynthetic activity and translocation to and accumulation of photosynthetic products in the leaves and bunches. Normal translocation and distribution patterns of photosynthates were apparently not affected by partial defoliation. Basal leaves (above the bunches) were the most important regarding the nourishing of bunches throughout the growth season. Total photosynthesis of recently matured, middle leaves was the highest, while that of old matured, bunch leaves (opposite and below the bunches) was the lowest at all developmental stages. It was evident that photosynthetic capacity of the vine may be underestimated if photosynthetic activity of only interior-canopy leaves is measured. Photosynthetic activity of all leaves generally decreased as the growth season progressed. Stimulation of photosynthetic activity by partial defoliation was the most pronounced until pea size stage, whereafter it decreased. The finding of a way to stimulate photosynthetic activity before and after pea size is emphasized. It was evident that chlorophyll concentration can not be regarded as a reliable index for photosynthetic activity of grapevine leaves. Photosynthesis and chlorophyll determinations proposed that excessive removal of metabolically active leaves should be avoided on the lower half of the canopy during early developmental stages of vines (until pea size) and on the apical parts from véraison to ripeness.

Remaining leaves of partially defoliated vines were in proportion photosynthetically more active and thus compensated adequately for the loss of leaves, provided that defoliation was not too severe. Considering the response of photosynthesis of all the leaves to increasing photon flux density, photosynthetic activity of middle and apical leaves increased more than expected, suggesting that besides improved light interception at these leaf positions, internal control also played a big role in photosynthetic expression.

The normal sigmoidal growth pattern of the vine was not affected by partial defoliation. No compensatory leaf growth occurred at subsequent developmental stages in reaction upon partial defoliation. Main shoot length decreased slightly, whereas lateral shoot length and number of laterals increased significantly with defoliation. Lateral growth was stimulated and cane mass reduced the earlier and more severe defoliation was applied. Yield was severely affected by 33 % defoliation prior to pea size and 66 % defoliation prior to véraison. Defoliation from véraison increased the fresh mass:cane mass ratio. Vines defoliated 33 % from pea size and véraison had leaf areas in accordance with the 10-12 cm^2 which is generally required to ripen one gram of fruit. Budding percentage was significantly improved by partial defoliation. Bud fertility was only improved by 33 % defoliation and was favoured by partial defoliation from just after bud break. A canopy microclimate beneficial to pest and disease control and higher grape quality was created by partial defoliation.

Subterranean growth was significantly stimulated by 33 % defoliation of the canopy, particularly when applied from pea size stage. Root density and the development of fine to medium diameter roots were increased. Yield and cane mass of partially defoliated vines coincided with subterranean growth. Generally, defoliations from early developmental stages (bud break, berry set) reduced root development compared to later defoliations (pea size, véraison). Partially defoliated vines had higher total root numbers in all soil layers. Roots were preferentially located in the 0-800 mm zone. Partially defoliated vines appeared to respond to the loss of leaves by forming new roots, creating a more efficient nutrient absorption capacity and utilization of soil and available water. It was evident that capacity of root systems may be misrepresented if only total root masses are determined.

In spite of much lower leaf areas, total soluble solids in berries of partially defoliated vines were still significantly higher than that of non-defoliated vines in some cases. Sugar accumulation was not affected by the time at which defoliation was commenced. Though not significant, total titratable acidity was generally slightly higher for partially defoliated vines and decreased the later defoliation commenced.

Grapes were extracted simultaneously for sugars and organic acids. Reliable recoveries were obtained. The extraction procedure comprised the extraction of freeze-dried berries with deionised water for 60 min. at room temperature, sample:solvent ratios of 1 g dry mass/50 cm^3 water up to véraison, 1 g dry mass/12,5 cm^3 water at ripeness and adsorption on 2 cm^3 anion exchange resin. Good resolution and reproducibility were obtained during HPLC analyses. Results of HPLC analyses compared well with those of enzymatic analyses. Glucose and fructose concentrations were unaffected by partial defoliation, whereas the concentration of tartaric acid was slightly increased and that of malic acid slightly decreased on a mg/g dry berry mass basis. The anthocyanin concentration of berry skins generally increased as a result of partial defoliation and increased the later during the growth season defoliation was commenced. Phenolic content was unaffected by partial defoliation. Improved pigmentation of berry skins probably resulted exclusively from better light conditions in the canopy interior. Berry volume decreased with increasing defoliation and tended to increase the later defoliation was commenced, thus lowering the pulp:skin ratio. The effects on berry volume and composition suggest higher grape quality. Wines made from grapes of partially defoliated vines were scored significantly higher for cultivar character and overall wine quality, regardless of the severity of defoliation or the developmental stage defoliation was commenced.

It was evident that partial defoliation as applied in this study changed the general metabolism of vines, mainly in terms of more favourable source:sink ratios, resulting in more efficient photosynthesis, subterranean performance and canopy microclimate. Important principles for use in canopy management strategies were established. Among others, the results suggest that an even removal of 33 % of leaves opposite and below bunches during the period from flowering or berry set to pea size may be applied. The results further suggest that existing vigorous and dense-canopy vines may be 33 % defoliated evenly on the lower half of the shoot (canopy) from pea size or véraison stage. This hypothesis was implemented and proved to be effective in improving canopy microclimate, photosynthetic activity and yield, whilst inhibiting vegetative growth. Grape and wine quality were improved with an increase in cultivar character.

On the whole, partial defoliation as applied in this study, is recommended as canopy management practice to facilitate the abolishment of deleterious effects of excessive vegetative growth and canopy density on balanced metabolic activity, fruit and wine quantity and quality as well as the longevity and healthiness of grapevines. On the contrary, these aspects can be improved when partial defoliation is applied correctly. It is, however, emphasized that partial defoliation can not solely be used as remedying or general practice, but that other canopy management practices such as suckering, shoot positioning, tipping and topping are equally important and should also be considered to obtain the required goal.