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EFFECT OF SHOOT NUMBER AND CROP LOAD ON DRY MATTER PARTITIONING AND CANOPY MORPHOLOGY OF POTTED CHAMBOURCIN GRAPEVINES

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ABSTRACT

EFFECT OF SHOOT NUMBER AND CROP LOAD ON DRY MATTER PARTITIONING AND CANOPY MORPHOLOGY OF POTTED CHAMBOURCIN GRAPEVINES

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The effects of shoot number and crop load on canopy morphology, shoot fruitfulness and dry matter production were studied in potted Chambourcin grapevines. Increasing shoot number per vine increased early-season leaf area but had no effect on dry matter production until veraison. Between veraison and harvest, continued carbohydrate sink activity caused vines with greater shoot numbers to produce about 20% more dry matter than single-shoot vines. Greater shoot numbers caused profound alterations in canopy morphology. Three- and six- shoot vines had shorter shoots, smaller leaves and lower specific shoot and leaf weight than did one-shoot vines, but greater shoot length and leaf area per vine. Flower cluster size and flower number per cluster were also reduced with increasing shoot numbers leading to a reduction in shoot fruitfulness but an increase in flower number per vine.

Growing vines with one- or four- shoots and no clusters (1/0 and 4/0), one-shoot and one-cluster (1/1), or four- shoots and one- (4/1), two- (4/2), three- (4/3) or four- (4/4) clusters, demonstrated that shoot number had a greater influence on canopy morphology than crop load. Four-shoot vines had shorter shoots and smaller leaves than did one-shoot vines, but crop load had little effect on most canopy parameters. Dry matter production was linearly related to berry number at harvest even though differences among treatments were small. Dry matter used in fruit production was derived from preferential partitioning of carbon to fruit at the expense of vegetative tissues, and at high crop loads, an increase in dry matter production relative to low crop load vines, particularly between veraison and harvest.

Increasing shoot number and early-season leaf area does not lead to greater early-season dry matter production. Increasing shoot number does alter canopy morphology and allow the vine to set more fruit. This increases the possibilities to balance the crop load with the vine's dry matter production capacity. As carbohydrate sink strength increases to a point, dry matter production per vine increases, maximizing the potential for production of both dry matter and fruit. Balancing carbon partitioning to fruit and vegetative tissues maximizes sustained fruit production.

DEDICATION

Dedicated to good friends, good times and good wines

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LIST OF SYMBOLS, ABBREVIATIONS OR NOMENCLATURE

A	CO_2 assimilation
°Brix	Sugar content
Ci	Internal CO_2 concentration
GDD	Growing degree days
g_s	Leaf conductance
g_m	Mesophyll conductance
MP	Minimally pruned vines
Pi	Inorganic phosphate
Pn	Net photosynthesis
PPFD	Photosynthetic photon flux density
RH	Relative humidity
SLW	Specific leaf weights
SPS	Sucrose-phosphate synthase
SSW	Specific shoot weigh
T	Leaf temperature

LITERATURE REVIEW

Grapevines are cultivated on six of the seven continents and in nearly every country on the face of the earth. They have been grown for the production of fresh fruit, raisins, grape seed oil and wine from before recorded history. Many of the cultivars used for grape and wine production today are traditional varieties which have been propagated for centuries by vegetative cuttings. While the varieties are ancient, the methods employed in growing them have changed rapidly during this century. Mullins (35) states that: "In viticulture, the main response to biological constraints or economic change has been to manipulate the existing traditional cultivars by applying progressively higher inputs of husbandry. Included are innovations in standard husbandry (rootstocks, pruning, training), in chemical-based husbandry (fertilizers, pesticides, herbicides, growth regulators), in mechanization (mechanical harvesting and pruning) and in postharvest technology and processing (winemaking)". The present economic climate has caused many growers to attempt to increase profitability by mechanizing vineyard operations. Mechanized harvesting has been used now for decades, but mechanical pruning has only recently met with success in some areas (7,34,37). The primary advantage of mechanization is reduced production costs (34). However, researchers have reported yield increases of as much as 200% in minimally pruned vines as compared to controls with no negative effects on fruit composition (7,8,10,37). It is thought that rapid canopy development resulting from the growth of many shoots found on hedged or minimally pruned vines leads to greater, season-long carbohydrate assimilation by the vine, effectively increasing the vine's "capacity" over a normally pruned vine (7,10,28,44). Capacity is defined by Winkler (52) as "the quantity of action with respect to total growth. The term refers to a vine's ability for total production rather than to rate of activity". It is known that the total annual carbohydrate assimilation by a plant is affected by the total exposed leaf surface (14,46,47) and the length of time that leaf surface is exposed to the sun (28,29,49,50). Of course, many other factors influence total carbon assimilation such as light intensity (3,14,28,29,35), water availability (14,35), nutrition (35), leaf age (27,36) and carbohydrate source/sink relations (6,14,17,49,50).

In the case of grapevines, studies with minimally pruned (MP) vs. spur pruned (spur) vines have shown clear, season-long leaf area differences (7,44). Other researchers have shown, however, that the leaf area of spur vines equaled that of MP vines by mid-season and surpassed it by veraison (10). It is not clear if the greater leaf area of the MP vines for several weeks early in the season produced a carbon assimilation advantage over the spur vines. Nonetheless, MP vines produced fruit yields of approximately twice that of controls. However, when canopy dry weights (both vegetative and reproductive tissues) were compared, no differences were found among treatments (10). Similar results were demonstrated when crop load was varied in potted vines (11,12,13). Thus, the larger crop produced by the MP vines may have resulted from greater partitioning of carbohydrates from other organs rather than greater total carbon assimilation relative to spur vines.

CANOPY DEVELOPMENT

As stated above, the rapid canopy deployment characteristic of MP vines is thought to increase annual carbon assimilation thereby "increasing" vine capacity (7,28,44). Starch reserves are mobilized in the spring to support the spring growth flush (21,35,38,53,54,55). During this period of leaf development, assimilated carbon is utilized for building leaf and later, shoot tissues (18,54,55). The basal leaves become net carbon exporters only after the fifth leaf has emerged from the shoot (18,54). By the time the seventh leaf emerges, vines are nearing bloom and the reserves are spent. At the end of the growth flush (around bloom), the new leaves support growth (54). Because leaves become net carbohydrate exporters so late in the growth flush, it is not clear what advantage there is in having large amounts of leaf area during the growth flush. It is possible that greater shoot numbers (i.e. vegetative sink strength) more efficiently utilize stored carbohydrates during the growth flush as compared to severely pruned vines thereby taking full advantage of a vine's ability to generate a canopy. This, however, has not been demonstrated.

Empirical data suggest that vines compensate for a small number of shoots relative to the size of the reserve pool by causing the few shoots to grow faster. Koblet and Perret (25) reported that Muller-Thurgau vines with a greater volume of perennial wood had more fruitful shoots and higher yields than did control vines. The increase in shoot fruitfulness was due to a slight increase in berry weight and berries per cluster which in turn lead to significant yield increases with no negative effect on fruit composition. These findings are supported by Howell et al. (20) where the volume of perennial wood varied greatly with vine training system. These studies maintained a similar vegetative sink strength (or shoot number) while varying the size of the carbohydrate source during the spring growth flush. Although leaf area was not determined, the increases in berry and cluster weight and the slight increase in berry number per cluster at similar fruit soluble solids suggests that more leaf area was available both at bloom and at harvest on vines with greater carbohydrate reserves. Greater leaf area at bloom has been shown to improve fruit set (4) and it may have been responsible for the higher berry number per cluster reported (20). The production of greater fruit yields with no effect on fruit composition suggests that there may have been additional leaf area available from veraison through harvest to support fruit maturation on the higher yielding vines. In support of these hypotheses, Koblet et al. (26) demonstrated a positive relationship between trunk volume and total leaf area, lateral leaf area, yield per vine, shoot fruitfulness, cluster weight, berries per cluster, must soluble solids and must pH. By increasing source size (trunk volume) at constant sink strength (shoot number) during the growth flush, greater leaf area was made available for the developing clusters. The precise mechanism by which this occurred is not clear, but it has been suggested that individual shoots grow at a faster rate (and apparently generate more leaf area per cluster) when shoot numbers are reduced relative to source size (40,41,42).

