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INFLUENCE OF BASAL LEAF REMOVAL AND CROPPING LEVEL ON GROWTH, YIELD, COLD HARDINESS AND BUD FRUITFULNESS IN SEYVAL GRAPEVINES (Vitis sp.)

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INFLUENCE OF BASAL LEAF REMOVAL AND CROPPING LEVEL ON GROWTH, YIELD, COLD HARDINESS AND BUD FRUITFULNESS IN SEYVAL GRAPEVINES (*Vitis sp.*)

By

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ABSTRACT

INFLUENCE OF BASAL LEAF REMOVAL AND CROPPING LEVEL ON GROWTH, YIELD, COLD HARDINESS AND BUD FRUITFULNESS IN SEYVAL GRAPEVINES (*Vitis sp.*)

By

Maria Teresa Franco de Barros

Basal leaf removal effects on growth and yield, and on the cold hardiness and fruitfulness of the shoot region subjected to leaf removal, were studied in differentially cropped own-rooted Seyval grapevines, whether young potted or mature field-grown vines.

Basal leaf removal had no significant effect on vine growth, flower-bud differentiation and primary bud hardiness, in both potted and mature vines. Evidence from potted vines suggested that an eventual compensation for leaf removal was more effective following leaf removal at berry pea size than at veraison. The net CO_2 assimilation rate per unit of leaf area (A) was enhanced by leaf removal at pea size, unlike at or shortly after veraison. Leaf removal had no significant effect on dry matter partitioning in potted vines, and little effect on starch and soluble carbohydrate concentration in canes, roots, and trunk in the early fall, mid- and late winter. In the few cases where a significant effect was found, carbohydrate concentration was higher in potted vines treated at pea size than in those treated at veraison. The presence of fruits increased A, especially on potted vines. Cane and trunk soluble carbohydrate per dry weight in the early fall (1.5 weeks after harvest) were higher in fruiting (3Cl) than in non-fruiting (0Cl) potted vines, in

correspondence to fall cane hardiness, but there was no clear relationship between hardiness and carbohydrate levels in the winter and early spring. Flower-bud differentiation was lower on 3Cl than on 0Cl vines.

On mature vines, basal leaf removal improved the light microclimate in the cluster region with no significant effect on yield and fruit composition. In 1990, when canopies were denser, leaf removal at veraison reduced the percentage of rotten clusters on the vines thinned to 1.5 clusters per node retained (1.5), but not on the less vigorous, unthinned (NT) vines. Carbohydrate storage in 1989 was presumably impaired due to an early leaf killing frost and, in mature vines, to a heavy 1989 crop. Field cold injury was greater in the 1989/90 than in the 1990/91 dormant seasons, as evidenced by a higher percentage of shootless nodes in 1990 than in 1991. This percentage was not significantly affected by leaf removal, and was lower on non-fruiting (0) than on NT vines. In 1990 the number of clusters per primary shoot was larger on 0 than on NT vines. Differences in yield, hardiness, cane maturity, and primary bud fertility between 1.5 and NT vines were not significant in any trial year.

To my parents who, from long ago, prepared the ground for this thesis, and my fiancé, the sunlight in its development. To my true friends.

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CHAPTER II

INTRODUCTION

Photosynthesis is the basis for the vegetative and reproductive processes in plants. However, not only is carbohydrate synthesis important, but so too is carbohydrate partitioning into the different plant organs.

During most of the vegetative season, the processes of fructification, growth, and floral differentiation for the next crop occur simultaneously in grapevines, thereby competing for carbohydrates. By the end of the season, enough carbohydrates should be available for accumulation in storage organs. An adequate accumulation of reserves assumes a special meaning in cold regions given the important role that carbohydrates are considered to play in the development and maintenance of cold hardiness (Howell, 1988).

Because the leaves are the main photosynthetic organs, leaf area and carbohydrate availability are intimately related. Leaf removal, as a means to improve the microclimate in the cluster zone, can be a practice of interest mainly for excessively vigorous grapevines because it may reduce bunch rot and enhance ripening (Wolf et al., 1986; Koblet, 1987,1988; Kliewer and Bledsoe, 1987; Bledsoe et al., 1988; Smith et al., 1988; English et al., 1989). However, leaf removal can also result in severe carbohydrate depletion, with serious consequences to the grapevines. Hence, it is no wonder that conflicting reports exist on the effects of leaf removal on vine growth and on yield parameters and quality. Even though leaf removal is an

existing management practice with proven economic benefits on high value cultivars (Smith et al., 1988), it is still uncertain 'how, when, where, and how many leaves must be removed' (Hunter and Visser, 1990).

The research team led by Dr. G. S. Howell at Michigan State University has been a pioneer in studying the impact of defoliation and other cultural practices on the cold hardiness of grapevines, beyond the effects on growth and productivity parameters. The defoliation studies conducted have involved the complete defoliation of the vines (Stergios and Howell, 1977; Howell et al., 1978) and either complete defoliation or the defoliation of alternate vine portions (cordon, shoots, leaves) (Mansfield and Howell, 1981). In the present study, leaves were removed from the cluster region, hence the basal portion of the shoots. Basal leaf removal implies that the buds axillary to the leaves removed are likely to be retained at pruning and give rise to the new shoot growth and crop in the following season. Therefore, the viability of these buds (which in cold climates is largely conditioned by their cold hardiness), as well as their fruitfulness, have an important cultural significance.

The main source of photosynthate for a bud seems to be the leaf subtending it (Hale and Weaver, 1962; Smart et al., 1982b). Hence, leaf removal may have a negative effect on the carbohydrate status of the buds axillary to the leaves removed and, consequently, on their fruitfulness and cold resistance. On the other hand, several authors suggested that grapevines have compensatory mechanisms for losses in leaf area, which may result in increased photosynthetic activity of the remaining foliage and increased leaf area on lateral shoots (Buttrose, 1966; Kliewer, 1970; Kliewer and Fuller, 1973; Hofäcker, 1978; Hunter and Visser, 1988a,b; Koblet, 1988;

Reynolds and Wardle, 1989a; Candolfi-Vasconcelos, 1990; Hunter and Visser, 1990). Moreover, an alteration in the carbohydrate transport was reported in response to leaf removal (Quilan and Weaver, 1970). These responses might attenuate, to some extent, a localized carbohydrate depletion due to leaf removal.

The objectives of this study were: 1) to investigate whether photosynthesis can be enhanced by removal of a few basal leaves on vines under different cropping regimes; 2) to assess the basal leaf removal and cropping effects on dry matter partitioning and on non-structural carbohydrate levels namely in the restricted shoot region subjected to leaf removal; 3) to evaluate the treatment effects on the cold hardiness and fruitfulness of the treated shoot region and their probable relationship with 1) and 2); 4) to evaluate the vine growth and yield responses to basal leaf removal and cropping level, and potential limitations of basal leaf removal derived from the localized effects analyzed in 3). The study was conducted on Seyval grapevines (Seyve-Villard 5-276), one of the most important white wine cultivars in the Eastern United States (Reynolds et al., 1985; Kaps and Cahoon, 1989). This French-American hybrid has a propensity to overcrop and produces large and compact clusters, extremely susceptible to bunch rot (Botrytis cinerea Pers). Leaf removal in the cluster region could be helpful in reducing this problem, if no adverse effects, namely on cold hardiness, are found to result from this practice.

LITERATURE REVIEW

Radiation Microclimate and Grapevine Physiology

Introduction

Radiation microclimate is known to influence several physiological processes in plants and in the grapevine in particular. The effects of radiation on plant physiology are mainly exerted through the supply of energy for photosynthesis, the supply of specific wavebands that regulate photomorphogenesis, and tissue heating (Kliewer, 1982).

Light is the region of the electromagnetic radiation spectrum to which the human vision is sensitive (Smart, 1987). However, for simplification, the term 'light' will refer in this review to Photosynthetically Active Radiation (PAR, 400-700 nm waveband). The flux of PAR will be termed Photosynthetic Photon Flux (PPF) and expressed as μmol of photons $m^{-2}s^{-1}$.

Light is the climatic component most affected by canopy density (Smart, 1985). In the interior of dense canopies, PPF is reduced to less than 1% of the above canopy level. Moreover, in dense canopies, the ratio 660 nm/730 nm radiation (red/far red) may decrease to less than 10% of the ambient (Smart, 1982; Smart et al., 1982a). This qualitative change in radiation has important physiological implications because it affects the phytochrome equilibrium and, hence, the processes

controlled by this pigment (Smart, 1987).

Shaded grapevine canopies exhibit an inferior development of shoots, buds, leaves and berries (Shaulis and Smart, 1974; Kliewer, 1982). In the interior of dense canopies, a reduced photosynthetic rate (Kriedemann, 1968; Kriedemann and Smart, 1971; Smart, 1974; Kliewer, 1982) and early leaf abscision (Shaulis and Smart, 1974; Kliewer, 1982) are observed. Shoots are affected in their carbohydrate content, periderm formation and vascular development (Shaulis and Smart, 1974; Kliewer, 1982). Fruitfulness (Shaulis et al., 1966; May et al., 1976; Shaulis and May, 1971; Shaulis and Smart, 1974) and cold hardiness (Shaulis and Smart, 1974; Stergios and Howell, 1977; Howell et al., 1978; Kliewer, 1982; Wolpert and Howell, 1985a; Howell, 1988) are decreased. Berry growth and composition are markedly impaired (Shaulis and Smart, 1974; Kliewer, 1982; Reynolds et al., 1985; Smart, 1987; Kliewer et al., 1988; Morrison, 1988; Archer and Strauss, 1989; Morrison and Nobel, 1990).

Smart (1987) stressed that a difficulty exists in determining the extent to which the radiation effects on fruit composition might be phytochrome mediated, as opposed to photosynthetic or thermal effects. The same might apply to the radiation effects on fruitfulness and cold hardiness, even though in grapevines the involvement of phytochrome in these processes is not clear, as can be inferred from further sections.

Light and Grapevine Photosynthesis

The light response curve of photosynthesis in grapevine leaves was shown to follow a rectangular hyperbola (Kriedemann, 1968; Kriedemann and Smart, 1971).

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In a study with cv. Gewurztraminer, Smart (1985) found a light compensation point of 15-20 μmol $m^{-2}s^{-1}$, i.e., less than 1% of full sunlight. Light saturation occurred at about 700 μmol $m^{-2}s^{-1}$, with a maximum photosynthetic rate of 0.55 mg CO_2 $m^{-2}s^{-1}$. Grapevines grown under reduced illumination show a lower light compensation point and lower saturation values than those developed under full sunlight (Kriedemann, 1968). Levels of PPF above saturation may result in decreased photosynthetic rate due to photoinhibition (Powles, 1984).

A wide range of values for the light compensation point, the light saturation levels, and the maximum photosynthetic rate in grapevine leaves are found in the literature, as reviewed by Carbonneau (1976), Koblet (1985), and Chaves (1986). The differences encountered might be due not only to the cultivar under study but also to the conditions of measurement. Indeed, temperature (Buttrose and Hale, 1971; Kriedemann, 1968, 1977) and vine water status (Kriedemann and Smart, 1971; Smart, 1974; Kriedemann, 1977) are important factors in determining the photosynthetic response. Other factors known to influence grapevine photosynthesis and that might also explain the differences found in the photosynthetic responses to light include leaf age (Kriedemann, 1968, 1977; Kriedemann et al., 1970), time of the day (Kriedemann and Smart, 1971; Loveys, 1984; Loveys and During, 1984; Chaves, 1986; Chaves et al., 1987; Downton et al., 1987), seasonal trends (Kriedemann, 1977; Pandey and Farmahan, 1977; Scholefield et al., 1982; Koblet, 1988), and source/sink relationships (Humphries and Thorne, 1964; Kriedemann and Lenz, 1972; Hofäcker, 1978; Herold, 1980; Chaves, 1984; Hunter and Visser, 1988a,b; Kaps and Cahoon, 1989; Candolfi-Vasconcelos, 1990).

The photosynthetic rates measured on individual leaves and those of the whole vine are not necessarily related. In a study with potted Seyval grapevines, Edson (1991) found no correlation between single leaf and whole vine photosynthesis. This was attributed, among other reasons, to the fact that the global plant photosynthesis results from the activity of a continuum of leaves of different physiological ages, some of them assimilating under suboptimal conditions. By contrast, the leaf angle to the sun, for instance, was optimized when measuring photosynthesis at individual leaves (Edson, 1991).

On standard canopies, the preferred leaf orientation is more vertical than horizontal (Smart, 1985). In Concord canopies Smart et al. (1982a) observed that leaves preferably formed an angle of about 45°C to the horizon. As quoted by Kriedemann and Smart (1971), the photosynthesis of the whole canopy is higher when the outer leaves are more or less pendulous, allowing for a greater penetration of direct sunlight.

Canopy management practices to maximize the interception of PAR in grapevine canopies have been intensively investigated since the pioneering studies of Dr. N. Shaulis in New York State (Smart et al., 1990). Canopy division and reduced vine spacing were both shown to enhance light interception by increasing canopy length per hectare (Shaulis et al., 1966; Shaulis and Smart, 1974; Carbonneau et al., 1981; Smart, 1985; Smart et al., 1990).

Close, high, vertical, and north-south oriented canopy walls allow for maximal light interception. However, they should not be so close and high as to result in a shaded canopy base (Smart, 1985; Smart et al., 1990). Divided canopy systems of

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training to improve the radiation microclimate include Geneva Double Curtain (GDC) (Shaulis et al., 1966), Lyre (Carbonneau et al., 1981; Carbonneau, 1985), and Te Kauwhata Two Tier (Smart, 1985).

Additional practices to improve the radiation microclimate in canopies, such as vigor control, shoot positioning, leaf removal, and shoot trimming are discussed by Kliewer (1982), Koblet (1988), and Smart et al. (1990).

Radiation Microclimate and Grapevine Fruitfulness

Buttrose (1974) presented a review on the climatic factors influencing fruitfulness in grapevines. Fruitfulness of grapevine buds is strongly promoted by temperature (an optimum range of 30-35°C being reported by Buttrose, 1969a), and light (May and Antcliff, 1963; May, 1965; Shaulis et al., 1966; Buttrose, 1970, 1974; Shaulis and May, 1971; Shaulis and Smart, 1974; Kliewer, 1982; Smart et al., 1982b; Morgan et al., 1985). These factors can readily be assumed to interact in influencing flowering and fruiting under field conditions.

May and Antcliff (1963) found that light intensity was important for flower bud formation in 'Sultana' grapevines and that shading inhibited fruitfulness when applied during the period of inflorescence initiation. The improvement of the light conditions in grapevine canopies may not only increase the fertility of the buds but also the number of buds that originate shoots (Kliewer, 1982). Moreover, light, along with temperature, is a major factor in influencing fruit set in grapevines (Roubelakis and Kliewer, 1976).

The importance of light exposure for flower bud formation and fruiting of fruit

trees is also well documented (Jackson and Sweet, 1972; Cain, 1973; Jackson, 1980; Flore, 1981). However, neither in grapevines (Kliewer, 1982) nor in fruit trees (Lakso, 1986) is the mechanism for this light effect entirely elucidated.

The hypothesis that the carbohydrate-nitrogen ratio was important for flower initiation in perennial fruit crops was already largely abandoned in the early 60's, even though carbohydrates were still considered essential for satisfactory flowering (May, 1965). The view that carbohydrates may play an important role in bud differentiation still exists, at least in the case of the grapevine (Shaulis and May, 1971; Buttrose, 1974; Winkler et al., 1974; Bains et al., 1981; Smart et al., 1982b; Morgan et al., 1985), even though there is insufficient evidence to suggest that bud development is limited by nutritional as opposed to hormonal regulation (Smart et al., 1982b). In grapevines, cytokinins have been shown to promote the growth of inflorescences (Mullins, 1967) and flowers (Pool, 1975), the development of pistils by staminate flowers (Negi and Olmo, 1972), and the production of inflorescences and flowers in tendrils (Srinivasan and Mullins, 1978). Cytokinins have also been implicated in the flowering of apple trees (Hoad and Abbott, 1986) and other species (Leopold and Kriedemann, 1975). Jackson and Sweet (1972) agreed with the argument of Evans (1969) that the differentiation of a flower, as of any other organ, is dependent on the spatial and temporal interaction of endogenous hormones and assimilates, rather than on a specific floral stimulus. This argument seems suitable for flower-bud initiation in woody plants (Jackson and Sweet, 1972).

The yield of grapevines is determined, among other factors, by the development of the buds and their inflorescence primordia, and the accumulation of

photosynthate in the season preceding harvest (Shaulis and May, 1971; Morgan et al., 1985). Smart et al. (1982b) observed a positive correlation between the illuminance of the leaf subtending a bud (evaluated by hemispherical photography) and the productivity of the shoot(s) arising from that bud in the following year. These authors suggested that a reason for this relationship might be that the leaf subtending the bud is the main source of photosynthate for that bud.

It is still under debate, though, whether the fertility of a bud is increased due to improved light conditions of its subtending leaf or to improved exposure of the bud itself (Kliewer, 1982). May (1965) found that in cv. Sultana shading of buds without shading of leaves reduced inflorescence formation. The leaf primordia inside shaded buds were etiolated, which supported a previous hypothesis (May, 1964) that initiation and development of inflorescences was determined, at least in part, by the growth of the vegetative components of the mixed grapevine bud. May (1965), however, did not rule out the idea of an external carbohydrate supply. Indeed, shading of buds might have reduced their import of assimilates at the time when inflorescence initiation was to occur, and thereby result in the lack of assimilates at the apex region where initiation should take place (May, 1965).

Roubelakis and Kliewer (1976) studied the influence of light/temperature regimes on the fruit set of five grapevine cultivars, and suggested that an insufficient availability of assimilates was responsible for the failure of fruit set observed at reduced light/temperature levels. Under these conditions, neither the cytokinin 6-benzyladenine nor CCC were effective in promoting fruit set. Both growth regulators have, however, been widely reported to enhance fruit set under favorable climatic

conditions, the former supposedly by attracting assimilates to the cluster and the latter by diverting assimilates from shoot tips to developing ovaries (Roubelakis and Kliewer, 1976).

Photoperiod does not influence flowering in many fruit and forest trees (Jackson and Sweet, 1972). Grapevine buds tend to be more fruitful when developed under long days, but the operative factor may be the extra production of photosynthates associated with long days (Buttrose, 1974). Buttrose (1969b) could not find an effect of photoperiod on grapevine fruitfulness. However, contradictory results have been obtained in studies under controlled vs. natural environments (Smart et al., 1982b). Varietal differences may also influence the response of fruitfulness to day length (Buttrose, 1969b).

The role of radiation quality in grapevine fruitfulness has not been conclusively determined. May (1965) observed that the shading of buds with different materials reduced the percentage of fruitful buds but this effect seemed to be related to a reduction in radiation intensity rather than to a change in quality. This study is sometimes quoted to illustrate that the quality of radiation is not important for grapevine fruitfulness (Morgan et al., 1985). However, Morgan et al. (1985), reported that both PPF and radiation quality influenced the fruitfulness of cv. Muller Thurgau, but the red/far red ratio had a minor effect, in contrast with PPF. There was a consistent trend for reduction in the number of clusters per shoot in the treatments with low red/far red ratio relatively to the treatments with a high ratio. Nevertheless, the number of flowers per cluster was not related to the red/far red ratio, neither was the fruitfulness index (number of flowers/total buds) (Morgan et al., 1985).

Given the diversity of the results obtained, the involvement of phytochrome in the grapevine fruitfulness needs to be further investigated (Kliewer, 1982; Smart et al., 1982b).

Radiation Microclimate and Cold Hardiness

Light and temperature are the main environmental effects controlling the development of cold hardiness in plants (Levitt, 1980). Photoperiod is also an important factor in the cold acclimation of some species (van Huystee et al., 1967; Howell and Weiser, 1970; Williams et al., 1972).

The major need for light seems to be due to a need for photosynthates (Levitt, 1980). A number of studies involving a wide range of species with different light cycles have supported the view that qualitative and quantitative changes in carbohydrates may be important for the development and maintenance of cold hardiness (Levitt, 1956, 1980). Changes in other cellular substances such as lipids (Ketchie, 1966; Kuiper, 1970; Uemura and Yoshida, 1984; Yoshida and Uemura, 1984; Lynch and Steponkus, 1987), nucleic acids (Li and Weiser, 1967; Brown and Sasaki, 1972; Gusta and Weiser, 1972; Guy et al., 1985; Mohapatra et al., 1987; Gilmour et al., 1988; Hajela et al., 1990), proteins (Siminovitch and Briggs, 1949, 1953; Li and Weiser, 1967; Brown and Sasaki, 1972; Gusta and Weiser, 1972; Yoshida and Uemura, 1984; Guy et al., 1985; Robertson et al., 1987; Mohapatra et al., 1988; Guy, 1990), and growth regulators, namely ABA (Irving, 1969; Perry and Hellmers, 1973; Daie and Campbell, 1981; Chen et al., 1983; Bray, 1989) have also been investigated for their possible involvement in cold acclimation. These metabolic

changes are necessarily related to alterations in enzyme activity or in gene expression (Bray, 1989). Levitt (1980) and Guy (1990) reviewed the physiological role that the metabolic and physiological changes might play in the hardening processes.

In mulberry (Sakai, 1960), peach (Layne and Ward, 1978), red-osier dogwood (Chen and Li, 1977), apple (Raese et al., 1978), and several other species (Levitt, 1956, 1980), a close relationship was found between the degree of hardiness and the levels of certain sugars or sugar derivatives. Sugars usually increase in fall as plants harden and decrease in spring with dehardening (Siminovitch et al., 1953; Levitt, 1956).

Even though carbohydrate conversions (namely starch-sucrose) are widely known to be related with hardening and dehardening, the enzymology of carbohydrate metabolism during cold acclimation is not yet elucidated (Guy, 1990).

The nature of the carbohydrates accumulated during cold hardening and of the prevalent carbohydrate has been found to vary from species to species and among different climates (Siminovitch et al., 1953). In grapevines, a conversion of starch to sugars (sucrose and reducing sugars) during the fall and early to mid-winter was reported by Richey and Bowers (1924), Schrader (1924), Winkler and Williams (1945), and Kliewer (1967), but its relationship with cold hardiness was not investigated in these studies. Recently, though, a positive correlation was noticed between sugar levels and cold hardiness in cv. Cabernet Sauvignon (Wample et al., 1988).

In contrast with the above findings, Steponkus and Lanphear (1968) found no parallelism between sugar content and hardiness levels in English ivy. A similar lack

of correlation was observed in other studies (Levitt, 1980). Despite these results, Steponkus and Lanphear (1968) did not deny to carbohydrates a role in the cold acclimation processes. Rather, they suggested that acclimation does not result merely from an accumulation of sugars and that a precise parallelism between the two would only be expected if sugar content were the rate limiting step in acclimation.

Some possible roles of carbohydrates in hardiness have been proposed. A suggestion by Levitt (1956) was that sugars would have an osmotic role in hardiness. Accumulation of sugars in the vacuole would lower the freezing point sufficiently to prevent freezing. However, there is evidence to suggest that the increase in sap concentration can solely account for a small increase in hardiness and may be important only for tender plants, unable to survive freezing (Levitt, 1956). In certain plants, such as hardy winter cereals, cell wall polysaccharides seem to play a role in hardiness by interfering with ice formation. Such interference resulted in more imperfect ice crystal development, which was associated with hardier tissues (Olien, 1965, 1967).

Two other roles of carbohydrates, with more pronounced effects on hardiness have been proposed: carbohydrates might increase hardiness by providing the energy required for the hardening processes or by preventing the denaturation of proteins (i.e., act as cryoprotectants) (Howell and Stackhouse, 1973).

Energy is needed for the acquisition of cold hardiness and its maintenance during mid-winter, and for hardiness recovery (rehardening) after spells of warm weather. Carbohydrates might therefore be important to meet these energetic demands (Howell, 1988).

In many plants, exposure to low temperatures leads to the accumulation of cryoprotectants, namely the carbohydrates sucrose, raffinose, and sorbitol. Of these, sucrose is the most commonly found in freezing-tolerant species (Guy, 1990). It was suggested that sugars might exert a direct protection of proteins either by replacing the water of hydration of the protein or by increasing the firmness of water binding (Steponkus and Lanphear, 1968). Sugars might also stabilize the membranes by interacting with the polar headgroups of the phospholipids (Anchordoguy et al., 1987). The role in membrane stabilization is of primordial importance, as several studies have indicated that cell membranes are one of the major targets of freezing injury, if not the primary site of injury (Steponkus and Wiest, 1978; Levitt, 1980; Palta et al., 1981; Steponkus, 1984). Heber and Santarius (1964), for instance, showed that in mitochondria and chloroplasts, sucrose could prevent the uncoupling of phosphorylation resulting from freezing.

Regardless of the mode of action of carbohydrates, and despite the fact that a cause-effect relationship between sugar levels and cold hardiness is not established, a high level of stored carbohydrates is considered important for cold hardiness of grapevines (Howell, 1988; Wample et al., 1988), and other woody perennials such as sour cherry (Howell and Stackhouse, 1973). Therefore, cultural practices that optimize light interception by the foliage (e.g. adequate training and pruning) and contribute to healthy leaves (e.g. pest and disease control) are important to increase hardiness because they result in improved carbohydrate production (Howell and Dennis, 1981; Howell, 1988).

Photoperiod was shown to induce cold acclimation in some woody species. In

apple trees (Howell and Weiser, 1970) and red-osier dogwood (van Huystee et al., 1967) cold acclimation occurs in two stages. The first stage is probably triggered in nature by short days (or, preferably, long nights) even though short days are not a necessary prerequisite for acclimation. Indeed, the first hardiness plateau (-25°C to -30°C in Haralson apple) can be induced not only by short days per se, but also by low temperature (Howell and Weiser, 1970). Other factors such as endogenous growth cycles or radiation quality may also be involved in the first stage of acclimation (Howell and Weiser, 1970). Temperature seems to be an absolute prerequisite for the second stage of acclimation, which can result in survival to temperatures as low as -55°C in Haralson apple trees (Howell and Weiser, 1970) or -196°C in red-osier dogwood (Smithberg and Weiser, 1968).

In stems of pine and English ivy and in the bark of black locust, a single-stage acclimation is observed, as quoted by Wolpert and Howell (1985b). This does not necessarily imply that photoperiod is not involved, given that the onset of low temperatures may coincide with the short-day effect, resulting in a single-stage pattern of acclimation (Wolpert and Howell, 1985a).

Photoperiodic effects on cold acclimation are probably associated with the production of translocatable hardiness promoters in 'short day' leaves (Irving and Lanphear, 1967c) and of cold hardiness inhibitors in 'long day' leaves (Irving and Lanphear, 1967b). In contrast, no translocatable factors seem to be involved in the low temperature-induced cold acclimation (Howell and Weiser, 1970).

In grapevines, photoperiod does not seem to influence acclimation (Wolpert and Howell, 1986b). It has often been assumed that growth cessation is a prerequisite

for the development of cold acclimation, even though it was shown that dormancy is not required (Irving and Lanphear, 1967a,b; Howell and Weiser, 1970). Growth cessation in grapevines seems to be under photoperiodic control, but the need of growth cessation for cold acclimation in this species is questionable (Wolpert and Howell, 1986a,b)

Leaf Removal Effects on Vine Growth and Yield

Introduction

Leaf removal is a recognized canopy management practice to improve the microclimate in the cluster zone, and thereby enhance ripening and reduce fungal diseases, namely bunch rot caused by Botrytis cinerea Pers. (Winkler et al., 1974; Weaver, 1976; Wolf et al., 1986; Gubler, 1987; Kliewer and Bledsoe, 1987; Koblet, 1987, 1988; Bledsoe et al., 1988; Smith et al., 1988; English et al., 1989). However, because leaf removal represents the removal of the main source of photosynthates, this practice can have a negative impact on the carbohydrate status of the grapevine and, therefore, on vine growth (Buttrose, 1966; Kliewer and Fuller, 1973; Howell et al., 1978), yield components (Weaver, 1963; Buttrose, 1966; May et al., 1969; Kliewer, 1970; Kliewer and Antcliff, 1970; Howell et al., 1978; Mansfield and Howell, 1981; Candolfi-Vasconcelos and Koblet, 1990), and cold hardiness (Stergios and Howell, 1977; Howell et al., 1978; Mansfield and Howell, 1981).

Several authors suggested that grapevines can compensate, to some extent, for losses in the functional leaf area by increasing the photosynthetic activity of the

remaining foliage and by expanding the leaf area on lateral shoots (Buttrose, 1966; Kliewer, 1970; Kliewer and Fuller, 1973; Hofäcker, 1978; Hunter and Visser, 1988a,b; Koblet, 1988; Reynolds and Wardle, 1989a; Candolfi-Vasconcelos, 1990; Candolfi-Vasconcelos and Koblet, 1990). Moreover, Hofäcker (1978), Hunter and Visser (1989) and Candolfi-Vasconcelos (1990) reported that defoliation increased the chlorophyll content of the remaining leaves.

Photosynthetic compensation for biological or physical leaf injury has also been reported for fruit (Hall and Ferree, 1976; Proctor et al., 1982) and forest species (Bassman and Dickmann, 1982), among others. Kriedemann (1977) attributed the increased photosynthetic rate following leaf removal to enhanced stomatal opening, increased enzyme activity, and freer carbohydrate movement to the growth sites. Candolfi-Vasconcelos (1990) observed that leaf removal led to an increase in both stomatal and mesophyll conductances, in agreement with previous reports (Kriedemann, 1977).

Compensation may only be partial (Chaves, 1986; Candolfi-Vasconcelos, 1990), and this might explain, for instance, why in the study of Kliewer and Fuller (1973) a significant decrease in the growth of roots, trunks and shoots was observed in severely defoliated vines (Chaves, 1986).

The ultimate response of a particular grapevine cultivar to leaf removal will depend not only on the technique of removal by itself but also on environmental factors, as will be discussed in the following sections.

Leaf Removal Effects on Vine Growth and Yield Components

Buttrose (1966) studied the effects of defoliation on the growth of roots, stems, and berries in cv. Muscat of Alexandria. He found that root dry weight was the most affected parameter, followed by dry weight of berries, shoots and trunks. In contrast, Kliewer and Fuller (1973) reported that in Thompson Seedless, leaf removal reduced more severely the accumulation of dry matter in the trunk than in the roots and canes.

Several authors reported a reduction in berry weight following defoliation (Weaver, 1963; Buttrose, 1966; May et al., 1969; Kliewer and Antcliff, 1970; Kingston and van Epenhuijsen, 1989). Others observed a decreased bud fruitfulness (number of clusters per node and/or number of berries per cluster) (May et al., 1969; Mansfield and Howell, 1981). In cv. Thompson Seedless, May et al. (1969) reported a 10% to 80% reduction in yield per node in the season following defoliation, the effect increasing with increased defoliation. Most of this reduction was accounted for by a decrease in the number of clusters per node (May et al., 1969). Similarly, leaf removal was shown to reduce flower bud initiation in fruit trees such as plums, apples, pears, and cherries (for references see Jackson and Sweet, 1972). The effect of leaf removal on flower initiation might be attributed to a loss of photosynthates or to a change in the hormonal balance (Jackson and Sweet, 1972).

The above results sharply contrast with those of Kliewer and Bledsoe (1987) and Bledsoe et al. (1988). In studies with Sauvignon blanc grapevines, these authors observed that leaf removal improved fruit composition without affecting the yield components (cluster number and weight, berry weight). Moreover, in the same

cultivar, Kliewer et al. (1988) observed that, on average over a period of three years, neither time nor severity of leaf removal significantly affected the yield components. In the third year of the trial, the vines subjected to the most intense leaf removal (removal of basal leaves plus leaves at the top of the canopy) were even significantly superior in number of clusters per shoot, flowers per inflorescence, and fruit set.

Some factors that may account for the discrepancies observed include: a) variety and clone; b) site climate; c) fruit exposure to sunlight; d) light environment, age, and position of the leaves removed; e) timing and severity of removal, and f) vine size (Kliewer and Bledsoe, 1987; Reynolds and Wardle, 1989b; Zoecklein, 1989).

Bledsoe et al. (1988) noted that most of the defoliation work preceding their study had been done on cv. Thompson Seedless in hot climates and used severe defoliation. Under these conditions, the berries would receive a substantial amount of direct solar radiation after defoliation, and their temperature could increase considerably. Radler (1965) reported that a high temperature by itself significantly reduced berry weight in cv. T. Seedless. In contrast, the trial of Bledsoe et al. (1988) was performed in a cool to moderate climate. Moreover, the number and position of the leaves removed were such that the fruits were not exposed to direct solar radiation for prolonged periods. This might explain the lack of berry weight reduction (Bledsoe et al., 1988).

Mansfield and Howell (1981) found that partial defoliation (50%) of Concord grapevines reduced cold hardiness and fruitfulness and delayed bud break in a manner dependent on the distance between the foliated and the defoliated parts of the vine.

In cv. Pinot noir, leaf removal within a critical period (up to 2-3 weeks after full bloom) resulted in intense flower and fruitlet abscision and reduced bud fertility, thereby decreasing the current year's and the following year's yield. Moreover, the presence of leaves on lateral shoots during fruit maturation was considered important to assure fruit quality and adequate starch reserves in the wood (Candolfi-Vasconcelos, 1990; Candolfi-Vasconcelos and Koblet, 1990).

Leaf Removal Effects on Fruit Quality

Some inconsistencies have also been found for the effects of leaf removal on berry composition, which might be explained, at least in part, by the same factors mentioned above.

Buttrose (1966) and Kliewer and Antcliff (1970) found a significant decrease in fruit soluble solids concentration, but in these studies an intense defoliation was applied. Several defoliation experiments have been conducted in an attempt to assess the leaf area required to mature a given weight of grapevine fruits. Numerous values have been obtained, ranging from 0.5 to 1.7 m^2/Kg of fruit, depending upon variety and experimental conditions (for references see Carbonneau et al, 1977; Chaves, 1986; Williams et al., 1987). In field experiments to determine this relationship the functional leaf area per vine, related to the canopy microclimate, has often been overlooked which may account for the diversity of results obtained (Williams et al., 1987).

Kliewer et al. (1988) reported that Sauvignon blanc grapevines with well exposed fruits prior to leaf removal showed no significant difference in fruit

composition relative to non-defoliated vines. In contrast, leaf removal improved fruit composition in vines subjected to training systems causing highly shaded fruits (4 to 5% of ambient PPF). The removal of leaves around the cluster between fruit set and veraison increased the total soluble solids and decreased the titratable acidity, malic acid, pH, and potassium concentration in the fruits (Bledsoe et al., 1988; Kliewer et al., 1988).

Smith et al. (1988) noticed that the most marked effect of leaf removal on fruit composition of Sauvignon blanc, Chardonnay and Cabernet Sauvignon was a reduction in titratable acidity, largely due to a decrease in malic acid; no significant reduction was observed when leaf removal was applied after veraison.

Leaf removal may affect fruit composition as a result of a change in radiation quality and temperature (Smart, 1987; Bledsoe et al., 1988; Zoecklein, 1989) and in photosynthesis and pattern of assimilate movement (Quilan and Weaver, 1970; Bledsoe et al., 1988; Zoecklein, 1989). Temperature will increase due to a greater exposure to sunlight caused by leaf removal. Such an increase, even if small, may explain the increased soluble solids in the fruits and the reduced titratable acidity and malic acid (Smart, 1982; Bledsoe et al., 1988; Kliewer et al., 1988; Zoecklein, 1989). The increase in soluble solids may also result from enhanced photosynthetic efficiency of the remaining leaves and increased movement of assimilates towards the cluster, due to the removal of basal leaves (Bledsoe et al., 1988). Moreover, a higher red/far red ratio was observed in the cluster region following leaf removal. This would affect the activity of the phytochrome and thereby some phytochrome regulated enzymes (e.g. malic enzyme, malic dehydrogenase, phenylalanine ammonia

lyase, and probably nitrate reductase), which are involved in reactions relevant for fruit composition (see Smart, 1987, for references).

English et al. (1989) studied the relationship between microclimate changes brought about by leaf removal around the clusters, and the incidence and severity of Botrytis bunch rot. Of the microclimate variables tested (temperature, atmospheric humidity, wind speed, and leaf wetness), wind speed was the most affected by leaf removal. However, the decrease in bunch rot associated with leaf removal was related to interactions between the microclimate variables rather than to a change in a single variable (English et al., 1989).

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CHAPTER I

Influence of Basal Leaf Removal and Cropping Level on Leaf Gas Exchange, Leaf Chlorophyll Content, Vegetative Growth, and Partitioning of Dry Matter and Non-structural Carbohydrates in Seyval Grapevines

Abstract

Own-rooted Seyval grapevines, either one-year-old potted vines or mature, field-grown vines were subjected to source/sink manipulative treatments consisting of basal leaf removal and cropping level.

On potted vines, leaf removal at berry pea size increased leaf net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E) at the basal and middle-shoot leaf positions, while total leaf chlorophyll content was not significantly influenced; removal at veraison had no significant effect on A, g_s, and E either on potted or on mature vines, and only a sporadic positive effect on WUE. A, g_s, and E were increased by the presence of fruits, specially on potted vines; the cropping effect on water use efficiency (WUE) was minimal and no consistent pattern was noticed. Fruiting (3Cl) potted vines had higher leaf chlorophyll content than non-fruiting (0Cl) ones but this was apparently not decisive for the enhanced A on the former.