By contrast, other researchers have varied vegetative sink strength while maintaining a relatively constant source size during the growth flush (7,8,10,33,43,44). This approach demonstrated that as vegetative sink (shoot and leaf) number increased, shoot fruitfulness and fruit soluble solids decreased (7,8,33,44). The decrease in shoot fruitfulness was due to fewer berries per cluster, reduced berry weight and fewer clusters per node (7,33). These data indicate that leaf area was limiting at bloom (evident in the reduced fruit set) and again from veraison through harvest as fruit matured as shown by the reduction in fruit soluble solids with increasing bud numbers and crop load. When leaf area was determined on lightly pruned vines, it was found that they had greater leaf area overall than did controls (44). However, individual shoots were shorter with smaller leaves and there was an inverse relationship between the number of buds retained at pruning and the number of buds producing shoots. Clingeleffer suggests that this is a means by which vines "self regulate" the amount of crop produced (7). It is known that as crop load increases, shoot length decreases (11,12). It appears that the presence of many shoots also causes a reduction in shoot length relative to severely pruned vines (7,8,10). Shoot length may be less in MP vines relative to severely pruned controls even before bloom suggesting that the large numbers of shoots are competing for limited resources (e.g. carbohydrate reserves, water, nutrients and root-produced growth regulators). The relative effects of crop load and competition among shoots on the length of individual shoots over the course of the growing season are difficult to separate. Thus, the relative influence that increasing crop load or increasing shoot numbers have on shoot length, either separately or combined, remains unclear.

FRUITFULNESS

The fruitfulness of a shoot might be influenced by the carbohydrate source/sink relationships during shoot development as discussed above. This apparently occurs even though buds of similar developmental morphology were used. It seems important to make a distinction between "bud" and "shoot" fruitfulness. Bud fruitfulness refers to the development of flower cluster primordia within a dormant bud (35,40,51). Shoot fruitfulness, by contrast, is the actual quantity of fruit produced on a shoot. It integrates environmental and vine growth variables in the current growing season while bud fruitfulness is a reflection of environmental and vine growth variables from the previous growing season. It has been shown that both bud (32,40,51) and shoot (7,33,39,44) fruitfulness can be influenced by carbohydrate availability. Given the strong fruit sinks on MP vines, carbohydrates may be limited for bud development since the developing bud is a relatively weak sink (32,49,50). However, it has also been shown that increasing the number of buds on a vine can cause a reduction in shoot fruitfulness (7,8,10,33,44). Thus, it is not clear if the reduction in fruitfulness observed in MP vines is due to poorer bud development relative to controls, increased carbohydrate competition during fruit set, or some combination of the two.

CARBOHYDRATE RELATIONS

The greater crop carried by MP vines represents a strong carbohydrate sink (49,50). The strength of a sink is defined as the sink size multiplied by its activity (29,48,49,50). It follows that doubling the size of the fruiting sink would double its strength if there is no change in metabolic activity. Chandler and Heinecke (6) demonstrated as early as 1926 that a strong fruiting sink in apple caused trees to produce a greater quantity of dry matter over a growing season as compared to a lightly cropped tree. Leaf photosynthesis can respond to increased sink demand by increasing the rate of CO_2 assimilation (4,14,17,29,49,50). This is known as photosynthetic compensation and is an important mechanism by which a plant maintains growth after losing foliage to disease or insects, or responds to increased carbohydrate demand such as occurs with high crop loads (4,30,31). As the leaf area ratio (LAR) is reduced, or sink strength increased, Pn per unit leaf area increases up to a maximum which is delimited by the rate of Rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase) regeneration (4,50). Photosynthetic compensation may reduce the expected differences in dry matter production caused by varying canopy size. For example, Candolfi-Vasconcelos (4) demonstrated that removing leaves from grapevines (effectively reducing the LAR) caused an increase in the rate of CO_2 assimilation per unit leaf area in the remaining leaves. It has been suggested that this phenomenon may be due to an increase in the quantity of water and root-supplied compounds available to the remaining leaves via the transpiration stream since the size of the root system remains unchanged (14). Severely pruned vines have a reduced LAR relative to MP vines for the early part of the growing season (10). This might lead to an increase in CO_2 assimilation per unit leaf area as a result of photosynthetic compensation. However, field vines did not show an increase in Pn per unit leaf area of spur pruned vines early in the season as suggested. Rather, MP vines had higher average rates of Pn per unit leaf area (10). Spur pruned vines in that study never had higher average rates of Pn than MP vines. The results are confounded though due to the fact that MP vines also had a much stronger fruiting sink than did controls.

More recently, attention has focused on the control of photosynthetic carbon fixation since it is the first step in dry matter production in higher plants. What has emerged is the hypothesis that photosynthetic carbon fixation is controlled by end-product inhibition of two important enzymes: fructose 1,6 phosphatase and sucrose-phosphate synthase (SPS) (16,47). As cytosolic sucrose levels rise due to low rates of sucrose utilization at sinks, sucrose production slows and the levels of hexose phosphates increase (45,46,47). This causes an increase in fructose 2,6 bisphosphate (47). As fructose 2,6 bisphosphate increases, synthesis of fructose 1,6 bisphosphate from triose phosphates is inhibited. Fructose 1,6 bisphosphate is the first six-carbon sugar formed from photosynthetically fixed carbon so it is an efficient control point from which carbon can be partitioned into sugar or starch production. When synthesis of hexose phosphates is inhibited, triose-phosphate concentrations in the cytosol increase. Triose-phosphate movement into the cytosol from the chloroplast is dependent upon a strict counter-exchange with inorganic phosphate (Pi) catalyzed by the phosphate translocator (47). When hexose synthesis slows, Pi remains bound to triose-phosphates and is unavailable for exchange with the chloroplast. Under this condition, the triose-phosphates accumulating in the chloroplast are diverted to starch production (16,47).

The control of sucrose production by SPS is also critical to cytosolic carbon partitioning (19). High rates of sucrose synthesis reduce the hexose pool and slow starch accumulation. Control of SPS is complex. It is influenced by light, increasing hexose-phosphates and decreasing inorganic phosphate (for a recent review, see Huber and Huber (19)). SPS is the final enzyme in the sucrose synthesis pathway and is therefore an important control point for the partitioning of carbon to sucrose for export to carbohydrate sinks.

If conditions exist in the whole plant which lead to continuing high levels of cytosolic hexose and starch in the chloroplast (such as a high ratio of carbohydrate sources to carbohydrate sinks), there may be a reduction in the rate of photosynthetically fixed carbon by Rubisco (15,16,31,46). By contrast, if sucrose utilization rates are high, the rate of sucrose synthesis rises to meet the demand. The rates of Rubisco regeneration and possibly sucrose transport are thought to limit the absolute rate of photosynthesis and plant growth. However, the ultimate controls regulating expression of the genes coding for photosynthetic proteins have yet to be fully deduced (for a recent review see Stitt and Quick (47)). Inhibition of sucrose synthesis due to low utilization rates by carbohydrate sinks is a condition where photosynthetic carbohydrate production is "sink limited" (14,49,50). When sink demand is greater than the available sugars supplied via photosynthesis, dry matter production is "source limited" (14,31,49,50). *Prunus cerasus* trees which were partially defoliated increased net CO_2 assimilation (A) and decreased leaf starch concentration within 24 hours (30,31). Exposure to continuous light caused a decrease in A within 24 hours. Chandler and Heinecke (6) and Edson (11) demonstrated higher rates of dry matter production per plant or per unit leaf area respectively when sink strength increased relative to source size. These facts lead one to the deduction that by increasing the crop on MP vines, it is possible to cause higher rates of Pn in leaves due to the greater sink demand represented by the developing fruits.