Leaf removal had no significant effect on vegetative growth and dry matter accumulation and partitioning on potted vines. Cropping influenced dry matter partitioning but not total dry weight; fruits developed at the expense of shoots, roots, leaves and, to a lesser degree, of the trunk. The lower cane dry weight of 3Cl relative to 0Cl vines reflected a reduction in shoot length, number of nodes, and internode diameter; the lower leaf dry weight resulted from fewer leaves and reduced area per leaf, while no significant differences in specific leaf weight were found.

In the early fall, the soluble carbohydrate per unit of dry weight was higher

in canes and trunk of 3Cl than of 0Cl vines; this was opposed to cane starch, both on a dry weight and a volume basis, and to cane total non-structural carbohydrate (TNC) on a volume basis. When all sampling dates were considered, 3Cl vines had lower cane starch and TNC than 0Cl vines on a volume basis, but higher concentration of starch and TNC in the trunk and of starch in roots; differences in root soluble carbohydrate and TNC between cropping levels were not significant.

Leaf removal had little effect on carbohydrate concentration. A significant effect was found for starch and TNC in roots if averaged across sampling dates; levels in vines defoliated at pea size (R1) were higher than in vines defoliated at veraison (R2), and similar (or higher, in the case of root TNC) to those of control (C) vines. If only 3Cl vines are considered, cane soluble carbohydrate and TNC (on a dry weight basis) at the March assessment were higher in R1 and C than in R2 vines.

Introduction

A number of studies in different crops have shown that the photosynthetic rate per unit of leaf area may increase with an increase in the strength of the sink (either reproductive or vegetative) relative to the size of the source (review by Flore and Lakso, 1989).

In grapevines, the presence of fruits (Loveys and Kriedemann, 1974; Kriedemann et al., 1975; Kriedemann, 1977; Chaves, 1984; Downton et al., 1987) and leaf removal (Hofäcker, 1978; Hunter and Visser, 1988,1989; Reynolds and Wardle,

1989; Candolfi-Vasconcelos, 1990), which decrease the source/sink ratio, were found to enhance the leaf net CO_2 assimilation rate (A). Earlier research before gas exchange systems were used, suggested the influence of the source/sink ratio on the photosynthetic rate based on dry matter accumulation in grapevines (Humphries and Thorne, 1964; Buttrose, 1966; May et al., 1969; Kliewer and Antcliff, 1970; Kliewer and Fuller, 1973) and in other crops (Flore and Lakso, 1989).

Increased photosynthetic rate following leaf removal or a higher photosynthetic rate of leaves on fruiting versus non-fruiting grapevines was shown to be associated with decreased mesophyll resistance and increased stomatal conductance (Kriedemann, 1977; Hofäcker, 1978; Chaves, 1984; Candolfi-Vasconcelos, 1990). However, the mechanism(s) responsible for a hypothesized regulation of the source by the strength of the sink has not been elucidated (Flore and Lakso, 1989). One hypothesis is the occurrence of end-product inhibition, whereby the accumulation of carbohydrates in the leaf due to insufficient sink strength or to excessive carbohydrate supply would reduce the photosynthetic rate (Neales and Incoll, 1968). However, hormonal changes (Loveys and Kriedemann, 1974; Kriedemann et al., 1975; Geiger, 1976; Hoad et al., 1977) and changes in the orthophosphate concentration (Walker and Herold, 1977) may also be involved in the regulation of photosynthesis by sink activity (Flore and Lakso, 1989).

Although widely reported, the photosynthetic response to the sink strength is not a general rule (Flore and Lakso, 1989). Moreover, despite the knowledge that the photosynthesis of grapevine leaves may respond positively to leaf removal, there is evidence that the enhancement of A as well as other compensatory responses such

as increased leaf area on lateral shoots (Kliewer, 1970; Kliewer and Fuller, 1973; Wolf et al., 1986; Reynolds and Wardle, 1989; Hunter and Visser, 1990) may only partially compensate for the loss of leaf area (Candolfi-Vasconcelos, 1990). Therefore, the use of basal leaf removal to improve the microclimate in the cluster region must be viewed with caution due to the potential carbohydrate loss it represents. The buds axillary to the basal leaves removed, located in the renewal zone, will in part be retained at pruning and originate the growth and crop in the following season. An adequate carbohydrate status of this particular cane region has considerable practical implications. This aspect is of special relevance in cold climate regions, because storage carbohydrates are probably involved in the physiological processes leading to the development and maintenance of cold hardiness (Howell, 1988).

The influence of the source/sink ratio on the photosynthetic rate has been generally investigated by studying a certain manipulative treatment per se. In only a few instances have both leaf removal and the cropping effect been simultaneously investigated in grapevines, and severe defoliation is usually applied. In the present study, the source/sink ratio was manipulated by combining the removal of a few basal leaves with total or partial cluster thinning. In two experiments, leaf removal was applied at or shortly after veraison. Based on the relationship between photosynthesis and leaf age reported by Kriedemann et al. (1970), the basal leaves (at least those on non-fruiting shoots) would at this time be in the period of gradual decline in photosynthesis. In another experiment, leaf removal at pea size (five weeks after full bloom) was also investigated. The effects of these manipulations on gas

exchange parameters of grapevine leaves (namely on A), leaf chlorophyll content, vine growth, leaf area, dry matter partitioning, and levels of non-structural carbohydrates (starch and soluble carbohydrates) in below and above-ground vine parts were studied. Some questions addressed were: a) Is photosynthesis of grapevine leaves sensitive enough to respond to the removal of a few basal leaves on mature and on young vines under differing cropping levels? b) Is there an effect of the source/sink manipulations performed on the total dry matter production and/or distribution? c) In particular, is there an effect of leaf removal and cropping level on non-structural carbohydrate concentration, namely in the restricted region of the cane subjected to leaf removal?

Materials and Methods

Plant Material and Treatments

Experiments I and II

These experiments were conducted at the Horticultural Research Center (HRC), East Lansing, Michigan, using one-year-old own-rooted Seyval (Seyve-Villard 5-276) grapevines. The vines were weighed and planted in May/1989 (Experiment I) or in May/1990 (Experiment II) in 19 l pots containing a sterilized loam, sand and peat mixture with good water holding and aeration properties. The potted vines were placed in a flat gravel-covered area at a 1.0 m x 1.2 m spacing which allowed good light exposure, and trained to two shoots. Vines were irrigated, fertilized (using a Peter's 20-20-20 solution), and sprayed for pest and disease control as needed.

Cropping level and leaf removal treatments were arranged as a two-factor factorial, set in a randomized block design; vine fresh weight at planting was used as the blocking variable.

Cropping level was either 0Cl (no clusters per vine) or 3Cl (three clusters per vine) and was imposed on June 22/89, four days before full bloom (Experiment I), or July 4/90, ten days after full bloom (Experiment II). On the vines thinned to three clusters, the basal cluster on one shoot and two clusters (the basal and the second) on the other shoot were retained. In Experiment I leaf removal levels were: C = no main leaves removed (control), and R = leaf removal near veraison (August 31/89, nine weeks after full bloom). In Experiment II leaf removal levels were C = control, R1 = leaf removal at pea size (July 27/90, five weeks after full bloom), and R2 = leaf removal at veraison (August 21/90, eight weeks after full bloom). Leaf removal consisted of removing three consecutive leaves in the fruiting region of both vine shoots. On fruiting vines, the leaves opposite, one node above and one node below the basal cluster were removed; on non-fruiting vines, leaves were removed from equivalent node positions. To avoid the variability associated with the erratic growth of lateral shoots (Buttrose, 1968), these shoots were removed at weekly intervals, regardless of the treatment combination.

Experiment III

Own-rooted, mature, bearing Seyval grapevines at the Clarksville Horticultural Experimental Station (CHES), Clarksville, Michigan, were used in this experiment. The vineyard was planted in 1983 in a Kalamazoo sandy loam soil with vine spacing

of 2.4 m x 3.0 m within and between rows and a N-S row orientation. The vines were trained to Hudson River Umbrella (a bilateral cordon at the top wire), with the top wire at 1.8 m height. The vines were balanced-pruned each year using a 15+10 pruning formula (15 nodes retained for the first 0.45 kg of dormant one-year cane prunings plus 10 nodes for each additional 0.45 kg), up to a maximum of 65 nodes retained per vine. Fertilization, irrigation, and pest and disease control were done according to standard procedures at CHES.

Prior to the 1989 growing season a randomized block design was established. Vine size (weight of one-year old cane prunings), which varied between 1.0 and 1.5 kg, was used as the blocking variable. Five blocks of six vines were defined, one vine per treatment combination.

Leaf removal and cropping level treatments were arranged as a 2x3 factorial. The leaf removal levels were: C = no leaves nor lateral shoots removed (control); R = main leaves and lateral shoots removed at three basal nodes on all the shoots of the vine, the same node positions defoliated in Experiments I and II. The cropping levels were: 0 = 0 clusters per vine; 1.5 = 1.5 clusters per node retained at pruning; NT = all clusters left (no thinning). Lateral shoots were allowed to develop normally, except for those at the three treated nodes on R vines. Each vine was subjected to the same treatment combination in 1989 and 1990. The data herein reported were collected in 1990. In this season, cluster thinning was applied on June 27 (nine days after full bloom) and leaf removal on August 15 (veraison, eight weeks after full bloom).

Leaf Gas Exchange Measurements

Gas exchange measurements on attached leaves were made on several occasions during the vegetative season using an ADC LCA-2 portable open gas exchange system (Analytical Development Co. Ltd., UK). The measurements were taken between 10:30H and 14:00H on well exposed leaves, with PPF above 1000 μmol $m^{-2}s^{-1}$ and leaf temperature between 24°C and 33°C, depending on the measurement date. At the time of measurement the leaves were held normal to the incident radiation. The time interval selected for gas exchange measurements represented a compromise between the number of measurements to take and the proximity to the 11:30H to 14:00H period, during which the photosynthetic rate of leaves on potted Seyval grapevines was found to remain relatively stable around the maximum value (Edson, 1991). Measurements were taken on successive blocks of vines, each block including one vine per treatment combination under evaluation. In Experiment II, only control vines (C/0Cl and C/3Cl) and vines defoliated at pea size (R1/0Cl and R1/3Cl vines) were used.

Measurements were taken on two (Experiments I and III) or one (Experiments II) shoots per vine on four (usually) or three replicates per treatment combination (eight or six replicates before leaf removal). Three leaves along the shoot were measured, except for the first measurement in Experiments I and II, when only two leaves per shoot were used due to the still reduced shoot length. The leaves measured were: 1) Basal leaf (BAS) - leaf usually at nodes three or four from the base on the measurements prior to leaf removal and at nodes five or six thereafter; 2) Middle shoot leaf (MID); 3) Apical leaf (AP) - in 1989 (Experiment I) the most

recently fully expanded leaf; in 1990 (Experiments II and III) a leaf near full size (80-90%), the most apical leaf with a hardened blade.

Net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE), were calculated using a BASIC program developed by Moon and Flore (1986). When two shoots per vine were measured, the calculated values for the gas exchange parameters were averaged by leaf position before statistical analysis.

Chlorophyll Extraction and Analysis

Leaf chlorophyll content was measured on four vines of Experiment II other than those used in gas exchange determinations but treated exactly the same way. As in the gas exchange measurements, only R1 and control vines were sampled. Ten leaf discs of 0.3378 cm^2 each were taken from BAS, MID, and AP leaves of each vine on August 24/90 (veraison) and September 19/90 (just before harvest). Five discs per leaf were used for chlorophyll extraction while the others were dried at 55°C and weighed to determine the specific leaf weight.

Chlorophyll extraction was based on Moran and Porath (1980). The five leaf discs per leaf were kept immersed in 9 ml of DMF (N,N-dimethylformamide) in darkness at 5°C for 30 hours. The absorbance of the extract was then measured at 664 nm, 647 nm and 625 nm, using a Spectronic 1001 (Bausch & Lomb) spectrophotometer. Chorophylls a and b, and total chlorophyll (chlorophylls a + b) were calculated as in Moran (1982). The total chlorophyll per unit of leaf area and of leaf dry weight were determined, as well as the chlorophyll a/b ratio.

Shoot Growth, Leaf Area, and Specific Leaf Dry Weight Determinations

Shoot length, the number of nodes per shoot, leaf area, and leaf dry weight were measured on both vine shoots of six replicates at the end of the 1989 (Experiment I) and 1990 (Experiment II) growing seasons. In Experiment II the diameter of the fifth internode from the base of each shoot was also determined (as the average over two perpendicular axes) and the mean value per vine was calculated. Total leaf area per vine was measured using an area meter (model LI-3000 from Li-Cor Inc., Nebraska, USA). Leaves were then oven-dried at 65°C until constant weight, and dry weight was recorded. The dry weight of the blades and the total leaf area per vine were used to calculate the specific leaf weight.

Dry Matter Partitioning

Part of the vines from Experiment II were partitioned in the early fall (September 30/90), mid-winter (January 10/91) and late winter (March 14/91). Nine blocks of vines were distributed by three groups (lighter, medium and heavier) according to vine weight before planting. One block per group was randomly selected to be partitioned at each date. The vines partitioned in January and March were kept outdoors during the dormant season, mulched with straw up to most of the trunk height.

For the vines partitioned on September 30, the parts considered were: leaves, clusters, current year's shoots, trunk, and roots. The clusters were included in the calculations relative to these vines even though they had been harvested on September 19. In the mid- and late winter, vines were partitioned into canes (current

year's shoots after leaf fall), trunk, and roots. For ease of expression the current year's shoots of the vines partitioned on September 30 will also be denominated 'canes'. The separation between the root system and the above-ground part of the vine was done at 2 cm above the uppermost insertion of the roots, a criterion previously adopted by Edson (1991). After sampling for non-structural carbohydrate analyses, the vine parts were oven-dried at 65°C until they achieved constant weight.

Non-structural Carbohydrate Evaluation in Storage Tissues

Non-structural carbohydrates (starch and total soluble carbohydrates) were measured in cane, root, and trunk samples collected on each vine partitioned (Experiment II). A cane segment was taken from both vine canes between nodes three and four. A segment of 3 to 5 cm long was taken from the basal end of the trunk. The root fragments sampled had a diameter of 2-3.5 mm and were well distributed throughout the root system. The length of the trunk and cane segments as well as the diameter across two transverse axes were measured for further volume estimation, assuming the transverse section to be elliptical. As the tissue samples were prepared, they were frozen in liquid nitrogen and then stored at -20°C. Prior to starch analysis, the samples were freeze-dried, weighed, ground in a Wiley mill, and passed through a 40-mesh screen. Fifty milligrams per sample were extracted four times using 2 ml of 80% ethanol per extraction. The homogenates were centrifuged at 3000x*g* for 5 min. after each extraction. Soluble carbohydrates were measured in the supernatants collected from the successive extractions, and starch in the remaining pellet, after evaporation to dryness using a Savant speedvac SC200

(Savant Instruments Inc., NY). Starch was measured using the method described by Roper et al. (1988). The pellets were heated in acetate buffer (0.1 M, pH 5.0) and then incubated for 16 h at 55°C with amyloglucosidase (Boehringer Mannheim 208 469). The glucose produced was colorimetrically assayed after reaction with PGO enzymes in the presence of o-dianisidine dihydrochloride (Sigma Chemical Co.). Absorbance at 440 nm was read with a Hitachi U-3110 UV/Vis spectrophotometer (Hitachi Ltd., Tokyo). Each sample was assayed three times. Soluble carbohydrates were measured by spectrophotometry (absorbance at 620 nm) after reaction with anthrone reagent (2 g anthrone/l 95% sulfuric acid) as described by Flore et al. (1983), except for the blanks used. Instead of using water as a blank, individual blanks for each sample extract were prepared by adding 1 ml of extract to 5 ml of water. Each sample was assayed three times. Appropriate glucose standard curves were used as reference for starch and soluble carbohydrate determinations.

Statistical Analysis

Leaf removal and cropping level (when both present) were analyzed as a two factor factorial set in a randomized block design. The effects of cropping level and leaf removal on gas exchange parameters were evaluated per leaf position at each measurement date. The effect of leaf position was evaluated at selected measurement dates in the season; in these analyses, leaf position was considered a split-plot on cropping and leaf removal (or on cropping alone, before leaf removal imposition). In all the analyses where two or more sampling dates were combined, sampling date was included as a blocking variable.

Data were analyzed by analysis of variance, using either the MSTAT-C software package (MSTAT Development Team, 1990) or the GLM (from General Linear Models) procedure of the Statistical Analysis System package (SAS Institute Inc., 1985). Percentage data were subjected to the arc-sine of the square root transformation prior to analysis of variance. When the F-values were significant at a 5% or lower level, mean separation was done using the LSD test or an equivalent test of the GLM procedure for the least-squares means. All mean separation tests were done at the 5% level. In Experiment II, when leaf removal had a significant effect and did not significantly interact with cropping level, orthogonal contrasts were used to compare the control against the average of the two leaf removal dates, and also the first against the second date.

Results

Leaf Gas Exchange Parameters

Prior to treatment imposition, no significant differences were found in any gas exchange parameters analyzed among the vines that were to be subjected to the different treatment combinations (data not shown).

Cropping Level Effects

On potted vines (Experiments I and II), the presence of fruits was almost invariably associated with higher A (significantly or not), regardless of the leaf position (Tables 1 and 2). On average through the whole season, the fruit effect on

Table 1. Influence of leaf removal and cropping level on the net CO_2 assimilation rate (A) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1989 - Experiment I).

Leaf position[z]	Treatment[y]	A (μmol $CO_2.m^{-2}.s^{-1}$)							Average	
		June 28 2 d PFB[x]	July 11 2 wk PFB	Aug.21 8 wk PFB	Aug.25 V	Aug.30 5 d PV	Sep.12 2.5 wk PV	Sep.18 1 wk BH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C						6.37	5.09		5.52
	R						6.42	5.76		5.98
							ns[w]	ns		ns
	Crop. level									
	0Cl	10.90	12.08	5.31b	6.76	7.99b	6.48	4.88	7.96b	5.41
	3Cl	12.12	12.41	7.82a	8.26	10.67a	6.31	5.97	9.38a	6.09
		ns	ns	*	ns	*	ns	ns	***	ns
	Interaction						ns	ns		ns
MID	Leaf removal									
	C						8.50	7.81		8.04
	R						7.79	7.81		7.81
							ns	ns		ns
	Crop. level									
	0Cl		11.46b	7.81b	8.78	10.28b	6.82	6.32b	8.54b	6.49b
	3Cl		12.79a	11.03a	12.07	15.00a	9.47	9.31a	11.36a	9.36a
			**	*	ns	**	ns	*	***	**
	Interaction						ns	ns		ns
AP	Leaf removal									
	C						10.54	9.23		9.67
	R						11.10	8.85		9.60
							ns	ns		ns
	Crop. level									
	0Cl	7.59b	7.12	8.36b	10.64	12.62b	10.53	7.52b	9.24b	8.52b
	3Cl	9.25a	7.42	11.83a	13.55	16.23a	11.12	10.56a	11.67a	10.74a
		*	ns	*	ns	*	ns	**	***	**
	Interaction						ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; V:Veraison; PV:post veraison; BH:before harvest
[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 2. Influence of leaf removal and cropping level on the net CO_2 assimilation rate (A) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990 - Experiment II).

Leaf position[z]	Treatment[y]	A (μmol $CO_2.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C			13.10	13.16b	13.41	10.66	4.56b		10.98b
	R1			14.82	14.99a	14.38	9.56	5.88a		11.93a
				ns[w]	*	ns	ns	*		*
	Crop. level									
	0Cl	12.00	12.92	12.94	13.84	11.69b	7.33b	5.66	10.79b	10.29b
	3Cl	13.22	13.31	14.98	14.31	16.10a	12.89a	4.79	12.76a	12.61a
		ns	ns	ns	ns	***	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
MID	Leaf removal									
	C			13.32b	13.15b	13.90	12.55	6.69b		11.92b
	R1			16.50a	15.01a	14.36	12.31	8.43a		13.32a
				*	*	ns	ns	**		**
	Crop. level									
	0Cl		12.44b	13.79	12.86b	12.37b	10.52b	8.03	11.64b	11.51b
	3Cl		15.63a	16.03	15.30a	15.89a	14.33a	7.10	13.98a	13.73a
			**	ns	**	*	**	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Leaf removal									
	C			9.63	10.76	11.93	10.86	4.50		9.54
	R1			11.14	12.24	11.50	10.33	4.62		9.97
				ns	ns	ns	ns	ns		ns
	Crop. level									
	0Cl	7.05b	9.21	9.30	9.75b	10.47b	8.49b	4.51	8.42b	8.50b
	3Cl	9.32a	10.90	11.46	13.25a	12.96a	12.70a	4.62	10.79a	11.00a
		*	ns	ns	**	*	*	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 3. Influence of leaf removal and cropping level on the net CO_2 assimilation rate (A) of BAS, MID, and AP leaves of mature field Seyval vines (CNES 1990 - Experiment III)

Leaf position[z]	Treatment[y]	A (μmol $CO_2.m^{-2}.s^{-1}$)				Average	
		July 18 4 wk PFB[x]	Sept. 4 3 wk PV	Sept. 25 H	Oct. 6 10 d PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal						
	C		11.57	8.66	6.69		9.18
	R		11.01	9.54	6.32		9.19
			ns[w]	ns	ns		ns
	Crop. level						
	0	9.36	10.40	9.89	7.14	9.33	9.32
	1.5	10.23	11.38	9.00	6.55	9.42	9.20
	NT	9.95	12.08	8.42	5.80	9.23	9.04
		ns	ns	ns	ns	ns	ns
	Interaction		ns	ns	ns		ns
MID	Leaf removal						
	C		14.39	12.11	9.25		12.16
	R		13.32	12.17	10.45		12.12
			ns	ns	ns		ns
	Crop. level						
	0	11.55	12.87	12.06	11.52	12.06	12.20
	1.5	12.40	14.65	11.67	9.41	12.19	12.14
	NT	12.62	14.05	12.69	8.63	12.19	12.08
		ns	ns	ns	ns	ns	ns
	Interaction		ns	ns	ns		ns
AP	Leaf removal						
	C		11.94	11.58	11.89		11.79
	R		10.64	11.88	10.89		11.16
			ns	ns	ns		ns
	Crop. level						
	0	5.83	7.94b	10.58b	11.80	9.07b	9.95b
	1.5	7.27	12.74a	12.77a	12.40	11.50a	12.66a
	NT	7.49	13.20a	11.83ab	9.98	10.89a	11.82a
		ns	**	*	ns	**	*
	Interaction		ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (no leaves removed); R:leaves removed on Aug. 15/90 (veraison)
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.

[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; H:harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

A was highly significant at every leaf position in both experiments with potted vines. The overall increase in A on 3Cl relative to 0Cl vines at BAS, MID, and AP leaves was, respectively, 18%, 33%, and 26% in Experiment I (Table 1) and 18%, 20%, and 28% in Experiment II (Table 2); an enhancement as high as 76% was found at BAS leaves in Experiment II one week before harvest. The response of mature field vines (Experiment III) to cropping was less marked than that of potted vines; only at the AP leaf position was a significant fruit effect on A observed (Table 3). In Experiment I, the presence of fruits increased A at the AP leaf position as early as two days after full bloom (Table 1). However, neither at this time (data not shown) nor at two weeks after full bloom (Table 4) was the cropping effect significant when all the leaf positions were considered, unlike at the first measurement in Experiment II, 3.5 weeks post full bloom (Table 5). On mature vines, A was higher on fruiting (1.5 and NT) than on non-fruiting (0) vines three weeks after veraison if leaf positions were analyzed together (Table 6). In the experiments conducted, g_s and E at each leaf position were, like A, usually higher on fruiting than on non-fruiting vines, and significantly higher when all the sampling dates were considered (except for E at MID leaves in Experiment III); cropping effects on WUE were seldom significant, regardless of the leaf position (Appendix A). When the leaf positions were combined, the 3Cl vines had higher WUE than the 0Cl vines at 3.5 weeks post full bloom in Experiment II (Table 5), while WUE was higher on non-fruiting than on fruiting field vines at harvest (Table 6).

Table 4. Influence of leaf removal, cropping level and leaf position on the net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) of leaves of potted Seyval grapevines at selected vine phenophases (HRC 1989 - Experiment I).

Factor	A (μmol $CO_2.m^{-2}.s^{-1}$)			g_s (mmol $CO_2.m^{-2}.s^{-1}$)			E (mmol $H_2O.m^{-2}.s^{-1}$)			WUE (mmol CO_2/mol H_2O)		
	July 11 2 wk PFB[z]	Aug. 30 5 d PV	Sep. 18 1 wk BH	July 11 2 wk PFB	Aug. 30 5 d PV	Sep. 18 1 wk BH	July 11 2 wk PFB	Aug. 30 5 d PV	Sep. 18 1 wk BH	July 11 2 wk PFB	Aug. 30 5 d PV	Sep. 18 1 wk BH
Leaf removal (DEF)[y]												
C			7.38			90.7			4.06			1.86
R			7.47			99.5			4.41			1.69
			ns			ns			ns			ns
Crop. level (CROP)[x]												
0Cl	10.22	10.30b	6.24	112.2	134.6b	72.5b	6.33	4.31b	3.61b	1.59	2.40	1.79
3Cl	10.87	13.97a	8.61	117.5	197.3a	117.7a	6.50	5.46a	4.86a	1.65	2.56	1.76
	ns[w]	**	(*)	ns	**	**	ns	**	**	ns	ns	ns
DEF*CROP			ns			ns			ns			ns
Leaf position (LPOS)[v]												
BAS	12.25a	9.33c	5.43	135.3a	140.7c	85.4b	7.25a	4.39c	3.88b	1.69a	2.13b	1.43b
MID	12.13a	12.64b	7.81	123.1b	163.3b	92.7b	6.75b	4.84b	4.13b	1.80a	2.62a	1.93a
AP	7.27b	14.43a	9.04	86.2c	193.9a	107.1a	5.24c	5.41a	4.69a	1.38b	2.67a	1.97a
	***	**	(***)	***	***	**	***	***	**	***	***	***
DEF*LPOS			ns			ns			ns			ns
CROP*LPOS	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
DEF*CROP*LPOS			ns			ns			ns			ns

[z]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest
[y]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
[x] 0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[v]BAS:basal; MID:middle shoot; AP:apical

Table 5. Influence of leaf removal, cropping level and leaf position on the net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) of leaves of potted Seyval grapevines at selected vine phenophases (HRC 1990 - Experiment II).

Factor	A (μmol $CO_2.m^{-2}.s^{-1}$)			g_s (mmol $CO_2.m^{-2}.s^{-1}$)			E (mmol $H_2O.m^{-2}.s^{-1}$)			WUE (mmol CO_2/mol H_2O)		
	July 19 3.5 wk PFB[z]	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH
Leaf removal (DEF)[y]												
C		13.08	11.35		113.2	102.1		5.24	4.65		2.53	2.46
R1		13.42	10.74		113.9	92.1		5.32	4.27		2.51	2.53
		ns	ns		ns	ns		ns	ns		ns	ns
Crop. level (CROP)[x]												
0Cl	9.53b	11.51b	8.78b	158.0	96.7b	75.2b	7.71	4.62b	3.66b	1.22b	2.50	2.43
3Cl	11.27a	14.98a	13.31a	157.0	130.4a	119.0a	7.66	5.94a	5.25a	1.48a	2.53	2.56
	*[w]	***	***	ns	***	***	ns	***	***	**	ns	ns
DEF*CROP		ns	ns		ns	ns		ns	ns		*	ns
Leaf position (LPOS)[v]												
BAS	12.61a	13.89b	10.11b	166.6a	112.1	82.5b	7.90a	5.21	3.90b	1.59a	2.68a	2.60
MID	—	14.13a	12.43a	—	114.7	101.0a	—	5.35	4.61a	—	2.66a	2.72
AP	8.19b	11.72c	10.60b	148.4b	113.8	107.9a	7.38b	5.28	4.87a	1.11b	2.21b	2.16
	***	**	**	***	ns	***	**	ns	***	***	***	(***)
DEF*LPOS		ns	ns		ns	ns		ns	ns		ns	ns
CROP*LPOS	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
DEF*CROP*LPOS		ns	ns		ns	ns		ns	ns		ns	*

[z]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
[x] 0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[v]BAS:basal; MID:middle shoot; AP:apical

Table 6. Influence of leaf removal, cropping level and leaf position on the net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) of leaves of mature field Seyval grapevines at selected vine phenophases (CMES 1990 - Experiment III).

Factor	A (μmol $CO_2.m^{-2}.s^{-1}$)			g_s (mmol $CO_2.m^{-2}.s^{-1}$)			E (mmol $H_2O.m^{-2}.s^{-1}$)			WUE (mmol CO_2/mol H_2O)		
	July 18 4 wk PFB[z]	Sept. 4 3 wk PV	Sep. 25 H	July 18 4 wk PFB[z]	Sept. 4 3 wk PV	Sep. 25 Harvest	July 18 4 wk PFB[z]	Sept. 4 3 wk PV	Sep. 25 Harvest	July 18 4 wk PFB[z]	Sept. 4 3 wk PV	Sep. 25 Harvest
Leaf removal (DEF)[y]												
C		12.63	10.78		112.5	117.9		5.47	3.41		2.33	3.24b
R		11.66	11.20		109.9	117.3		5.10	3.21		2.31	3.62a
		ns	ns		ns	ns		ns	ns		ns	**
Crop. level (CROP)[x]												
0	8.91	10.40b	10.84	62.8b	93.1b	106.0b	3.43b	4.61b	3.04	2.88	2.29	3.65a
1.5	9.97	12.93a	11.15	69.6a	118.4a	126.0a	3.72a	5.47a	3.48	2.74	2.37	3.30b
NT	10.02	13.11a	10.98	73.4a	122.0a	120.8a	3.84a	5.78a	3.41	2.67	2.31	3.36b
	ns[w]	*	ns	**	**	*	*	**	ns[v]	ns	ns	*
DEF*CROP		ns	ns		ns	ns		ns	ns		ns	ns
Leaf position (LPOS)[u]												
BAS	9.85b	11.29b	9.10	69.3b	107.6b	111.7b	3.71b	5.17b	3.19b	2.74ab	2.23	2.96b
MID	12.19a	13.86a	12.14	77.3a	124.3a	125.3a	4.05a	5.75a	3.45a	3.10a	2.44	3.61a
AP	6.87c	11.29b	11.73	59.2c	101.6b	115.8b	3.22c	4.93b	3.29ab	2.45b	2.30	3.73a
	***	***	(***)	***	**	**	***	**	*	*	ns	***
DEF*LPOS		ns	ns		ns	ns		ns	ns		ns	ns
CROP*LPOS	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
DEF*CROP*LPOS		ns	ns		ns	ns		ns	ns		ns	ns

[z]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; H:harvest.
[y]C:control (no leaves removed); R:leaves removed on August 15/90 (veraison)
[x] 0:0 clusters per vine; 1.5: 1.5 clusters per node retained; NT: unthinned. Thinning date: June 27/90.
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[v]P=0.0509
[u]BAS:basal; MID:middle shoot; AP:apical

Leaf Removal Effects

Leaf removal at pea size (R1) increased A, g_s, and E at the BAS and MID leaf positions (Experiment II) at either one or both measurements in the pre-veraison period (August 2 and August 9, one and two weeks after leaf removal, respectively), at the post-harvest measurement, and on average across the measurements following leaf removal (Table 2; Appendix A). The AP leaf position showed no significant leaf removal effect on A, and a significant effect on g_s and E was observed only once. Leaf removal at on shortly after veraison whether on potted (Experiment I) or on field vines (Experiment III) had no significant effect on A, g_s, and E (Tables 1, 3, 4 and 6; Appendix A), and no or only a sporadic effect on WUE at each leaf position (Appendix A). When leaf positions were analyzed together, a significant leaf removal effect on WUE was found on field vines at harvest (Table 6). Whenever the leaf removal effect was significant, WUE was higher on defoliated than on control vines.

Leaf Chlorophyll Content

The total chlorophyll content of BAS leaves was not significantly affected by leaf removal at pea size nor by cropping level; a tendency for higher chlorophyll levels at BAS leaves of R1 than of C vines, and of 3Cl than of 0Cl vines was observed, though (Table 7). At MID and AP leaves there was no clear pattern of response in total chlorophyll to leaf removal. At these leaves, the chlorophyll content on a dry weight basis was higher on 3Cl than on 0Cl vines both at veraison and at harvest; on a leaf area basis this effect was also evidenced, except that at harvest it was significant for the MID leaves of R1 but not of C vines (data not shown).

Table 7. Influence of leaf removal and cropping level on the total chlorophyll content, chlorophyll a/b ratio, and specific leaf weight (SLW) of BAS, MID and AP leaves of potted Seyval vines at veraison (August 24) and at harvest (September 19) (HRC 1990 - Experiment II).

Leaf position[z]	Treatment[y]	Total chlorophyll (chl. a + b) µg/cm²		Total chlorophyll (chl. a + b) mg/g dry weight		chlorophyll a/b		SLW (mg/cm²)	
		Veraison	Harvest	Veraison	Harvest	Veraison	Harvest	Veraison	Harvest
BAS	Leaf removal								
	C	43.52	29.10	7.00	4.42	4.17	3.36	6.22	6.62
	R1	48.62	31.73	7.77	4.62	3.88	3.46	6.26	7.00
		ns[x]	ns	ns	ns	ns	ns	ns	ns
	Crop. level								
	0Cl	44.37	28.82	6.91	4.13	3.98	3.47	6.42	7.02
	3Cl	47.77	32.02	7.86	4.90	4.07	3.35	6.06	6.59
		ns	ns	ns	ns	ns	ns	ns	ns
	Interaction	ns	ns	ns	ns	ns	ns	ns	*
MID	Leaf removal								
	C	46.54	35.84	7.71	5.63	4.28	3.68	6.06	6.39
	R1	48.73	30.37	8.22	4.91	4.07	3.55	5.94	6.26
		ns	(*)	ns	ns	ns	ns	ns	ns
	Crop. level								
	0Cl	44.61b	29.79	7.46b	4.61b	4.14	3.57	6.00	6.46
	3Cl	50.66a	36.42	8.48a	5.94a	4.21	3.65	6.00	6.19
		*	(**)	*	**	ns	ns	ns	ns
	Interaction	ns	*	ns	ns	ns	ns	ns	ns
AP	Leaf removal								
	C	27.71	14.75	6.78	3.10	3.59b	3.50	4.08	4.88
	R1	24.92	17.23	6.01	3.55	4.24a	3.25	4.15	4.91
		ns	(*)	ns	ns	*	ns	ns	ns
	Crop. level								
	0Cl	23.13b	12.86	5.54b	2.52b	3.87	3.15	4.17	5.12a
	3Cl	29.49a	19.12	7.25a	4.13a	3.96	3.60	4.07	4.67b
		*	(***)	**	***	ns	ns	ns	*
	Interaction	ns	*	ns	ns	ns	ns	ns	ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.

Neither leaf removal at pea size nor cropping level had a significant effect on the chlorophyll a/b ratio, except for AP leaves at veraison, when the ratio was higher on R1 than on C vines (Table 7).

Vegetative Growth and Dry Matter Partitioning

Leaf removal had no significant effect on shoot growth, leaf area, and specific leaf weight on potted vines (Tables 8 and 9), nor on total dry matter accumulation and distribution among vine components whether at the end of the 1990 season (Table 10) or when the partitioning dates were combined (Table 11).

Cropping level had no significant effect on the total dry weight per vine at the end of the season (Table 10), but influenced dry matter allocation (Tables 10 and 11). The fruits represented approximately 45% of the overall dry weight of 3Cl vines. Fruit development was detrimental to dry matter accumulation in all the vegetative fractions considered; the canes (leaves excluded) were the most affected, followed by roots, leaves and trunk. Cane dry weight was decreased by about 70% due to the presence of fruits, while a reduction of about 40% was found in the dry weight of roots and leaves and of 18% in trunk dry weight. The lower cane dry weight of the 3Cl vines reflected highly significant differences in shoot length, number of nodes, internode length and internode diameter between cropping levels (Table 9). The lower leaf dry weight resulted from a lower leaf area per vine due to a reduction in both the number of leaves (nodes) and the area per leaf; the specific leaf weight did not significantly differ between 3Cl and 0Cl vines. The above differences in shoot growth parameters, leaf area, and leaf dry weight between 0Cl and 3Cl vines in

Table 8. Influence of leaf removal and cropping level on shoot growth parameters, leaf area, and specific leaf weight of potted Seyval grapevines (HRC 1989 - Experiment I).

Treatment[z]	Total shoot length/vine (cm)	No. of nodes/ vine	Internode length (cm)	Total leaf area /vine (cm^2)	Single leaf area (cm^2)	Specific leaf weight (mg/cm^2)
Leaf removal						
C	305.2	65.8	4.5	5035.5	82.1	7.80
R	290.9	63.2	4.5	4661.3	88.2	7.05
	ns[y]	ns	ns	ns	ns	ns
Crop. level						
0Cl	384.1a	73.6a	5.2a	6044.8a	97.3a	7.85
3Cl	227.8b	56.9b	3.9b	3853.8b	76.1b	7.01
	***	**	***	*	*	ns
Interaction	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 9. Influence of leaf removal and cropping level on shoot growth parameters, leaf area, and specific leaf weight of potted Seyval grapevines (HRC 1990 - Experiment II).

Treatment[z]	Total shoot length/vine (cm)	No. of nodes/ vine	Internode length (cm)	Diameter of 5th internode (mm)	Total leaf area/vine (cm^2)	Single leaf area (cm^2)	Specific leaf weight (mg/cm^2)
Leaf removal							
C	198.3	52.1	3.8	5.8	3292.3	65.7	6.42
R1	223.2	56.1	3.9	5.5	3624.7	75.1	6.29
R2	208.3	54.0	3.8	5.5	3425.8	75.8	6.37
	ns[y]	ns	ns	ns	ns	ns	ns
Crop. level							
0Cl	247.3a	59.3a	4.1a	6.2a	4100.4a	78.7a	6.37
3Cl	172.6b	48.9b	3.5b	5.0b	2805.4b	65.9b	6.34
	***	***	***	***	**	**	ns
Interaction	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 10. Influence of leaf removal and cropping level in 1990 on the dry weight partitioning of potted Seyval grapevines at the end of the season (September 30/90) (Experiment II).

Treatment[z]	Dry weight (g)					Total dry weight (g)	Percent of total dry weight				
	Fruits	Leaves	Canes	Trunk	Roots		Fruits	Leaves	Canes	Trunk	Roots
Leaf removal											
C	31.8	24.6	26.3	13.8	41.8	138.2	21.7	17.8	19.1	10.9	30.5
R1	32.2	28.2	31.4	14.3	42.2	148.4	22.4	18.9	20.7	9.8	28.2
R2	28.6	22.6	25.0	15.6	38.0	129.7	23.4	17.1	18.4	12.2	28.8
	ns[y]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level											
0Cl	0b	31.1a	42.1a	16.0a	50.8a	139.9	0b	22.1a	29.6a	12.1	36.1a
3Cl	61.7a	19.1b	13.1b	13.1b	30.5b	137.6	45.0a	13.8b	9.1b	9.9	22.2b
	***	**	***	*	**	ns	***	***	***	ns	***
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 11. Influence of leaf removal and cropping level in the 1990 season on the dry weight of canes, trunk and roots of potted Seyval grapevines, on average across partitioning dates in the fall and winter of 1990/91 (Experiment II).

Treatment[z]		Dry weight (g)			
		Canes	Trunk	Roots	Total of the three vine parts
Leaf removal:	C	34.5	13.2	42.8	90.5
	R1	30.8	14.2	38.1	83.9
	R2	29.3	14.1	36.3	79.7
		ns[y]	ns	ns	ns
Crop. level:	0Cl	45.8a	15.1a	48.0a	108.9a
	3Cl	17.3b	12.5b	30.2b	59.9b
		***	**	***	***
Interaction		ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Experiment II were consistent with the results obtained in Experiment I (Table 8).

Non-structural Carbohydrates in Storage Tissues

Of the vine tissues analyzed (Tables 12, 13 and 14), the roots had the highest concentration of soluble carbohydrates and starch and, consequently, of total non-structural carbohydrates (TNC) at any partitioning date; canes had higher soluble carbohydrate concentration than the trunk, while the trunk had higher starch and TNC concentration.

Regardless of the vine tissue, treatment, and basis of evaluation (dry weight or volume), the soluble carbohydrate content had a sharp increase from September 30 to January 10, followed by a much smoother reduction from January to March. The changes in soluble carbohydrate between sampling dates were proportionally larger in the trunk and canes than in the roots. In canes (Table 12) and trunk (Table 13), the fluctuations in starch content were opposite to those in soluble carbohydrates. In roots, however, starch levels decreased not only from September 30 to January 10 but also from January 10 to March 14 (Table 14).

Leaf removal had no significant effect on cane carbohydrate levels on September 30 and January 10 (Table 12). In March, the leaf removal x cropping level interaction was significant for cane soluble carbohydrate and TNC expressed on a dry weight basis. If only 3Cl vines are considered, the vines defoliated at veraison had lower levels of these carbohydrates than the vines that were either not defoliated or defoliated at pea size; on 0Cl vines, though, higher levels were found on control than on defoliated vines, regardless of the defoliation date (data not shown). Leaf removal

Table 12. Influence of leaf removal and cropping level on starch, soluble carbohydrate, and total non-structural carbohydrate content per unit of dry weight and per unit of volume of canes of potted Seyval grapevines (MRC 1990/91 - Experiment II)

Treatment[z]		Starch				Soluble carbohydrate				TNC[x]			
		Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average
		mg/g cane dry weight											
Leaf removal:	C	85.17	10.38	23.01	39.52	28.60	152.51	128.05	103.05	113.77	162.89	151.06	142.57
	R1	84.42	9.90	20.43	38.25	29.24	154.17	124.77	103.11	113.66	162.52	145.20	140.84
	R2	89.74	10.09	21.10	40.41	33.32	153.38	115.31	100.43	123.06	163.47	136.41	140.83
		ns[y]	ns	ns	ns	ns	ns	(**)	ns	ns	ns	(*)	ns
Crop. level:	0Cl	92.34a	10.12	21.01	41.16	27.77b	153.40	120.92	100.70	120.12	163.52	141.93	141.85
	3Cl	80.54b	10.13	22.01	37.62	33.00a	153.31	124.51	103.70	113.55	162.40	146.52	140.97
		*	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns
Interaction		ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*	ns
		mg/cm^3 fresh cane tissue											
Leaf removal:	C	50.47	6.39	13.73	23.53	16.48	93.35	76.59	62.14	66.95	99.73	90.32	85.67
	R1	49.77	5.76	12.07	22.53	16.89	89.30	73.81	60.35	66.66	94.11	85.88	82.52
	R2	53.37	6.40	13.11	24.55	19.48	95.40	72.79	62.31	72.84	101.80	85.90	86.85
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level:	0Cl	58.75a	6.35	13.21	26.10a	17.60	95.45	76.59	63.21	76.35a	101.80	89.80	89.32a
	3Cl	43.66b	6.02	12.73	20.97b	17.63	89.91	72.21	59.98	61.28b	95.29	84.94	80.71b
		*	ns	ns	*	ns	ns	ns	ns	*	ns	ns	**
Interaction		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[x]TNC:Total Non-structural Carbohydrate (starch + soluble carbohydrate).

Table 13. Influence of leaf removal and cropping level on starch, soluble carbohydrate, and total non-structural carbohydrate content per unit of dry weight and per unit of volume of trunk of potted Seyval grapevines (HRC 1990/91 - Experiment II)

Treatment[z]		Starch				Soluble carbohydrate				TNC[x]			
		Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average
		mg/g trunk dry weight											
Leaf removal:	C	152.19	33.21	77.17	87.52	26.04	136.70	104.64	89.13	178.24	169.91	181.82	176.65
	R1	147.33	35.66	81.46	88.15	26.85	135.56	102.34	87.42	174.19	171.22	178.99	174.55
	R2	141.65	34.65	67.48	81.26	24.69	139.72	106.24	90.21	166.33	174.36	173.71	171.47
		ns[y]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level:	0Cl	143.02	28.17b	61.20b	77.46b	24.25b	140.50	107.92	90.89	167.27	168.67	169.12	168.35b
	3Cl	152.00	40.84a	89.54a	93.82a	27.47a	134.15	100.72	86.94	178.57	174.99	188.26	180.31a
		ns	*	*	**	*	ns	ns	ns	ns	ns	ns	*
Interaction		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
		mg/cm^3 fresh trunk tissue											
Leaf removal:	C	90.96	18.20	40.91	50.02	15.73	76.29	55.72	49.24	106.68	94.48	96.62	99.26
	R1	84.87	19.54	42.33	48.91	15.48	75.41	52.70	47.58	100.34	94.95	92.43	96.11
	R2	83.35	19.41	34.49	45.75	14.88	77.80	55.20	49.29	98.23	97.21	89.69	95.04
		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level:	0Cl	83.19	15.74b	31.43b	43.45b	14.19	78.84	55.43	49.49	97.38	94.58	86.86b	92.94b
	3Cl	89.60	22.35a	47.06a	53.00a	16.53	74.16	53.77	47.94	106.13	96.51	99.79a	100.85a
		ns	*	*	***	ns	ns	ns	ns	ns	ns	*	**
Interaction		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.
[x]TNC:Total Non-structural Carbohydrate (starch + soluble carbohydrate).

Table 14. Influence of leaf removal and cropping level on starch, soluble carbohydrate, and total non-structural carbohydrate content per unit of dry weight of roots of potted Seyval grapevines (HRC 1990/91 - Experiment II)

Treatment[z]	Starch (mg/g root dry weight)				Soluble carbohydrate (mg/g root dry weight)				TNC[x] (mg/g root dry weight)			
	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average	Sept. 30/90	Jan. 10/91	Mar. 14/91	Average
Leaf removal												
C	205.51	143.73	122.33	157.19ab	44.51	180.52	161.89	128.98	250.03	324.25	284.22	286.17b
R1	206.05	190.79	140.15	179.00a	46.65	186.10	180.16	137.60	252.69	376.89	320.31	316.63a
R2	175.88	160.78	107.94	148.20b	52.44	181.10	158.95	130.83	228.32	341.88	266.89	279.03b
	ns[y]	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	*
Crop. level												
0Cl	189.67	142.55b	114.58	148.94b	50.97	187.76	174.46	137.73	240.64	330.32	289.04	286.67
3Cl	201.95	187.65a	132.36	173.96a	44.76	177.39	159.54	127.23	246.71	365.03	291.90	301.22
	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%
[x]TNC:Total Non-structural Carbohydrate (starch + soluble carbohydrate)

had no significant effect on starch, soluble carbohydrate and TNC levels in roots and trunk at any partitioning date (Tables 13 and 14). When all sampling dates were considered, though, the R1 vines had higher root starch content than the R2 vines, and higher root TNC than either C or R2 vines.

Cropping level effects on carbohydrate levels varied markedly with sampling date and vine tissue. In canes, the cropping effect was only significant on September 30, 1.5 weeks after harvest (Table 12). At this time, cane, as well as trunk (Table 13) soluble carbohydrate content on a dry weight basis were higher on 3Cl than on 0Cl vines, in contrast with cane starch both on a dry weight and on a volume basis, and cane TNC per unit of volume. Across sampling dates, the canes of 3Cl vines had lower starch and TNC than those of 0Cl vines, on a volume basis (Table 12); by contrast, the concentration of starch and TNC in the trunk (Table 13) and of starch in roots (Table 14) were higher on 3Cl vines. Cropping had no significant effect on soluble carbohydrate and TNC levels in roots (Table 14). In mid-winter, the root soluble carbohydrate content was higher on 0Cl than on 3Cl vines but only for non-defoliated (C) vines (data not shown).

Discussion

Leaf Removal and Cropping Level Effects on Gas Exchange and Chlorophyll Content at Individual Leaf Positions

In Experiments I and II, in which gas exchange measurements were taken relatively often, the course of the net CO_2 assimilation rate per unit of leaf area (A)

throughout the growing season and some differences in A among leaf positions reflect, in part, the aging effect reported in grapevines (Kriedemann, 1968, Kriedemann et al., 1970) and other species (Flore and Lakso, 1989). Environmental factors, and changes in sink activity and proximity to a carbon source, among other factors (Flore and Lakso, 1989) also conceivably contributed to the results found.

In grapevine leaves, A increased as the leaf expanded, achieved a maximum with full expansion, and declined later, toward senescence (Kriedemann, 1968, Kriedemann et al., 1970). In the present study, higher A values were initially found at BAS or MID leaves but, as the season progressed, the AP or the MID leaves (in 1989 and 1990, respectively) became the most active. In 1989 (Tables 1 and 4), as in the study of Edson (1991), the AP leaves became dominant, while in 1990 (Tables 2 and 5), as in Chaves (1984), A increased from the BAS to the MID leaf and then decreased to the AP leaf. The difference between years is probably due to the fact that in 1989, as in Edson (1991), the AP leaves measured were fully expanded, while in 1990, like in Chaves (1984) they had not yet reached that stage.

Leaf aging was conceivably greatly responsible for the decline in A towards the end of the season. The rate of development of new leaves decreased late in the season; therefore, even though the position of the MID and AP leaves measured evolved with shoot elongation, these leaves were successively older, like the BAS ones. This is consistent with the decline in total leaf chlorophyll content and chlorophyll a/b ratio from veraison to harvest (Table 7). Ribulose-1,5-bisphosphate carboxylase activity has been reported to decrease with leaf aging (Zima and Šesták, 1985). Besides, given the hypothesis of photosynthesis regulation by sink activity

(Neales and Incoll, 1968; Geiger, 1976), it can also be suggested that decreased daylength late in the season restricted the vegetative growth, which lowered the photosynthetic demand and amplified the decline in the photosynthetic rate associated with leaf aging (Kriedemann, 1977).

In Experiment II (Table 2), leaf removal at pea size (five weeks after full bloom) presumably created a source limitation despite the reduced number of leaves removed. The higher A at BAS and MID leaves on defoliated (R1) relative to control (C) vines might have represented a compensatory response; E and g_s were likewise higher on R1 than on C vines (Appendix A). Increased A, g_s, and E in response to leaf removal has been previously reported (Hunter and Visser, 1988; Candolfi-Vasconcelos, 1990). By contrast, no significant effect on A, g_s, and E was observed here following leaf removal at or shortly after veraison on potted (Experiment I) or on mature vines (Experiment III); if an effect occurred it could have been limited to a short period following treatment, before the first post-leaf removal assessment. Although on potted vines the same number of leaves was removed either at pea size or shortly after veraison, the leaves removed on the latter date were proportionally less important due to the larger area available at this time of the season. Differences in leaf physiological stage at the time of treatment conceivably influenced the intensity of the photosynthetic response to the source/sink manipulation. In Experiment II, the MID leaves were the most responsive to leaf removal. The BAS leaves were closer to the leaves removed but could not react as intensively as the MID leaves presumably because they were older. By contrast, the AP leaves had probably not fully developed the mechanisms to sense or to react to

the leaf removal stimulus or, because these leaves were further away from the defoliation zone, they might have received a weaker 'signal'. In Experiment I, where leaf removal was imposed near veraison, the BAS and MID leaves had probably already passed the stage when they could adjust the photosynthetic apparatus to an increased demand, hence the absence of a significant response in A. WUE has been reported to increase following leaf removal (Hunter and Visser, 1988; Candolfi-Vasconcelos, 1990). This effect was only sporadically found here, in Experiments I and III (Appendix A).

In the experiments conducted, the enhancement of A due to the presence of fruits is consistent with previous studies on grapevines (Loveys and Kriedemann, 1974; Kriedemann et al., 1975; Kriedemann, 1977; Chaves, 1984; Downton et al., 1987) and several fruit crops (Flore and Lakso, 1989). Hale and Weaver (1962) observed that early in the post-bloom period the clusters are relatively weak sinks, and they become very powerful sinks only after fruit set. This may explain the finding that, when the leaf positions were considered, the presence of fruits increased A at 3.5 weeks after full bloom in Experiment II (Table 5) but had no significant in Experiment I either at two days (data not shown) or at two weeks after full bloom (Table 4). It can be argued that A remained higher on fruiting vines due to high photosynthate demand and translocation toward the fruits, which would prevent or minimize a hypothesized end-product inhibition of photosynthesis (Neales and Incoll, 1968). Hormonal control is also a possibility, as suggested by studies where the decline in A following fruit removal was accompanied by a raise in phaseic acid and abscisic acid (ABA) in leaves (Loveys and Kriedemann, 1974), and by a reduction

in gibberellin levels (Hoad et al, 1977). ABA has been implicated in the reduction of stomatal conductance (Loveys and Kriedemann, 1974; Downton et al., 1988), and gibberellin levels were found to be positively correlated to the activity of ribulose-1,5-bisphosphate carboxylase (Treharne and Stoddart, 1968).

Reduced light levels may lead to a lack of photosynthetic enhancement in response to increased sink strength (Flore and Lakso, 1989). However, in another experiment with potted vines conducted under the same conditions of Experiment II except that cropping level was combined with vine shading to 24% of sunlight, a significant increase in A due to the presence of fruits was likewise observed (Appendix B). It seems, therefore that a stronger light reduction than that imposed would be needed to prevent the fruit effect on A from occurring on grapevine leaves.

On mature vines (Tables 3 and 6), the response of A to the presence of fruits was noticeably lower than on young potted vines. In a previous study with field grown grapevines, no significant differences in A were found between fruiting and non-fruiting vines (Williams, 1986). Similarly, Kriedemann (1977) mentioned that the photosynthetic adjustment to fruiting demands is more evident on small potted vines, where shoot growth (therefore leaf number) is limited. In the experiments with potted vines (Experiments I and II), removal of all the lateral shoots likely enhanced the cropping effect on A, by intensifying the photosynthate demand to the main source leaves. Predictable differences in water status and in carbohydrate accumulation between potted and field vines may have also accounted for a different degree of photosynthetic response to leaf removal and cropping level. On mature vines, the fruit effect on A was particularly evident at the assessment three weeks

after veraison (Tables 3 and 6), probably reflecting a high photosynthate demand for fruit ripening. On other occasions, this effect was probably masked due to competitive vegetative sinks (Flore and Lakso, 1989). The intense vegetative growth of the mature non-fruiting vines might have created a photosynthate demand similar to that associated with the presence of fruits on 1.5 and NT vines.

A hypothetical relationship between photosynthetic rate and chlorophyll level has been investigated but conflicting results have been reported (Buttery and Buzzell, 1977; Hunter and Visser, 1989). In this study, as in Hunter and Visser (1989), there were situations where such a relationship apparently occurred, but this was not a general rule. At the gas exchange measurements between chlorophyll assessments in Experiment II (August 29 and September 13), A was higher on 3Cl than on 0Cl vines at every leaf position (Table 2). This was in correspondence to higher chlorophyll levels at MID and AP leaves on the former vines (Table 7). However, at BAS leaves, where the fruit effect on A was more strongly marked, the chlorophyll levels were not significantly higher on 3Cl than on 0Cl vines. This suggests that differences in leaf chlorophyll concentration were not decisive for the enhanced A on fruiting vines. Chlorophyll levels were found to increase in response to defoliation (Hofäcker, 1978; Hunter and Visser, 1989; Candolfi-Vasconcelos, 1990). Probably due to the reduced number of leaves removed, no clear leaf removal effect on total leaf chlorophyll was noticed in this study.

Leaf Removal and Cropping Level Effects on Vegetative Growth and Dry Matter and Non-structural Carbohydrate Partitioning

Although either one or both source/sink manipulation treatments imposed had a significant effect on the net CO_2 assimilation rate per unit of leaf area (A), it must be noted that this rate may not be well correlated with that of the vine as a whole (Edson, 1991), nor with total dry matter production (Kramer, 1981). At individual leaves, A responded positively to an increased cropping level, but there was no significant correlation between cropping and net CO_2 assimilation rate of the whole vine; the lower A on slightly cropped vines appeared to be compensated for by a larger leaf area (Edson, 1991). In the present study, the CO_2 assimilation of the whole vine was not evaluated, but the absence of a significant cropping effect on total dry matter accumulation (Table 10) may indicate a lack of photosynthetic response at the whole vine level. This suggestion must be viewed with caution, though, given that the overall dry matter accumulation resulted from assimilate production and utilization over an extended period; besides, a similar total dry weight may reflect a different photosynthate production, due to differences both in dry matter partitioning, and in the respiration rate (Amthor, 1989) and energy content per unit of dry weight (Gifford et al., 1984) of the different plant parts.

The lack of a significant cropping effect on total dry weight (Table 10) is consistent with the findings of Eibach and Alleweldt (1985) and Edson (1991); in both studies, as in the present one, cropping level had a marked influence, however, on dry matter partitioning. Similar results were reported by Lenz (1979) in citrus. Assimilates were allocated into the fruits at the expense of canes, roots and leaves

(Tables 10 and 11), in agreement with the generalized observation that fruits are successful competitive sinks (Wardlaw, 1968).

The vines partitioned on September 30/90 were still holding functional leaves, while those partitioned in January and March of 1991 had their leaves naturally abscised and carbohydrate accumulation proceeded normally. This may explain the observation that in canes (Table 12) and roots (Table 14) the levels of TNC were higher on January 10 than on September 30, despite the consumption of reserves in maintenance processes that occurred meanwhile. Respiratory losses most certainly accounted for the decrease in TNC from January and March. The observed high concentration of storage carbohydrates in roots is consistent with previous results (Schrader, 1924; Winkler and Williams, 1945). Cell walls are proportionally more developed in stem than in root tissues; this would lead to a higher concentration of non-structural carbohydrates in roots even if the cell content were similar in both tissues (Winkler and Williams, 1945). Even though carbohydrate accumulation was not completed on September 30, the fact that starch was the most abundant non-structural carbohydrate in all the tissues analyzed and that its concentration largely changed during the dormant season agrees with previous studies with grapevines where starch was found to be the main storage carbohydrate (Richey and Bowers, 1924; Winkler and Williams, 1945). In this study, the number of sampling dates does not allow for a detailed description of carbohydrate evolution. Nevertheless, the increase in soluble carbohydrates between September 30/90 and January 10/91 and the concomitant reduction in starch (Tables 12, 13 and 14) seem to agree with previous reports of a starch:sugar conversion during the fall and in early to mid-

winter, in grapevines (Richey and Bowers, 1924; Schrader, 1924; Winkler and Williams, 1945) and several other species (Siminovitch et al., 1953; Levitt, 1956). This conversion appeared to occur in all vine tissues analyzed. In the trunk, where the TNC levels changed only slightly between September 30 and January 10 (unlike in canes and roots), the evidence of a starch:sugar conversion is particularly suggestive; the increase of 111.5 mg/g dry weight in soluble carbohydrate content between these dates closely approached the decrease in starch concentration (Table 13). The increase in starch and decrease in soluble carbohydrates noticed in canes (Table 12) and trunk (Table 13) between January and March of 1991 is consistent with the suggestion of a sugar:starch conversion in the late winter, before the above-ground growth starts (Schrader, 1924; Kliewer, 1967). In roots, however, starch decreased again between January and March (Table 14). This was probably due to larger respirational losses in the roots in late winter due to higher soil than air temperature, and root growth (Winkler and Williams, 1945).

The reduced leaf removal effect on the carbohydrate content of the tissues analyzed is conceivably due to the low number of leaves removed. In the few cases when the leaf removal effect was significant (root starch and TNC levels averaged across sampling dates) the vines defoliated at pea size (R1) had higher carbohydrate levels than those defoliated at veraison (R2), and similar or even higher (in the case of root TNC) levels than the control vines. In March, cane soluble carbohydrate and TNC on a dry weight basis were higher in R1 than in R2 vines in the case of 3Cl vines; when only 0Cl vines were considered, levels were lower on R1 and R2 than on control vines. It appears that the presence of fruits during the treatment season

was needed for a carbohydrate compensation to occur in canes of R1 vines. Carbohydrate translocation might have been altered by leaf removal at pea size, unlike by removal at veraison; this hypothesis needs further investigation. Besides, the enhancement of A at BAS and MID leaves in response to leaf removal at pea size has probably contributed to attenuate the leaf removal effects on carbohydrate levels.

Several reasons may have contributed to the variation in cropping effects on carbohydrate levels among sampling dates and vine tissues. On September 30, 1.5 weeks after harvest, the canes of 3Cl vines had lower starch concentration than those of 0Cl vines (Table 12), conceivably because they had been deprived of carbohydrates for the benefit of the clusters, the dominant sink after berry set (Hale and Weaver, 1962). Besides photosynthates translocated from the leaves, the ripening berries may import sugars derived from carbohydrate reserves in shoots (Matsui et al., 1979), or shoots, roots and trunk (Mansfield and Howell, 1981). Following harvest, carbohydrate allocation to storage tissues was conceivably greatly enhanced on 3Cl vines, while until then carbohydrates were mainly diverted towards the clusters. Limitations in the capacity of the vascular system to adjust to the altered translocation pattern may explain the finding that on September 30 the levels of soluble carbohydrates in canes (Table 12) and trunk (Table 13) were higher, on a dry weight basis, on 3Cl than on 0Cl vines. Moreover, the wood/bark ratio was conceivably lower in canes of 3Cl than of 0Cl vines due to the smaller diameter of the former canes (Table 9); this may have further contributed to the lower starch and higher soluble carbohydrate content in the canes of 3Cl vines. Indeed, Winkler and

Williams (1945) found that starch concentration was higher in the wood than in the bark of basal cane portions, while Kliewer (1967) noticed that the soluble carbohydrate content in the early fall was higher in the shoot bark than in the wood. In spite of the large amount of photosynthate diverted to the clusters, 3Cl vines had higher starch concentration in the trunk (Table 13) and roots (Table 14) than 0Cl vines. The physical constraint created by the smaller size of the root system and trunk of 3Cl vines (Table 9), and lower respirational losses in these vines to meet maintenance needs during the dormant season, are possible explanations for the above results.

Conclusions

Basal leaf removal at pea size (five weeks after full bloom) increased the leaf net CO_2 assimilation rate (A) at basal and middle-shoot leaf positions on potted vines, while removal at veraison had no significant effect on A, whether on potted or on mature field vines. As in previous studies with grapevines and other crops, the presence of fruits increased A at individual leaves. This effect was more clearly evidenced on young potted than on mature field vines. The observed changes in A are likely due to an influence of the source/sink manipulative treatments on the photosynthate demand at individual leaves. Fruiting and non-fruiting potted vines had a similar total dry weight, a coarse indication that cropping level had probably little influence on the net photosynthesis of the vine as a whole. The presence of fruits had, on the other hand, a marked effect on dry matter allocation; the fruits

developed at the expense of all the vegetative components.

Fruit development increased, on a dry weight basis, the soluble carbohydrate content in canes and trunk of potted vines in the early fall (1.5 weeks after harvest), but decreased the starch and total non-structural carbohydrate (TNC) in canes (on a fresh volume basis) when the early fall, mid-, and late winter data were combined. On the other hand, the concentration of starch and TNC in the trunk and of starch in roots were higher on the vines that had borne fruit, conceivably due to decreased storage capacity associated with the lower vegetative development of these vines. Basal leaf removal had no significant effect on growth, total dry weight and dry matter partitioning in potted vines, and little influence on carbohydrate concentration in the tissues analyzed. In the few instances when a significant effect was found, carbohydrate concentration was favored by leaf removal at pea size relative to leaf removal at veraison. The observed enhancement of A following leaf removal at pea size and, probably an alteration in translocation pattern, may have contributed to the above results. Probable implications of these findings on the cold hardiness of bud and cane tissues and on bud fruitfulness will be discussed in further chapters.

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CHAPTER II

Influence of Basal Leaf Removal and Cropping Level on the Cold Hardiness of Primary Bud and Cane Tissues of Seyval Grapevines

Abstract

On potted vines, basal leaf removal in 1990 had no significant effect on primary bud and cane hardiness in the 1990/91 dormant season. Hardiness was higher on fruiting than on non-fruiting vines, supposedly due to improved acclimation of the former vines, resulting from less vigorous growth.

On mature vines, treatment effects on hardiness were more marked in 1989/90 than in 1990/91. Carbohydrate storage in the 1989 fall was probably impaired due to an early leaf killing frost and, in fruiting vines, to a heavy 1989 crop. Basal leaf removal 2.5 weeks after veraison in 1989 decreased cane hardiness when all sampling dates of 1989/90 were considered; removal at veraison in 1990 had no significant effect on tissue hardiness in 1990/91. Leaf removal had no significant effect on the number of canes with five or more mature nodes before pruning in the following April, but reduced the number and percentage of canes with less than five mature nodes. The percentage of shootless nodes was not significantly affected by leaf removal in the previous season. Cropping level affected primary bud hardiness when the sampling dates in the 1989/90 dormant season were combined. Non-fruiting (0) vines had hardier buds than unthinned (NT) ones; vines thinned to 1.5 clusters/node retained (1.5) had intermediate bud hardiness. The percentage of shootless nodes in 1990 was accordingly affected by cropping level. In 1990/91, an overall difference of 1°C separated the primary bud hardiness of fruiting and non-fruiting vines; this difference was not significant but appeared to be viticulturally relevant, given the higher percentage of shootless nodes on the former vines in 1991.

The number of canes with five or more mature nodes before pruning was higher on non-fruiting than on fruiting vines, but the percentage relative to the total number of canes/vine did not significantly differ among cropping levels. There were no significant differences in hardiness, cane maturity and percentage of shootless nodes between 1.5 and NT vines in any of the trial years.

Introduction

Winter cold is a serious problem of the grape industry at (but not limited to) the northern limits of culture (Wolpert and Howell, 1985). In Northeastern viticultural areas of the U.S.A. cold injury is a major concern (Dethier and Shaulis, 1964; Shaulis et al., 1968; Howell and Shaulis, 1980) and has motivated an intense effort to determine the factors that influence cold resistance, and to evaluate the impact of diverse cultural practices on grapevine hardiness (Stergios and Howell, 1977; Byrne and Howell, 1978; Howell et al., 1978; Howell and Shaulis, 1980; Mansfield and Howell, 1981; Wolpert and Howell, 1985; Howell, 1988; Miller et al., 1988).

The dormant season can be subdivided into distinct periods characterized by differences in environmental conditions and in the expression of hardiness (Howell, 1988). The first period is acclimation, or the transition from the non-hardy to the hardy condition. The second period, mid-winter, is the time when cold is most severe and the vines exhibit the maximum hardiness (Müllner and Mayer, 1978; Howell, 1988). The third is a post-rest period, in which cold hardiness fluctuates in response

to fluctuating temperatures. This is followed by a period of gradual warming when deacclimation takes place (Howell, 1988).

The internal mechanisms responsible for the above changes in hardiness are not well understood. 'Several thousand' papers have been written on cold hardiness and freezing injury (Steponkus and Wiest, 1978). Nevertheless, given the complexity of the processes involved in cold acclimation, freezing injury or recovery from injury, a general theory to explain these phenomena has not been found. A large number of metabolic and physiological changes accompanying cold acclimation have been investigated for possible involvement in the hardening processes. These include qualitative and quantitative changes in cellular compounds such as carbohydrates, lipids, nucleic acids, proteins, and growth regulators, namely ABA (for a review see Levitt, 1980; Guy, 1990). It still remains to be clarified, though, whether correlations rather than cause-effect relationships may link those changes and the hardiness responses.

Carbohydrates have been suggested to play an osmotic role in hardiness (Levitt, 1956), act as cryoprotectants, or as source of energy for hardening processes (Howell and Stackhouse, 1973). Whichever their actual role is, a reduced carbohydrate storage resulting from defoliation treatments was considered detrimental to tissue hardiness and winter survival in grapevines (Howell et al., 1978; Mansfield and Howell, 1981; Howell, 1988) and sour cherry (Howell and Stackhouse, 1973).

Previous research conducted in our laboratory to evaluate the influence of defoliation on grapevine hardiness utilized a severe defoliation stress: removing 100%

(Stergios and Howell, 1977; Howell et al., 1978) and either 100% or 50% of the leaves (Mansfield and Howell, 1981). In the current study, fruiting and non-fruiting vines were subjected to the removal of only a few basal leaves in the cluster region (or equivalent in non-fruiting vines) and the effects of cropping level and leaf removal on cane maturity and on the hardiness of cane and primary bud tissues taken from the defoliated region were investigated. This study may represent a step towards the evaluation of the applicability of basal leaf removal in a region like Michigan, where cold hardiness is crucial for a successful grape growing. If, as suggested by Hale and Weaver (1962) and Smart et al. (1982), the leaf subtending a bud is the main photosynthate source for that bud, it might be anticipated that the buds axillary to the leaves removed are affected in their carbohydrate status and cold resistance, unless there is some mechanism to attenuate or compensate for a localized carbohydrate depletion, or the carbohydrate levels are simply not limiting the hardening processes.

Materials and Methods

Plant material and treatments applied

Experiment I

Own-rooted, mature, bearing Seyval (Seyve-Villard 5-276) grapevines in a vineyard at the Clarksville Horticultural Experimental Station (CHES), Clarksville, Michigan, were used in this experiment. The vineyard was planted in 1983 in a Kalamazoo sandy loam soil, with a spacing of 2.4 m x 3.0 m within and between rows,

and a N-S row orientation. The vines were trained to Hudson River Umbrella (a bilateral cordon at the top wire), with the top wire at 1.8 m height. The vines were balanced pruned using a 15+10 pruning formula (Reynolds et al., 1986), up to a maximum of 65 nodes retained per vine. Other details regarding vineyard maintenance were presented in Chapter I.

Prior to the 1989 growing season, a randomized block design was established. Vine size (weight of one-year old cane prunings), which varied between 1.0 and 1.5 kg, was used as the blocking variable. Five blocks of six vines were defined, one vine per treatment combination. Treatments were arranged as a 2x3 factorial with leaf removal and cropping level as factors. The leaf removal levels were: C = no leaves nor lateral shoots removed (control); R = main leaves and lateral shoots removed at three consecutive basal nodes on all the shoots of the vine. The cropping levels were: 0 = 0 clusters per vine; 1.5 = 1.5 clusters per node retained at pruning; NT = all clusters left (no thinning). The treatment combinations are abbreviated as C/0, C/1.5, C/NT, R/0, R/1.5, and R/NT. In the 1990 growing season each vine received the same treatment combination assigned in 1989. Cluster thinning was done on June 12/1989 (one week before full bloom) and June 27/1990 (nine days after full bloom). Leaf removal was imposed on September 10/1989 (2.5 weeks after veraison) and August 15/1990 (veraison). On fruiting shoots, leaves and lateral shoots opposite, one node above, and one node below the basal cluster were removed. On non-fruiting shoots, leaves and laterals were removed from equivalent node positions. The position of the defoliated nodes was marked on the shoots for further reference. Lateral shoots were allowed to develop normally except for those at the three treated

nodes on the defoliated vines.

Experiment II

This experiment was initiated in 1990 at the Horticultural Research Center (HRC), East Lansing, Michigan, at the same site and simultaneously with another leaf removal experiment in potted vines described in a previous chapter (Experiment II, Chapter I). The installation procedure, cultural practices (training, removal of lateral shoots, irrigation, fertilization and spraying) and the treatments imposed were exactly the same and performed on the same dates in both experiments.

In May/1990 two-year-old own-rooted Seyval grapevines were weighed and planted in 19 l pots containing a sterilized loam, sand and peat mixture with good water holding and aeration properties. Nine blocks of six vines each were used in this experiment; vine fresh weight before planting was used as the blocking variable. The potted vines were placed on a flat gravel-covered area at a 1.0 m x 1.2 m spacing, allowing for good light exposure, and trained to two shoots. Treatments were arranged in a 3x2 factorial, with leaf removal and cropping level as factors. The leaf removal levels used were: C = no main leaves removed (control); R1 = main leaves removed at three consecutive basal nodes at pea size (July 27, five weeks after full bloom); R2 = main leaves removed at three consecutive basal nodes at veraison (Aug. 21, eight weeks after full bloom). The cropping level was either 0Cl = 0 clusters per vine or 3Cl = 3 clusters per vine. Treatment combinations are abbreviated as C/0Cl, C/3Cl, R1/0Cl, R1/3Cl, R2/0Cl, and R2/3Cl.

Thinning was imposed on July 4 (10 days after full bloom). On the vines

thinned to 3 clusters, the basal cluster on one shoot and two clusters (the basal and the second) on the other shoot were retained. Leaves were removed on both vine shoots at the three node positions indicated for mature field vines (Experiment I). Unlike Experiment I, all the lateral shoots were removed at weekly intervals, regardless of the treatment combination. This was done to avoid the variability that would result from an erratic lateral growth (Buttrose, 1968).

During the 1990/91 dormant season, the vines were kept outdoors mulched with straw up to most of the trunk height.

Cane sampling for controlled freezing tests

Experiment I

Canes were collected at three occasions during the 1989/90 and 1990/91 dormant seasons: late fall, mid-winter, and early spring before bud-burst. Cane sampling considered the factors known to influence cold hardiness, as reported by Howell and Shaulis (1980). Well exposed canes with dark periderm and a medium diameter (7-10 mm, averaged over two perpendicular directions between nodes four and five) were collected at all sampling dates. On the third sampling date of 1990/91 (March 26/91), the non-thinned vines were not sampled, due to insufficient number of canes with the desired characteristics. The canes removed from each vine were weighed so that, at pruning in 1990 and 1991, the vine size was obtained by adding the weight of the cane prunings from each vine to the weight of the canes removed from that vine for cold hardiness assessments in the previous dormant season.

Only the cane segments containing the three nodes subjected to leaf removal

in the previous season (or equivalent nodes in the case of the non-defoliated vines) were used in the freezing tests. These segments were put in plastic bags, kept in styrofoam containers with ice during transport to the laboratory, and then stored at 0°C until being used in the freezing runs within 24 hours.

Experiment II

Canes were sampled during the 1990/91 dormant season, at the same occasions as in Experiment I. The nine blocks of vines were distributed into three groups (lighter, medium and heavier) according to the initial fresh weight of the vines. One block per group was randomly selected to be used at each sampling date. Both canes of each vine were sampled regardless of their diameter. All canes were well exposed and dark, but canes from fruiting (3Cl) vines had smaller diameters than those from non-fruiting (0Cl) ones (data not shown). Three-node cane segments were taken from the same cane position selected in Experiment I.

Controlled freezing tests

Controlled freezing tests were conducted to evaluate the cold hardiness of cane and primary bud tissues. Sample preparation was based on the procedure described by Howell and Weiser (1970) and Howell et al. (1978).