Source/sink relationships are complex and change as the growing season progresses (4,14,21,49,50). During the spring growth flush, shoot tips and expanding leaves are the primary carbohydrate sink and starch reserves are the primary source (18,53,54,55). By bloom, starch reserves are depleted and fully developed leaves become the primary carbohydrate source (18,54). While shoot tips and leaves are strong sinks during the growth flush, flower clusters become relatively strong sinks during bloom (1,2,22). After anthesis, fruit becomes an active sink as berries grow (11,13,14,35,49,50). Vegetative sinks are active between anthesis and veraison as well. During fruit ripening, berries are a very active sink but this is also a very important period for building the reserves which will support growth the following spring (55). The actual strength of the fruit sink, as mentioned above, is dependent on the number of berries present. Several researchers have determined that a minimum of 10 cm^2 of exposed leaf area are required to mature one gram of fruit (23,24,27,52). This is the relationship which must exist at harvest. If the leaf area per gram of fruit drops below this value because of overcropping or loss of leaf area to biotic or abiotic factors, insufficient carbohydrates are produced to either mature fruit for commercial use or rebuild reserves. In this case, both the current season's crop and the subsequent season's vine capacity will suffer. Between harvest and leaf fall, root tissues are the most active carbohydrate sink (35,52) so a period of active photosynthesis between harvest and leaf fall is beneficial to the building of starch reserves and vine capacity for the following season.

The timing of sink activity in grapevines and the effects of varying the relative strength of sinks have been demonstrated in several studies (11,35,52). When potted grapevines were grown with varying crop loads, the total quantity of dry matter produced by vines was not different among treatments ranging from one to six clusters (11). However, the partitioning of carbohydrate was altered so that less was allocated to vegetative sinks and more was partitioned to fruit. In general, there is an inverse relationship between crop load and leaf size (11), leaf area and shoot length (11,12) resulting from preferential partitioning of carbohydrate to fruit. Given these data, it is apparent that some of the carbohydrates used to produce crop in MP vines is derived from greater allocation of carbohydrate to fruit at the expense of vegetative organs. The higher crop loads of MP vines may cause higher rates of photosynthesis and therefore dry matter production because of the strength of the fruiting sink. High sink activity has been shown to increase the rate of A per unit leaf area (11,12,14,17,30,31), so it is possible that the greater sink activity present on MP vines is actually in closer "balance" with the vine's capacity, thereby causing the leaves to be more efficient at carbohydrate production. In summary, the higher productivity of MP vines likely results from the interplay of several factors rather than being caused solely by higher photosynthetic rates.

MINIMALLY PRUNED VINES

Minimally pruned vines have produced large crops in both warm (7,8) and cool (37) climates. Results are in conflict, however, regarding the estimate of whole-canopy photosynthesis over the course of the growing season (7,10). It is not clear if MP vines actually assimilate more carbon over the growing season or if they even need to produce more dry matter in order to produce larger crops. Large morphological changes occur in the vegetative structures of MP vines compared to spur pruned vines (7,8,10,44) including shorter shoots, smaller leaves and a reduction in shoot fruitfulness. It has also been shown that MP vines produce a smaller quantity of lignified, one-year-old wood than a spur pruned vine at a similar vine capacity (7,10). Altered shoot morphology has been observed in MP vines even though the shoot fruitfulness is reduced (7), indicating that factors other than fruitfulness are involved. Thus, the relative influences of crop load and vine "self regulation" are not clear regarding their effects on bud and shoot fruitfulness, shoot length and leaf size. Similarly, the relative influences of filling the canopy early and increasing the strength of the reproductive sink(s) on whole-season carbohydrate assimilation remain to be resolved. Finally, the amount of carbohydrate either selectively partitioned to fruit during normal growth, or remobilized from other vine organs for fruit maturation with increasing crop load are not known.

To summarize, a number of morphological and physiological changes accompany light pruning of grapevines as compared to severely pruned controls. The relative strengths of the greater numbers of vegetative and fruiting sinks in MP vines and their influence on vine physiology and morphology are not known. The purpose of this research was to broaden our understanding of these factors.

There are several working hypotheses to be tested: (1) greater shoot numbers present during the spring growth flush more completely utilize stored reserves thereby allowing a vine to maximize its capacity for dry matter production; (2) competition among shoots for carbohydrates, water, nutrients and growth regulators during both the spring growth flush and the remainder of the growing season has a large effect on shoot, leaf and cluster morphology; (3) there is a positive relationship between shoot number, early-season leaf area and whole vine CO_2 assimilation/seasonal dry matter production; (4) the source of carbohydrates used for the production of fruit as crop load increases is due largely to a preferential partitioning to fruit at the expense of vegetative organs; and (5) the stronger fruiting sink on MP vines causes more dry matter assimilation per unit exposed leaf area.

Four chapters describe the experiments conducted to test the above hypotheses. The first chapter describes a whole plant photosynthesis chamber which was developed to measure the rate of CO_2 exchange of whole grapevines when grown with varying numbers of vegetative and reproductive sinks. The second chapter focuses on the rate of canopy development, canopy morphology and whole vine carbon exchange when increasing numbers of shoots are retained. The third chapter examines the rate of starch utilization during the growth flush, dry matter partitioning during the growing season and the rate of dry matter production during the growing season when vines are allowed to develop leaf area more rapidly in the spring. This experiment is designed to test the hypothesis that by simply having more leaf area, vines will accumulate more dry matter. The fourth chapter is an experiment in which both leaf area and fruit-sink strength are varied to determine (a) the contribution of greater leaf area; and (b) the contribution of greater sink strength, in affecting seasonal dry matter production. This experiment is also designed to determine the source of carbohydrate used to produce fruit as crop load increases.

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I. AN INEXPENSIVE, WHOLE PLANT, OPEN GAS EXCHANGE SYSTEM FOR THE MEASUREMENT OF Pn IN POTTED WOODY PLANTS

ABSTRACT

The measurement of whole plant CO_2 exchange integrates leaf to leaf variability which arises from sources such as angle of incident radiation, source/sink relationships, age and biotic or abiotic factors, and respiration of above ground vegetative and reproductive sinks into the final determination of whole plant CO_2 assimilation. While estimates of whole plant CO_2 uptake based on single leaf determinations have been used, they do not accurately reflect actual whole plant assimilation. Chambers were constructed to measure gas exchange of entire potted grapevines. The design and construction are simple, inexpensive and easy to use, allowing for the measurement of many plants in a relatively short period of time. This enables the researcher to make replicated comparisons of the whole plant CO_2 assimilation of various treatments throughout the growing season. While CO_2 measurement was the focus of this project, it is also possible to measure whole plant transpiration with this system.

INTRODUCTION

Measurement of leaf gas exchange is an important technique used to estimate photosynthesis. However, individual leaf photosynthetic determinations have limitations when used to estimate whole plant CO_2 exchange. Leaf Pn can be highly variable due to differences in leaf age (Poni et al., 1994a), chlorophyll content (Candolfi-Vasconcellos and Koblet, 1991; Flore and Lakso, 1989; Poni et al. 1994b), angle of incident radiation (Flore and Lakso, 1989), leaf shading (Flore, 1994) leaf age (Poni et al., 1994a), respiration of leaves, perennial structures and fruit (Corelli-Grappadelli and Manganini, 1993) or due to biotic or abiotic stress. In addition, variability may result from differences within and between plants due to crop load, the proximity of carbohydrate sinks and other source/sink relationships (Edson, 1991; Flore, 1994; Gucci et al., 1991). Consequently, individual leaf measurements indicate the relative carbon uptake per unit leaf area, but they are problematic when used to extrapolate whole plant assimilation.