The three-node cane segments were cut into single node sections and the sections from the vines subjected to the same treatment combination were pooled together. Three single node sections per temperature per treatment combination were used. The base of the single node cane sections was wrapped in moistened

cheese cloth to inoculate the tissues with ice and thereby reduce the degree of supercooling during the freezing test (McKenzie and Weiser, 1975). To monitor the progress of the freezing run, a thermocouple (26 gauge copper-constantan) was inserted into the pith of a cane section in each set including all the treatment combinations. The sets were then wrapped in aluminum foil. In 1989/90 they were further placed in vacuum flasks to promote a gradual decrease in tissue temperature. Then they were placed in a Revco Ultra Low freezer where the temperature was manually lowered to achieve a temperature decline of 3 to 5°C/hour. In 1990/91 no vacuum flasks were considered necessary because a steady temperature decrease of 4.0°C/hour was automatically controlled using a computer program.

Five target freezing temperatures and a non-freezing one were used per sampling date. The unfrozen tissues were held at 5°C during the freezing runs and thereafter subjected to the same procedures as the frozen materials. Target temperatures were separated by 3 or 4°C, depending on the time of sampling. The temperature range used aimed at obtaining 100% of survival at the uppermost temperature and 100% of tissue death at the lowest one.

The samples were removed from the freezer when the appropriate target temperatures were attained and then allowed to gradually thaw at 2°C until the following day. Then they were placed in aerated humid chambers at room temperature (approx. 20°C). Ten days later the mortality of primary buds and cane tissues was evaluated under a binocular microscope using the browning test (Howell and Weiser, 1970; Stergios and Howell, 1973). Primary buds were considered dead if the primordia were brown and water soaked; canes were rated as dead if the

cambium/phloem area was brown in most of its extension.

Cane maturity and percentage of shootless nodes on mature field vines

On April 13/90 and April 1/91, before pruning, each vine was evaluated for the number of canes with five or more mature nodes. On April 1/91, after two treatment seasons, the total number of canes per vine and the number of canes with five or more mature nodes and medium diameter (7-10mm between nodes four and five) were also assessed. These values were corrected by adding the number of canes removed from each vine for cold hardiness assessments in the preceding dormant season.

The percentage of shootless nodes was assessed in the early summer of 1990 (July 5) and 1991 (June 20), about two weeks after full bloom. It was assumed that by this time all the shoots for the current season had emerged. This percentage was calculated by counting the number of nodes that failed to develop and dividing it by the total number of buds retained at pruning.

Statistical analysis

A modified Spearman-Karber equation (Bittenbender and Howell, 1974) was used to estimate the temperature at which 50% mortality occurred (T_{50}). For ease of exposition, statistical significance was indicated in the tables relative to the T_{50} values. However, the hardiness data analyzed were the discrete injury data for canes and primary buds at the temperatures tested. The number of dead tissues at each temperature for every treatment combination was converted to percentage and then

subjected to the arc-sine of the square root transformation. The transformed data were then analyzed using the GLM (from General Linear Models) procedure of the Statistical Analysis System package (SAS Institute Inc., 1985). Stressing temperature was included in the model as a covariate. The analysis was done for each sampling date of both seasons, as well as for the pooled data of the three sampling dates in 1989/90, for the first two dates of 1990/91 (due to the unavailability of cane material of the NT level of cropping at the third assessment), and for the three dates of 1990/91 (not considering the NT level in the calculations). When more than one sampling date was analyzed, sampling date was included in the model as a blocking variable. Because stressing temperatures varied with sampling date, temperature was considered nested within date.

Data on percentage of shootless nodes and percentage of canes per maturity class were subjected to the arc-sine of the square root transformation and then analyzed by analysis of variance.

In all the statistical analyses when the F-values were significant at the 5% or lower level, mean separation was done using the LSD test at the 5% level.

Results and Discussion

Cane and primary bud hardiness

On mature, field-grown vines, basal leaf removal (R) had a significant effect on cane hardiness in the mid-winter of 1989/90 and across that dormant season; canes were hardier on control (C) than on R vines, as evidenced by lower T_{50} on the

former (Table 1). When the three sampling dates of 1989/90 were considered, primary bud hardiness was lower on fruiting than on non-fruiting vines; the vines thinned to 1.5 clusters per node retained (1.5 vines) had intermediate bud hardiness between unthinned (NT) and non-fruiting (0) vines, not significantly different from any of the two.

In 1990/91 (Table 2), treatment effects on the hardiness of mature vines were, in general, less marked than in 1989/90 (Table 1). Cane hardiness was not significantly affected by leaf removal neither was primary bud hardiness by cropping level, unlike in 1989/90. On the other hand, canes were hardier on 1.5 than on non-fruiting vines when all sampling dates of 1990/91 were considered, although no significant cropping effect was observed for individual sampling dates. Data were not analyzed across years; however, cane and primary bud hardiness were clearly higher in 1990/91 than in 1989/90 at comparable sampling dates, an exception being cane hardiness in March (Tables 1 and 2; Figures 1 and 2).

On mature vines, leaf removal consisted of removing not only basal main leaves but also lateral shoots (hence lateral leaves) at the defoliated nodes. During the post-veraison period, the leaves on lateral shoots are a very active source of assimilates not only for the ripening cluster but also for carbohydrate storage in the wood (Candolfi-Vasconcelos, 1990). Under the conditions of Experiment I, the possibility that some compensatory response might have attenuated the effects of leaf removal is remote. In a study earlier presented (Chapter I), there was no significant enhancement of the CO_2 assimilation rate following leaf removal at veraison. Besides, based on Hunter and Visser (1990), a compensatory increase in lateral shoot growth

Table 1. Influence of leaf removal and cropping level on cold hardiness (T_{50}) of primary bud and cane tissues of mature, field-grown Seyval grapevines (CHES 1989/90 - Experiment I).

Treatment[z]	Dec. 1/89		Jan. 25/90		Mar. 23/90		Average of the three sampling dates	
	1[er]bud	Cane	1[er]bud	Cane	1[er]bud	Cane	1[er]bud	Cane
Leaf removal								
C	-19.5	-18.5	-17.5	-21.0a	-13.0	-18.0	-16.5	-19.0a
R	-19.0	-17.0	-15.0	-17.0b	-15.0	-17.0	-16.5	-17.0b
	ns[y]	ns	ns	*	ns	ns	ns	*
Crop. level								
0	-20.5	-19.5	-17.0	-18.5	-15.0	-18.0	-17.5a	-18.5
1.5	-19.0	-16.5	-17.0	-20.5	-14.0	-17.5	-16.5ab	-18.0
NT	-18.5	-17.5	-15.0	-18.5	-12.5	-17.5	-15.5b	-18.0
	ns	ns	ns	ns	ns	ns	*	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on September 10/89 (2.5 weeks after veraison).
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 12/89.
[y]ns, * Non-significant or significant at the 5% level, respectively. Mean separation whithin columns using the LSD test at 5%.

Table 2. Influence of leaf removal and cropping level on cold hardiness (T_{50}) of primary bud and cane tissues of mature field grown Seyval grapevines (CHES, 1990/91 - Experiment I).

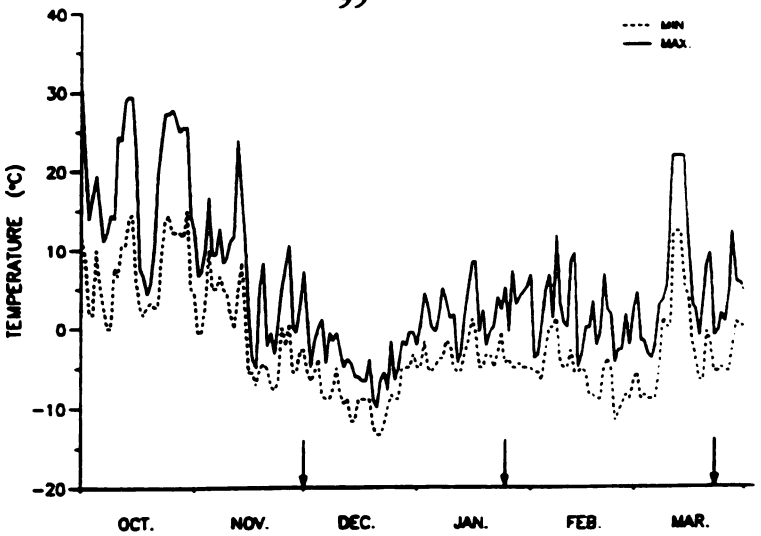
Treatment[z]	Nov. 30/90		Feb. 26/91		Mar. 26/91		Average of Nov. 30/90 and Feb. 26/91		Average of the three sampling dates	
	1[ery]bud	Cane	1[ery]bud	Cane	1[ery]bud	Cane	1[ery]bud	Cane	1[ery]bud	Cane
Leaf removal										
C	-20.5	-22.0	-24.0	-26.5	-15.5	-15.5	-22.5	-24.5	-20.0	-21.0
R	-21.0	-22.0	-23.5	-25.5	-17.5	-17.5	-22.5	-23.5	-21.0	-21.5
	ns[y]	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level										
0	-21.5	-20.5	-25.0	-25.5	-16.5	-15.5	-23.0	-23.0	-21.0	-20.5b
1.5	-20.0	-22.0	-24.0	-27.5	-16.0	-17.5	-22.0	-25.0	-20.0	-22.5a
NT	-21.5	-23.5	-22.5	-25.5	NA[x]	NA	-22.0	-24.5	NA	NA
	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

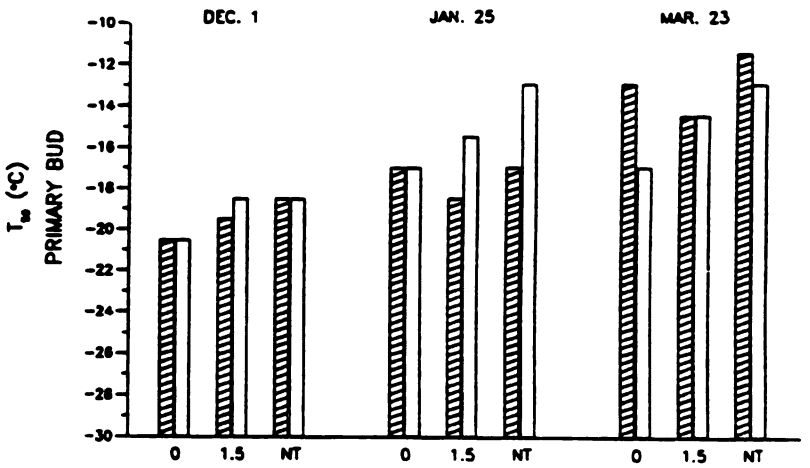
[z]C:control (no leaves removed); R:leaves removed on Aug. 15/90 (veraison)
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.
[y]ns, * Non-significant or significant at the 5% level, respectively.
[x]NA: Not available.

Figure 1. Maximum-minimum temperature profile for the 1989/90 dormant season at the site of Experiment I (Clarksville) and the cold hardiness (T_{50}) of primary bud and cane tissues per cropping level x leaf removal treatment combination on mature Seyval grapevines in the late fall, mid-winter and early spring of 1989/90 (sampling dates indicated by arrows in the upper graph). Means per treatment level are presented in Table 1.

Leaf removal:
▨ C: control (no leaves removed)
▭ R: basal leaves removed on September 10/89

Cropping level (imposed on June 12/89):
0 : 0 clusters per vine
1.5 : thinned to 1.5 clusters /node retained
NT: unthinned





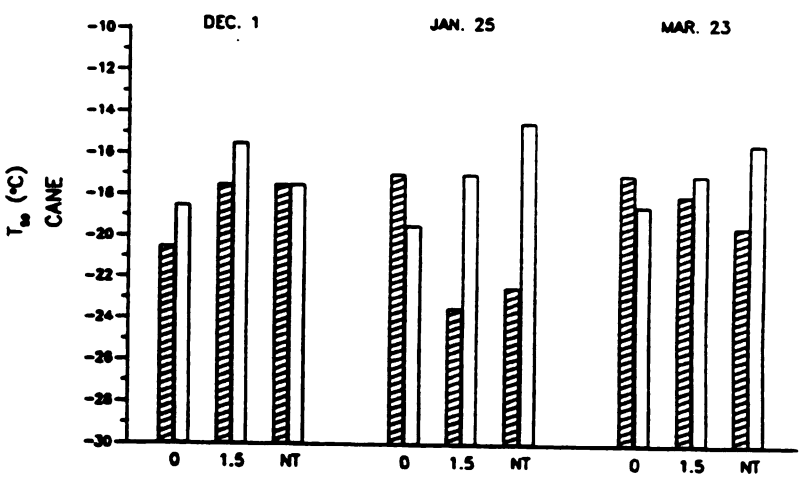


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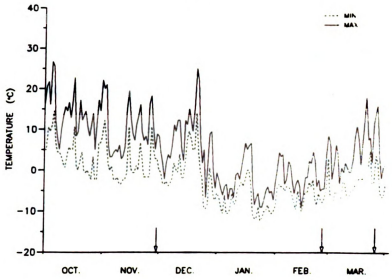
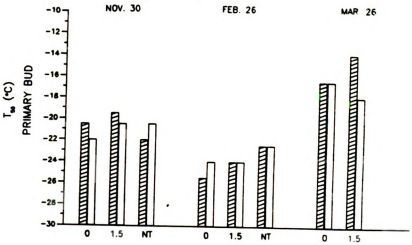
Figure 2. Maximum-minimum temperature profile for the 1990/91 dormant season at the site of Experiment I (Clarksville)[z] and the cold hardiness (T_{50}) of primary bud and cane tissues per cropping x leaf removal treatment combination on mature Seyval grapevines in the late fall, mid-winter and early spring of 1990/91 (sampling dates indicated by arrows in the upper graph). Means per treatment level are presented in Table 2.

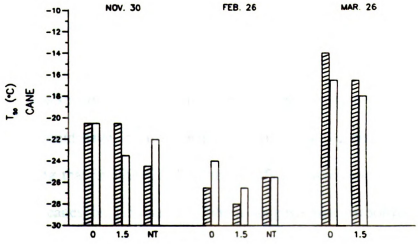
Leaf removal:
▨ C: control (no leaves removed)
▭ R: basal leaves removed on August 15/90

Cropping level (imposed on June 27/90):
0 : 0 clusters per vine
1.5 : thinned to 1.5 clusters /node retained
NT: unthinned

[z]Except for the period from Feb. 9 to Feb. 25 when data at Clarksville were not available and maximum and minimum temperature were estimated by regression from the values at a nearby station (Grand Rapids). The regression equations were fitted considering the temperature at both sites in the 10-day period immediately before and after the period of missing data. The equations used were: $Y=0.5003X + 10.518$ ($R^2=0.843$) for minimum temperature and $Y= 0.7061X + 4.3309$ ($R^2=0.9003$) for maximum temperature, where Y and X are the temperature (°F) at Clarksville and Grand Rapids, respectively.


TEMPERATURE (°C)
40
30
20
10
0
−10
−20
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.


T_{50} (°C)
PRIMARY BUD
NOV. 30
FEB. 26
MAR. 26
0
1.5
NT
0
1.5
NT
0
1.5


T_{50} (°C)
CANE
NOV. 30
FEB. 26
MAR. 26
0
1.5
NT
0
1.5
NT
0
1.5

following leaf removal as late as veraison seems unlikely.

One possible reason for the differences in treatment effects between the 1989/90 and the 1990/91 dormant seasons is a heavier crop and stronger growth inhibition in fruiting vines in 1989 than in 1990 (Chapter III). Moreover, an unseasonably early leaf killing frost in the fall of 1989 presumably affected carbohydrate storage for the 1989/1990 dormant season aggravating, in fruiting vines, the stress resulting from the heavy 1989 crop. The fact that primary bud hardiness in 1989/90 was affected by the 1989 crop may be due to insufficient carbohydrate accumulation. Previous studies showed that cluster thinning, presumably by reducing competition for carbohydrates, improved hardiness on heavily stressed vines (Howell et al., 1978; Howell, 1988). An inspection of the T_{50} means in 1989/90 for each treatment combination (Figure 1) revealed that the mid-winter reduction in cane hardiness by leaf removal in 1989 derived solely from the response of the fruiting (1.5 and NT) vines. The difference in T_{50} values between C and R vines was as large as 8°C and 6.5°C for canes of NT and of 1.5 vines, respectively; on fruiting vines, mid-winter primary bud hardiness was also apparently affected by leaf removal although to a lesser, non-significant degree. The above results suggest that the activity of the leaves removed from fruiting vines would otherwise have been particularly important in 1989/90 because not only the heavy crop in 1989 but also the shorter season due to early frost would have led to impaired carbohydrate accumulation. On the other hand, the finding that in 1990/91 the only significant treatment mean difference was that of hardier canes on 1.5 than on 0 vines suggests that carbohydrate storage was less critical for hardiness in 1990/91, following the 1990 season when fruiting vines

yielded a light crop and growth was relatively intense.

On potted vines, leaf removal in 1990 had no significant effect on cane and primary bud hardiness during the 1990/91 dormant season (Table 3). Fruiting (3Cl) potted vines had hardier canes than non-fruiting (0Cl) ones in the late fall of 1990 and in the early spring of 1991, as well as hardier primary bud and cane tissues when the three sampling dates of 1990/91 were considered. Thus, cropping level effects on hardiness were more marked on potted (Table 3) than on mature vines (Table 2) during the same dormant season. Either on potted or on field vines, dark, well exposed canes were sampled for hardiness assessments. However, while the canes from mature vines were selected for a defined diameter range, those from potted vines were not subjected to diameter selection and the canes sampled from 3Cl vines had smaller diameter than those from 0Cl vines (data not shown). The lower vigor of the canes from 3Cl vines conceivably allowed for a better maturation and acclimation and hence for an increased cane and bud hardiness. On the other hand, the use of cane diameter as a sampling criterion on mature field vines, and the fact that mature vines were balanced-pruned throughout this study probably attenuated the treatment effects on cold hardiness (Howell and Shaulis, 1980; Wolpert and Howell, 1985).

Changes in hardiness degree have often been found to correspond to carbohydrate conversions (Guy, 1990). Sugar levels usually raise in the fall as plants harden and decrease in spring with dehardening (Siminovitch et al., 1953; Levitt, 1956). In grapevine (Wample et al., 1988) and several other species (Sakai, 1960; Layne and Ward, 1978; Raese et al., 1978; Levitt, 1980) a close relationship was

Table 3. Influence of leaf removal and cropping level on the cold hardiness (T_{50}) of primary bud and cane tissues of 2-year-old potted Seyval grapevines (HRC 1990/91 - Experiment II).

Treatment[z]	Nov. 30/90		Feb. 27/91		Mar. 27/91		Average of the three sampling dates	
	1[ere]bud	Cane	1[ere]bud	Cane	1[ere]bud	Cane	1[ere]bud	Cane
Leaf removal								
C	-23.0	-24.0	-23.5	-31.0	-15.5	-19.0	-20.5	-24.5
R1	-21.5	-25.0	-21.5	-29.0	-15.0	-19.5	-19.5	-24.5
R2	-21.0	-24.0	-19.5	-26.5	-16.0	-18.0	-19.0	-23.0
	ns[y]	ns	ns	ns	ns	ns	ns	ns
Crop. level								
0Cl	-20.5	-22.0b	-20.5	-29.0	-14.5	-17.0b	-18.5b	-22.5b
3Cl	-22.5	-26.5a	-22.0	-28.5	-16.5	-20.5a	-20.5a	-25.0a
	ns	*	ns	ns	ns	*	*	*
Interaction	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, * Non-significant or significant at the 5% level, respectively.

noticed between sugar content and hardiness levels, but that was not true for other studies (Steponkus and Lanphear, 1968; references in Levitt, 1980). These findings can be resolved considering that cold acclimation is not solely due to an accumulation of sugars, thus a direct parallelism between the levels of sugars and of cold hardiness would occur only if sugar content was limiting the rate or degree of acclimation (Steponkus and Lanphear, 1968).

In a study presented earlier (Chapter I), carbohydrate analyses (starch and soluble carbohydrates) were done on potted vines grown under the same conditions and subjected to the same treatments as those in Experiment II. Internodal cane samples were taken in the early fall, mid- and late winter of 1990/91 within the cane region used in the hardiness determinations here presented. The sampling dates for carbohydrate evaluation did not correspond to those for hardiness assessments during the same dormant season, but still some inferences can be drawn by comparing the results from both studies. In the early fall, cane soluble carbohydrate concentration (in contrast with starch concentration) was higher on fruiting (3Cl) than on non-fruiting (0Cl) vines; no significant differences were found in total non-structural carbohydrate. Assuming that this relationship was valid throughout the fall, it can be suggested that higher soluble carbohydrate levels may have contributed to hardier cane tissues on 3Cl than on 0Cl vines at the first hardiness assessment of 1990/91 (Table 3). On mature field vines, by analogy with the potted ones, the relatively high hardiness levels of cane and primary bud tissues on C/NT vines in the late fall of 1990 (Figure 2) could also be associated with a relatively high soluble carbohydrate content in the canes of these vines. In March/91, differences in cane hardiness

between 3Cl and 0Cl vines would not have been anticipated from carbohydrate analyses (Table 12 of Chapter I). Indeed, only on R1 vines and solely for soluble carbohydrate content was there in March a significant difference between canes of 3Cl and 0Cl vines (higher levels in the former), while hardiness differences between the two cropping levels were particularly marked for R2 and C vines (results not shown). It can be suggested that cane carbohydrate content was probably not a decisive factor for hardiness at this time of the 1990/91 season.

On mature field vines, no carbohydrate analyses were done. However, as previously discussed, carbohydrate content might have limited cold hardiness in situations where carbohydrate insufficiency was more likely to occur, namely during the 1989/90 dormant season. In contrast, there were instances where such possibility appeared unlikely, such as in assessments where leaf removal apparently (though not significantly) improved cane and/or primary hardiness, in spite of the expectation that cane carbohydrate levels would be affected (Figures 1 and 2). These include the assessments in January/1990 for canes of non-fruiting (0) vines, in the fall of 1990 for 0 and 1.5 vines, in March/1990 for primary buds, and in March/1991 for both canes and primary buds (Figures 1 and 2). In the late March assessments, inconsistent hardiness results may in part be due to changeable hardiness levels due to large fluctuations in ambient temperature (Figures 1 and 2). The possibility also exists that, at least in some of those situations other factors, perhaps hormonal in nature, were more decisive to hardiness than carbohydrate levels.

Although some exceptions occur, growth inhibitors have been found to promote and growth promoters to reduce hardiness levels. There is evidence

suggesting that ABA and gibberellin may be endogenous hardiness promoter and inhibitor, respectively, but some contradictory results have been reported (Howell and Dennis, 1981). Besides their antagonistic effects on growth, the fact that ABA has been associated with dormancy in woody plants and gibberellin with dormancy inhibition (Roberts and Hooley, 1988) is consistent with a hypothetical role of these growth regulators in cold hardiness. Indeed, even though dormancy is not required for hardening (Irving and Lanphear, 1967a,b), still a rapid onset of rest and a prolonged rest period are considered important for winter survival (Brierley and Landon, 1946; Edgerton, 1954; Proebsting, 1963; Irving and Lanphear, 1967c; Howell and Dennis, 1981). It is worth to recall that in Experiment I leaf removal comprised not only the removal of main leaves but also of lateral shoots at the treated nodes of R vines. Howell and Shaulis (1980) found that the lack of persistent lateral canes favored the hardiness of cane and primary bud tissues in cvs. Vignoles and Riesling. Even though in that study, as in the present one, well exposed canes were sampled, the presence of large lateral shoots conceivably resulted in poor light exposure of the node from which the lateral shoot arose (Howell and Shaulis, 1980). Thus, the bud at the insertion of a large lateral shoot (namely on a vigorous, non-fruiting vine), would be relatively shaded compared to another bud at an equivalent node position on a R vine, whose lateral shoot was removed. The import of assimilates might be reduced due to shading in the former bud (May, 1965). However, it could also be the case that growth inhibitor levels were higher in the latter, better exposed bud. Light induces the formation of the growth inhibitor xanthoxin and can probably stimulate ABA synthesis, given the evidence that xanthoxin is an ABA precursor (Burden et

al., 1971). Moreover, the removal of lateral shoots probably corresponded to the elimination of a source of gibberellins or of any hardiness inhibitor. This would favor cold hardiness in situations where such removal did not drive the carbohydrate content to a level below a critical point.

Cane maturity and percentage of shootless nodes on mature field vines

Leaf removal in 1989 and 1990 had no significant effect on the number of canes per vine with five or more mature nodes prior to pruning in the following April, nor on the number and percentage of these canes that had the most favorable (medium) diameter in April/1991, after two treatment seasons (Table 4). This may suggest that leaf removal effects on cane maturity were of reduced practical meaning. However, the number and percentage of canes with less than five mature nodes in April/1991 was lower on R than on C vines, indicating that leaf removal enhanced periderm development at the basal shoot region, conceivably due to improved light conditions. This improvement would benefit the canes, regardless of their number of mature nodes. Neither in 1990 nor in 1991 was the percentage of shootless nodes significantly influenced by leaf removal in the preceding season (Table 5).

The number of canes per vine with five or more mature nodes was higher on non-fruiting (0) than on fruiting (1.5 and NT) vines, both in 1990 and 1991. As evaluated in April/1991, this effect was associated with a higher total number of canes on the former vines, while the frequency distribution per cane diameter and maturity classes was not significantly influenced by cropping level. In a previous study with Seyval, thinning improved cane maturity (Reynolds et al., 1986); however, the

Table 4. Influence of leaf removal and cropping level during the 1989 and 1990 seasons on the number of canes per vine with 5 or more mature nodes before pruning at the end of the following winter (April 13/90 and April 1/91), and on the within vine distribution of canes on April 1/91 by diameter and maturity categories related to cold resistance (Experiment I).

Treatment[z]	Canes per vine with 5 or more mature nodes on April 13/90	Canes with 5 or more mature nodes on April 1/91						Canes with less than 5 mature nodes on April 1/91		Total canes per vine on April 1/91
		Canes/vine	% of total	Medium (7-10mm) diameter		Large or small diameter (above or below 7-10mm)				
				Canes/vine	% of total	Canes/vine	% of total	Canes/vine	% of total	
Leaf removal										
C	30	32	65.3b	15	31.3	17	34.0	16a	34.7a	48
R	24	31	74.9a	17	40.2	14	34.8	10b	25.1b	41
	ns[y]	ns	*	ns	ns	ns	ns	*	*	ns
Crop. level										
0	43a	48a	76.0	22a	37.0	25a	39.0	15	24.0	63a
1.5	21b	25b	67.4	14b	36.3	12b	31.2	13	32.5	38b
NT	16b	22b	66.8	12b	33.9	10b	33.0	11	33.2	33b
	***	***	ns	**	ns	***	ns	ns	ns	***
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90;
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning dates: June 12/89 and June 27/90.
[y]ns, *, **, *** Non-significant or significant at the 5%, 1%, or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 5. Number of nodes retained on mature field grown Seyval grapevines prior to treatment imposition (1989), and influence of leaf removal and cropping level in the 1989 and 1990 seasons on the number of nodes retained at pruning and on the percentage of shootless nodes in the seasons following treatment application (Experiment I).

Treatment[z]	Number of nodes retained			Percentage of shootless nodes	
	1989[y]	1990	1991	July 5/90	June 20/91
Leaf removal:					
C	32	33	39	32.1	17.5
R	31	31	37	29.6	17.0
	ns[x]	ns	ns	ns	ns
Crop. level:					
0	32	58a	62a	15.9b	10.6b
1.5	32	22b	28b	34.8ab	19.9a
NT	31	15c	24b	41.8a	21.2a
	ns	***	***	**	*
Interaction	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90; 0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned
[y]At pruning prior to treatment imposition
[x]ns, *, ** Non-significant or significant at the 5% or 1% level, respectively. Mean separation within columns using the LSD test at 5%

vines were not balanced-pruned, which renders the results of that and of the present study hardly comparable. The larger number of canes on non-fruiting vines in April 1991 (Table 4) reflects a larger number of nodes retained on these vines in 1990 (a direct consequence of their larger size), and a lower percentage of nodes that failed to develop subsequently (Table 5). In 1991 the percentage of shootless nodes was, like in 1990, lower on non-fruiting than on fruiting (1.5 and NT) vines. The total number of canes before pruning in 1991 was similar on 1.5 and NT vines (Table 4). The NT vines had lower number and percentage of count-canes than the 1.5 vines, though (data not shown), due to fewer nodes retained at pruning in 1990 and a subsequently higher (but not significant) percentage of shootless nodes (Table 5).

Although data were not analyzed across years, the percentage of shootless nodes was clearly higher in 1990 than in 1991 (Table 5), in agreement with lower cold hardiness in the 1989/90 than in the 1990/91 dormant seasons (Tables 1 and 2). Primary bud hardiness data were more consistent with the percentage of shootless nodes than were cane hardiness data. In 1989/90, for instance, canes were hardier on C than on R vines when all sampling dates were considered but the percentage of shootless nodes in 1990 was similar in these vines. Moreover, in 1991 the lower percentage of shootless nodes on non-fruiting (0) vines was not in correspondence with the overall cane hardiness during the 1990/91 dormant season, which was lower on 0 vines than on 1.5 vines. A relatively better agreement between bud hardiness and percentage of shootless nodes was to be expected not only because the shoots arise directly from the buds, but also because on mature vines (Tables 1 and 2), as well as on the potted ones (Table 3) and in previous studies (Pogosyan and

Sarkisova, 1967; Byrne and Howell, 1978; Howell and Shaulis, 1980), bud tissues were generally more cold sensitive than cane tissues. Differences in primary bud hardiness between C and R vines across 1989/90 and 1990/91 were not significant, the same being true for differences in the percentage of shootless nodes in 1990 and 1991. When all sampling dates in 1989/90 were considered, primary buds from 0 vines were 2°C hardier than those from NT vines (Table 1). This was consistent with an enhanced field survival of the buds on 0 vines (approximately 16% of shootless nodes in July/90 vs. 42% on NT vines) (Table 5). The influence of cropping level on primary bud hardiness and on the percentage of shootless nodes continued, although to a lesser degree, into the second year of the study. On average across the 1990/91 dormant season, there was a 1°C difference in primary bud hardiness between fruiting and non-fruiting vines (Table 2); this difference was not statistically significant but appeared to be of viticultural importance, as inferred from a lower percentage of shootless nodes on non-fruiting relatively to fruiting vines in 1991 (about 11% on 0 vines compared to 20% and 21% on 1.5 and NT vines, respectively) (Table 5). Differences in percentage of shootless nodes, as in cane maturity and cold hardiness between 1.5 and NT vines were not significant in any of the trial years.

Conclusions

Cane and primary bud hardiness of young potted vines were not significantly affected by leaf removal, neither was primary bud hardiness on mature field vines. Leaf removal reduced cane hardiness on mature vines in 1989/90, but this was of no

consequence to field survival during that dormant season. Indeed, the percentage of shootless nodes in the field was more consistent with primary bud than with cane hardiness data, and was not significantly affected by leaf removal in any trial years.

Mature field vines unthinned in 1989 and 1990 (NT vines) had lower primary bud hardiness through the 1989/90 dormant season, and lower field bud survival in 1989/90 and 1990/91 than non-fruiting (0) vines. Differences in tissue hardiness, cane maturity and percentage of shootless nodes between NT vines and vines thinned to 1.5 clusters per node retained (1.5 vines) were not statistically significant in any of the trial years. In 1990/91, canes were hardier on 1.5 than on 0 mature vines; in that dormant season, fruiting potted vines had hardier cane and primary bud tissues than non-fruiting ones.

Carbohydrate shortage conceivably limited cold hardiness on mature vines in 1989/90. An impaired carbohydrate accumulation in the fall of 1989 due to an early leaf killing frost apparently aggravated the stress created by a heavy crop and by leaf removal in 1989. This may in part explain the more pronounced treatment effects in 1989/90 than in 1990/91, and the relatively high T_{50} values and low field bud survival during the former dormant season. However, in some situations during the course of this study, other factors were probably more relevant to hardiness than carbohydrate levels. The removal of basal leaves and large lateral shoots in invigorated grapevines, besides improving radiation microclimate at the basal shoot region, might have decreased the supply to the buds of gibberellins or other likely hardiness inhibitor, and/or increased the levels of abscisic acid, a supposed hardiness promotor. This could have minimized, or even overridden a potential negative influence of leaf

removal on cold hardiness, specially under non-limiting carbohydrate conditions. This hypothesis needs further investigation.

Some relationships were noticed in this study that were not statistically significant but defined consistent patterns. Among them, there was, on mature vines, a tendency for leaf removal to decrease primary bud hardiness in the mid-winter and to increase it in the early spring, probably by delaying spring bud activity (Fuchigami et al., 1977; Mansfield and Howell, 1981). This may explain the lack of a significant leaf removal effect on the percentage of shootless nodes following the dormant seasons under study. Mid-winter hardiness data for potted vines suggested that hardiness may be less affected by leaf removal at berry pea size than by removal at veraison, which could indicate that an eventual compensation for leaf removal is probably more effective following the earlier treatment date. This could not be proven here, however, but should be given further, detailed evaluation in future experimentation, because viticultural implications are very important.

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CHAPTER III

Influence of Basal Leaf Removal and Cropping Level on the Growth, Canopy Microclimate, Yield and Fruit Composition of Seyval Grapevines

Abstract

Basal leaf removal (R) had no significant effect on vine growth, yield, and fruit composition in either 1989 or 1990. Canopy microclimate was improved by leaf removal; the photosynthetic photon flux at the cluster region prior to harvest for R vines was about twice that of control (C) vines. Leaf removal in 1989 had no significant effect on bunch rot levels. In 1990, when canopies were denser, a significant leaf removal x cropping level interaction was observed; leaf removal decreased the rot incidence on vines thinned to 1.5 clusters per node retained (1.5 vines) but had no significant effect on unthinned (NT) vines.

Thinning to 1.5 clusters per node retained had no significant effect on vine yield. In 1989 the lower number of clusters on 1.5 relative to NT vines was compensated for by heavier clusters; in 1990 there were no significant differences in yield components between 1.5 and NT vines. Two consecutive non-thinned years followed by one year of thinning to 1.5 clusters per node retained had no significant effect on final vegetative growth, relative to annual thinning to 1.5 clusters per node retained. In 1991, when all vines were thinned to 1.5 clusters per node retained, yield was highest on the vines that did not bear fruit in the preceding two seasons (0 vines). This was due to these vines having larger size in 1991, hence larger number of nodes and clusters retained; no significant differences in other yield components were found. Unlike in previous years, the final shoot length in 1991 and the vine size in 1992 did not significantly differ among vines that were defruited and those that bore fruit in 1989 and 1990.

In 1989 fruit titratable acidity was higher on 1.5 than on NT vines while no significant differences in °Brix and pH were observed. Thinning had no significant effect on fruit composition in 1990. In 1991 °Brix was highest on the vines that had been unthinned in 1989 and 1990 and lowest on the vines that bore no clusters in those years. In the first trial year, bunch rot incidence was lower on NT than on 1.5 vines, probably due to lower cluster compactness on the former vines. No significant differences in rot scores among cropping levels were observed thereafter.

Introduction

Seyval (Seyve-Villard 5-276) is an important white wine cultivar in Eastern United States viticulture (Reynolds et al., 1985; Kaps and Cahoon, 1989). It produces large, compact clusters, is susceptible to bunch rot, and has a propensity to overcrop. In Seyval grapevines, as in many French-American hybrids, pruning alone does not seem to provide adequate crop control, and adjustment by thinning has been used (Fisher et al., 1977; Pool et al., 1978; Reynolds et al., 1986; Kaps and Cahoon, 1989). Thinning to 1.5 clusters per node retained at pruning is a recommended practice to complement balanced-pruning of Seyval vines. Basal leaf removal, by improving the microclimate in the cluster zone, may reduce the incidence of bunch rot as observed on other cultivars (Wolf et al., 1986; Gubler, 1987; Koblet, 1987,1988; Kliewer and Bledsoe, 1987; Bledsoe et al., 1988; Smith et al., 1988; English et al., 1989).

The economical advantage of leaf removal has been proven on some high value cultivars (Smith et al., 1988). The value of this cultural practice can not be

generalized, though, given conflicting reports of leaf removal effects on vine growth, yield and fruit composition. Defoliation reduced berry weight (Weaver, 1963; Buttrose, 1966; May et al., 1969; Kliewer and Antcliff, 1970; Kingston and van Epenhuijsen, 1989), clusters per node, and/or berries per cluster (May et al., 1969; Mansfield and Howell, 1981). This contrasts with reports where yield was not affected (Kliewer and Bledsoe, 1987; Bledsoe et al., 1988). Buttrose (1966) and Kliewer and Antcliff (1970) reported a reduction in % soluble solids, while Kliewer et al. (1988) showed fruit composition to be either unaffected or enhanced by leaf removal. This diversity can be attributed to differences in variety, site climate, fruit exposure to sunlight, nature of the leaves removed (age, position, light environment), timing and severity of removal, and vine size, among other factors (Kliewer and Bledsoe, 1987; Reynolds and Wardle, 1989; Zoecklein, 1989).

In temperate zone grape regions a relevant aspect in the adoption of any new cultural practice is its potential influence on cold hardiness. In a previous chapter of this work it was shown that the removal of basal leaves had no significant effect on primary bud hardiness in the dormant season following removal, nor on the percentage of nodes that developed in the next growing season. This study aimed at estimating the impact of this practice on the vegetative growth, light microclimate, yield, fruit composition, and bunch rot incidence on mature, differentially cropped field-grown Seyval grapevines.

Materials and Methods

Plant material and treatments applied

Own-rooted, mature, bearing Seyval grapevines planted in 1983 at the Clarksville Horticultural Experimental Station (CHES), Clarksville, Michigan, were used in this experiment. Vine spacing was 2.4 m x 3.0 m within and between the rows and the vines were trained to Hudson River Umbrella (a bilateral cordon at the top wire) with the top wire at 1.8 m height and a N-S row orientation. The vines were balanced-pruned using a 15+10 pruning formula (Reynolds et al., 1986) up to a maximum of 65 nodes retained per vine. A more detailed description of the vineyard installation and maintenance was presented in Chapter I.

Prior to the 1989 growing season a randomized block design was established. Vine size (assessed by the weight of one-year old cane prunings), which varied between 1.0 kg and 1.5 kg), was used as the blocking variable. Five blocks of six vines were defined, one vine per treatment combination.

Leaf removal and cropping level treatments were arranged in a 2x3 factorial. The leaf removal levels were: C = no leaves nor lateral shoots removed (control); R = main leaves and lateral shoots removed at three basal nodes on all the shoots of the vine. The cropping levels were: 0 = 0 clusters per vine; 1.5 = 1.5 clusters per node retained at pruning; NT = all clusters retained (no thinning). In 1990 each vine was treated as in 1989. In 1991, all vines were thinned to 1.5 clusters per node retained and no leaf removal was applied. Cluster thinning was done on June 12/89 (one week before full bloom), June 27/90 (9 days after full bloom), and June 15/91

(12 days after full bloom). Leaf removal was imposed on September 10/89 (2.5 weeks after veraison) and August 15/90 (veraison). On fruiting shoots, leaves and lateral shoots opposite, one node above, and one node below the basal cluster were removed. On non-fruiting shoots, leaves and laterals were removed from equivalent node positions. Lateral shoots were allowed to develop normally except for those at the three treated nodes on the defoliated vines.

Of the total number of buds retained at pruning in 1990 and thereafter (calculated by the 15+10 pruning formula), two-thirds were left on 6-node canes and the remaining on 2-node spurs. By doing so, not only the ratio of buds on canes:buds on spurs was maintained but also, in the case of the vines that had been previously subjected to leaf removal, the proportion of the buds that were retained at defoliated node positions was standardized. Indeed, given the position of the defoliated nodes, this procedure resulted in retaining 50% of the count-buds (buds counted in balanced-pruning) at positions defoliated in the previous season and 50% at non-defoliated positions.

Canopy microclimate measurements

Instantaneous photosynthetic photon flux (PPF) was measured at 1.5 weeks before harvest in 1989 and on five occasions during the 1990 growing season, using Li-Cor LI-1000 quantum sensors connected to a data logger. Three sensors were attached to a wooden bar. The bar was horizontally inserted perpendicular to the row, across the fruiting zone of each vine (about 0.15 m below the cordon), at seven (in 1989) or five (in 1990) locations in the canopy. The two lateral sensors were at

0.20 m from the cordon; the middle one was offset towards the west side of the canopy, not to be positioned directly below the cordon. Measurements were taken on sunny days between 11:00H and 14:00H. PPF data were expressed as the percentage relative to the ambient horizontal above the canopy, determined just before the measurements for each vine. Analysis was done for the mean percentage PPF per vine, calculated as the average over all the observations on the vine.

Canopy structure was evaluated using the point quadrat technique (Wilson, 1960; Smart, 1982; Smart and Smith, 1988). A thin, 1 m needle, was inserted at a 45° angle across the fruiting zone. Assessments were made on the day before harvest in 1989 and through the 1990 vegetative season. At each measurement date, ten random insertions per vine were done, giving a total of fifty insertions per treatment combination. The sequence of contacts with leaves and clusters as well as the number of gaps was recorded. Leaf layer number (LLN), percent gaps, percent interior leaves and percent interior clusters were calculated as proposed by Smart and Smith (1988).

Vine yield, yield components and fruit composition

Harvest was done on September 27/89, September 25/90 and September 6/91. Immediately prior to harvest, five random clusters per vine were evaluated for the incidence of bunch rot, Botrytis cinerea Pers. The following 5-point scale was used, based on the approximate percentage of rotten berries per cluster: 1- ≈100%; 2- ≈75%; 3- ≈50%; 4- ≈25%; 5- ≈0%. In addition, each vine was scored according to the percentage of rotten clusters (i.e., clusters in classes four or lower), using a 5-point scale as follows: 1- 80-100%; 2- 60-80%; 3- 40-60%; 4- 20-40%; 5- 0-20%.

Also just before harvest, a sample of berries was obtained from each replicate (vine) for berry weight assessment and fruit analysis. In 1989 and 1990, two apical berries from twenty-five randomly selected clusters per vine (excluding clusters on lateral shoots) were sampled. Vines were harvested individually. The clusters on lateral shoots (second crop) were not picked. Mean cluster weight was calculated by dividing yield by cluster number. Berries per cluster was calculated by dividing cluster weight by berry weight. In 1991, five apical berries were taken from each of two clusters on five previously tagged shoots per vine. These shoots had been selected two weeks after full bloom for being representative of the vine's shoots and for their node of origin. Only shoots at node positions two and three from the base of the spurs and canes were tagged (defoliated in 1990 in the case of R vines). Clusters from the selected shoots were harvested and weighed separately from the other clusters of the vine. Total number of clusters and yield per vine were measured and used to calculate the overall mean cluster weight per vine; in addition, the mean cluster weight, berry weight and number of berries per shoot were calculated based on the harvest data for the tagged shoots.

The berries taken from each vine were crushed, the juice was strained through cheesecloth, and analyzed for total % soluble solids (°Brix), titratable acidity and pH using standard analytical methods described by Ough and Amerine (1988).

Shoot growth parameters and vine size

On October 23/1989, October 24/1990 and October 18/1991 (approximately one month after harvest), five random canes per vine (twenty-five canes per

treatment combination) were randomly selected. Cane length, number of nodes per cane and internode length were determined, and the mean values per vine were calculated.

Vine size was assessed every year at pruning as the weight of 1-year-old cane prunings. In 1990 and 1991 vine size was obtained by adding the weight of the cane prunings from each vine to the weight of the canes removed from that vine for cold hardiness assessments in the previous dormant season.

Statistical analysis

Data (except point quadrat determinations) were subjected to analysis of variance using the GLM procedure of the Statistical Analysis System (SAS Institute Inc., 1985). Leaf removal and cropping treatments were analyzed as a two-factor factorial set in a randomized block design.

Percentage of PPF values were subjected to the arc-sine of the square root transformation prior to analysis. When more than one PPF measurement date was analyzed, date was considered a blocking variable. In the analyses of harvest data for 1989 and 1990 the two levels of leaf removal (C and R) were combined with two cropping levels (1.5 and NT). Because all vines were treated alike in 1991, the harvest data that year reflects the carryover effect of the treatments applied in 1989 and 1990; therefore three cropping levels (0, 1.5, and NT) and two leaf removal levels (C and R) were considered.

When the F-values were significant at 5% or lower level, mean separation was done using the LSD test at the 5% level.

Results and Discussion

Leaf removal had no significant effect on vine growth, yield components and fruit composition during the trial years (Tables 1, 2, 3 and 4); similar results were found in the treatment season in two leaf removal experiments with potted Seyval vines (results not shown). The low intensity and the timing of leaf removal might have contributed to the lack of significant effects. Nevertheless, in a study with Sauvignon blanc grapevines in which four leaf removal levels (control plus low to moderate removal intensities) and three treatment dates (fruit set, four and seven weeks after fruit set) were investigated, no treatment effects on yield and yield components were likewise observed (Kliewer et al., 1988; Bledsoe et al, 1988). Similarly, berry number and berry weight were not significantly affected by leaf removal applied to Sauvignon blanc and Cabernet Sauvignon as early as flowering and early fruit set (Smith et al., 1988). Significant reductions in berry weight in the season of leaf removal have been reported (Weaver, 1963; Buttrose, 1966; May et al., 1969; Kliewer, 1970; Kliewer and Antcliff, 1970; Kingston and Van Epenhuijsen, 1989; Candolfi-Vasconcelos and Koblet, 1990) but they occurred under severe defoliation and/or hot climate conditions. When both conditions are present, the berries are conceivably exposed to high radiation levels for prolonged periods and a concomitant rise in temperature may, by itself, cause a reduction in berry weight (Bledsoe et al., 1988).

No significant differences in yield were found between the vines thinned to 1.5 clusters per node retained (1.5 vines) and the unthinned (NT) ones, in either 1989

or 1990 (Tables 1 and 2). Because vine size was the blocking variable in the establishment of this experiment in 1989, vine size and number of nodes retained at pruning in 1989 were similar among the vines subjected to the different treatments. In that year, reduced cluster number on 1.5 relative to NT vines was compensated for by heavier clusters, resulting from an additive effect on the number of berries per cluster and berry weight, although neither component was significantly influenced per se (Table 1). The vegetative development of the NT vines in 1989 was more affected by cropping than that of 1.5 vines, as evidenced by a smaller size of the former vines at pruning in 1990 (Table 2). This suggests that a similar yield is more demanding of the vine when distributed over a larger number of clusters. In 1990, balanced-pruning resulted in fewer nodes retained on NT than on 1.5 vines; at harvest there were no significant differences in cluster number or other yield components between the two (Table 2). In previous studies, an increase in berry weight in the year of thinning minimized or compensated for the reduction in vine cluster number (Looney, 1981; Bravdo et al., 1984; Reynolds et al., 1986; Kaps and Cahoon, 1989). In 'Carignane' grapevines, thinning immediately after full bloom reduced yield only when at least two-thirds of the clusters were removed (Bravdo et al., 1984). Thinning was applied at an earlier stage in 1989 (one week before full bloom) than in 1990 (nine days after full bloom). The lack of a significant thinning effect on the number of berries per cluster in either year reflects a reduced cluster thinning influence on berry set, in agreement with previous works (Hale and Weaver, 1962; Looney, 1981). Hale and Weaver (1962) observed that clusters were relatively weak sinks during the pre-bloom and setting period. They concluded that during these stages the practices

Table 1. Vine size and number of nodes retained per vine prior to treatment imposition and influence of leaf removal and cropping level on the yield, fruit composition and rot levels of mature field Seyval grapevines in 1989 (Year 1). Harvest date: September 27/89.

Treatment[z]	Vine size (Kg/vine) (Year 1)[y]	Nodes retained /vine[y]	Yield (Kg/vine)	Yield components				Fruit composition			Rot levels	
				Clusters /vine	Cluster Wt.(g)	Berries/ cluster	Berry Wt.(g)	Soluble solids (°Brix)	pH	Titratable acidity ($g.L^{-1}$)	Cluster rot[x]	Vine rot[w]
Leaf removal												
C	1.15	32	14.3	59	250.2	142	1.78	16.5	3.39	0.93	4.7	4.4
R	1.16	31	13.3	56	247.9	150	1.70	16.6	3.36	0.97	4.8	4.4
	ns[v]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level												
0	1.18	32	—	—	—	—	—	—	—	—	—	—
1.5	1.17	32	13.2	48b	278.1a	160	1.80	16.4	3.34	1.02a	4.5b	3.9b
NT	1.12	31	14.4	67a	221.8b	132	1.68	16.7	3.41	0.88b	4.9a	4.9a
	ns	ns	ns	*	*	ns	ns	ns	ns	**	**	*
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on September 10/89
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 12/89.
[y]At pruning prior to treatment imposition.
[x]In a 5-point scale based on the approximate percentage of rotten berries per cluster, as follows: 1- ≈100%; 2- ≈75%; 3- ≈50%; 4- ≈25%; 5- ≈0%
[w]In a 5-point scale based on the approximate percentage of rotten clusters per vine, as follows: 1- 80-100%; 2- 60-80%; 3- 40-60%; 4- 20-40%; 5- 0-20%.
[v]ns, *, ** Non significant or significant at the 5% or 1% level, respectively.

Table 2. Influence of leaf removal and cropping level on the vine size and number of nodes retained per vine at pruning after the first treatment season and on the yield, fruit composition and rot levels of mature field Seyval grapevines in 1990 (Year 2). Harvest date: September 25/90.

Treatment[z]	Vine size (Kg/vine)	Nodes retained /vine	Yield (Kg/vine)	Yield components				Fruit composition			Rot levels	
				Clusters /vine	Cluster Wt.(g)	Berries/ cluster	Berry Wt.(g)	Soluble solids (°Brix)	pH	Titratable acidity ($g.L^{-1}$)	Cluster rot[y]	Vine rot[x]
Leaf removal												
C	1.57	33	7.1	39	188.2	104	1.81	19.0	3.33	1.02	4.4	3.7
R	1.24	31	6.8	36	191.0	108	1.78	18.7	3.31	1.00	4.4	4.2
	ns[w]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level												
0	3.23a	58a	—	—	—	—	—	—	—	—	—	—
1.5	0.74b	22b	6.9	35	198.7	108	1.85	18.9	3.31	1.01	4.3	3.9
NT	0.25c	15c	7.0	40	180.5	105	1.73	18.9	3.33	1.01	4.5	4.0
	***	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*

[z]C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90.
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.
[y]In a 5-point scale based on the approximate percentage of rotten berries per cluster, as follows: 1- ≈100%; 2- ≈75%; 3- ≈50%; 4- ≈25%; 5- ≈0%
[x]In a 5-point scale based on the approximate percentage of rotten clusters per vine, as follows: 1- 80-100%; 2- 60-80%; 3- 40-60%; 4- 20-40%; 5- 0-20%.
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%.

that can be expected to influence set are those like topping or girdling, which modify or eliminate either of the two major sinks for assimilates at that time, i.e., the shoot tips or the parent vine.

In 1991, when all vines were treated similarly, vine cluster number and yield did not significantly differ between the vines that bore fruit in 1989 and 1990, regardless of thinning treatment (NT vs. 1.5) in those years. Non-bearing vines in 1989 and 1990 had the largest size in 1990 and 1991. Consequently, they were ascribed the highest number of nodes and clusters in 1991, and achieved the highest yield. However, no significant differences in cluster weight, berries per cluster and berry weight were found among cropping levels in 1991 (Table 3). This could in part reflect a greater homogeneity of the clusters as a consequence of the shoot selection criteria used in 1991; however, differences were also non-significant when the mean cluster weight was calculated considering all clusters on the vine. At the end of 1991, there were no significant differences in shoot length among differently cropped vines in 1989 and 1990 (Table 4); similarly, no significant differences in vine size were found at pruning in 1992 (Table 3).

Data were not analyzed across years, but a reduction in yield from 1989 to 1990 is clear (Tables 1 and 2). The lower yield in 1990 allowed for more vegetative growth, as evidenced by longer canes on fruiting vines at the end of the 1990 compared to the 1989 season (Table 4) and, specially, by the increase in vine size of 1.5 and NT vines from 1990 to 1991 (Tables 2 and 3). The main reasons that might have contributed to the low 1990 yield are: a) inflorescence primordia formation inhibited on the fruiting (1.5 and NT) vines in the 1989 season due to a relatively

Table 3. Influence of leaf removal and cropping level treatments in 1989 (Year 1) and 1990 (Year 2) on the vine size and number of nodes retained per vine in 1991 and 1992, and on the yield, fruit composition and rot levels of mature field Seyval grapevines in 1991 (Year-3), when no differential treatments were applied. Harvest date: September 6/91.

Treatment[z]	Vine size (Kg/vine) (1991)	Nodes retained /vine (1991)	Yield (Kg/vine)	Yield components					Fruit composition			Rot levels		Vine size (Kg/vine) (1992)	Nodes retained /vine (1992)
				Clusters /vine	Cluster Wt.(g)		Berries/ cluster[y]	Berry Wt.(g)[y]	Soluble solids (°Brix)[y]	pH[y]	Titratable acidity[y] ($g.L^{-1}$)	Cluster rot[x]	Vine rot[w]		
					all the clusters included	clusters on selec. shoots[y]									
Leaf removal															
C	2.03	39	15.8	60	246.2	226.7	128	1.95	19.4	3.26	0.83	4.4	3.6	0.62	23
R	1.59	37	14.0	56	247.3	219.8	128	1.92	19.9	3.28	0.83	4.6	4.2	0.81	27
	ns[v]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level															
0	3.64a	62a	23.8a	94a	261.3	213.5	136	1.91	17.8c	3.24b	0.90	4.6	4.1	0.87	28
1.5	1.04b	28b	11.2b	43b	226.3	224.6	116	1.96	19.6b	3.24b	0.79	4.6	4.1	0.60	23
NT	0.74b	24b	9.8b	36b	252.7	231.5	132	1.92	21.5a	3.33a	0.81	4.2	3.5	0.68	24
	***	***	***	***	ns	ns	ns	ns	***	*	(*)	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns

[z]Relative to 1989 and 1990:
C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90.
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning dates: June 12/89 and June 27/90.
In 1991 no leaf removal was applied and all the vines were thinned to 1.5 clusters per node retained on June 15/91.
[y]Evaluated on the clusters of five selected shoots per vine
[x]In a 5-point scale based on the approximate percentage of rotten berries per cluster, as follows: 1- ≈100%; 2- ≈75%; 3- ≈50%; 4- ≈25%; 5- ≈0%
[w]In a 5-point scale based on the approximate percentage of rotten clusters per vine, as follows: 1- 80-100%; 2- 60-80%; 3- 40-60%; 4- 20-40%; 5- 0-20%.
[v]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.

Table 4. Influence of 1989 (Year 1) and 1990 (Year 2) leaf removal and cropping level treatments on shoot growth parameters of mature field Seyval vines at the end of the treatment seasons and of the 1991 (Year 3) season, in which no differential treatments were applied.

Treatment[z]	1989 October 23			1990 October 24			1991 October 18		
	Cane length (cm)	Nodes/ cane	Internode length (cm)	Cane length (cm)	Nodes/ cane	Internode length (cm)	Cane length (cm)	Nodes/ cane	Internode length (cm)
Leaf removal									
C	143.5	24.5	5.7	175.9	31.8	5.5	125.9	25.7	4.8
R	144.4	25.2	5.6	183.9	32.8	5.5	133.5	25.3	5.2
	ns[y]	ns	ns	ns	ns	ns	ns	ns	ns
Crop. level									
0	209.2a	31.8a	6.6a	214.0a	35.4a	6.0a	135.9	24.7	5.5
1.5	122.2b	22.3b	5.5b	181.1a	32.4ab	5.6a	117.8	25.1	4.6
NT	100.3b	20.6b	4.9b	144.6b	29.2b	4.9b	135.4	26.7	5.0
	**	**	**	**	*	**	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C: control (no leaves removed); R: leaves removed on September 10/89 and August 15/90
0: 0 clusters per vine; 1.5: 1.5 clusters per node retained; NT: unthinned
[y]ns, *, ** Non significant or significant at 5% or 1% level, respectively. Mean separation within columns using the LSD test at 5%

high crop (Chapter IV); b) inhibited growth of the fruiting vines in 1989; hence the number of nodes retained at pruning and the number of clusters per vine were lower in 1990 than in 1989; c) high bud mortality in the 1989/90 dormant season, expressed by a high percentage of shootless nodes in 1990 on the fruiting vines (Chapter II) and, therefore, a low percentage of clusters on shoots originated from count-nodes. Indeed, prior to thinning in 1990, clusters from count-nodes represented only 45% and 25% of the total number of clusters on 1.5 and NT vines, respectively (data not shown). This percentage was higher in 1991 (63% and 64% on 1.5 and NT vines respectively) following the milder 1990/91 dormant season, and probably also in 1989 (not evaluated) due to low bud mortality during the 1988/89 dormant season at the experimental Seyval plot (Howell, 1989). Clusters arising from count positions have been shown to be heavier than clusters from non-count positions (Pool et al., 1978; Wolpert et al., 1983).

Cropping level had no significant effect on fruit % soluble solids and pH in 1989 and 1990 (Tables 1 and 2), unlike in reports where thinned vines had higher °Brix (Fisher et al., 1977; Looney, 1981; Howell et al., 1987; Kaps and Cahoon, 1989). In a previous Seyval study, only two of four years showed a decrease in °Brix with decreasing thinning levels from 10 to 25 clusters/500g of cane prunings (Reynolds et al., 1986). In 1989, titratable acidity was lower on NT than on 1.5 vines for a comparable °Brix (Table 1); based on Bravdo et al. (1984), this suggests that the NT vines were overcropped. In 1991 there were clear differences in fruit composition among 0, 1.5, and NT vines (abbreviations relative to cropping treatments in 1989 and 1990) (Table 3). The highest °Brix was found on the NT vines followed, in order,

by the 1.5 and the 0 vines; the NT vines also had the highest pH. The lower composition value of the 0 vines was probably due to the high yield of these vines, leaf and cluster shading resulting from shoot crowding, or both.

The point quadrat and PPF assessments prior to harvest in the treatment seasons (mid to late September) clearly reflect the higher vegetative growth in 1990 compared to 1989 (Tables 5, 6, 7 and 8). Leaf removal improved the light microclimate and the canopy characteristics in both seasons and conceivably increased air movement in the cluster region. At the preharvest measurement, the mean percentage of PPF reaching the cluster region was about twice as high on defoliated than on control vines both in 1989 and 1990 (Tables 6 and 8). However, no significant leaf removal effect on cluster and vine rot scores was found in 1989. In that year, rot incidence was lower on NT than on 1.5 vines, probably due to lower cluster compactness on the former vines (Table 1; Smithyman, 1992). In 1990 the vine rot score was influenced by a significant leaf removal x cropping level interaction (Table 2); an inspection of the treatment combination means revealed that leaf removal reduced the percentage of rotten clusters on 1.5 vines but had no significant effect on NT vines (data not shown).

Conclusions

The removal of three basal leaves and adjacent laterals on all vine shoots had little impact on vine growth, yield, yield components and fruit composition in the treatment seasons (1989 and 1990). Light microclimate and canopy parameters were

Table 5. Influence of leaf removal and cropping level on canopy parameters of mature Seyval grapevines on September 26/89, the day before harvest in the first treatment season, as evaluated by point quadrat analysis.[z]

Treatment[y]		Leaf layer number (LLN)	% Gaps	% Interior leaves	% Interior clusters
Leaf removal:	C	1.81	4.4	23.9	32.0
	R	1.27	10.6	13.5	7.0
Crop. level:	0	1.83	12.1	19.8	—
	1.5	1.38	5.3	17.7	13.2
	NT	1.40	5.9	20.5	26.6

[z]Based on 50 insertions per treatment combination (150 and 100 insertions per leaf removal level and per cropping level, respectively)
[y]C:control (no leaves removed); R:leaves removed on September 10/89
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned.
Thinning date: June 12/89.

Table 6. Influence of leaf removal and cropping level on the percentage of photosynthetic photon flux (PPF) reaching the cluster region of the canopy of mature Seyval grapevines on September 17/89, 1.5 weeks before harvest in the first treatment season.[z]

Treatment[y]		PPF (% of ambient)
Leaf removal:	C	15.5b
	R	33.1a
		***[x]
Crop. level:	0	17.4b
	1.5	29.3a
	NT	26.3ab
		*
Interaction		ns

[z]Based on 105 readings per treatment combination (315 readings per leaf removal level and 210 readings per cropping level, respectively)
[y]C:control (no leaves removed); R:leaves removed on September 10/89
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned.
Thinning date: June 12/89
[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%.

Table 7. Influence of leaf removal and cropping level on canopy parameters of mature Seyval grapevines during 1990, the second treatment season, as evaluated by point quadrat analysis.[z]

Treatment[y]	June 28 1.5 wk PFB[x]	July 9 3 wk PFB	July 18 4 wk PFB	July 25 5 wk PFB	Aug. 7 1 wk BV	Aug. 14 V	Aug. 31 2 wk PV[w]	Sep. 17 1 wk BH	Average Over the 1990 season	Average Since leaf removal
	Leaf Layer Number (LLN)									
Leaf removal										
C	1.26	2.35	3.07	3.17	3.53	3.83	4.63	4.60		4.62
R	1.02	2.01	2.57	2.47	3.05	3.29	3.03	3.50		3.27
Crop. level										
0	1.28	2.57	3.52	3.77	4.46	4.82	4.81	4.94	3.77	4.88
1.5	1.12	1.96	2.47	2.43	3.01	3.00	3.53	3.74	2.66	3.64
NT	1.02	2.02	2.47	2.27	2.40	2.85	3.14	3.47	2.46	3.31
	% Gaps									
Leaf removal										
C	19.4	2.5	0	0	0	0	0	0		0
R	17.9	5.4	4.7	2.7	1.3	1.3	0.7	0		0.7
Crop. level										
0	22.2	1.6	1.0	1.0	0	0	0	0	3.2	0
1.5	21.0	1.1	1.0	0	0	0	0	0	2.9	0
NT	25.7	9.3	5.0	3.0	2.0	2.0	1.0	0	6.0	0.5
	% Interior leaves									
Leaf removal										
C	8.4	28.0	41.4	42.9	50.1	51.9	58.4	57.2		57.8
R	10.9	21.0	33.8	35.9	43.2	44.8	41.9	48.0		45.0
Crop. level										
0	9.3	30.0	42.9	47.2	55.2	58.5	58.4	59.5	45.1	59.0
1.5	10.6	18.5	34.0	36.2	44.2	41.0	49.3	51.3	35.6	50.3
NT	8.6	24.1	34.8	31.7	35.0	40.0	44.6	46.4	33.2	45.5
	% Interior clusters									
Leaf removal										
C	30.6	54.5	56.9	55.6	56.3	61.7	81.0	91.2		86.1
R	11.1	45.9	49.0	38.2	42.3	58.7	50.0	56.5		53.3
Crop. level										
0	—	—	—	—	—	—	—	—	—	—
1.5	18.4	47.6	54.7	42.9	54.7	62.7	65.5	67.2	51.7	66.4
NT	15.2	53.7	51.1	44.6	45.8	57.4	63.0	78.7	51.2	70.9

[z]Based on 50 insertions per treatment combination (150 and 100 insertions per leaf removal level and per cropping level, respectively)
[y]C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning dates: June 12/89 and June 27/90
[x]Time in weeks (wk) relative to vine phenophases:
PFB:post full bloom; BV:before veraison; V: veraison; PV:post veraison; BH:before harvest
[w]First assessment after leaf removal in 1990.

Table 8. Influence of leaf removal and cropping level on the percentage of photosynthetic photon flux (PPF) reaching the cluster region of the canopy of mature Seyval grapevines during 1990, the second treatment season.[z]

Treatment[y]	PPF (% of ambient)					Average	
	July 16 4 wk PFB[x]	July 24 5 wk PFB	Aug.7 1 wk BV	Aug. 31 2 wk PV[w]	Sep. 15 1.5 wk BH	Over the 1990 season	Since leaf removal
Leaf removal							
C	27.0	18.9	14.9	11.6b	10.8b		11.2b
R	28.3	26.3	19.2	21.7a	19.9a		20.8a
	ns[v]	ns[u]	ns	**	*		***
Crop. level							
0	22.6	12.2b	11.1b	10.5b	10.2	12.5c	10.4b
1.5	26.2	22.5ab	16.8ab	16.6ab	16.2	18.5b	16.4a
NT	37.5	33.0a	23.0a	22.9a	19.6	25.5a	21.2a
	ns	***	*	**	ns	***	***
Interaction	ns	ns	ns	ns	ns		ns

[z]Based on 75 readings per treatment combination (225 and 150 readings per leaf removal level and per cropping level, respectively)
[y]C:control (no leaves removed); R:leaves removed on September 10/89 and August 15/90
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning dates: June 12/89 and June 27/90
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; BV:before veraison; V: veraison; PV:post veraison; BH:before harvest
[w]First assessment taken after leaf removal in 1990.
[v]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%.
[u]P=0.0542

improved by leaf removal in both seasons. In 1990 a light crop was associated with an intense growth and high canopy density, which may have contributed to increased Botrytis infection. Leaf removal had no significant effect on cluster and vine rot scores in 1989; in 1990, however, leaf removal reduced the percentage of rotten clusters on vines thinned to 1.5 clusters per node retained (1.5 vines) but had no significant effect on unthinned (NT) vines. The above results are consistent with the view that vines with denser canopies are more likely to benefit from an improved Botrytis control by leaf removal. There is, however, a need to further evaluate the practice as well as the economics of leaf removal in Seyval, before recommendations can be made.

During this study, yield and yield components were not significantly different on 1.5 and NT vines, except for a higher cluster weight on 1.5 vines in 1989, which compensated for a lower cluster number. In that year, Botrytis incidence was lower on NT than on 1.5 vines, probably due to less compact clusters on the former. Two consecutive non-thinned years followed by one year of thinning to 1.5 clusters per node retained increased the °Brix in the third year, with no significant reduction in the final vegetative growth (as compared to annual thinning to 1.5 clusters per node retained). The initial vine size (which ranged from 1.0 to 1.5 kg) appeared to be sufficient to support two consecutive seasons without thinning. Moreover, the fact that all vines were balanced-pruned undoubtedly contributed to minimize any eventual vegetative/reproductive imbalance resulting from unthinning. The above results and the increased labor costs associated with cluster thinning make systematic thinning questionable and motivate a further investigation on the value of pluriannual

cluster thinning in Seyval.

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CHAPTER IV

Influence of Basal Leaf Removal and Cropping Level on the Fruitfulness of Primary Buds of Seyval Grapevines. Localized and Positional Treatment Effects.

Abstract

The removal of leaves at three nodes within the fruiting zone of young potted (Experiments I and II) or mature field-grown (Experiment III) Seyval grapevines (at the node of the basal cluster, one node above and one node below that node) had minimal influence on flower-bud differentiation for Year 2' s crop. In particular, leaf removal at a node had no significant effect on the differentiation of the primary bud developing at that node, despite the evidence (Experiment II) that differentiation was still underway when leaves were removed, whether at berry pea size or at veraison. In Experiment II, leaf removal increased the percentage of berry set, berries per fruitful primary shoot, and berries per cluster in Year 2; yield in Year 2 was not significantly influenced.

The percentage of fruitful primary shoots and the number of clusters per vine and per primary shoot in Year 2 were higher on non-bearing (0Cl) than on bearing (3Cl) potted vines (Experiments I and II). The same relationship was found in Experiment II for the number of flowers per cluster and per primary shoot in Year 2; however, the 0Cl vines had lower percentage of berry set, number of berries per cluster at harvest and cluster weight than the 3Cl vines, which counteracted the advantage in cluster number. On mature vines, the percentage of fruitful primary shoots in 1990 and 1991 (Years 2 and 3) was not significantly affected by cropping level. The unthinned (NT) vines had fewer clusters per primary shoot in 1990 than the non-fruiting ones; the vines thinned to 1.5 clusters per node retained, had an intermediate response, not significantly different from that of the other cropping

levels. A similar but non-significant trend was found in 1991. The heavier crop in 1989 than in 1990 may be a reason for a significant cropping effect in 1990 but not in 1991.

The presence of a cluster at a specific node had no significant influence on the Year 2 fruitfulness of the primary bud developing at that node, in any of the experiments. By contrast, bud position on the 6-node cane had a highly significant effect on most fruitfulness responses evaluated. As in previous studies, an increased fruitfulness from the base to the apex of the 6-node cane was generally found.

Introduction

Seyval (Seyve-Villard 5-276) has a propensity to overcrop (Reynolds et al.,1986; Kaps and Cahoon, 1989) which is largely due to a high fruitfulness of the buds at the base of the canes (Pool et al., 1978) and not counted in balanced-pruning. To prevent overcropping and reduce the contribution of the non-count crop, cluster thinning (Fisher et al., 1977; Reynolds et al., 1986; Kaps and Cahoon, 1989) and cane pruning combined with removal of excess basal shoots (Pool et al., 1978) have been employed.

Despite overcropping, adequate primary bud fruitfulness is a goal in the evaluation of new cultural practices. Clusters on primary shoots are heavier than those on either secondary (Mansfield and Howell, 1981) or non-count shoots (Pool et al., 1978; Wolpert et al., 1983). Hence, an increased percentage of fruitful primary shoots may help minimize crop losses following a dormant season in which high bud

mortality occurred. Moreover, Wolpert et al. (1983) found that count-crop was of better quality than non-count crop, although the differences were small.

Light is an important factor for fruitfulness in grapevines (May and Antcliff, 1963; May, 1965; Shaulis et al., 1966; Buttrose, 1970, 1974; Shaulis and May, 1971; Shaulis and Smart, 1974; Kliewer, 1982; Smart et al., 1982; Morgan et al., 1985). An adequate light microclimate at the basal portion of grapevine shoots will not only benefit the current season's but also the following season's crop, because buds there will be retained at pruning and produce next season's crop.

Basal leaf removal can improve the microclimate in the cluster region and reduce bunch rot (Wolf et al., 1986; Koblet, 1987,1988; Kliewer and Bledsoe, 1987; Bledsoe et al., 1988; Smith et al., 1988; English et al., 1989), with proven economical advantage on some high value cultivars (Smith et al., 1988). However, leaf removal has reduced bud fruitfulness (May et al., 1969; Mansfield and Howell, 1981; Kingston and van Epenhuijsen, 1989; Candolfi-Vasconcelos and Koblet, 1990), but this is not a general rule (Kliewer et al., 1988). The influence of leaf removal on flower-bud initiation may be linked to a loss of photosynthate or to a change in the hormonal balance (Jackson and Sweet, 1972). Carbohydrate accumulation and flower-bud formation are associated in grapevines (May, 1965; Shaulis and May, 1971; Buttrose, 1974; Winkler et al., 1974; Bains et al., 1981; Smart et al, 1982), although a direct involvement of carbohydrates has not been proven (Winkler et al., 1974; Smart et al., 1982). Hale and Weaver (1962) suggested that the leaf subtending a bud is the major source of photosynthate for that bud. Thus, carbohydrate status and bud fruitfulness may be affected by removing its subtending leaf, unless some compensatory response

occurs.

Previously in this research effort, the yield responses of mature, field-grown own-rooted Seyval grapevines to basal leaf removal were investigated (Chapter III). This study is aimed at providing greater detail concerning the influence of basal leaf removal on the reproductive development in Seyval. Toward that end, fruitfulness responses to leaf removal were assessed for primary buds at specific node positions on six-node canes, both on potted and on mature field grown-Seyval grapevines subjected to different cropping levels.

Materials and Methods

Plant Material and Treatments

Experiments with Young Potted Vines (Experiments I and II)

These experiments were conducted at the Horticultural Research Center (HRC), East Lansing, Michigan, using one-year-old own-rooted Seyval (Seyve-Villard 5-276) grapevines. The vines were weighed and planted in May/1989 (Experiment I) or in May/1990 (Experiment II) in 19 l pots containing a sterilized loam, sand and peat mixture with good water holding and aeration properties. The potted vines were placed on a flat gravel-covered area at a 1.0 m x 1.2 m spacing which allowed for good light exposure, and trained to two shoots. Vines were irrigated, fertilized (using a Peter's 20-20-20 solution), and sprayed for pest and disease control as needed.

Cropping level and leaf removal treatments were arranged as a two-factor factorial, set in a randomized block design; vine fresh weight at planting was used as

the blocking variable. Cropping level was either 0Cl (no clusters per vine) or 3Cl (three clusters per vine) and was imposed on June 22/89, four days before full bloom (Experiment I), or July 4/90, ten days after full bloom (Experiment II). On the vines thinned to three clusters, the basal cluster on one shoot and two clusters (the basal and the second) on the other shoot were retained.

In Experiment I, leaf removal levels were: C = no main leaves removed (control), and R = leaf removal near veraison (August 31/89, nine weeks after full bloom). In Experiment II an additional leaf removal date was included. Leaf removal levels were C = control, R1 = leaf removal at pea size (July 27/90, five weeks after full bloom), and R2 = leaf removal at veraison (August 21/90, eight weeks after full bloom). Leaf removal consisted of removing three consecutive leaves in the fruiting region of both vine shoots. On vines bearing fruit, the leaves opposite, one node above and one node below the basal cluster were removed. On non-fruiting vines, the leaves were removed from equivalent node positions. Lateral shoots were removed at weekly intervals regardless of the treatment combination.

To prevent injury due to naturally occurring freezing temperatures, the vines in their pots were stored in a controlled temperature room at ≈4 °C from late October until mid May. During storage, the humidity was monitored to avoid tissue desiccation; molding was prevented by anti-Botrytis sprays. In May, the vines were returned to the outdoor gravel pad and both retained canes were pruned to six nodes. No differential treatments were applied during the second trial year. The observations on the vines treated in 1989 (Experiment I) ended at three weeks after bloom in 1990 with the counting of set berries. The vines treated in 1990

(Experiment II) were maintained until harvest in 1991; the shoots arising from the 6-node canes were kept well exposed to sunlight forming a vertical wall supported by a 3-wire trellis.

Experiment with Mature Field Vines (Experiment III)

Own-rooted, mature, bearing Seyval grapevines planted in 1983 at the Clarksville Horticultural Experimental Station (CHES), Clarksville, Michigan, were used. Vine spacing was 2.4 m x 3.0 m within and between rows, and the vines were trained to Hudson River Umbrella (a bilateral cordon at the top wire) with the top wire at 1.8 m height and a N-S row orientation. The vines were balanced-pruned using a 15+10 pruning formula (Reynolds et al., 1986) up to a maximum of 65 nodes retained per vine. A more detailed description of vineyard installation and maintenance was presented in Chapter I.

Prior to the 1989 growing season, a randomized block design was established. Vine size (weight of one-year old cane prunings), which varied between 1.0 and 1.5 kg, was used as the blocking variable. Five blocks of six vines were defined, one vine per treatment combination.