An accurate assessment of the total, net carbon uptake of whole plants is essential if production per unit land area is to be maximized. One approach is to place the entire plant in a whole plant gas exchange system. This integrates all factors which influence Pn as well as respiration of the various plant parts (Corelli-Grappadelli, 1993; Katerji et al., 1994). Heinecke and Childers (1937) first devised a system for a whole apple tree in 1935. Since then, modern materials and portable gas analysis equipment have allowed for construction of chambers which are easier to use (Long and Hallgren, 1985). The expense, power requirements and the necessity for cooling have been limitations of these systems. Recently, the performance of polyethylene chambers used continuously in the field on apple trees (Corelli-Grappadelli, 1993) and grapevines (Katerji et al., 1994) was reported. These chambers have the advantage of being inexpensive, easy to build, and they do not require cooling because they do not trap significant quantities of infra-red radiation, and the high flow rates used insure rapid exchange of air within the chamber. Additionally, polyethylene blocks very little of the incident radiation in the photosynthetically active range aloowing full sun to provide saturating light conditions. The authors were able to monitor whole plant photosynthesis for extended periods. The chambers described here are not easily moved from plant to plant so the number of treatments or replicates which could be monitored was limited, but the results suggest the utility of this approach.

The goal of this project was to design, build and test an open, gas exchange system for whole, potted plants. I wanted the following attributes: (1) low cost; (2) easily constructed from off-the-shelf items; (3) low volume relative to plant size so high flow rates could be used; (4) no need for cooling; (5) rapid equilibration for higher throughput of plant materials; and (6) easily assembled and disassembled making it somewhat portable. I also wanted chamber conditions to be near ambient so leaf temperature and gas environment would not affect photosynthetic processes. To maximize the number of plants which could be measured in a given interval, two chambers were employed: one in which a plant could equilibrate while the other was being measured.

Work by other researchers (Corelli-Grappadelli, 1993; Alan Lakso, personal communication) suggested that the easiest and least expensive approach to achieve these goals was to construct open system chambers that were essentially "balloons" made of Mylar. Such chambers operate under a slight positive pressure, thus no other means of support is generally necessary and any small leaks in the system flow out of the chamber so there is no affect on ΔCO_2 readings. A benefit of an open system is that small chamber leaks are acceptable.

MATERIALS AND METHODS

Chamber Construction

Building materials available at a local hardware store, with the exception of the Mylar™ film were used in system construction. The plant chambers were constructed around a wood base (Figure. 1) 43.0 cm in length and 39.5 cm in width. This was cut in an obovate shape from 1.6 cm thick plywood. Holes were cut to accommodate the plant stem (in this case a grapevine) [3.8 cm dia.] and the air inlet pipe [5.7 cm dia.]. The base was then cut in half through the trunk opening so it could be moved on and off of vines (Figure 1b). To hold the halves together during operation, two chest-latches were used, one on each side of the vine opening. Wooden "biscuits" were inserted into the faces of the two halves of the base to aid in alignment during assembly and to insure that the base would not fold when the latches were secured. A sleeve of non-porous foam, the type used to insulate hot water pipes, was placed around the vine trunk. This was slightly larger in diameter than the opening for the vine trunk which enabled the chamber base to compress the sleeve and form a relatively tight seal around the trunk. This design separated the vine from the potting soil to eliminate the effects of soil and root respiration on CO_2 determinations.

The actual chambers consisted of Mylar M-30 film (polyethylene terephthalate, polyvinylidene chloride coated, DuPont Inc., Wilmington, DE) which had been rolled into a cylinder of a diameter slightly larger than that of the wood bases to facilitate assembly of the base/chamber system. This cylinder was sealed with clear box tape along the seam. An outlet port of 5.1 cm i.d. PVC pipe was attached using tape and rubber bands to draw the distal end of the chamber together forming a roughly hemispherical top above a cylindrical chamber. The chambers were attached to the base using an elastic band fitted into a groove cut around the periphery of the base (Figure 1b inset). The bands used here was the type used to attach garbage bags to 30 gallon garbage containers.

Mylar's light transmition and gas permeation qualities are excellent. Light transmission in the photosynthetically active range of radiation was about 90% (similar to polyethylene) (R. Richmond, DuPont Inc., Wilmington, DE, personal communication), and permeability to CO_2, H_2O and O_2 is quite low relative to other films (Pauly, 1989). In addition, the high flow rates used here reduced gaseous losses or gains which might occur through the film thereby reducing variation arising from this source. However, light quality and quantity may be influenced by any commercially available film, and this should be considered when interpreting data collected with a film between the light source and leaves.

The air supply system consisted of a small, squirrel-cage fan of the type used for forced-air heating systems with a maximum, unrestricted output of 4530 $l\ min^{-1}$ (Model #IC982B, Dayton Inc., Dayton, OH). This was attached to a 10.2 cm i.d. PVC pipe "T" which served as a manifold to distribute the air to the two chambers. After the flow was divided by the manifold, air flowed through two, 1.2m lengths of 10.2 cm i.d. PVC pipe. This section of the air supply system was kept at 10.2 cm i.d. because it was necessary to have piping of this diameter or larger in order to accurately measure air flow using a hot-wire anemometer. The air supply pipe diameter was reduced to 5.1cm before the inlet into the chambers. Using a smaller inlet pipe reduced the diameter of the chamber base and helped keep chamber volume low. Air flow was regulated using a 120 V, 10 A rheostat to control fan speed.

Air flow and temperature measurement were accomplished using a thermal anemometer (Cole-Parmer Model #37000-00, Cole-Parmer Inc., Chicago, IL). Air flow was measured midway on the inlet pipe by taking 8 readings of equal cross-sectional area and then averaging these (Dr. R. Beaudry, personal communication). Volume of air was calculated from linear flow data by the equation:

$$V=\frac{\Pi r^{2}\ l}{1000}$$

Where: V = volume of air in liters sec^{-1}
r= the inside radius of the air supply line in cm
l=the linear flow rate of air in cm sec^{-1}

Once the volume of air flow was calculated, it was corrected using the chamber calibration curve described below. Laminar flow from the chamber inlet to its outlet was prevented by placing an air diffuser over the chamber inlet. The diffuser, a piece of tape, created turbulence in the air stream thereby insuring that chamber air was completely mixed. This was later verified by introducing smoke to visualize flow into a chamber containing a vine.

Chamber influence on leaf temperature was determined by comparing a leaf on a vine inside a chamber with a leaf on a vine outside of the chamber simultaneously over a range of air flow rates. This was accomplished by inserting a copper-constantan "needle" thermocouple probe into a leaf on each vine. Leaf temperatures were determined using an Omega model HH23 handheld microprocessor thermometer. Temperature data (not shown) indicated that leaf temperatures inside the chamber were 1 to 2°C higher when air flow rates were similar to those used for determination of A. At very low flow rates, leaf temperature increased inside the chamber 5 to 6°C above that of vine leaves under ambient conditions, indicating the need to use the highest flow rates that will still allow accurate determination of ΔCO_2 (ΔCO_2 readings in the 15 to 35 ppm range).

Measurement of ΔCO_2 was accomplished using an ADC LCA-2 portable infrared gas analyzer (IRGA) (Analytical Development Co., Hoddesdon, U.K.). A reference sample was obtained from one of the inlet pipes in the same region that the air flow was measured. The sample CO_2 measurement was then taken at the chamber outlet. ΔCO_2 concentrations were determined only after vines had equilibrated in the chambers for about 5 minutes after which the IRGA readings had stabilized.

Whole vine CO_2 assimilation (μmol vine^{-1} sec^{-1}) was calculated as follows:

$$A(\mu mol\ vine^{-1}\ \mathrm{sec}^{-1}) = \frac{(\Delta CO_2)\,\mu l\ l^{-1}\ x\ (flow)\,l\ \mathrm{min}^{-1}}{29.2\mu l\ \mu mol^{-1}\ x\ 60\mathrm{sec}\ \mathrm{min}^{-1}}$$

Where: $\Delta CO2 = [CO_2]_{in} - [CO_2]_{out}$

"Flow" was calculated from anemometer readings. The value of 29.2 μl μmol^{-1} to convert CO_2 volume to CO_2 concentration was calculated at standard temperature (20°C). At the higher temperatures often encountered in the chambers (26 - 36°C), 29.2μl was less than 1μmol. However, the change in CO_2 concentration only introduced about a 0.5% error over the range of temperatures listed above.

Chamber Calibration

Air flow in the inlet pipe was more turbulent than expected in the area of air flow measurement due to the reduction of inlet pipe diameter at the chamber. This required verification of flow readings from the thermal anemometer which was accomplished by calculating air flow into an empty chamber by measuring the dilution of a stream of CO_2 of known concentration and flow rate. The values obtained over a range of flow rates were then regressed on values obtained using the thermal anemometer at the same flow rates. The regression equation ($Y = .51x - 0.10$. $r^2=0.99$) was used to correct the flow calculated from the anemometer readings (see Figure 2).

Chamber Use For Pn Measurement

To use the chambers, the air supply system was set up, connecting the pipes with duct tape. Typically, the air supply system was shaded to reduce heat buildup in the system. Two vines were placed in position at the ends of the air inlet pipes and air flow was set on high. The non-porous foam sleeves were placed around the vine trunks and the chamber bases latched into place, resting on the pot. The elastic bands were then placed loosely around the pot so they would be in place when needed for bag attachment. The Mylar balloons were carefully lowered over the vines, taking care to not damage leaves, shoot tips or fruit and their bases constricted around the chamber base and allowed to fill with air. Finally, the elastic bands were moved into place to attach the balloons to the chamber base.

Once inflated, air flow to the balloons was reduced to a rheostat setting of between 20% and 35% of maximum (air flow of 80 to 250 L min^{-1}) depending on vine leaf area, and the IRGA sample line was placed in the chamber outlet. After air flow and chamber pressure had stabilized, air flow was measured and recorded. A ΔCO_2determination was made when the IRGA readings stabilized. The IRGA was then set up to sample the second chamber, which at that point was in dynamic equilibrium, and the measurement process used for the first chamber repeated.

After completing readings for two vines (about 15 to 20 minutes), the air flow was increased and the balloons removed. Bases and foam sleeves were removed. Two more vines were then set up. It was possible to measure twelve vines in as little as 1.5 hours. Data were collected on four replicate vines.

Single Leaf Pn Measurements

Pn of single leaves was measured at the same physiological growth stages as were whole vines with the exception of harvest. Data were collected on a recently, fully expanded leaf using an ADC LCA-2 portable, open gas exchange system equipped with a Parkinson broad leaf chamber and an air supply unit (Analytical Development Co., Hoddesdon, U.K.). These data were then used to estimate whole vine Pn by multiplying the Pn rate per unit leaf area by the estimated leaf area of the vines. It was then possible to compare the actual whole vine data with the calculated values.

PLANT MATERIALS

The plant materials used were one-year-old Chambourcin grapevines grafted to 5-C rootstock and potted in 19-L pots using 45% sand, 45% loam and 10% peat. The vines were watered regularly and fertilized monthly. Vines were divided by their fresh weight prior to planting, into four blocks and and trained to 3-shoots per individual vine.

The relationship between leaf area and shoot length was determined previously (10) to be ($y = 15.69x - 27.83$; $r^2 = .88$). Shoot length measurements were then used to estimate leaf area at each date of measurement.

RESULTS AND DISCUSSION

The chamber calibration curve is shown in Figure 2. Actual flow rates were lower than those indicated by the hot-wire anemometer which was likely due to turbulence caused by the reduction of inlet pipe diameter at the chamber entrance. The observed differences demonstrate the necessity for chamber calibration for accurate and precise data.

CO_2 assimilation per unit leaf area (μmol CO_2 m^{-2} sec^{-1}) was measured on an individual leaf or was calculated from whole vine measurements (Figure 3a). Net assimilation determined using a single leaf measurement was less than the average assimilation rate per unit leaf area as determined from the whole vine only at veraison.

Net CO_2 assimilation per vine (μmol CO_2 $vine^{-1}$ sec^{-1}) was either measured for entire vines or estimated from single leaf measurements (Figure 3b). Whole vine Pn measured for entire vines was greater than the single leaf estimate at veraison only. The data indicate that using single leaf Pn measurements to estimate whole vine A (in a potted-vine system with no fruit present) gives good results early in the season. However, as the season progresses and more leaf area is generated (about 3000 cm^2 at harvest), estimates of whole vine A using a recently, fully expanded leaf, are too low.

If one were measuring the carbon uptake of the most rapidly photosynthesizing leaf and using it to estimate whole plant Pn, an overestimation would occur. This, however, was not the case here. Compared to the whole vine data, the estimate of whole plant A from single leaf determinations was similar at bloom and at the 5mm berry stage and low at veraison. While we used a recently fully expanded leaf for consistency among treatments (as do many studies -Edson, 1991; Gucci et al., 1991), this leaf position was shown by Poni et al. (1994a) to be photosynthesizing at the highest rate on the plant only during mid-season in grape. Earlier in the season (around bloom), more basal leaves showed the highest photosynthetic rates whereas apical leaves had the highest rates late in the season (veraison through harvest).

Apparently, as the plant grows and the canopy becomes more complex, it is increasingly difficult to select a leaf which will give a meaningful estimate of the average Pn of the plant. It is for this reason that whole plant Pn chambers are necessary for accurate and precise whole plant Pn measurement. Whole plant chambers integrate Pn from all leaf types as well as respiration from the various aerial organs of the plant and give a good estimate of whole plant carbon assimilation (Figure 4). In addition, using potted, one-year old grapevines at veraison, there was a positive, linear relationship between whole vine Pn and whole vine dry weight. However, more data are required to verify this observation both at veraison and at other phenological stages.

Corellii-Grappadelli and Manganini (1993) demonstrated the use of the Parkinson broad leaf chamber to measure total transpirational losses from trees in their chamber. While this was not attempted, it is possible that it could work on the whole-plant chambers described herein as well.

Considerable variability exists among vines in their photosynthetic responses to treatments. Pre-selection of plant materials is therefore recommended prior to attempting whole plant measurements (e.g. blocking by fresh weight prior to planting). It would also be useful to have a group of plants from which those to be measured could be selected based on uniformity of growth.

CONCLUSION

Use of whole plant, open gas exchange systems gives a more accurate indication of carbon assimilation under various conditions. Attempting to infer whole plant responses from single leaves involves many assumptions (e.g. all leaves photosynthesize at the same rate; all leaves are perpendicular to incident radiation) and cannot integrate respiration by organs other than leaves. The whole plant gas exchange system described measures Pn of potted plants, integrating respiration and other factors affecting Pn to give a better measure of whole plant carbon assimilation.