Leaf removal and cropping level treatments were arranged as a 2x3 factorial. Leaf removal levels were: C = no leaves nor lateral shoots removed (control); R = main leaves and lateral shoots removed on all vine shoots at the same three basal nodes positions defoliated in Experiments I and II. Vines were cropped to: 0 = 0 clusters per vine; 1.5 = 1.5 clusters per node retained at pruning; NT = all clusters retained (no thinning). Lateral shoots were allowed to develop normally, except for

those at the three treated nodes on defoliated vines.

In the 1990 growing season, each vine was treated as in 1989. Cluster thinning was done on June 12/89 (one week before full bloom) and June 27/90 (nine days after full bloom). Leaf removal was imposed on September 10/89 (2.5 weeks after veraison) and August 15/90 (veraison).

Fruitfulness of the Buds on Nodes One to Six in the Year Following Treatment

Fruitfulness evaluations were done on six, four, and five replicates (vines) of Experiments I, II and III, respectively, on canes that originated from count nodes, were well-matured in the fall, and had the position of the nodes that had borne a cluster or that had been defoliated adequately marked (on fruiting or defoliated vines, respectively). Cane diameter was smaller on 3Cl than on 0Cl potted vines (Chapter I); on mature field vines, only canes with medium diameter (7-10 mm averaged over two perpendicular directions between nodes four and five) were used. Canes were pruned to six nodes in May/90 (Experiment I), May/91 (Experiment II), April/90 and April/91 (Experiment III). The nodes were numbered from the base to the apex of the 6-node canes.

Two 6-node canes per vine in the experiments with potted vines and four or five 6-node canes per mature field vine were used to evaluate the percentage of fruitful primary shoots relative to the primary shoots evolved, and the number of clusters (including zero) on the primary shoot (if any) arising from each node position. On potted vines additional fruitfulness evaluations were performed. In Experiment I, the number of set berries was assessed at three weeks after bloom on

every cluster of each primary shoot arising from both 6-node canes. In Experiment II, the primary shoots arising from one of the 6-node canes (the cane from which more clusters were originated) were allowed to yield crop in 1991. These shoots were left unthinned while the remaining vine shoots were deblossomed. On every cluster of the former shoots, the flowers were counted just prior to bloom and the set berries were counted three weeks after bloom. At harvest (September 3/91), each cluster was weighed and its berries were counted. The basal cluster of each shoot was crushed and the seeds were counted to calculate the mean number of seeds per berry.

Statistical Analysis

Data (except for binary and ordinal responses) were tested for normality using the UNIVARIATE procedure of the Statistical Analysis System package (SAS Institute Inc., 1985a,b). When there was no sufficient evidence for normality of a given variable, it was brought closer to normality before analysis using the Box-Cox power transformation with an appropriate power value (Box and Cox, 1964; Draper and Smith, 1981).

Fruitfulness responses were evaluated on both a whole vine and an individual bud basis. Data evaluated on a per-vine basis were subjected to analysis of variance using the GLM (from General Linear Models) procedure of SAS. The factors included in these analyses were the leaf removal and cropping treatments applied to the vine in the preceding season; they were analyzed as a two-factor factorial set in a randomized block design. For a given response, the data relative to all the buds on

the 6-node canes retained per vine were combined to give a single observation.

In the analyses of fruitfulness on an individual bud basis, the conditions under which each specific node had developed were considered, as well as the treatments applied to the vine in the previous season. Considered in these analyses were replicate (REP), cropping level (CROP), leaf removal (DEF), the position of the bud on the 6-node cane (BP), the presence/absence of a cluster opposite the bud in question in the season preceding the fruitfulness evaluation (PCL), and the removal (yes or no) in that season of the leaf (or leaf plus lateral shoot in Experiment III) that subtended each specific bud (BDEF). PCL and BDEF were considered nested within CROP and DEF, respectively. For each fruitfulness response analyzed an initial, a priori intentionally overparametrized model was defined, which included the above factors and the interactions that could have some biological meaning. This model included REP, DEF, CROP, BP, PCL(CROP), BDEF(DEF), DEF*CROP, DEF*BP, CROP*BP, DEF*CROP*BP, CROP*BDEF(DEF), BP*BDEF(DEF), DEF*PCL(CROP), and BP*PCL(CROP). Starting with the above model, a backward elimination procedure was followed, orderly deleting from the model the non-significant interactions (Draper and Smith, 1981). Despite its restrictions (Draper and Smith, 1981) the backward elimination method was sought as an adequate one, given its relative simplicity in eliminating the non-significant interactions in order to achieve a more parsimonious model. In the analyses presented, the shootless nodes were considered as missing. Binary and ordinal responses for the individual buds were analyzed using the GLIM package (Healy, 1988), assuming the binomial and the Poisson error distribution, respectively. These responses were, respectively, the

fruitful/unfruitful condition of a bud (whether it originated a primary shoot with at least one cluster or with none), and the number of clusters (zero to four) per primary shoot. In all the other fruitfulness analyses at the individual bud level, the GLM procedure of SAS was used and only the fruitful primary shoots were considered.

In the analyses performed with GLM, mean separation tests were done at the 5% level when the F values were significant at 5% or lower level. The LSD test or an equivalent test of the GLM procedure for the least-squares means was used, except for the separation of means for bud position where, due to the large number of levels, Duncan's multiple range test was applied. In Experiment II, when leaf removal was significant and was not included in significant interactions, orthogonal contrasts were used to compare the control against the two leaf removal dates, and also the first against the second treatment date; in Experiment III, orthogonal contrasts were occasionally used to compare the responses of non-fruiting (0) against those of fruiting (1.5 and NT) vines, and of the 1.5 vines against those of the NT ones.

Results and Discussion

For the interpretation of the fruitfulness responses, one needs to consider the stages involved in the ontogeny and development of inflorescences and flowers in grapevines: 1) formation of Anlagen, club-shaped meristematic protuberances arising from bud apices, which may or not give rise to inflorescence primordia; 2) differentiation of the Anlagen to form inflorescence primordia; and 3) differentiation

of the inflorescence primordia to form flowers (see references in Srinivasan and Mullins, 1981; Swanepoel and Archer, 1988). Stages 1) and 2) occur during the vegetative season preceding the year of flowering and fruiting. The time of initiation and the rate of development of an inflorescence depend, among other factors, on the region and the season, the cultivar, the position of the bud on the shoot, and the position of the inflorescence on the condensed shoot within the bud (Pratt, 1971; Winkler et al., 1974). The formation of flowers (stage 3) is generally considered to start after the latent buds are activated the following spring (Pratt, 1971; Buttrose, 1974; Srinavasan and Mullins, 1976; 1978; 1981; Swanepoel and Archer, 1988).

Leaf Removal Effects

Basal leaf removal had little influence on flower-bud differentiation for the following season's crop, whether evaluated at the whole vine (Tables 1, 2, and 3) or at the individual bud level (Tables 4 to 9).

The reduced number of leaves removed and the timing of removal are probable explanations for the above results. However, at least in Experiment II, inflorescence primordia formation was probably not accomplished when leaf removal was imposed whether at pea size (July 27/90) (R1) or, less predictably, at veraison (August 21/90) (R2). Evidence for this was obtained from a shading experiment conducted in parallel with Experiment II. Vine shading to about 24% of ambient photosynthetic photon flux starting at one or the other date reduced the percentage of fruitful primary shoots and the number of clusters per primary shoot in the following year (Appendix B). Some authors suggested a relationship between shoot

Table 1. Influence of 1989 (Year 1) leaf removal and cropping level treatments on the fruitfulness of potted Seyval grapevines in 1990 (Year 2), evaluated on a vine basis (Experiment I)

Treatment[z] in Year 1	% of fruitful 1[ary] shoots[y]	No. clusters			No. berries set at 3 weeks PFB[x]			
		Vine	1[ary] shoot	fruitful 1[ary] shoot	1[ary] shoot	fruitful 1[ary] shoot	cluster	basal cluster
Leaf removal								
C	60.9	13.0	1.19	1.96	115	195	99	104
R	54.9	11.2	1.01	1.84	99	170	92	97
	ns[w]	ns	ns	ns	ns	ns	ns	ns
Crop. level								
0Cl	71.0a	15.2a	1.37a	1.96	122a	176	90	93
3Cl	44.7b	9.0b	0.83b	1.84	92b	191	101	109
	***	***	***	ns	*	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R:leaves removed on August 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]Relatively to the total of primary shoots evolved from both 6-node canes retained at pruning per vine
[x]PFB: post full bloom
[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively

Table 2. Influence of 1990 (Year 1) leaf removal and cropping level treatments on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a vine basis (Experiment II)

Treatment[z] in Year 1	% of fruitful 1[ary] shoots[y]	No. clusters				No. flowers				No. berries set at 3 weeks PFB[v]				% set at 3 weeks PFB	
		Vine[x]	Selec. 6-node cane[w]	1[ary] shoot[x]	fruitful 1[ary] shoot[x]	1[ary] shoot	fruitful cluster 1[ary] shoot		basal cluster	1[ary] shoot	fruitful cluster 1[ary] shoot		basal cluster	all the clusters included	basal cluster
Leaf removal															
C	80.9	17.4	10.0	1.58	2.07	598	665	322	417	67	74	36	37	11.2b	9.0
R1	76.6	16.6	9.9	1.50	2.10	491	595	279	357	66	90	43	44	17.3ab	14.0
R2	71.9	15.4	8.6	1.36	2.09	434	615	278	397	71	110	52	54	19.9a	15.4
	ns[u]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns[t]	*	ns[s]
Crop. level															
OCl	85.6a	19.0a	10.8a	1.72a	2.20	634a	719	318	436	69	81	38	49	13.0b	10.7b
3Cl	67.3b	13.9b	8.3b	1.24b	1.98	382b	531	268	345	66	102	50	50	19.3a	14.9a
	**	*	*	**	ns	*	ns	ns	ns	ns	ns	ns	ns	*	*
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
OCl:0 clusters per vine; 3Cl:3 clusters per vine
[y]Relatively to the total of primary shoots evolved from both 6-node canes retained at pruning per vine
[x]Considering both 6-node canes retained at pruning per vine
[w]Clusters on the primary shoots evolved from the 6-node cane selected for further fruitfulness evaluations
[v]PFB: post full bloom
[u]ns, *, ** Non significant or significant at the 5% or 1% level, respectively. Mean separation within columns using the LSD test at 5%.
[t]P=0.0545
[s]P=0.0674

Table 2 (cont'd).

Treatment[z] in Year 1	Yield (g)			Cluster Wt. (g)		No. berries at harvest				% berries at harvest		Berry weight (g)		No. seeds/ berry
	vine	1[ary] shoot	fruitful 1[ary] shoot	all the clusters included	basal cluster	1[ary] shoot	fruitful 1[ary] shoot	cluster	basal cluster	all the clusters included	basal cluster	all the clusters included	basal cluster	
Leaf removal														
C	399.6	74.2	82.1	40.4	43.6	47	52	26	28	8.0	6.7	1.48	1.49	2.95a
R1	378.4	66.4	95.8	45.7	48.6	46	63	30	32	12.3	10.2	1.38	1.43	3.03a
R2	406.1	69.6	108.1	51.5	56.2	50	79	37	40	14.2	11.4	1.34	1.34	2.45b
	ns[y]	ns	ns	ns	ns	ns	ns	ns	ns	ns[x]	ns	ns	ns	*
Crop. level														
0Cl	381.2	67.9	80.0b	37.3b	42.9	47	56	26b	30	9.0b	7.8b	1.35	1.36	2.81
3Cl	408.1	72.2	110.7a	54.5a	56.1	48	73	36a	37	14.0a	11.0a	1.45	1.48	2.81
	ns	ns	*	*	(**)	ns	ns	*	ns	**	*	ns	ns	ns
Interaction	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]ns, *, **, *** Non significant or significant at the 5% or 1% level, respectively. Mean separation within columns using the LSD test at 5%. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed.
[x]P=0.0523

Table 3. Influence of 1989 (Year 1) and 1990 (Year 2) leaf removal and cropping level treatments on the percentage of fruitful primary shoots and on the number of clusters per shoot in mature field Seyval grapevines in 1990 (Year 2) and 1991 (Year 3), evaluated on a vine basis (Experiment III)

Treatment[z]	1990 (Year 2)			1991 (Year 3)		
	% of fruitful 1[ary] shoots[y]	No. Clusters		% of fruitful 1[ary] shoots	No. Clusters	
		1[ary] shoot	fruitful 1[ary] shoot		1[ary] shoot	fruitful 1[ary] shoot
Leaf removal						
C	92.6	1.91	2.05	98.3	2.43	2.47
R	92.3	1.81	1.95	96.1	2.27	2.36
	ns[w]	ns	ns	ns	ns	ns
Crop. level						
0	96.0	2.11a	2.19	98.9	2.50	2.53
1.5	94.1	1.88ab	2.00	98.5	2.34	2.38
NT	87.3	1.59b	1.82	94.2	2.02	2.34
	ns	*	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns

[z]C: control (no leaves removed); R: leaves removed on September 10/89 and August 15/90
0: 0 clusters per vine; 1.5: 1.5 clusters per node retained; NT: unthinned
[y]Relatively to the total of primary shoots evolved from the 6-node canes retained per vine
[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%.

development and the evolvement of the inflorescences for the following season's crop (Lavee et al., 1967; Bozhinova-Boneva, 1975). In 'Alphonse Lavallée' and 'Sultana' grapevines, at least 18 to 21 leaves apical to the examined buds were needed to achieve the maximum percentage of differentiated buds at the bud position under analysis (Lavee et al., 1967). The shoot growth of the potted vines in 1990 (Year 1 of Experiment II) was relatively small compared to that in 1989 (Year 1 of Experiment I) (Chapter I). On August 21/90 there were 19 to 27 nodes per shoot, with an average of 21 and 24 nodes per shoot on fruiting (3Cl) and non-fruiting (0Cl) vines, respectively (data not shown). The limited 1990 growth conceivably delayed the development of a sufficient number of leaves to complete flower-bud differentiation, and inflorescence primordia formation was probably scattered over an extended period.

In all experiments there was a trend for higher percentage of fruitful primary shoots and number of clusters per primary shoot on control than on vines subjected to leaf removal (Tables 1, 2 and 3); flower number responded similarly in Experiment II. These responses were not statistically significant, however. By contrast, in Experiment II, basal leaf removal increased the percentage of berry set at three weeks after bloom in Year 2, both at the vine (Table 2) and at the individual bud level (Table 7); the number of seeds per berry was higher on C and R1 than on R2 treated vines. On an individual bud basis, additional leaf removal effects were found on the number of berries per fruitful primary shoot, per cluster and per basal cluster, both at three weeks post full bloom and at harvest. In each case, C vines had fewer berries than the vines subjected to leaf removal (Table 7).

Table 4. Significance[z] of the effects of 1989 (Year 1) leaf removal (DEF), cropping level (CROP), bud position (BP), defoliation at a specific node (BDEF), presence of a cluster at a specific node (PCL), and interactions, on the fruitfulness and yield components of potted Seyval grapevines in 1990 (Year 2), evaluated on a bud basis (Experiment I). Mean values for DEF, CROP, and BP levels relative to these analyses are presented in Table 5.

Factor or Interaction	No. clusters per 1[ary] shoot	No. set berries at 3 weeks PFB[y]		
		fruitful 1[ary] shoot	cluster	basal cluster
DEF	ns[x]	ns	ns	ns
CROP	**	ns	ns	ns
BP	***	***	**	**
BDEF(DEF)[w]	ns	ns	ns	ns
PCL(CROP)[v]	ns	ns	ns	ns
DEF*CROP				
DEF*BP				
CROP*BP				
CROP*BDEF(DEF)				
BP*BDEF(DEF)				
DEF*PCL(CROP)				
BP*PCL(CROP)				
DEF*CROP*BP				

[z]The level of significance is indicated for the main effects and interactions present in the final model obtained from backwards elimination starting at an overparametrized model that contained all the factors and interactions listed. The main effects were always kept in the sucessive models, regardless of their significance

[y]PFB: post full bloom

[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

[w]BDEF(DEF): BDEF nested within DEF

[v]PCL(CROP): PCL nested within CROP

Table 5. Influence of bud position and 1989 (Year 1) leaf removal and cropping level treatments on the fruitfulness of potted Seyval grapevines in 1990 (Year 2), evaluated on a bud basis (Experiment I)

Factor	No. clusters per 1^{ary} shoot	No. set berries at 3 weeks PFB[z]		
		fruitful 1^{ary} shoot	cluster	basal cluster
Leaf removal[y]				
C	1.19	181	90.4	101
R	1.01	165	88.1	95
	ns[x]	ns	ns	ns
Crop. level[w]				
0Cl	1.37a	167	84	93
3Cl	0.82b	182	98	106
	**	ns	ns	ns
Bud position				
1	0.15	84bc	59c	68b
2	0.28	76c	69bc	70b
3	0.79	116bc	80ab	85ab
4	1.00	133b	83ab	89ab
5	1.94	205a	96a	105a
6	2.22	232a	99a	115a
	***	***	**	***

[z]PFB: post full bloom.
[y]C:control (no leaves removed); R:leaves removed on August 31/89 (near veraison).
[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Means for bud position were separated using Duncan's New Multiple Range test at the 5% level.
[w]0Cl:0 clusters per vine; 3Cl:3 clusters per vine.

Table 6. Significance[z] of the effects of 1990 (Year 1) leaf removal (DEF), cropping level (CROP), bud position (BP), defoliation at a specific node (BDEF), presence of a cluster at a specific node (PCL), and interactions, on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a bud basis (Experiment II). Mean values for DEF, CROP, and BP levels relative to these analyses are presented in Table 7.

Factor or Interaction	No. clusters per 1[ary] shoot	No. flowers			No. set berries at 3 weeks PFB[y]			% set at 3 weeks PFB	
		fruitful 1[ary] shoot	cluster	basal cluster	fruitful 1[ary] shoot	cluster	basal cluster	all the clusters included	basal cluster
DEF	ns[x]	ns	ns	ns	*	***	**	***	**
CROP	*	***	**	**	ns	ns	ns	***	***
BP	***	***	***	***	***	***	***	ns	ns
BDEF(DEF)[w]	ns	ns	ns	ns	ns	ns	ns	ns	ns
PCL(CROP)[v]	ns	ns	ns	ns	ns	ns	ns	ns	ns
DEF*CROP		*		*					*
DEF*BP			ns	ns					
CROP*BP						*			
CROP*BDEF(DEF)									
BP*BDEF(DEF)			*	*					
DEF*PCL(CROP)									
BP*PCL(CROP)									
DEF*CROP*BP									

[z]The level of significance is indicated for the main effects and interactions present in the final model obtained from backwards elimination starting at an overparametrized model that contained all the factors and interactions listed. The main effects were always kept in the sucessive models, regardless of their significance

[y]PFB: post full bloom

[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

[w]BDEF(DEF): BDEF nested within DEF

[v]PCL(CROP): PCL nested within CROP

Table 6 (cont'd).

Factor or Interaction	Yield per fruitful 1^{ary} shoot (g)	Cluster Wt. (g)		No. berries at harvest			% berries at harvest		Berry Wt. (g)		No. seeds/ berry
		all the clusters included	basal cluster	fruitful 1^{ary} shoot	cluster	basal cluster	all the clusters included	basal cluster	all the clusters included	basal cluster	
DEF	ns[z]	ns	ns	*	**	**	***	**	ns	ns	*
CROP	*	***	**	ns	**	ns	***	***	***	***	ns
BP	***	***	***	***	***	***	ns	ns	***	***	ns
BDEF(DEF)	ns	ns	ns	ns	ns	ns	ns	ns	***	**	ns
PCL(CROP)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
DEF*CROP							*	*	**		
DEF*BP									*	*	
CROP*BP					*						
CROP*BDEF(DEF)											
BP*BDEF(DEF)											
DEF*PCL(CROP)											
BP*PCL(CROP)											
DEF*CROP*BP											

[z]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 7. Influence of bud position and 1990 (Year 1) leaf removal and cropping level treatments on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a bud basis (Experiment II)

Factor		No. clusters per 1[any] shoot	No. flowers			No. set berries at 3 weeks PFB[z]			% set at 3 weeks PFB	
			fruitful 1[any] shoot	cluster	basal cluster	fruitful 1[any] shoot	cluster	basal cluster	all clusters included	basal cluster
Leaf removal[y]:	C	1.58	640	309	403	71b	34b	36b	12.9b	11.1
	R1	1.51	624	283	369	81ab	37b	40ab	15.2ab	13.4
	R2	1.35	566	274	373	94a	46a	48a	18.6a	15.1
		ns[x]	ns	ns	ns	*	***	**	***	(**)
C vs. R1 and R2						**	**	**	***	
R1 vs. R2						ns	*	ns	ns	
Crop. level[w]:	0Cl	1.73a	697	320a	420	77	36	39	12.4b	10.5
	3Cl	1.24b	509	252b	337	88	43	44	19.1a	16.2
		*	(***)	**	(**)	ns	ns	ns	***	(***)
Bud position:	1	0.46	272d	179	213	32c	23	26c	18.0	17.4
	2	0.83	352cd	228	267	36c	24	25c	14.4	13.2
	3	1.15	446bc	257	325	49b	29	32b	13.4	11.4
	4	1.41	609b	326	396	59b	32	32b	11.4	9.4
	5	2.28	813a	346	470	130a	59	61a	18.4	14.6
	6	2.46	859a	316	475	129a	48	52a	17.1	14.1
		***	***	(***)	(***)	***	(***)	***	ns	ns

[z]PFB: post full bloom.
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison).
[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Least-squares means for leaf removal were separated at the 5% level. Means for bud position were separated using Duncan's New Multiple Range test at the 5% level.Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed.
[w]0Cl:0 clusters per vine; 3Cl:3 clusters per vine.

Table 7 (cont'd).

Factor		Yield per fruitful 1^{ary} shoot (g)	Cluster Wt. (g)		No. berries at harvest			% berries at harvest		Berry Wt. (g)		No. seeds/ berry
			all the clusters included	basal cluster	fruitful 1^{ary} shoot	cluster	basal cluster	all the clusters included	basal cluster	all the clusters included	basal cluster	
Leaf removal[z]:	C	79.9	37.3	42.2	50b	24b	27b	8.6	7.6	1.41	1.44	2.93a
	R1	84.2	38.7	44.0	56ab	26b	29ab	10.7	9.6	1.34	1.37	2.91a
	R2	92.8	45.4	50.8	66a	32a	36a	12.9	10.8	1.32	1.36	2.64b
		ns[y]	ns	ns	*	**	**	(***)	(**)	ns	ns	*
C vs. R1 and R2					**	**	**					ns
R1 vs. R2					ns	*	ns					*
Crop. level[x]:	0Cl	75.0b	33.9b	40.4b	52	24	28	8.4	7.6	1.29	1.31b	2.81
	3Cl	97.8a	47.9a	51.5a	64	31	33	13.3	11.3	1.44	1.48a	2.86
		*	***	**	ns	(**)	ns	(***)	(***)	(***)	***	ns
Bud position:	1	24.6c	17.8d	21.2c	20c	15	17d	9.6	9.5	1.11	1.13	2.58
	2	31.7c	21.4cd	24.1c	25c	16	18cd	10.4	9.7	1.20	1.24	2.69
	3	47.9b	28.4bc	32.9b	34b	20	22bc	9.0	7.8	1.33	1.40	2.74
	4	58.7b	31.7b	36.0b	39b	21	23b	7.8	6.8	1.39	1.44	2.99
	5	146.7a	67.2a	73.1a	94a	43	46a	13.2	10.9	1.49	1.53	2.92
	6	135.4a	51.4a	59.4a	91a	34	40a	12.2	10.4	1.43	1.43	2.89
		***	***	***	***	(***)	***	ns	ns	(***)	(***)	ns

[z]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size); R2:leaves removed on Aug.21/90 (veraison).
[y]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Least-squares means for leaf removal were separated at the 5% level. Means for bud position were separated using Duncan's New Multiple Range test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed.
[x]0Cl:0 clusters per vine; 3Cl:3 clusters per vine.

Unexpectedly, potted vines subjected to leaf removal at pea size usually had intermediate fruitfulness responses between control vines and vines treated at veraison.

A discrepancy between cluster and flower number on one hand, and the percentage of berry set and berry number on the other, was also observed in Experiment II when cropping level means were compared. Probable reasons for this will be discussed in the next section.

To summarize, the data reported for statistically significant responses showed either no negative effects or, in a few cases (related to fruit set in Experiment II), a positive leaf removal response. What is a nagging concern, however, are the array of data suggesting potentially negative responses on flower-bud differentiation, yet non-significant at the $\alpha = 0.05$ level of probability. Indeed, these data may not represent real differences. There is also the chance that the differences are real and inadequate replication has resulted in a Type II statistical error (Steel and Torrie, 1980). This possibility cannot serve as any weight for this discussion, but should be a consideration in further effort in this area of viticultural research.

Cropping Level Effects

The fruits developing in a given season may influence bud development and differentiation for the following season's crop by competing with the buds for metabolites or by interfering with the hormonal balance (Jackson and Sweet, 1972). In this study, as in Antcliff and Webster (1955), flower-bud differentiation for Year 2' s crop was affected by cropping in Year 1, especially on young potted vines.

Potted vines that bore fruit in Year 1 (3Cl) had lower percentage of fruitful primary shoots and fewer clusters per vine and per primary shoot than non-bearing (0Cl) potted vines (Tables 1 and 2); the number of flowers per primary shoot (Experiment II) was likewise lower on the 3Cl vines. However, cropping had no significant influence on the number of clusters per fruitful primary shoot, whether on potted or on mature vines. Apparently, fruit development in Year 1 reduced the number of differentiated primary buds, but after the first inflorescence was formed within the bud this factor probably had little influence on the number of inflorescences per bud.

On mature vines, the percentage of fruitful primary shoots (which was higher than on potted vines) did not significantly differ among cropping levels in Years 2 and 3 (1990 and 1991) (Table 3). At the individual bud level, though, cropping in 1989 had a significant effect on the fruitful condition of the primary buds in 1990; the propensity to be fruitful in 1990 was higher for the primary buds on vines that did not bear fruit in 1989 (0 vines) than on fruiting (1.5 and NT) vines (data not shown). In 1991 the cropping effect was not clearly evidenced, due to significant interactions (data not shown). Cluster number per primary shoot in 1990 was lower on NT than on 0-treated vines; 1.5 vines had an intermediate value, not significantly different from that of 0 and NT vines. Cropping level had no significant effect on the number of clusters per primary shoot in 1991 (Tables 3, 8 and 9).

On mature vines, the differences in response intensity between the two years under analysis could be due to: a) earlier cluster thinning in 1989 (one week before full bloom) than in 1990 (nine days after full bloom); hence, the advantage of the

Table 8. Significance[z] of the effects of 1989 (Year 1) and 1990 (Year 2) leaf removal (DEF), cropping level (CROP), bud position (BP), defoliation at a specific node (BDEF), presence of a cluster at a specific node (PCL), and interactions, on the number of clusters per primary shoot of mature field Seyval grapevines in 1990 (Year 2) and in 1991 (Year 3), evaluated on a bud basis (Experiment III).Mean values for DEF, CROP, and BP levels relative to these analyses are presented in Table 9.

Factor or Interaction	No. clusters per primary shoot	
	1990 (Year 2)	1991 (Year 3)
DEF	ns[y]	ns
CROP	*	ns
BP	ns	**
BDEF(DEF)[x]	ns	ns
PCL(CROP)[w]	ns	ns
DEF*CROP		
DEF*BP		
CROP*BP		
CROP*BDEF(DEF)		
BP*BDEF(DEF)		
DEF*PCL(CROP)		
BP*PCL(CROP)		
DEF*CROP*BP		

[z]The level of significance is indicated for the main effects and interactions present in the final model obtained from backwards elimination starting at an overparametrized model that contained all the factors and interactions listed. The main effects were always kept in the sucessive models, regardless of their significance
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.
[x]BDEF(DEF): BDEF nested within DEF
[w]PCL(CROP): PCL nested within CROP

Table 9. Influence of bud position, and 1989 (Year 1) and 1990 (Year 2) leaf removal and cropping level treatments on the number of clusters per primary shoot of mature Seyval grapevines in 1990 (Year 2) and 1991 (Year 3), evaluated on a bud basis (Experiment III)

Factor		No. clusters per primary shoot	
		1990 (Year 2)	1991 (Year 3)
Leaf removal:[z]	C	2.05	2.43
	R	1.90	2.30
		ns[y]	ns
Crop. level:[x]	0	2.16	2.51
	1.5	1.93	2.34
	NT	1.66	2.25
		*	ns
0 vs. 1.5 and NT		*	
1.5 vs. NT		ns	
Bud position:	1	1.78	1.94
	2	1.84	1.95
	3	1.92	2.24
	4	1.92	2.58
	5	2.03	2.63
	6	2.17	2.63
		ns	**

[z]C: control (no leaves removed); R: leaves removed on September 10/89 and August 15/90.
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.
[x]0: 0 clusters per vine; 1.5: 1.5 clusters per node retained; NT: unthinned.

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buds developing on non-fruiting vines would have been implemented at an earlier stage of bud differentiation in 1989. Indeed, the initiation of the first Anlage at the basal bud was found to occur at 12 to 15 days before bloom on 'Chenin blanc' grapevines (Swanepoel and Archer, 1988), and an earlier date was suggested by Pratt (1979) on 'Concord'; b) heavier crop on 1.5 and NT vines in 1989 than in 1990 (Chapter III); cropping in 1989 would consequently be more depressive to bud fertility in 1990 than would cropping in 1990 be to bud fertility in 1991. Reason a) is probably not relevant from the standpoint of competition for photosynthate between clusters and developing buds. Indeed, Hale and Weaver (1962) found that the inflorescences (clusters) were strong sinks while rapidly increasing in size, but from about 10 to 14 days before bloom until 10 days after full bloom they were relatively weak sinks compared to the shoot tip and the parent vine; only after berry set did the clusters become a powerful sink again, in contrast with the axillary buds, which were minor sinks. Both in 1989 and 1990, thinning was imposed while the clusters were conceivably still a weak sink for photosynthate. Thus, if any influence of thinning date on bud fertility occurred, it was most probably exerted via a process other than competition for assimilates.

The lower responsiveness to cropping level of mature as compared to potted vines was to be expected, not only because the degree of homeostasis is conceivably higher on the former vines, but also because the canes for fruitfulness evaluation on mature vines were selected for a defined diameter range (unlike on potted vines where cane diameter was smaller on 3Cl than on 0Cl vines).

It is important to emphasize that under field conditions cropping has an

additional, indirect effect, on yield of the following year by influencing bud burst. The heavy crop in 1989 not only reduced flower-bud differentiation for 1990 but also aggravated the primary bud mortality associated with freezing temperatures during the severe 1989/90 dormant season (Chapter II).

In Experiment II, flower-bud differentiation and fruit set in Year 2 were not influenced in the same manner by the treatments applied in Year 1. In contrast with the percentage of fruitful primary shoots and the number of clusters and flowers, the percentage of fruit set in Year 2 was higher on 3Cl than on 0Cl vines (Table 2). During the massive differentiation to individual flower parts, which occurs shortly before and after bud-burst (Buttrose, 1974), the inflorescence primordia were conceivably strong sinks. The 0Cl vines, less stressed in Year 1 than the 3Cl vines, would then have the advantage resulting from greater reserve availability. This may explain the higher number of flowers per cluster (on an individual bud basis) (Table 7) and, along with more clusters per primary shoot, the higher number of flowers per primary shoot on 0Cl than on 3Cl vines (Table 2). The initial advantage of the 0Cl vines was probably reduced when the inflorescence became a weak sink, including during the period when most berry set occurred (Hale and Weaver, 1962). Given the limited capacity of the potted vines (namely those of Experiment II), the markedly higher number of clusters and of flowers per cluster on 0Cl than on 3Cl vines conceivably created a stronger competition in the former vines and exerted a negative influence on berry set. The number of clusters per fruitful primary shoot was not significantly different on 0Cl and 3Cl vines; however, as suggested by Looney (1981), within-cluster competition is probably more critical for berry set than

competition among clusters on the same shoot. As both nutritional and hormonal hypotheses have been proposed for the regulation of berry set in grapevines (Winkler et al, 1974), there is also the possibility that the hormonal balance on 3Cl vines was more favorable to fruit set than on 0Cl vines. Similar arguments could also explain the opposite trends in number of flowers and number of berries among control vines and vines subjected to leaf removal in Experiment II. Yield per primary shoot and per vine in Year 2 was similar for 0Cl and 3Cl vines. The higher number of berries per cluster on 3Cl than on 0Cl vines contributed to heavier clusters on the former vines, which compensated for their lower number of clusters (Table 2).

Bud Position

On potted vines, the propensity of a primary bud to originate a fruitful shoot tended to increase from the base to the apex of the 6-node cane (data not shown). In Experiment I, the meaning of this observation is restricted due to significant interactions involving bud position (BP), while in Experiment II the BP effect was highly significant. However, on mature vines, where a relatively large percentage of the primary shoots that evolved were fruitful (Table 3), the propensity of a viable bud to be fruitful was either not significantly affected by BP (Year 2) or the BP effect was confounded by significant interactions (Year 3); in both cases this propensity was relatively uniform along the 6-node cane (data not shown). Whether on potted or on mature vines, the number of clusters per primary shoot increased from nodes one to six (Tables 5, 7 and 9). In Year 2, unlike in Year 3 of Experiment III, this effect was not significant, though; this may be due to a lower number of

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observations in the former year, resulting from severe winter damage during the 1989/90 dormant season.

For most of the remaining responses evaluated on potted vines, a gradient of increasing fruitfulness from the base to the apex of the 6-node canes was usually found, with only a few minor deviations (Tables 5 and 7). These results are consistent with the widely reported increase in fruitfulness from the basal to the mid-nodes of grapevine canes, after which fruitfulness gradually declines towards the apical cane portion (Partridge, 1921; Buttrose, 1974; Champagnol, 1984; Huglin, 1986; Howell et al., 1993). BP had no significant influence on the percentage of berry set and on the number of seeds per berry, though (Table 7). The lack of a significant effect on the percentage of berry set is understandable given that BP strongly influenced in the same direction both the number of berries and the number of flowers per fruitful primary shoot.

Removal of the Subtending Leaf

The leaf subtending a grapevine bud is probably the major source of photosynthate for that bud (Hale and Weaver (1962). Alternatively, leaf removal can alter the pattern of photosynthate translocation in grapevines, originating a compensatory movement of photosynthate to the treated shoot region (Quilan and Weaver, 1970). In the present study, the removal of the leaf subtending a given bud (or leaf plus lateral shoot in Experiment III) (BDEF) had no significant effect on the differentiation of that bud (Tables 4 to 9) despite the evidence (for Experiment II) that inflorescence primordia formation was still underway when leaves were removed.

A bud whose subtending leaf was removed probably benefitted from a compensatory photosynthate movement, which may explain the lack of a significant reduction in its fertility. In fruit trees, buds lacking a subtending leaf accumulated ^{14}C applied to other leaves on the shoot as readily as did buds with intact leaves (Minnis, 1970), suggesting that a bud may attract and utilize carbohydrates from a source other than the subtending leaf (Jackson and Sweet, 1972).

Presence of a Cluster at an Individual Node

The presence of a cluster at a specific node position in Year 1 (PCL) had no significant effect on the Year 2 fruitfulness responses of the primary bud located at that node (Tables 4, 6, 8). Grapevine clusters, unlike the inflorescences of most plants, have an extra-axillary, leaf-opposed position on the shoot (hence opposed to the axillary buds) (Pratt, 1971; Srinavasan and Mullins, 1976). This feature, by itself, does not prevent the cluster from using carbohydrates or other substances produced by the opposite leaf. Hale and Weaver (1962) found that after berry set the grape cluster can not only attract photosynthate from the opposite leaf but also divert the photosynthate moving down the shoot from the originally vertical path. Because of its polarizing power, a cluster can conceivably affect several axillary buds on the shoot, besides the one developing on that same node. Conversely, as this study suggests, the cropping effect on the fruitfulness of a given bud may derive mostly from the fruiting condition (bearer or not) of the shoot in Year 1, rather than from the condition (presence/absence of a cluster) of the node where the bud developed.

Significant Interactions Influencing Bud Fruitfulness

In the fruitfulness evaluations at the individual bud level, several significant interactions were observed; to avoid an extensive description, only the most relevant will be discussed. There were instances, specially in the analyses of the fruitful condition (differentiated or not) of a primary bud, where some interactions could not be resolved, because the pattern of the responses resulted in excessively high variances that compromised the realization of contrasts.

In Experiment II and in Year 3 of Experiment III, the fruitful condition of a primary bud was influenced by a significant leaf removal x cropping interaction (data not shown). In Experiment II, leaf removal decreased the propensity of the primary buds of 3Cl vines to be fruitful, but had no significant effect in the case of 0Cl vines; this reflects the synergism of two negative influences (leaf removal and cropping) which by themselves were not significantly influential. As for Year 3 of Experiment III, contrasts were not feasible; the fruiting propensity of the buds was relatively high for all treatment combinations but leaf removal appeared to increase that propensity on non-fruiting vines and to decrease it on NT vines (data not shown). This may be explained by improved light exposure of the buds on non-fruiting vines resulting from the removal of their subtending leaf and lateral shoot. Though only well-matured canes were used in the fruitfulness evaluations, the presence of a lateral shoot (whose growth was particularly favored on non-fruiting vines) would conceivably affect the exposure of the bud on the node at which the lateral shoot developed (Howell and Shaulis, 1980).

Conclusions

Basal leaf removal had little influence on flower-bud differentiation for the following season's crop, whether evaluated at the vine or at the individual bud level. In particular, the removal of the leaf subtending a bud had no significant effect on the differentiation of that bud. The small number of leaves removed and the timing of removal are probable explanations for the above results. However, at least in one experiment with potted vines, there is evidence that inflorescence primordia formation was not yet completed on the 6-node canes when leaf removal was applied whether at pea size or at veraison.

Cropping in Year 1 inhibited flower-bud differentiation for Year 2' s crop, especially on young potted vines. On mature vines, cropping reduced the number of clusters per primary shoot in 1990 but not in 1991, conceivably due to a heavier yield (hence stronger inhibition of flower-bud differentiation) in 1989 than in 1990. It must be noted that under field conditions a heavy crop may have a further effect on the following year's yield by reducing bud burst, especially if in conjunction with severe winter conditions as in the 1989/90 dormant season. The presence of a cluster at a specific node had no significant effect on the fruitfulness of the primary bud developing at that node, regardless of the experiment. The fruiting condition in Year 1 of the vine or the shoot where the bud developed (bearer or not), rather than the presence or absence of a cluster at the same node of the developing bud, was probably the determining factor in the fruitfulness response of that bud to cropping level. On the other hand, the position of a bud on the 6-node cane had a highly

significant effect on most fruitfulness responses. An increasing fruitfulness from the base to the apex of the 6-node cane was consistently found, in agreement with previous studies.

Treatment effects on flower-bud differentiation and on fruit set in Year 2 were not in correspondence, as evaluated in one of the experiments with potted vines. Opposite trends in cluster number on one hand and in the number of berries per cluster and cluster weight on the other, resulted in a lack of significant treatment effects on yield per vine and per primary shoot in Year 2.

A trend was noticed in all the experiments conducted for higher flower-bud differentiation on control than on vines subjected to leaf removal; unexpectedly, though, potted vines subjected to leaf removal at pea size appeared to have intermediate bud differentiation between control vines and vines treated at veraison. This trend was not statistically proven in this study. However, its viticultural interest suggested that it should be investigated with more detail in future experimentation.

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SUMMARY AND CONCLUSIONS

On young potted Seyval grapevines, basal leaf removal at berry pea size (five weeks after full bloom) increased the net CO_2 assimilation rate per unit of leaf area (A), in contrast with leaf removal at veraison, which had no significant effect on A whether on potted or on mature field vines. Fruit development enhanced A, particularly on potted vines. The observed increase in A following a reduction in the source/sink ratio was probably a consequence of increased photosynthate demand at individual leaves, as hypothesized by other authors.

On mature, field-grown Seyval, the removal of basal leaves and adjacent laterals at veraison or 2.5 weeks after improved the light microclimate in the cluster region, with no significant negative effects on global vine growth and yield, nor on the fruitfulness and cold hardiness of the primary buds on the treated shoot region. Leaf removal reduced cane hardiness in the 1989/90 dormant season. However, the percentage of nodes evolved in the field, which was more consistent with primary bud than with cane hardiness data (as expected from a higher cold sensitivity of the primary buds), was not significantly affected by leaf removal in any of the trial years. Similarly, no significant adverse effects of basal leaf removal were observed on potted vines. These results suggest that the use of basal leaf removal to improve canopy microclimate and, thereby, the control of bunch rot (Botrytis cinerea Pers.) can be broadened to regions where cold injury is an actual concern.

The economical value of basal leaf removal is comprehensibly dependent on a number of factors influencing the degree of Botrytis infection. Data from field-grown vines supported the view that vines with dense canopies are more likely to benefit from an improved Botrytis control, and less prone to suffer from a potential loss of carbohydrate due to leaf removal. It could be of interest to increase the number of basal leaves removed per shoot (to say, five or six), and assess whether compensatory responses would be implemented and still prevent the expression of negative effects at the primary bud and whole vine levels.

Fruiting mature vines yielded a heavier crop in 1989 than in 1990. This, aggravated by an early leaf killing frost in the fall of 1989, may explain the finding that cropping in the former year had a stronger impact on cold hardiness, field bud survival, and bud fertility. Mature field vines left unthinned in the first two (1989 and 1990) trial seasons (NT vines) had lower primary bud hardiness in 1989/90, lower field bud survival in 1989/90 and 1990/91, and fewer clusters per primary shoot in 1990 than non-fruiting (0) ones. The vines thinned to 1.5 clusters per node retained (1.5 vines) had intermediate values, not significantly different from those of NT vines. Yield was similar for 1.5 and NT vines. The NT vines had lower Botrytis infection in 1989 (presumably due to lower cluster compactness), a prompt growth recovery by thinning to 1.5 clusters per node retained in the third trial year, and a higher °Brix in the recovery year than the 1.5 vines. The vine size at the beginning of the experiment (1.0 to 1.5 kg) appeared to be sufficient to support two consecutive seasons of unthinning, and balanced-pruning undoubtedly minimized any potential vegetative/reproductive imbalance resulting from unthinning. These findings and the

labor costs of cluster thinning motivate further research on the value of pluriannual as compared to annual cluster thinning in Seyval.

In this study, there were situations where carbohydrate shortage probably limited hardiness development and maintenance, while in other instances such a possibility appeared unlikely. This reinforces the view that by no means should carbohydrate content be systematically invoked to justify differences in hardiness degree. Hormonal regulation might have been important in situations where leaf removal or cropping did not drive carbohydrate levels below a critical point. It would be of interest to investigate the hypothesis of a hormonal involvement (namely of ABA) in hardiness responses to basal leaf removal.

During the course of this study, there were a number of trends that consistently emerged, but lacked statistical significance. Their consistency and viticultural interest suggested that they should be tested in further experiments with increased number of observations. On mature vines, there was a tendency for leaf removal to decrease primary bud hardiness in the mid-winter and to increase it in the early spring, which could have contributed to the lack of a significant leaf removal effect on field bud survival through the dormant season. On potted vines, leaf removal at pea size may have triggered compensatory responses (such as the observed photosynthetic enhancement and, presumably, an alteration in translocation patterns), that either did not develop or were less effective when leaf removal was applied at veraison. This may explain the observation that mid-winter hardiness and flower-bud differentiation were apparently less affected by leaf removal at pea size than by leaf removal at veraison. There was no sufficient evidence to corroborate this

trend, however. If real, it would have important viticultural implications, which motivates further, detailed experimentation. So far, the absence of a significant negative leaf removal effect on the physiological responses analyzed is a point in favor of leaf removal at pea size relative to removal at veraison given that an earlier treatment, besides increased easiness of application, is more likely to provide an effective bunch rot control.

APPENDICES

APPENDIX A

Influence of Basal Leaf Removal and Cropping Level on the Stomatal Conductance, Transpiration Rate, and Water use Efficiency at Basal, Middle-shoot and Apical Leaves of Seyval Grapevines

Influence of Basal Leaf Removal and Cropping Level on the Stomatal Conductance, Transpiration Rate, and Water use Efficiency at Basal, Middle- shoot and Apical Leaves of Seyval Grapevines

Summary

The effects of basal leaf removal and cropping treatments on gas exchange were evaluated at basal (BAS), middle-shoot (MID) and apical (AP) leaves of own-rooted Seyval grapevines, either one-year-old potted vines (Experiments I, II) or mature, field-grown vines (Experiment III).

Potted vines were trained to two shoots and lateral shoots were removed weekly. Leaf removal consisted of the removal of three consecutive leaves in the fruiting region of both vine shoots. On the potted vines used in gas exchange determinations leaf removal levels were C (control, no leaves removed) and R (leaf removal near veraison) in Experiment I, or C (control) and R1 (leaf removal at pea size, 5 weeks after full bloom) in Experiment II. Cropping level was either 0Cl (no clusters per vine) or 3Cl (3 clusters per vine) in both experiments. Mature vines, trained to Hudson River Umbrella (a high bilateral cordon), were cropped at levels 0 (no clusters per vine), 1.5 (1.5 clusters per node retained at pruning) and NT (all clusters retained, no thinning). Leaf removal levels were C (control), and R (main leaves and lateral shoots removed at veraison at three consecutive basal nodes on all vine shoots). Lateral shoots were allowed to develop normally except for those at the treated nodes of the R treatment vines. Details regarding trial installation and vine

maintenance, as well as equipment and procedures used in gas exchange determinations were described in Chapter I.

The gas exchange parameters measured were net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE). The data herein reported concern the g_s, E, and WUE evaluations at the individual leaf positions on each measurement date and for the combination of the measurement dates through the season. The responses in A at individual leaves, as well as in gas exchange parameters for the combination of leaf positions were presented in Chapter I.

Basal leaf removal at pea size on potted vines (Experiment II) increased g_s, and E at BAS and MID leaves at either one or both measurements taken in the pre-veraison period (August 2 and August 9, one and two weeks after leaf removal, respectively), at the post-harvest measurement, and on average across the measurement dates following leaf removal (Tables 4 and 5). At AP leaves, this effect was significant only for the measurement taken two weeks after leaf removal. The observed increase in g_s, and E in response to leaf removal is consistent with previous results (Hunter and Visser, 1988; Candolfi-Vasconcelos, 1990). The increase in g_s besides increasing E, is conceivably one reason for the enhanced A at BAS and MID leaves in response to leaf removal at pea size (Chapter I). On the other hand, leaf removal at or shortly after veraison whether in potted (Experiment I) or in mature vines (Experiment III) had no significant effect on A (Chapter I), nor on g_s and E. Leaf removal at pea size presumably created a source limitation despite the reduced number of leaves removed; the observed increase in A, g_s and E might have

represented a compensatory response. At veraison, the source/sink ratio was conceivably less affected by leaf removal, due to a proportionally less important area and physiological activity of the leaves removed. Moreover, leaf aging might have prevented a compensatory response to leaf removal at veraison. WUE has been reported to increase in response to defoliation (Hunter and Visser, 1988; Candolfi-Vasconcelos, 1990). However, no significant effect on WUE was found following leaf removal at pea size (Table 6); leaf removal at or near veraison led to a sporadic increase in WUE, but this effect was not significant when the measurements since leaf imposition were combined (Tables 3 and 9).

In the experiments conducted, g_s and E were generally higher on fruiting than on non-fruiting vines. At the last measurement in Experiment II, unlike at previous ones, g_s and E were lower at BAS leaves of 3Cl than of 0Cl vines (Tables 4 and 5); however, at this time the clusters of the 3Cl vines had already been harvested. These results are consistent with the cropping level effects on A (Chapter I), which suggest a photosynthetic enhancement in response to increased sink demand resulting from fruit development. By contrast, cropping effects on WUE were seldom observed, regardless of the leaf position, and no consistent pattern was noticed. On average across sampling dates, the fruiting potted vines in Experiment II had higher WUE at AP leaves than the non-fruiting ones (Table 6), but the opposite relationship was found at MID leaves in mature field vines (Table 9).

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Table 1. Influence of leaf removal and cropping level on the stomatal conductance (g_s) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1989 - Experiment I).

Leaf position[z]	Treatment[y]	g_s (mmol $CO_2.m^{-2}.s^{-1}$)							Average	
		June 28 2 d PFB[x]	July 11 2 wk PFB	Aug.21 8 wk PFB	Aug.25 V	Aug.30 5 d PV	Sep.12 2.5 wk PV	Sep.18 1 wk BH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C						94.3	75.0		81.4
	R						95.7	95.8		95.8
							ns[w]	ns		ns
	Crop. level									
	0Cl	109.6	131.3	51.4b	70.8b	115.2b	92.8	71.2b	93.4b	78.4
	3Cl	119.9	139.4	78.5a	129.3a	166.1a	97.2	99.6a	119.3a	98.8
		ns	ns	*	ns	*	ns	*	***	ns
	Interaction						ns	ns		ns
MID	Leaf removal									
	C						95.8	88.7		91.0
	R						77.9	96.8		90.5
							ns	ns		ns
	Crop. level									
	0Cl		117.6b	57.6	87.3b	121.8b	67.5	68.0b	86.5b	67.8b
	3Cl		128.6a	83.1	155.5a	204.7a	106.2	117.5a	125.0a	113.7a
			*	ns	*	**	ns	**	***	**
	Interaction						ns	ns		ns
AP	Leaf removal									
	C						129.5	108.4		115.4
	R						113.4	105.8		108.3
							ns	ns		ns
	Crop. level									
	0Cl	76.6	87.8	68.4b	119.9	166.8b	112.5	78.2b	103.5b	89.6b
	3Cl	85.4	84.6	104.8a	188.2	220.9a	130.3	135.9a	141.1a	134.0a
		ns	ns	**	ns	*	ns	**	**	***
	Interaction						ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; V:Veraison; PV:post veraison; BH:before harvest
[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 2. Influence of leaf removal and cropping level on the transpiration rate (E) of BAS,MID, and AP leaves of potted Seyval vines (HRC 1989 - Experiment I).

Leaf position[z]	Treatment[y]	E (mmol $H_2O.m^{-2}.s^{-1}$)							Average	
		June 28 2 d PFB[x]	July 11 2 wk PFB	Aug.21 8 wk PFB	Aug.25 V	Aug.30 5 d PV	Sep.12 2.5 wk PV	Sep.18 1 wk BH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C						3.47	3.53		3.51
	R						3.44	4.24		3.97
							ns[w]	ns		ns
	Crop. level									
	0Cl	4.63	7.10	2.76	2.79b	3.83b	3.38	3.52	4.16b	3.47
	3Cl	4.88	7.40	3.08	4.34a	4.96a	3.53	4.25	4.87a	4.01
		ns	ns	ns	**	*	ns	ns	***	ns
	Interaction						ns	ns		ns
MID	Leaf removal									
	C						3.33	3.95		3.74
	R						2.98	4.32		3.87
							ns	ns		ns
	Crop. level									
	0Cl		6.59b	3.09	3.26b	4.08b	2.46	3.42b	3.81b	3.10b
	3Cl		6.91a	3.81	4.97a	5.60a	3.85	4.84a	4.89a	4.51a
			**	ns	**	**	ns	*	***	**
	Interaction						ns	ns		ns
AP	Leaf removal									
	C						4.32	4.70		4.57
	R						3.94	4.68		4.43
							ns	ns		ns
	Crop. level									
	0Cl	3.39	5.29	3.39b	4.20	5.02	3.88	3.87b	4.32b	3.88b
	3Cl	3.75	5.18	4.71a	5.53	5.81	4.37	5.50a	5.23a	5.13a
		ns	ns	*	ns	ns	ns	**	***	***
	Interaction						ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; V:Veraison; PV:post veraison; BH:before harvest
[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 3. Influence of leaf removal and cropping level on the water use efficiency (WUE) of BAS, MID leaves of potted Seyval vines (HRC 1989 - Experiment I).

Leaf position[z]	Treatment[y]	WUE (mmol CO_2/mol H_2O)							Average	
		June 28 2 d PFB[x]	July 11 2 wk PFB	Aug.21 8 wk PFB	Aug.25 V	Aug.30 5 d PV	Sep.12 2.5 wk PV	Sep.18 1 wk BH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C						1.98	1.50		1.66
	R						2.02	1.36		1.58
							ns[w]	ns		ns
	Crop. level									
	0Cl	2.39	1.71	2.37	2.42a	2.08	2.08	1.45	2.04	1.66
	3Cl	2.49	1.68	2.35	1.92b	2.17	1.92	1.42	2.00	1.58
		ns	ns	ns	*	ns	ns	ns	ns	ns
	Interaction						ns	ns		ns
MID	Leaf removal									
	C						3.01	2.02		2.36
	R						2.63	1.82		2.09
							ns	ns		ns
	Crop. level									
	0Cl		1.74b	2.64	2.72	2.56	3.11	1.89	2.35	2.30
	3Cl		1.86a	3.30	2.44	2.68	2.53	1.96	2.46	2.15
			*	ns	ns	ns	ns	ns	ns	ns
	Interaction						ns	ns		ns
AP	Leaf removal									
	C						2.52b	2.04		2.20
	R						2.84a	1.90		2.21
							**	ns		ns
	Crop. level									
	0Cl	2.35	1.34	3.02	2.59	2.54	2.75a	2.02	2.32	2.26
	3Cl	2.47	1.42	2.84	2.44	2.80	2.61b	1.92	2.30	2.15
		ns	ns	ns	ns	ns	*	ns	ns	ns
	Interaction						ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R:leaves removed on Aug. 31/89 (near veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; V:Veraison; PV:post veraison; BH:before harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 4. Influence of leaf removal and cropping level on the stomatal conductance (g_s) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990 - Experiment II).

Leaf position[z]	Treatment[y]	g_s (mmol $CO_2.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C			109.4b	118.4	107.6	87.4	37.2b		92.0b
	R1			137.1a	126.4	116.7	77.5	52.7a		102.1a
				*[w]	ns	ns	ns	**		*
	Crop. level									
	0Cl	165.5	123.6	110.7b	115.5	93.6b	59.0b	52.2a	99.7b	86.2b
	3Cl	167.7	136.3	135.9a	129.4	130.7a	105.9a	37.7b	118.1a	107.9a
		ns	ns	*	ns	**	**	**	***	***
	Interaction			ns	ns	ns	ns	ns		ns
MID	Leaf removal									
	C			105.6b	115.7b	115.9	104.4	57.7b		99.8b
	R1			148.2a	137.1a	113.5	97	77.3a		114.8a
				*	**	ns	ns	*		**
	Crop. level									
	0Cl		112.4b	109.1b	112.7b	98.0b	80.1b	74.1	97.1b	94.8b
	3Cl		154.5a	144.6a	140.1a	131.4a	121.9a	61.0	124.3a	119.8a
			*	**	***	**	**	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Leaf removal									
	C			70.3	87.0b	116.1	114.5	39.1		85.4
	R1			88.8	117.8a	111.5	101.3	41.6		92.2
				ns	**	ns	ns	ns		ns
	Crop. level									
	0Cl	150.6	89.2	75.6	92.2	98.6b	86.6b	43.2	88.6b	79.2b
	3Cl	146.3	102.5	83.5	112.7	129.0a	129.2a	37.5	104.4a	98.4a
		ns	ns	ns	ns	*	*	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 5. Influence of leaf removal and cropping level on the transpiration rate (E) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990 - Experiment II).

Leaf position[z]	Treatment[y]	E ($mmol\ H_2O.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C			5.38b	5.94	5.05	4.12	1.49b		4.40b
	R1			6.31a	6.43	5.36	3.68	2.06a		4.77a
				*[w]	ns	ns	ns	*		*
	Crop. level									
	0Cl	8.00	6.32	5.36	5.82	4.44b	3.00b	2.02a	4.83b	4.13b
	3Cl	7.98	6.91	6.33	6.55	5.97a	4.80a	1.52b	5.59a	5.03a
		ns	ns	ns	ns	***	**	*	***	***
	Interaction			ns	ns	ns	ns	ns		ns
MID	Leaf removal									
	C			5.28b	5.91b	5.34	4.74	2.19b		4.69b
	R1			6.62a	6.89a	5.36	4.47	2.83a		5.23a
				*	**	ns	ns	*		**
	Crop. level									
	0Cl		5.95b	6.54a	5.80b	4.68b	3.83b	2.72	4.67b	4.48b
	3Cl		7.48a	5.36b	7.00a	6.01a	5.38a	2.30	5.71a	5.44a
			***	*	***	**	**	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Leaf removal									
	C			3.72	4.79b	5.34	5.09	1.60		4.11
	R1			4.50	6.00a	5.23	4.65	1.68		4.41
				ns	**	ns	ns	ns		ns
	Crop. level									
	0Cl	7.42	5.04	3.92	4.89b	4.72b	4.16b	1.75	4.43b	3.89b
	3Cl	7.33	5.59	4.31	5.90a	5.85a	5.58a	1.53	5.05a	4.63a
		ns	ns	ns	**	**	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 6. Influence of leaf removal and cropping level on the water use efficiency (WUE) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990 - Experiment II).

Leaf position[z]	Treatment[y]	WUE (mmol CO_2/mol H_2O)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal									
	C			2.44	2.29	2.69	2.56	3.30		2.65
	R1			2.36	2.35	2.67	2.65	2.88		2.58
				ns[w]	ns	ns	ns	ns		ns
	Crop. level									
	0Cl	1.50	2.04	2.43	2.44	2.64	2.50	2.83	2.38	2.57
	3Cl	1.68	1.94	2.37	2.20	2.72	2.70	3.34	2.47	2.67
		ns	ns	ns	ns	ns	ns	ns	ns	ns
	Interaction			ns	ns	ns	**	ns		ns
MID	Leaf removal									
	C			2.55	2.26	2.64	2.68	3.17		2.66
	R1			2.50	2.19	2.68	2.76	3.02		2.63
				ns	ns	ns	ns	ns		ns
	Crop. level									
	0Cl		2.09	2.59	2.25	2.66	2.76	3.02	2.58	2.66
	3Cl		2.09	2.46	2.20	2.66	2.69	3.17	2.56	2.63
			ns	ns	ns	ns	ns	ns	ns	ns
	Interaction			ns	ns	ns	ns	ns		ns
AP	Leaf removal									
	C			2.64	2.32	2.25	2.12	2.77		2.42
	R1			2.49	2.03	2.18	2.20	2.81		2.34
				ns	ns	ns	ns	ns		ns
	Crop. level									
	0Cl	0.94b	1.84	2.45	2.11	2.21	2.04	2.59	2.07b	2.28b
	3Cl	1.28a	1.96	2.68	2.24	2.21	2.28	2.99	2.28a	2.48a
		***	ns	ns	ns	ns	ns	ns	**	*
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (no leaves removed); R1:leaves removed on July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 7. Influence of leaf removal and cropping level on the stomatal conductance (g_s) of BAS, MID, and AP leaves of mature field Seyval vines (CHES 1990 - Experiment III).

Leaf position[z]	Treatment[y]	g_s (mmol $CO_2.m^{-2}.s^{-1}$)				Average	
		July 18 4 wk PFB[x]	Sept. 4 3 wk PV	Sept. 25 H	Oct. 6 10 d PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal						
	C		108.1	113.4	83.9		103.4
	R		107.1	110.1	79.1		100.5
			ns[w]	ns	ns		ns
	Crop. level						
	0	62.2	95.8	103.8	74.0	86.3b	92.8b
	1.5	71.3	109.2	117.7	86.8	98.7a	106.2a
	NT	70.1	117.8	113.7	83.5	99.9a	106.9a
		ns	ns	ns	ns	**	*
	Interaction		ns	ns	ns		ns
MID	Leaf removal						
	C		126.8	126.3	103.0		120.1
	R		121.9	124.2	101.0		117.0
			ns	ns	ns		ns
	Crop. level						
	0	74.7	107.0	111.4b	105.6	101.0b	108.2b
	1.5	75.6	133.8	130.5a	108.5	115.0a	125.7a
	NT	81.6	132.2	133.9	91.9	113.2a	121.8ab
		ns	(**)	*	ns	*	*
	Interaction		**	ns	ns		ns
AP	Leaf removal						
	C		102.6	113.9	117.3		110.7
	R		100.6	117.7	99.4		106.5
			ns	ns	ns		ns
	Crop. level						
	0	51.2b	76.6b	102.9b	112.5	86.3b	95.9b
	1.5	61.8a	112.1a	129.7a	119.6	108.0a	120.5a
	NT	64.6a	116.0a	114.9ab	93.0	99.8ab	109.3ab
		*	*	*	ns	*	*
	Interaction		ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (no leaves removed); R:leaves removed on Aug. 15/90 (veraison)
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.

[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; H:harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 8. Influence of leaf removal and cropping level on the transpiration rate (E) of BAS, MID, and AP leaves of mature field Seyval vines (CHES 1990 - Experiment III).

Leaf position[z]	Treatment[y]	E (mmol $H_2O.m^{-2}.s^{-1}$)				Average	
		July 18 4 wk PFB[x]	Sept. 4 3 wk PV	Sept. 25 H	Oct. 6 10 d PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal						
	C		5.32	3.32	3.44		4.08
	R		5.02	3.06	3.16		3.80
			ns[w]	ns	ns		ns
	Crop. level						
	0	3.42	4.73	2.98	3.07	3.59b	3.64b
	1.5	3.82	5.14	3.34	3.38	3.97a	4.01a
	NT	3.89	5.64	3.27	3.45	4.12a	4.18a
		ns	ns	ns	ns	*	*
	Interaction		ns	ns	ns		ns
MID	Leaf removal						
	C		6.01	3.56	3.96		4.56
	R		5.49	3.35	3.80		4.25
			(*)	ns	ns		ns
	Crop. level						
	0	3.99	5.12	3.15b	4.03	4.08	4.11
	1.5	3.98	5.96	3.54ab	3.89	4.40	4.52
	NT	4.19	6.16	3.67a	3.72	4.50	4.59
		ns	(**)	*	ns	ns	ns
	Interaction		**	ns	ns		ns
AP	Leaf removal						
	C		5.08	3.35	4.33		4.25
	R		4.78	3.22	3.65		3.91
			ns	ns	ns		ns
	Crop. level						
	0	2.88b	3.97b	3.01	4.15	3.50b	3.67
	1.5	3.35a	5.29a	3.56	4.17	4.14a	4.35
	NT	3.44a	5.54a	3.30	3.64	4.04a	4.21
		*	*	ns	ns	*	ns
	Interaction		ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (no leaves removed); R:leaves removed on Aug. 15/90 (veraison)
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.

[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; H:harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 9. Influence of leaf removal and cropping level on the water use efficiency (WUE) of BAS, MID, and AP leaves of mature field Seyval vines (CHES 1990 - Experiment III).

Leaf position[z]	Treatment[y]	WUE (mmol CO_2 /mol H_2O)				Average	
		July 18 4 wk PFB[x]	Sept. 4 3 wk PV	Sept. 25 H	Oct. 6 10 d PH	Over the whole season	Since leaf removal imposition
BAS	Leaf removal						
	C		2.24	2.62b	1.97		2.30
	R		2.22	3.31a	1.99		2.55
			ns[w]	**	ns		ns
	Crop. level						
	0	2.86	2.21	3.35	2.37	2.71	2.67
	1.5	2.74	2.23	2.82	1.87	2.43	2.35
	NT	2.62	2.25	2.72	1.70	2.35	2.27
		ns	ns	ns	ns	ns	ns
	Interaction		ns	ns	ns		ns
MID	Leaf removal						
	C		2.40	3.47	2.33		2.77
	R		2.48	3.75	2.69		3.00
			ns	ns	ns		ns
	Crop. level						
	0	2.98	2.57	3.91a	2.89	3.11	3.15a
	1.5	3.26	2.46	3.35b	2.37	2.87	2.76b
	NT	3.05	2.29	3.57ab	2.27	2.81	2.75b
		ns	ns	*	ns	ns	*
	Interaction		ns	ns	ns		ns
AP	Leaf removal						
	C		2.37	3.63	2.70b		2.92
	R		2.23	3.82	3.02a		3.02
			ns	ns	**		ns
	Crop. level						
	0	2.79	2.08	3.68	2.90	2.86	2.88
	1.5	2.22	2.41	3.73	2.96	2.86	3.04
	NT	2.35	2.40	3.78	2.72	2.85	2.99
		ns	ns	ns	ns	ns	ns
	Interaction		ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (no leaves removed); R:leaves removed on Aug. 15/90 (veraison)
0:0 clusters per vine; 1.5:1.5 clusters per node retained; NT:unthinned. Thinning date: June 27/90.

[x]Time in days (d) or weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison; H:harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

APPENDIX B

Influence of Vine Shading and Cropping Level on Leaf Gas Exchange, Vegetative Growth, Dry Matter Accumulation, and Fruitfulness of Young Potted Seyval Grapevines

Influence of Vine Shading and Cropping Level on Leaf Gas Exchange, Vegetative Growth, Dry Matter Accumulation, and Fruitfulness of Young Potted Seyval Grapevines

Abstract

In 1990 an experiment using one-year-old, own-rooted potted Seyval grapevines was conducted to evaluate the influence of cropping level and vine shading to 24% of full sun on leaf gas exchange and several vegetative and reproductive vine parameters.

The presence of fruits increased leaf net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E) when the measurements across the vegetative season were considered, but had little effect on water use efficiency (WUE). Shading since berry pea size had no significant effect on A at basal (BAS) and middle-shoot (MID) leaf positions, but reduced A at the apical (AP) position when the measurements following shading were analyzed together; g_s and E at BAS leaves were increased by shading, unlike at the MID and AP positions where no overall significant effect was observed. WUE was reduced by shading; this effect was highly significant at the BAS and MID leaf positions when all measurement dates were considered.

Shading since pea size increased the total chlorophyll content on a dry weight basis at veraison and/or at harvest (except for BAS leaves) and reduced the chlorophyll a/b ratio. Chlorophyll content was higher on fruiting than on non-fruiting

vines at the AP leaf position. At BAS and MID leaf positions a significant cropping x shading interaction was observed at harvest; the presence of fruits magnified the shade-induced compensatory increase in leaf chlorophyll.

Cropping level had no significant effect on total dry matter accumulation, but markedly influenced dry matter partitioning. The fruits developed at the expense of shoots, roots, and leaves, while trunk dry weight was not significantly affected. Shading increased the percentage of dry matter in leaves in the early fall and reduced the dry weight of roots and canes when all partitioning dates were considered. Root dry weight and the sum of the dry weight of roots, canes and trunk were negatively correlated with the number of days under shading.

Both fruit development and shading in Year 1 reduced the percentage of fruitful primary shoots and the number of clusters per vine and per primary shoot in the following year; they increased, however, the number of berries per cluster and cluster weight. Yield in Year 2 was reduced by shading in Year 1, but did not significantly differ between vines that bore fruit in Year 1 and non-bearing vines.

The presence of a cluster at a specific node in Year 1 had no significant effect on the fruitfulness of the primary bud developing at that node. In contrast, the position of the bud on the 6-node cane had a highly significant influence on all fruitfulness responses analyzed, except for the number of seeds per berry; fruitfulness generally increased from the base to the apex of the 6-node canes.

Introduction

The negative effects of shading on grape yield and quality have been widely reported since the studies of N. J. Shaulis in the mid 60's (Shaulis et al., 1966). An adequate light microclimate at the base of the shoots is of special relevance, because in this zone are not only the clusters but also the nodes to be retained at pruning (Shaulis, 1982; Smart et al., 1990). Shading of this zone, besides affecting wine quality (see references in Smart et al., 1990) reduces inflorescence initiation, bud burst, fruit set, berry size (Shaulis and Smart, 1974; Smart et al., 1990) and tissue cold hardiness (Shaulis and Smart, 1974; Stergios and Howell, 1977; Howell et al., 1978; Howell and Shaulis, 1980; Kliewer, 1982; Wolpert and Howell, 1985; Howell, 1988).

Reduced light is one of the factors that may prevent the photosynthetic enhancement response to increased sink strength; during an extended period of cloudy weather or immediately thereafter, when the plant is still carbohydrate depleted, there may be no detectable difference in the leaf net CO_2 assimilation rate (A) between fruiting and non-fruiting plants (Flore and Lakso, 1989).

In this study, the effects of shading and cropping on A and related gas exchange parameters were investigated at individual leaf positions on fruiting and non-fruiting potted Seyval grapevines grown under full sun until berry pea size and thereafter shaded to 24% of full sun. Moreover, the influence of shading post- pea size or post- veraison on several vegetative and reproductive vine parameters was evaluated, to complement the information obtained from a parallel leaf removal study with potted Seyval vines, and from a study with mature field Seyval vines where

the light microclimate was modified by differential cropping and leaf removal treatments.

Materials and Methods

Plant Material and Treatments

This experiment, installed in May/1990, was set and conducted in parallel with Experiment II of Chapters I and IV at the Horticultural Research Center (HRC) in East Lansing, Michigan, and used similar one-year-old own-rooted Seyval (Seyve-Villard 5-276) grapevines. Cultural practices were common to both experiments, except that shading was imposed instead of leaf removal; cropping level and shading treatments were applied on the same dates as cropping level and leaf removal in the parallel experiment. The treatments were likewise arranged in a 3x2 factorial set in a randomized block design, using vine fresh weight at planting as the blocking variable. The vines used in this experiment were from the same blocks of those used in the leaf removal experiment, and the control vines were common to both experiments. Shading levels were: C = unshaded (control); S1 = shaded starting at pea size (July 27/90, five weeks after full bloom); and S2 = shaded starting at veraison (August 21/90, eight weeks after full bloom). Shading was maintained until the end of October. Cropping level was either 0Cl (no clusters per vine) or 3Cl (3 clusters per vine) and was imposed on July 4/90, 10 days after full bloom. Treatment combinations are abbreviated as C/0Cl, C/3Cl, S1/0Cl, S1/3Cl, S2/0Cl, and S2/3Cl.

Shading was accomplished by placing the vines in a wooden framed shading

structure built in the same gravel area where the unshaded vines were kept. The cover and walls of this structure were made of a 73% polypropylene black shade cloth from Chicopee Manufacturing Company (Cornelia, GA, USA). This fabric transmitted an average of 24 % of the Photosynthetic Photon Flux (PPF), as measured with Li-Cor LI-1000 quantum sensors. In a previous study, spectral measurements through shade fabrics from the same origin and identical to the one used except for density (92% and 55% in the manufacturer's designation) were made (Long, 1980). None of the fabrics seemed to influence the spectral distribution within the range of wavelengths tested ($\approx$ 380 nm to 1500 nm). Therefore it was assumed that the fabric herein used was likewise neutral.

Data Collection

The timing of data collection and the methodology used were the same described for Experiment II in Chapters I and IV, except for the particularities that follow. The shaded vines were moved to full sun for about 30 minutes prior to gas exchange determinations; indeed, on the first measurement date after shading, a period of 20 to 30 minutes was found to be needed for the leaves to equilibrate at their maximum photosynthetic capacity.

In this experiment no carbohydrate analyses were done, unlike in Experiment II (Chapter I), and fewer fruitfulness parameters were evaluated than in Experiment II (Chapter IV), because the number of flowers was not assessed.

Statistical Analysis

Statistical analyses were performed as mentioned for Experiment II in Chapters I and IV, except as described next.

In this experiment the data on dry matter partitioning were further analyzed by linear regression to test the relationship between the dry weight of the different vine parts and the number of days of foliage shading (0, 65, and 90 days for C, S2, and S1 vines, respectively, counted since shading imposition until the first leaf killing frost in the fall).

In the analyses of fruitfulness on a whole vine basis the factors included were replicate (REP), and the cropping (CROP) and shading (SH) treatments applied to the vine in the season (Year 1) preceding the fruitfulness evaluation. In the fruitfulness evaluations on an individual bud basis, two additional factors were included, to consider the conditions under which each specific node had developed. These factors were BP - the position of the bud on the 6-node cane, and PCL - the presence/absence in Year 1 of a cluster opposite the bud under analysis. PCL was considered nested within CROP. For each fruitfulness response at the individual bud level an initial, overparametrized model was set (see Chapter IV), which included the above factors and the interactions SH*CROP, SH*BP, CROP*BP, SH*CROP*BP, SH*PCL(CROP), and BP*PCL(CROP). Starting at the above model, a backward elimination procedure was followed, orderly deleting from the model the non-significant interactions (Draper and Smith, 1981).

Results and Discussion

Leaf Gas Exchange Parameters

Cropping Level Effects

Cropping level had a highly significant effect on the leaf net CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration rate (E) at every leaf position when all the measurements across the vegetative season were considered. Higher values were found on fruiting (3Cl) than on non-fruiting (0Cl) vines (Tables 1, 2 and 3), as in the parallel experiment where the potted vines were grown under full sunlight throughout the whole season (Experiment II of Chapter I). In both experiments, however, the effects of cropping on water use efficiency (WUE) were minimal, regardless of the leaf position (Table 4); when the leaf positions were analyzed together, WUE was higher on 3Cl than on 0Cl vines at 3.5 weeks post full bloom (Table 5).

Increased A in response to the presence of fruits (and to a decreased source/sink ratio in general), has been reported in grapevines (Loveys and Kriedemann, 1974; Kriedemann et al., 1975; Kriedemann, 1977; Chaves, 1984; Downton et al., 1987) and several fruit crops (Flore and Lakso, 1989), and has been attributed, among other factors, to increased photosynthate demand; this would prevent or minimize a hypothesized end-product inhibition of photosynthesis (Neales and Incoll, 1968). The photosynthetic enhancement may not be observed during or immediately after an extended period of reduced light levels (Flore and Lakso, 1989). However, the shading intensity applied in this experiment was not sufficient to

Table 1. Influence of shading and cropping level on the net CO_2 assimilation rate (A) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990).

Leaf position[z]	Treatment[y]	A (µmol $CO_2.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since shading imposition
BAS	Shading									
	C			13.10	13.16	13.41a	10.66	4.56		10.98
	S1			14.51	13.98	11.13b	9.87	6.81		11.00
				ns[w]	ns	*	ns	(***)		ns
	Crop. level									
	0Cl	11.90	12.75	12.74	13.54	11.48	8.20	5.19	10.81b	10.10b
	3Cl	12.51	13.29	14.42	13.60	13.06	12.33	6.18	12.18a	11.85a
		ns	ns	ns	ns	ns	(**)	(*)	**	***
	Interaction			ns	ns	ns	*	**		ns
MID	Shading									
	C			13.32	13.15b	13.90a	12.55a	6.69		11.92
	S1			15.26	13.86a	10.92b	10.56b	7.27		11.17
				ns	*	**	**	ns		ns
	Crop. level									
	0Cl		12.59	12.78	12.30	11.21b	10.13b	7.33	11.01b	10.64b
	3Cl		15.14[v]	15.16	14.71	13.61a	12.98a	6.64	12.99a	12.48a
			ns	ns	ns	*	**	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Shading									
	C			9.63	10.76	11.93a	10.86	4.50		9.54a
	S1			8.22	10.52	8.13b	7.22	3.82		7.51b
				ns	ns	*	**	ns		***
	Crop. level									
	0Cl	6.97b	9.91	7.99	9.02b	8.41b	6.96b	3.82	7.60b	7.20b
	3Cl	9.14a	11.11	10.34	12.26a	11.65a	11.12a	4.51	10.01a	9.96a
		*	ns	ns	**	*	**	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine

[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison of C vines; BH:before harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in a significant interaction; therefore no mean separation was performed for the main effect.