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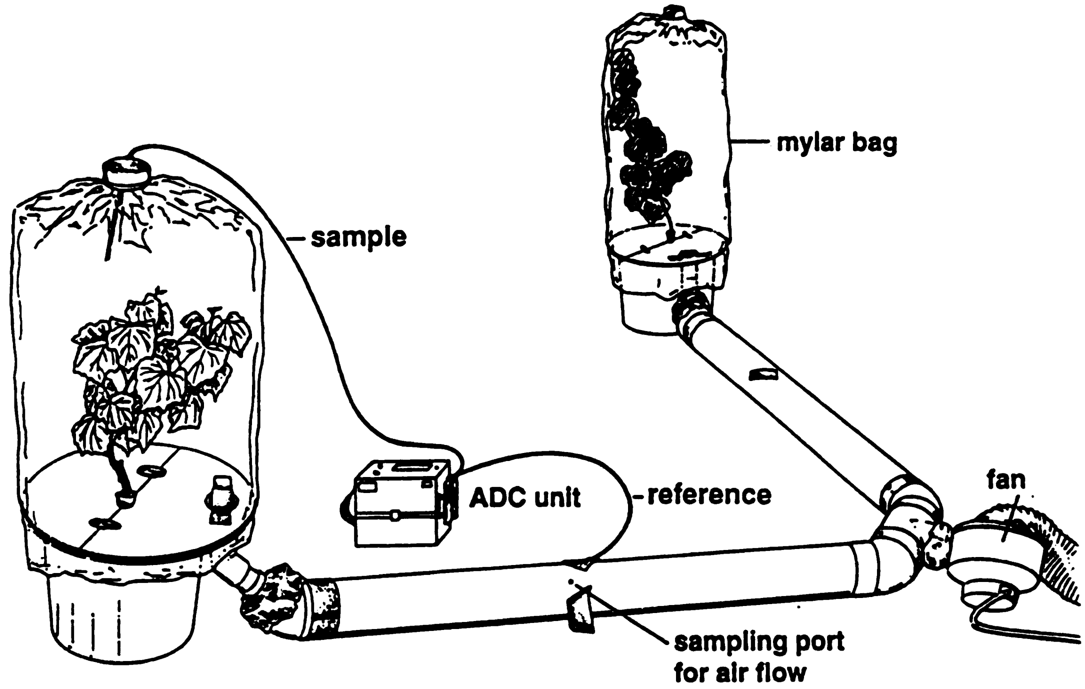

Figure 1a. Whole-plant gas-exchange system showing both chambers, air supply system, location of air flow measurement ports and IRGA hookup.

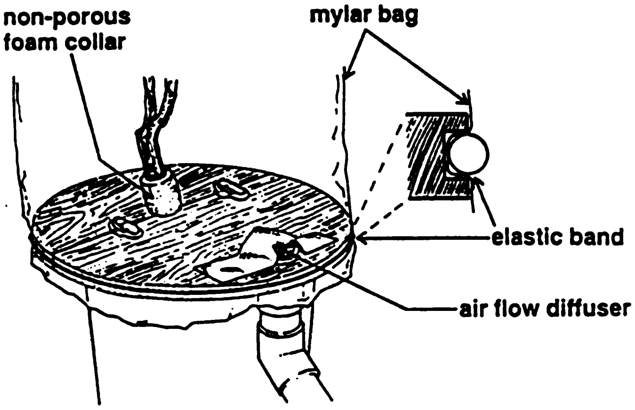

Figure 1b. Detail of chamber base showing, non-porous foam collar sealing the trunk, latches for fastening chamber halves, air diffuser, and attachment of Mylar balloon with elastic band. Inset shows detail of elastic band positioning and attachment.

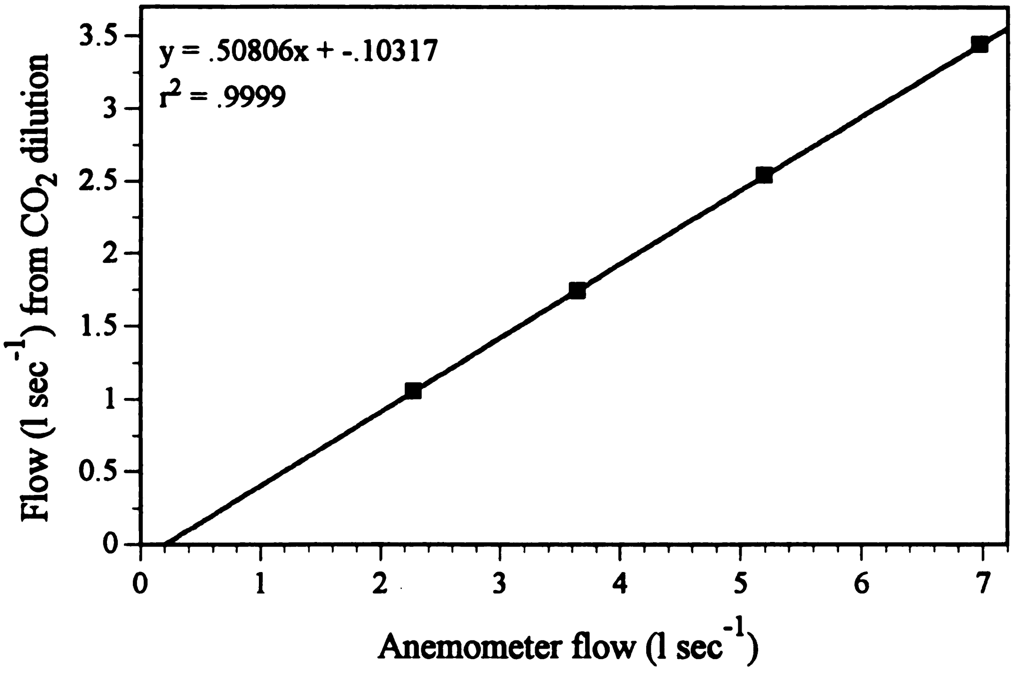

Figure 2. Relationship between actual flow rate (as determined by dilution of CO_2) and flow as measured by hot-wire anemometer.

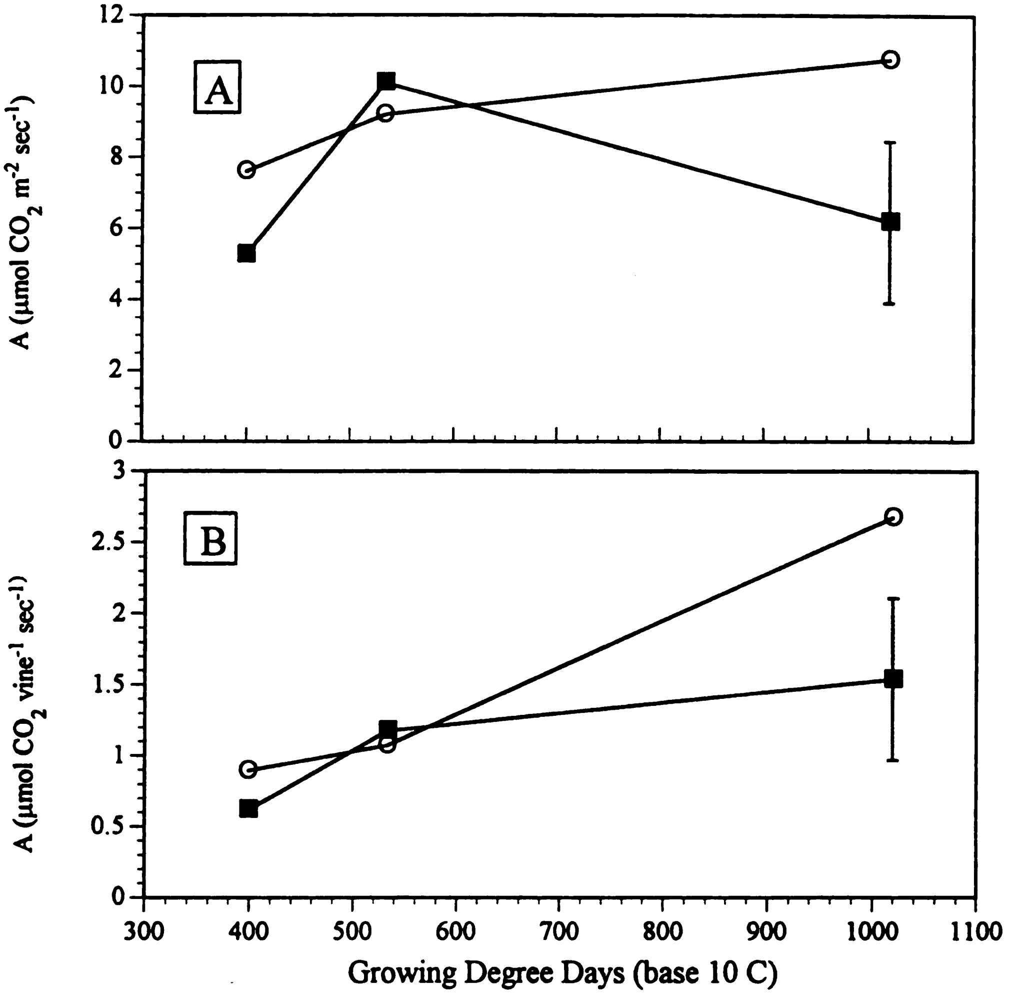

Figure 3. CO_2 assimilation (A) of Chambourcin grapevines. Measurment using a Parkinson broad-leaf chamber (■); or whole-plant chambers (O). A) CO_2 assimilation per unit leaf area (µmol CO_2 m^{-2} sec^{-1}) and; B) CO_2 assimilation per vine(µmol CO_2 $vine^{-1}$ sec^{-1}). Bars represent the LSD at $p = 0.05$.