[v]Almost significant at the 5% level (P=0.0567)

Table 2. Influence of shading and cropping level on the stomatal conductance (g_s) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990).

Leaf position[z]	Treatment[y]	g_s (mmol $CO_2.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since shading imposition
BAS	Shading									
	C			109.4	118.4	107.6	87.4	37.2		92.0b
	S1			135.0	120.3	98.2	96.0	77.4		102.9a
				ns[w]	ns	ns	ns	(***)		*
	Crop. level									
	0Cl	165.7	122.2	106.1	117.4	90.7b	72.3b	50.8	104.9b	86.5b
	3Cl	167.1	137.6	130.5	121.3	115.2a	111.2a	63.8	121.9a	107.8a
		ns	ns	ns	ns	*	**	ns	***	***
	Interaction			ns	ns	ns	ns	***		ns
MID	Shading									
	C			105.6	115.7	115.9a	104.4	57.7		99.8
	S1			124.6	114.8	94.5b	98.1	76.8		99.2
				ns	ns	*	ns	ns		ns
	Crop. level									
	0Cl		117.3b	92.5b	98.3b	92.8b	78.8b	71.9	92.4b	86.6b
	3Cl		149.7a	131.3a	132.2a	117.6a	123.7a	62.6	119.6a	112.5a
			*	*	**	*	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Shading									
	C			70.3	87.0	116.1a	114.5	39.1		85.4
	S1			59.5	89.4	79.6b	103.9	41.7		76.5
				ns	ns	*	ns	ns		ns
	Crop. level									
	0Cl	139.8	88.8	58.5	70.5b	76.2b	82.7b	37.2	81.1b	65.4b
	3Cl	146.5	105.7	74.8	105.9a	119.6a	135.7a	43.6	106.4a	97.0a
		ns	ns	ns	*	**	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison of C vines; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in a significant interaction; therefore no mean separation was performed for the main effect.

Table 3. Influence of shading and cropping level on the transpiration rate (E) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990).

Leaf position[z]	Treatment[y]	E (mmol $H_2O.m^{-2}.s^{-1}$)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since shading imposition
BAS	Shading									
	C			5.38	5.94	5.05	4.12	1.49		4.40b
	S1			6.72	6.58	4.89	4.36	2.86		4.95a
				ns[w]	ns	ns	ns	(***)		**
	Crop. level									
	0Cl	7.98	6.34	5.40	6.17	4.36b	3.52b	2.01	5.18b	4.23b
	3Cl	7.91	6.87	6.32	6.34	5.58a	4.96a	2.33	5.81a	5.08a
		ns	ns	ns	ns	**	**	ns	***	***
	Interaction			ns	ns	ns	ns	**		ns
MID	Shading									
	C			5.28	5.91	4.74	4.74	2.19		4.69
	S1			6.37	6.32	5.36	4.33	2.89		4.77
				ns	ns	ns	ns	ns		ns
	Crop. level									
	0Cl		6.20b	4.97b	5.46b	4.42b	3.74b	2.71	4.60b	4.22b
	3Cl		7.26a	6.32a	6.77a	5.65a	5.33a	2.36	5.62a	5.23a
			*	*	**	**	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns
AP	Shading									
	C			3.72	4.79	5.34a	5.09	1.60		4.11
	S1			3.60	5.18	4.02b	4.48	1.62		3.80
				ns	ns	*	ns	ns		ns
	Crop. level									
	0Cl	7.06	5.06	3.24	4.21b	3.80b	3.91b	1.51	4.21b	3.37b
	3Cl	7.27	5.63	4.13	5.76a	5.56a	5.66a	1.72	5.19a	4.59a
		ns	ns	ns	*	**	***	ns	***	***
	Interaction			ns	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical

[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine

[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison of C vines; BH:before harvest; PH:post harvest

[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in a significant interaction; therefore no mean separation was performed for the main effect.

Table 4. Influence of shading and cropping level on the water use efficiency (WUE) of BAS, MID, and AP leaves of potted Seyval vines (HRC 1990).

Leaf position[z]	Treatment[y]	WUE (mmol CO_2/mol H_2O)							Average	
		July 19 3.5 wk PFB[x]	July 25 4.5 wk PFB	Aug.2 5.5 wk PFB	Aug.9 6.5 wk PFB	Aug.29 1 wk PV	Sep.13 1 wk BH	Sep.26 1 wk PH	Over the whole season	Since shading imposition
BAS	Shading									
	C			2.44	2.29	2.69a	2.56	3.30a		2.65a
	S1			2.19	2.14	2.30b	2.30	2.44b		2.28b
				ns[w]	ns	*	ns	*		***
	Crop. level									
	0Cl	1.49	2.01	2.40	2.27	2.64	2.32	2.64	2.23	2.46
	3Cl	1.59	1.94	2.30	2.16	2.35	2.53	3.09	2.26	2.49
		ns	ns	ns	ns	ns	ns	ns	ns	ns
	Interaction			ns	ns	ns	*	ns		ns
MID	Shading									
	C			2.55	2.26	2.64a	2.68	3.17		2.66a
	S1			2.45	2.21	2.31b	2.49	2.62		2.41b
				ns	ns	*	ns	ns		**
	Crop. level									
	0Cl		2.03	2.61	2.30	2.54	2.72a	2.80	2.48	2.59
	3Cl		2.09	2.42	2.17	2.42	2.45b	2.99	2.42	2.49
			ns	ns	ns	ns	*	ns	ns	ns
	Interaction			ns	ns	ns	ns	ns		ns
AP	Shading									
	C			2.64	2.32	2.25	2.12a	2.77		2.42
	S1			2.40	2.06	2.01	1.60b	2.68		2.34
				ns	ns	ns	***	ns		ns
	Crop. level									
	0Cl	0.99b	1.98	2.59	2.22	2.19	1.76	2.67	2.02	2.27
	3Cl	1.26a	1.98	2.53	2.15	2.07	1.96	2.78	2.08	2.29
		*	ns	ns	ns	ns	ns	ns	ns	ns
	Interaction			*	ns	ns	ns	ns		ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison of C vines; BH:before harvest; PH:post harvest
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

Table 5. Influence of shading, cropping level and leaf position on the net CO_2 assimilation rate (A), stomatal conductance (g_s), transpiration rate (E) and water use efficiency (WUE) of leaves of potted Seyval grapevines at selected vine phenophases (HRC 1990).

Factor	A (μmol $CO_2.m^{-2}.s^{-1}$)			g_s (mmol $CO_2.m^{-2}.s^{-1}$)			E (mmol $H_2O.m^{-2}.s^{-1}$)			WUE (mmol CO_2/mol H_2O)		
	July 19 3.5 wk PFB[z]	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH	July 19 3.5 wk PFB	Aug. 29 1 wk PV	Sep. 13 1 wk BH
Shading (SH)[y]												
C		13.08a	11.35		113.2a	102.1		5.24a	4.65		2.52	2.46
S1		10.06b	9.22		90.8b	99.3		4.55b	4.39		2.31	2.13
		***	(*)		**	ns		*	ns		ns	ns
Crop. level (CROP)[x]												
0Cl	9.44b	10.37b	8.43	152.7	86.5b	77.9b	7.52	4.19b	3.72	1.24b	2.53	2.27
3Cl	10.83a	12.77a	12.14	156.8	117.4a	123.5a	7.59	5.60a	5.32	1.43a	2.21	2.31
	*[w]	***	(***)	ns	***	***	ns	**	(***)	**	ns	ns
SH*CROP		ns	ns		ns	ns		ns	ns		ns	ns
Leaf position (LPOS)[y]												
BAS	12.21a	12.27a	10.26	166.4a	102.9	91.7	7.95a	4.97	4.24	1.54a	2.50a	2.43
MID	—	12.41a	11.55	—	105.2	101.2	—	5.04	4.54	—	2.48a	2.59
AP	8.05b	10.03b	9.04	143.1b	97.9	109.2	7.17b	4.68	4.78	1.13b	2.13b	1.86
	***	**	(***)	***	ns	(***)	***	ns	(***)	***	***	(***)
SH*LPOS		ns	**		ns	*		ns	**		ns	ns
CROP*LPOS	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
SH*CROP*LPOS		ns	**		ns	ns		ns	*		ns	ns

[z]Time in weeks (wk) relative to vine phenophases
PFB:post full bloom; PV:post veraison of C vines; BH:before harvest
[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
[x] 0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[y]BAS:basal; MID:middle shoot; AP:apical

prevent a cropping effect on A, although at BAS leaves (and, to a lesser extent, at MID leaves) this effect was less marked than in Experiment II of Chapter I.

Shading Effects

When the measurements after shading were analyzed together, shading had no significant effect on A at the BAS and MID leaf positions, but had a highly significant negative effect on A at AP leaves (Table 1). Shading increased g_s and E at the BAS leaf position, unlike at the MID and AP leaf positions, where no significant effect was observed on average across measurement dates (Tables 2 and 3). WUE was reduced by shading; this effect was highly significant at the BAS and MID leaf positions when the measurement dates following shading were combined (Table 4).

Reduced light conditions decrease the activity of Rubisco (ribulose-1,5-bisphosphate carboxylase), not only because the production of ribulose bisphosphate depends upon the production of ATP and NADPH, but also due to reduced Rubisco regeneration and to regulatory mechanisms of the enzyme's activity (Robinson, 1986; Seemann, 1989). A significant negative shading effect on A was not observed at any leaf position, though, until the measurement of August 29. At this time A was lower on S1 than on C vines at every leaf position (Table 1), and the same was found for A, g_s, and E when all the leaf positions were analyzed together (Table 5). Interestingly, at the first two measurements following shading (August 2 and August 9, one and two weeks since shading imposition) there was a tendency for higher A at the BAS and MID leaf positions of S1 as compared to C vines, which was

significant for MID leaves on August 9.

Shading x Cropping Level Interaction

One week before harvest, A at the BAS leaf position was influenced by a significant shading x cropping interaction; the same was observed at this leaf position for A, g_s, and E

on the last measurement date, one week after harvest (Tables 1, 2 and 3); a significant interaction was likewise observed at the BAS leaf position at one week before harvest. At one week before harvest, the presence of fruits increased A at BAS leaves of C but not of S1 vines; among C vines, A was about 95% higher on 3Cl than on 0Cl vines, while among S1 vines the difference was only of 15% (data not shown). At this time, A was higher at BAS leaves of C/3Cl than of S1/3Cl vines. On C/3Cl vines, however, A, g_s and E declined sharply from one week before to one week after harvest, while on S1/3Cl vines the decline was slight. At one week after harvest A, g_s, and E at BAS leaves were not significantly different on C/3Cl and C/0Cl vines, but were higher on S1/3Cl than on S1/0Cl vines, and on S1/3Cl than on C/3Cl vines (data not shown). It seems therefore, that at the BAS leaf position of 3Cl vines, shading reduced the enhancement of A in response to cropping, but prevented a dramatic decline in A after harvest. Decreased A following harvest has been attributed to increased source/sink ratio, which could lead to end-product inhibition of photosynthesis (Neales and Incoll, 1968). Moreover, fruit removal was found to increase the concentration of abscisic acid in the leaves (Loveys and Kriedemann, 1974), and this would reduce g_s and A (Loveys and Kriedemann, 1974;

Downton et al., 1988). On C, unlike on S1 vines, fruit removal probably resulted in a marked raise in leaf ABA, which could explain the sharp decrease in g_s and A from the pre- to the post-harvest measurements observed on the former but not on the latter vines. An increase in an ABA precursor might have occurred on S1 vines; however, based on Burden et al. (1971), light would be needed for its conversion into ABA. Higher chlorophyll concentration in the BAS leaves of S1/3Cl relative to C/3Cl vines, as will be discussed further on, may further explain the higher A of the former leaves at the post harvest measurement.

Exposure During and After Leaf Development

Differences in leaf age and in light conditions during leaf development may have accounted for the differences in gas exchange responses to shading and cropping level among leaf positions. The BAS leaves measured on S1 vines were already fully expanded when the vines were transferred to shading conditions. The same is true for the MID leaves on the first two measurements following shading, while those used thereafter had a successively longer period of growth and development under shade. The AP leaves, however, accomplished either most or all of their expansion under shading. The activity of Rubisco was probably more affected by shading at AP than at BAS and MID leaf positions. Moreover, photoinhibition (Powles, 1984) might have occurred on S1 vines due to high radiation levels (PPF above 1000 μmol $m^{-2}s^{-1}$) during the gas exchange evaluations, and the AP leaves were conceivably more sensitive than BAS and MID leaves. The above may explain the fact that at AP but not at BAS and MID leaves, shading reduced A when the measurements after

treatment were combined, and the tendency for a shade-induced decrease in A was observed since the first measurement after shading (Table 1). Even though the BAS leaves were expanded before transfer to shade, they still experienced (though less markedly than MID and AP leaves) changes in leaf chlorophyll and in specific dry weight induced by shading (Table 6). This agrees with the results of Barden (1974) in apple trees.

Leaf Chlorophyll Content

Adaptation to reduced light environments involve several morphological, physiological, and biochemical changes (Berry, 1975; Björkman, 1981; Seemann, 1989; Knapp and Smith, 1990). Shading increased the chlorophyll content per unit of dry weight of AP leaves both at veraison and at harvest, and of MID leaves at veraison (Table 6). In MID leaves, however, the chlorophyll content at harvest was lower on S1 than on C vines, if expressed on a leaf area basis. This reflects a shade-induced reduction in specific leaf weight, which was highly significant at every leaf position, and particularly marked for MID leaves at harvest. Shade-induced changes in leaf chlorophyll probably took place soon after treatment imposition; this may explain the delayed decrease in A following shading, and the higher A at MID leaves of S1 relative to C vines two weeks after treatment. Chlorophyll changes could not prevent, however, the occurrence on August 29 and September 13 of lower A on S1 vines (Table 1). Fruiting vines had higher chlorophyll content than non-fruiting ones at the AP leaf position both at veraison and at harvest and, on a leaf area basis, at the MID position at harvest. The chlorophyll concentration in MID (on a dry weight basis) and

Table 6. Influence of shading and cropping level on the total chlorophyll content, chlorophyll a/b ratio, and specific leaf weight (SLW) of BAS, MID and AP leaves of potted Seyval vines at veraison (Aug. 24) and at harvest (Sept. 19) (HRC 1990).

Leaf position[z]	Treatment[y]	Total chlorophyll (chl a + b) µg/cm²		Total chlorophyll (chl a + b) mg/g dry weight		chlorophyll a/b		SLW (mg/cm²)	
		Veraison[x]	Harvest	Veraison	Harvest	Veraison	Harvest	Veraison	Harvest
BAS	Shading								
	C	43.52	29.10	7.00	4.42	4.17	3.36a	6.22a	6.62a
	S1	48.36	34.77	9.00	6.42	3.90	2.99b	5.24b	5.46b
		ns[w]	(**)	ns	(***)	ns	*	***	***
	Crop. level								
	0Cl	46.10	29.25	8.01	4.82	4.09	3.29	5.87	6.13
	3Cl	45.77	34.62	8.22	6.02	3.98	3.06	5.59	5.95
		ns	(**)	ns	(**)	ns	ns	ns	ns
	Interaction	ns	**	ns	**	ns	ns	ns	ns
MID	Shading								
	C	46.54	35.84a	7.71b	5.63	4.28a	3.68a	6.06a	6.39a
	S1	49.63	28.78b	12.78a	9.11	3.75b	3.00b	3.96b	3.26b
		ns	***	***	(***)	**	***	***	***
	Crop. level								
	0Cl	46.04	30.55b	9.50	6.39	4.02	3.37	5.14	5.03
	3Cl	50.13	34.08a	11.00	8.36	4.01	3.31	4.89	4.62
		ns	*	ns	(**)	ns	ns	ns	ns
	Interaction	ns	ns	ns	*	ns	ns	ns	ns
AP	Shading								
	C	27.71	14.75	6.78b	3.10b	3.59	3.50	4.08a	4.88a
	S1	24.92	15.83	13.01a	5.66a	3.50	2.86	2.41b	2.93b
		ns	ns	***	**	ns	ns[v]	***	***
	Crop. level								
	0Cl	23.13b	13.14b	9.14b	3.26b	3.55	2.97	3.31	4.26a
	3Cl	29.49a	17.43a	10.65a	5.49a	3.53	3.39	3.19	3.54b
		*	*	**	**	ns	ns	ns	***
	Interaction	ns	ns	ns	ns	ns	ns	ns	ns

[z]BAS:basal; MID:middle shoot; AP:apical
[y]C:control (unshaded); S1:shaded since July 27/90 (pea size)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[x]Relatively to unshaded (C) vines
[w]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.
[v]Almost significant at the 5% level (P=0.0517)

BAS leaves at harvest was influenced by a significant cropping x shading interaction. Mean comparison among treatment combinations revealed that the presence of fruits intensified the shading-induced increase in leaf chlorophyll. Indeed, the difference in total chlorophyll content between S1/0Cl and C/0Cl vines was significant at the 5% level for MID leaves but not significant (though also positive) for BAS leaves, while a highly significant positive difference between S1/3Cl and C/3Cl was found at both leaf positions (data not shown). Shading decreased the chlorophyll a/b ratio. This effect was highly significant for MID leaves on both measurement dates, and significant or almost significant ($P = 0.0517$) for BAS and AP leaves, respectively, at harvest. The lower chlorophyll a/b ratio on S1 vines may reflect a proportionally higher contribution of the light-harvesting complex to the total chlorophyll complement of the chloroplast (Björkman, 1981).

Vegetative Growth and Dry Matter Accumulation and Partitioning

In this experiment, as in Experiment II of Chapter I, the fruiting (3Cl) vines had lower number of leaves (nodes), area per leaf and, consequently, total leaf area, than the non-fruiting (0Cl) ones; no significant differences in the overall specific leaf weight were observed (Table 7). The length of shoots and internodes was influenced by a significant shading x cropping level interaction. The comparison of treatment combination means revealed that both on 0Cl and 3Cl vines, shoot and internode length were higher on vines shaded since pea size (S1) than on control (C) vines; on 0Cl vines the means for the three shading levels were clearly separated, while on 3Cl vines no significant differences in shoot and internode length were found between

Table 7. Influence of shading and cropping level on shoot growth parameters, leaf area, and specific leaf weight of potted Seyval grapevines (HRC 1990).

Treatment[z]	Total shoot length/vine (cm)	No. of nodes/ /vine	Internode length (cm)	Diameter of 5th internode (mm)	Total leaf area/vine (cm^2)	Single leaf area (cm^2)	Specific leaf weight (mg/cm^2)
Shading							
C	198.3	52.1	3.8	5.8a	3292.5b	65.8b	6.42a
S1	317.8	56.2	5.6	4.7c	5021.6a	92.8a	4.12c
S2	256.1	56.5	4.4	5.3b	4001.6ab	75.3b	4.97b
	(***)[y]	ns	(***)	***	**	***	***
C vs. shaded				***	**	***	***
S1 vs. S2				**	ns	**	***
Crop. level							
0Cl	314.0	60.4a	5.1	5.9a	4877.3a	85.4a	5.12
3Cl	200.8	49.4b	4.0	4.6b	3518.5b	72.7b	5.17
	(***)	***	(***)	***	***	*	ns
Interaction	*	ns	*	ns	ns	ns	ns

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.
Mean separation within columns using the LSD test at 5%. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed for the main effect.

vines shaded since veraison (S2) and control vines (data not shown). Shoot diameter was highly significantly reduced by fruit development and by shading. Shaded vines had larger total leaf area and area per leaf than the unshaded ones but lower specific leaf weight; the number of leaves (nodes) was not significantly affected by shading (Table 7).

As in Experiment II of Chapter I, cropping level had a significant effect on dry matter allocation but not on total dry weight at the end of the vegetative season (September 30); this is consistent with the results of Eibach and Alleweldt (1985) and Edson (1991). The fact that the total dry matter accumulation was similar in fruiting and non-fruiting potted vines may be viewed as a rough indication of a lack of photosynthetic response to cropping at the whole vine level, in contrast with the enhancement of A by fruiting at individual leaf positions. Similarly, Edson (1991) found that A at individual leaves responded positively to an increased cropping level, but there was no significant correlation between cropping level and net CO_2 assimilation rate of the whole vine; he concluded that the lower A on slightly cropped vines was compensated for by the larger leaf area of these vines.

At the end of the season, the fruits represented 39% of the overall mean dry weight of 3Cl vines. The presence of fruits resulted in a significant decrease of about 70%, 39%, and 37% in the dry weight of canes, roots and leaves, respectively. By contrast, the trunk dry weight was not significantly affected by cropping level (Table 8). At this time, no significant shading effect on the dry weight of the different vine parts was found, but the percentage of dry matter in leaves was higher on shaded than on control vines, and the percentage of matter in canes was higher on S1 than

Table 8. Influence of shading and cropping level in 1990 on the dry weight partitioning of potted Seyval grapevines at the end of the season (September 30/90).

Treatment[z]	Dry weight (g)					Total dry weight (g)	Percent of total dry weight				
	Fruits	Leaves	Canes	Trunk	Roots		Fruits	Leaves	Canes	Trunk	Roots
Shading											
C	31.8	24.6	26.3	13.8	41.8	138.2	21.7	17.8b	19.1b	10.9	30.5
S1	18.2	25.8	28.7	11.1	28.9	112.6	17.9	22.5a	23.9a	9.9	25.7
S2	20.5	24.7	22.1	16.8	33.2	117.4	18.9	20.9ab	18.2b	14.2	27.8
	ns[y]	ns	ns	ns	ns	ns	ns	**	*	ns	ns
C vs. shaded								**	ns		
S1 vs. S2								ns	*		
Crop. level											
0Cl	0b	31.2a	39.6a	14.2	42.6a	127.6	0a	24.4a	30.7a	11.5	33.3a
3Cl	47.0a	18.9b	11.8b	13.6	26.7b	118.0	39.0b	16.4b	10.0b	11.8	22.7b
	***	**	***	ns	*	ns	***	***	***	ns	***
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 9. Influence of shading and cropping level during the 1990 season on the dry weight of canes, trunk and roots of potted Seyval grapevines, on average across partitioning dates in the fall and winter of 1990/91.

Treatment[z]		Dry weight (g)			
		Canes	Trunk	Roots	Total of the three vine parts
Shading:	C	34.5a	13.2ab	42.8a	90.5a
	S1	28.7ab	10.7b	25.9b	65.2b
	S2	26.1b	14.5a	31.0b	71.6b
		*[y]	*	***	***
C vs. shaded		*	ns	***	***
S1 vs. S2		ns	**	ns	ns
Crop. level:	0Cl	44.7a	13.5	40.5a	98.7a
	3Cl	14.8b	12.1	25.9b	52.8b
		***	ns	***	***
Interaction		ns	ns	ns	ns

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl: 3 clusters per vine
[y]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

on S2 vines. When the three partitioning dates were analyzed together, the dry weight of both canes and roots was lower on shaded than on control vines, and trunk dry weight was lower on S1 than on S2 vines (Table 9). Root dry weight and the sum of the dry weight of roots, canes and trunk were negatively correlated with the number of days under shading, when all the partitioned vines were included in the analyses (data not shown).

Fruitfulness of the Primary Buds on Nodes One to Six in Year 2 (1991)

Shading Effects

Vine shading reduced the percentage of fruitful primary shoots and the number of clusters per vine and per primary shoot in the year following treatment (Year 2), as evaluated at the whole vine level (Table 10). This is consistent with previous reports of an inhibitory shading effect on inflorescence formation (May and Antcliff, 1963; May, 1965). This reduction was especially pronounced following shading since pea size (S1) but was still significant when shading was imposed post-veraison (S2). Thus, it can be inferred that inflorescence primordia formation was probably not yet completed as late as veraison (August 21/90). Given the suggestion of a relationship between shoot development and inflorescence ontogeny (Lavee et al., 1967), the reduced vine growth of the potted vines prior to shading in 1990 probably contributed to a delay in the completion of inflorescence primordia formation, as discussed in Chapter IV. On the other hand, no significant shading effect on the number of clusters per fruitful primary shoot was observed, whether at the vine (Table 10) or at the individual bud level (Tables 11 and 12). Hence, shading

Table 10. Influence of 1990 (Year 1) shading and cropping level treatments on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a vine basis.

Treatment[z] in Year 1	% of fruitful 1[ary] shoots[y]	No. clusters				No. berries set at 3 weeks PFB[v]			
		Vine[x]	Selec. 6-node cane[w]	1[ary] shoot[x]	fruitful 1[ary] shoot[x]	1[ary] shoot	fruitful 1[ary] shoot	cluster	basal cluster
Shading									
C	80.9a	17.4a	10.0a	1.58a	2.07	67a	74b	36b	37
S1	38.9c	8.0c	4.5c	0.71c	1.90	43b	105a	55a	61
S2	56.2b	11.9b	6.9b	1.13b	1.91	59a	95ab	52a	54
	***[u]	***	***	***	ns	*	*	*	(*)
C vs. shaded	***	***	***	***		*	*	**	
S1 vs S2	*	*	*	*		*	ns	ns	
Crop. level									
0Cl	66.7a	14.8a	8.3a	1.38a	2.18a	62	91	42b	47
3Cl	50.6b	10.1b	5.9b	0.90b	1.73b	51	90	53a	54
	*	**	*	***	**	ns	ns	*	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	*

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]Relatively to the total of primary shoots evolved from both 6-node canes retained at pruning per vine
[x]Considering the primary shoots evolved from both 6-node canes retained at pruning per vine
[w]Clusters on the primary shoots evolved from the 6-node cane selected for further fruitfulness evaluations
[v]PFB: post full bloom
[u]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 10 (cont'd).

Treatment[z] in Year 1	Yield (g)			Cluster Wt. (g)		No. berries at harvest				Berry weight (g)		No. seeds/ berry
	vine	1[ery] shoot	fruitful 1[ery] shoot	all the clusters included	basal cluster	1[ery] shoot	fruitful 1[ery] shoot	cluster	basal cluster	all the clusters included	basal cluster	
Shading												
C	399.6a	74.2a	82.1	40.4b	43.6b	47a	52	26b	28b	1.48	1.49	2.95
S1	264.2b	46.3b	116.2	61.7a	70.7a	29b	73	39a	44a	1.50	1.50	2.94
S2	351.8ab	67.9a	109.0	59.6a	63.8ab	43a	70	38a	41a	1.48	1.48	2.99
	*[y]	*	ns	*	*	**	ns	*	*	ns	ns	ns
C vs. shaded	*	*		**	*	*		**	*			
S1 vs. S2	ns	*		ns	ns	*		ns	ns			
Crop. level												
0Cl	356.4	67.5	99.0	45.7b	53.1	43	64	29b	34	1.47	1.46	2.93
3Cl	320.7	58.1	105.0	62.2a	65.2	37	66	39a	41	1.51	1.52	3.00
	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
0Cl:0 clusters per vine; 3Cl:3 clusters per vine
[y]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Mean separation within columns using the LSD test at 5%

Table 11. Significance[z] of the effects of 1990 (Year 1) shading (SH), cropping level (CROP), bud position (BP), presence of a cluster at a specific node (PCL), and interactions, on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a bud basis. Mean values for SH, CROP, and BP levels relative to these analyses are presented in Table 12.

Factor or Interaction	No. clusters per 1[ary] shoot	No. set berries at 3 weeks PFB[y]		
		fruitful 1[ary] shoot	cluster	basal cluster
SH	***[x]	ns	**	**
CROP	*	ns	**	ns
BP	***	***	***	***
PCL(CROP)[w]	ns	ns	ns	ns
SH*CROP			***	**
SH*BP				
CROP*BP				
SH*PCL(CROP)				
BP*PCL(CROP)				
SH*CROP*BP				

[z]The level of significance is indicated for the main effects and interactions present in the final model obtained from backwards elimination starting at an overparametrized model that contained all the factors and interactions listed. The main effects were always kept in the sucessive models, regardless of their significance

[y]PFB: post full bloom

[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively.

[w]PCL(CROP): PCL nested within CROP

Table 11 (cont'd).

Factor or Interaction	Yield per fruitful 1^{ary} shoot (g)	Cluster Wt. (g)		No. berries at harvest			Berry Wt. (g)		No. seeds/ berry
		all the clusters included	basal cluster	fruitful 1^{ary} shoot	cluster	basal cluster	all the clusters included	basal cluster	
SH	ns[z]	*	ns	ns	**	**	ns	ns	ns
CROP	ns	***	*	ns	***	ns	*	ns	ns
BP	***	***	***	***	***	***	***	**	ns
PCL(CROP)	ns	ns	ns	ns	ns	ns	ns	ns	ns
SH*CROP					**	**	**		
SH*BP									
CROP*BP									
SH*PCL(CROP)									
BP*PCL(CROP)									
SH*CROP*BP									

[z]ns, *, **, *** Non significant or significant at 5%, 1% or 0.1% level, respectively.

Table 12. Influence of bud position and 1990 (Year 1) shading and cropping level treatments on the fruitfulness and yield components of potted Seyval grapevines in 1991 (Year 2), evaluated on a bud basis.

Factor		No. clusters per 1[ery] shoot	No. set berries at 3 weeks PFB[z]		
			fruitful 1[ery] shoot	cluster	basal cluster
Shading[y]:	C	1.58	71	34	36
	S1	0.70	103	54	59
	S2	1.10	91	46	49
		***[x]	ns	(**)	(**)
C vs. shaded		***			
S1 vs. S2		ns			
Crop. level[w]:	0Cl	1.37	84	38	42
	3Cl	0.89	86	47	48
		*	ns	(**)	ns
Bud position:	1	0.14	28c	22c	25c
	2	0.53	37c	24c	23c
	3	0.59	31c	23c	25c
	4	1.02	68b	36b	36b
	5	2.02	119a	56a	60a
	6	2.08	117a	52a	58a
		***	***	***	***

[z]PFB: post full bloom
[y]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
[x]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Least-squares means for leaf removal were separated at the 5% level. Means for bud position were separated using Duncan's New Multiple Range test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed.
[w]0Cl:0 clusters per vine; 3Cl:3 clusters per vine

Table 12 (cont'd).

Factor		Yield per fruitful 1[ary] shoot (g)	Cluster Wt. (g)		No. berries at harvest			Berry Wt. (g)		No. seeds/ berry
			all the clusters included	basal cluster	fruitful 1[ary] shoot	cluster	basal cluster	all the clusters included	basal cluster	
Shading[z]:	C	79.9	37.3b	42.2	50	24	27	1.41	1.45	2.93
	S1	111.2	58.3a	67.0	71	37	42	1.47	1.47	2.94
	S2	104.2	52.1a	57.9	67	34	37	1.45	1.45	2.94
		ns[y]	*	ns	ns	(**)	(**)	ns	ns	ns
C vs. shaded			**							
S1 vs. S2			ns							
Crop. level[x]:	0Cl	91.0	40.4b	48.2b	58	26	31	1.40	1.41	2.90
	3Cl	98.7	54.0a	58.0a	62	34	36	1.48	1.50	2.98
		ns	***	*	ns	(***)	ns	(*)	ns	ns
Bud position:	1	29.9c	23.5c	27.2c	20c	16c	18c	1.32b	1.32b	2.98
	2	33.8c	21.4c	22.1c	24c	15c	15c	1.27b	1.32b	2.73
	3	28.8c	21.3c	24.0c	20c	15c	17c	1.29b	1.32b	2.72
	4	72.7b	38.5b	42.5b	47b	25b	27b	1.46a	1.50ab	3.05
	5	137.2a	65.4a	71.0a	85a	40a	44a	1.52a	1.51a	2.95
	6	134.8a	60.1a	72.3a	86a	38a	45a	1.49a	1.50ab	3.03
		***	***	***	***	***	***	***	***	ns

[z]C:control (unshaded); S1:shaded since July 27/90 (pea size); S2:shaded since Aug.21/90 (veraison)
[y]ns, *, **, *** Non significant or significant at the 5%, 1% or 0.1% level, respectively. Least-squares means for leaf removal were separated at the 5% level. Means for bud position were separated using Duncan's New Multiple Range test at the 5% level. Brackets indicate that the factor is involved in significant interactions; therefore no mean separation was performed.
[x]0Cl:0 clusters per vine; 3Cl:3 clusters per vine

might have inhibited the formation of the first but not of subsequent inflorescences within the bud. In Year 2, the number of berries per primary shoot at three weeks post full bloom was higher on control (C) than on shaded vines, when evaluated on a vine basis. This resulted from a higher number of clusters per primary shoot on C vines, since these vines had a lower number of berries per cluster than the shaded ones (Table 10). Due to a higher number of clusters (and conceivably of flowers) on C than on shaded vines, the competition among setting berries was probably stronger and fruit set more affected on the former vines. Shading reduced the yield per vine and per primary shoot in Year 2, while the berry weight and the number of seeds per berry were not significantly influenced (Table 10). The higher cluster weight of shaded as compared to C vines was not sufficient to compensate for the shade-induced reduction in cluster number.

Cropping Level Effects

Fruit development in Year 1 reduced the percentage of fruitful primary shoots and the number of clusters in Year 2, whether expressed per vine, per primary shoot, or per fruitful primary shoot (Table 10). This is consistent with previous reports of a negative cropping effect on flower-bud differentiation for next season's crop in grapevines (Antcliff and Webster, 1955) and other woody plants (Jackson and Sweet, 1972). The vines that bore fruits in Year 1 (3Cl) had, on the other hand, a higher number of berries per cluster in Year 2 than non-bearing (0Cl) vines (Table 10). As discussed for Experiment II of Chapter IV, fruit set in Year 2 was probably lower on 0Cl than on 3Cl vines due to a stronger nutritional competition among developing

berries or to a less favorable hormone balance for fruit set on the former vines. As in Experiment II of Chapter IV, the higher number of berries per cluster on 3Cl than on 0Cl vines resulted in heavier clusters on the former vines, which compensated for their lower number of clusters; hence, no significant differences in yield between 3Cl and 0Cl vines were found in Year 2 (Table 10).

Bud Position (BP) Effects

The position of the bud on the 6-node cane had a highly significant effect on all the fruitfulness responses evaluated except the number of seeds per berry (Tables 11 and 12). An increased fruitfulness from the base to the apex of the 6-node cane was clearly evidenced, as in the experiments of Chapter IV and in previous studies (Partridge, 1921; Buttrose, 1974; Champagnol, 1984; Huglin, 1986; Howell et al., 1993).

Presence of a Cluster at an Individual Node (PCL)

As in the experiments described in Chapter IV, the presence of a cluster at a specific node had no significant influence on the Year 2 fruitfulness parameters of the primary bud developing on that node (Table 11). This suggests that the cropping effect on the fruitfulness of a given bud may derive mostly from the fruiting condition (bearer or not) of the shoot in Year 1, rather than from the presence or absence of a cluster at the particular node where the bud developed.

Conclusions

Vine shading to 24% of full sunlight after pea size had no significant effect on the net CO_2 assimilation rate (A) at BAS and MID leaf positions when all the measurements after shading imposition were considered, but reduced A at the AP leaf position. Differences in exposure during and after leaf development are probable explanations for the above results. The shade-induced increase in leaf chlorophyll content and decrease in chlorophyll a/b ratio, conceivably attenuated an inhibitory shading effect on A. Shading did not preclude a photosynthetic enhancement in response to the presence of fruits, although it appeared to decrease the intensity of this effect at the BAS and, to a lesser extent, at the MID leaf positions. Alternatively, shading prevented a dramatic decline in A at BAS leaves after harvest. This was probably due to delayed senescence of the BAS leaves on shaded fruiting vines, to the lack of a sharp post-harvest increase in ABA in these leaves, or both.

Shading increased the percentage of dry matter in leaves in the early fall, and reduced the dry weight of roots and canes when all the partitioning dates were considered. Whether applied post- pea size or post-veraison, shading reduced the percentage of fruitful primary shoots and the number of clusters per vine and per primary shoot in the following year, suggesting that inflorescence primordia formation was not completed as late as veraison. This resulted in lower Year 2 yield on vines shaded in the preceding season as compared to control vines, despite a larger number of berries per cluster and heavier clusters on the former vines.

As in Experiment II of Chapter I, cropping had a significant effect on dry

matter allocation unlike on total dry weight per vine. Shoots, roots, and leaves were particularly affected by fruiting. Fruit development in Year 1 inhibited flower-bud differentiation for the following season's crop. This inhibition was not significantly related to the presence of a cluster developing at the same node of a bud. Yield in Year 2 was similar on vines that bore fruit in Year 1 and on non-bearing vines, though, due to a compensatory increase in cluster weight on the former vines, resulting from a higher number of berries per cluster. Bud position on the 6-node cane had a highly significant effect on all the fruitfulness responses except for the number of seeds per berry. The observed increase in bud fruitfulness along the 6-node cane is consistent with the widely reported raise in fruitfulness from the basal to the middle region of grapevine canes.

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