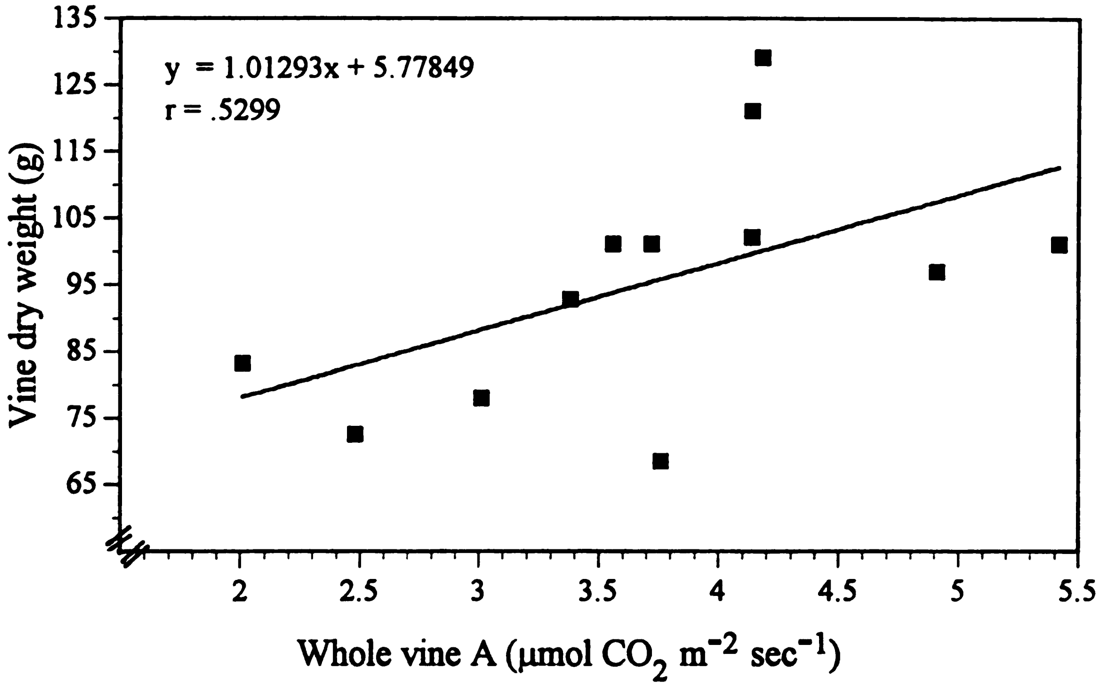

Figure 4. Relationship between whole vine CO_2 uptake at veraison and vine dry weight at harvest for potted Chambourcin grapevines.

II. EFFECT OF SHOOT NUMBER ON POTTED GRAPEVINES: I. CANOPY DEVELOPMENT AND MORPHOLOGY

ABSTRACT

Potted, one-year-old Chambourcin grapevines grafted to 5-C rootstock were grown with one- three- or six-shoots in the absence of fruit to determine the effect of competition between vegetative sinks on canopy morphology and development. As shoot number increased, leaf area per shoot, shoot length, leaf size and flower cluster length decreased for individual organs. On a whole vine basis, total leaf area, shoot length and flower cluster length increased with increasing shoot number. Leaf area of three- and six-shoot vines was 38% greater than that of one-shoot vines at harvest. Vine dry weight at harvest, however, was greater for three- and six-shoot vines only at $p \geq 0.10$. Whole vine photosynthesis (Pn) measurements showed no differences among treatments at bloom, but Pn had a positive, linear relationship to shoot number both at 5mm-berry size and at veraison. These data indicate that: (1) smaller flower clusters and less leaf area per shoot are responsible in part for the reduction in shoot fruitfulness observed in vines with many shoots; (2) many shoots allow a vine to develop greater leaf area relative to vines with few shoots earlier in the growing season and produce more vegetative sinks for carbohydrates; and (3) the presence of relatively large shoot numbers causes important morphological changes in canopy vegetative structure. These include shorter shoots and smaller leaves and flower clusters but greater shoot length, leaf area and flower cluster length per vine.

INTRODUCTION

Grapevine canopy management seeks to maximize leaf capture of solar radiation, while at the same time providing an optimum environment for fruit maturation and development (17,18,19,20). Research has shown that the high bud numbers retained on minimally pruned (MP) vines allow the canopy to develop more rapidly during the spring growth flush (3,4,5,14). Studies using vines which were skirted to remove low-hanging canes (3,4) or hedged (14) showed dramatic increases in yields over controls. The authors of those studies hypothesized that the large, early-season canopy surface increased the capacity of MP vines to produce crop, thereby causing the large yields. However, since the MP vines also had larger cluster and berry numbers relative to spur pruned controls, it is unclear if the large early-season leaf surface of MP vines is the sole cause of the increased yields, particularly in the absence of vine dry weight data over a growing season. Wilson (23) demonstrated that growth in *Brassica* and *Helianthus* was sink limited; the factor most limiting to growth rate was rate of leaf production (sinks during development). This may also be true in severely pruned grapevines. Additionally, the relatively small number of shoots on severely pruned vines may carry insufficient fruit to fully utilize the vines fruit production potential.

Carbohydrate reserves support canopy development during the spring growth flush (9,15,26,27,28). It follows that as the quantity of reserves varies, so will the quantity of growth that they can support or, conversely, that a given quantity of reserves will support a finite amount of growth. Yang and Hori (26,27) and Yang, et al. (28) demonstrated that carbohydrate reserves are utilized to support shoot growth up to appearance of the tenth leaf. Mobilization of reserves increased through the expansion of the sixth leaf, then declined. By contrast, basal leaves began exporting current assimilates after the fifth leaf emerged. Maximum shoot growth rates occurred when both reserves and current assimilate were available as energy substrates. McLaughlin et al. (9) calculated the energy required to support the growth flush of the canopy of a mature white oak (*Quercus alba* L.). However, to our knowledge, no work has been done to quantify the amount of canopy that can be generated during the growth flush by grapevines with a given quantity of reserves or to quantify the influence of varying canopy leaf area at the end of the growth flush on net, annual dry weight accumulation for whole vines.

To maximize the production potential of grapevine's , it is critical to have a better understanding of source/sink relationships which occur during the growth flush as the canopy is developing. The objectives of this experiment were to determine: (1) if competition from vegetative sinks alters canopy morphology; (2) whether greater shoot numbers result in greater dry matter production; (3) at what point during the growing season shoot number might influence dry matter production; and (4) if changes in canopy morphology can influence shoot fruitfulness.

Fruit are active sinks that are very competitive with vegetative tissues for carbohydrates (2,6,23,24,25). It is difficult for experimental purposes, however, to establish fruiting sinks of the same relative strength on vines with varying canopy morphologies. Therefore, to study the effect of competition among shoots on canopy morphology, it is necessary to conduct the experiments in the absence of fruit. It is also necessary to use potted vines to adequately assess canopy morphology and tissue dry weights.

MATERIALS AND METHODS

Plant Material

One-year-old Chambourcin grapevines grafted to 5-C rootstock were planted in 19 liter plastic pots with a 45% sand, 45% loam and 10% peat sterile potting mix on May 26, 1993. The potted vines were placed on pea-gravel in full sun and watered regularly. Fertilizer was applied as a balanced N,P,K solution once per month. Pesticides were applied occasionally as conditions warranted.

When buds were at the swell-two stage (7) of development (elongated sphere prior to burst), their numbers were adjusted to retain three treatments in which one, three or six buds which were allowed to develop. As the vines grew, all laterals were removed once per week. Flower clusters were retained for measurement until bloom at which time they were removed. Fruit was retained on several additional monitor vines not in the experiment but selected from the same group of vines so fruit phenology could be followed and used as a reference as the season progressed. While the non-fruiting vines may have had slightly altered phenology from the fruited vines, this approach gave a reasonable estimate of phenological stage of development. Phenological stages used in the study were: "bloom" (50% of flowers in bloom); 5mm berries; veraison (30% of berries showing coloration); harvest (fruit at 20 °brix and pH 3.45); and dormancy (all leaves fallen).

Vines were blocked by fresh weight prior to planting producing four blocks. Treatments were randomly assigned to 12 vines for each treatment in each block. At various intervals (described below), one vine of each treatment within each block was selected for destructive harvest. The experimental design was a randomized complete block with three treatments and four replicates, harvested on nine dates for a total of 108 vines.

Leaf Area and Canopy Measurements

Vines were destructively harvested at approximately five-day intervals (reported as growing degree days (GDD) base 10°C) during the period from bud burst through bloom, on dates when monitor vines achieved 5mm berry diameter, veraison and at fruit harvest for a total of nine harvests. Leaf area was determined using a Li-Cor LI-3000 portable leaf area meter (Lambda Instrument Corp., Lincoln, Nebraska). Length was recorded for individual shoots and cluster primordia until the time of cluster removal, after which only vegetative structures were measured.

Vine Dry Weight

Dry weight was determined at each destructive harvest by partitioning the vine into its various organs and recording the fresh weight of each. The tissues were then placed into paper bags in a drying oven at 60°C until no further weight reduction occurred (approximately 4 days). After drying, tissue weights were recorded and percentage water content calculated. Only the dry weight recorded at the date of monitor vine fruit harvest is reported here.

Photosynthesis

CO_2 assimilation(A), leaf conductance (g_s), photosynthetic photon flux density (PPFD), leaf temperature (T) and air relative humidity (RH) were determined for single leaves and CO_2 assimilation only was determined for whole vines. Single leaf

A was determined on a recently fully expanded leaf using an ADC LCA-2 portable open gas exchange system equipped with a Parkinson broad leaf chamber and an air supply unit (Analytical Development Co., Hoddesdon, UK). Whole vine A was determined using a whole plant open gas exchange, Mylar chamber as described in Chapter 1. Air flow rates of 400 ml min^{-1} were used for single leaf measurements and 180-250 L min^{-1} used for whole vines. Measurements were at 20% full bloom, after anthesis when berries of monitor vines were 5 mm diameter, and at veraison for single leaves and whole vines. Only single leaf A was determined at harvest as weather conditions would not permit a whole vine determination. Both single leaf and whole vine measurements were made between 11:00 and 13:00 hours (solar time) when PPFD levels were at least 1000 μmols m^{-2} sec^{-1}.

Data Analysis

Means were calculated on a per shoot and per vine basis using Lotus 123 Release 4 (Lotus Development Corp., Cambridge, MA). These data were further analyzed with the MSTATC statistical package (MSTATC, Michigan State University, East Lansing, MI) using a two-way Analysis of Variance and orthogonal contrasts where appropriate. Regression analyses were performed using DeltaGraph (Delta Point Inc., Monterey, CA).

RESULTS

Leaf Area

Leaf area per shoot was inversely related to shoot number at every destructive harvest (Figure 1a). Leaf area per shoot of three-shoot vines was greater than that of six-shoot vines only at bloom, veraison and harvest.

Leaf area per vine varied after bud burst until about 1-week before bloom (305 GDD) (Figure 1b). After that point, there was a positive, quadratic relationship between leaf area per vine and shoot number at every date. Leaf area per vine differences were established by 385 GDD. Leaf area per vine increased in all treatments from bud burst through veraison but continued to increase from veraison through harvest (1020 to 1141 GDD) for three- and six-shoot vines only (Figure 1b). The rate of leaf area increase per vine was similar for all treatments between 385 and 1020 GDD (Figures 1b and 2a). The rate of leaf area increase for three- and six-shoot vines reached a maximum at 384 and 219 GDD, respectively, while one-shoot vines reached a maximum rate at 219 GDD (Figure 2a). Three- and six-shoot vines had approximately 1.3 and 1.6 x the leaf area of one-shoot vines at veraison and harvest, respectively (Figure 1b).

Leaf size was inversely related to shoot number on every date (Figure 1c). Leaf size of three- and six-shoot vines was always similar.

Leaf number per shoot was inversely related to shoot number on every date (Figure 2b). Three-shoot vines had more leaves per shoot than did six-shoot vines after 305 GDD. Leaf number per shoot in one-shoot vines was nearly twice that of six-shoot vines at bloom (8.3 vs. 4.4) and harvest (20.5 vs. 11.7).

There was a positive, linear relationship between leaf number per vine and shoot number starting shortly after bud burst (Figure 2c). Leaf numbers of three- and six-shoot vines were 2 and 2.5 x respectively those of one-shoot vines on nearly every date. After veraison, leaf production ceased on one-shoot vines but continued on three- and six-shoot vines.

Shoot Growth

Mean individual shoot length was inversely related to shoot number per vine throughout the growing season (Figure 3a). Shoots of three-shoot vines were longer than those of six-shoot vines at harvest only.

A positive relationship existed between shoot length per vine and shoot number at each date except at bloom and in dormant vines when no differences were found (Figure 3b). Dormant cane lengths and shoot lengths at harvest of one-shoot vines were similar. Dormant cane lengths of three-and six-shoot vines, however, were dramatically less than their harvest shoot length due to a loss of non-lignified tissue to frost. The percentage of nodes which lignified was inversely related to shoot number (90%, 70%, and 57% for one, three and six shoots, respectively).

Internode length varied among treatments before bloom but was inversely related to shoot number at every date between bloom and dormancy (Figure 3c). Internode length was generally the shortest in six-shoot vines. However, at bloom internode length of six-shoot vines was intermediate to that of one- and three-shoot vines.

Flower Cluster Development

Flower cluster development was linearly related to both mean leaf size and mean shoot length per shoot (Figures 4a and 4b). The result was flower clusters which were nearly twice as long on one-shoot vines as those on six-shoot vines (70.3 mm vs. 38.3 mm). At bloom, mean cluster length per shoot was 27 mm for six-shoot vines compared to 123 mm for one-shoot vines. One- and six-shoot vines had 1.8 and 0.7 clusters per shoot, respectively. Cluster length per vine was linearly related to shoot length per vine (Figure 4c) resulting in greater flower cluster length per vine as shoot number (and shoot length) per vine increased.

Dry Weight of Vines

Dry weights of trunks, roots, shoots and whole vines were not different among treatments at 1141 GDD (harvest in this experiment) (Figure 5). Whole vine dry weight increased linearly with shoot number ($y = 3.59x + 83.53$; $r^2 = .526$) at that time but the relationship was significant only at $p \leq 0.10$. Leaf dry weight was greatest in three- and six-shoot vines. Shoots of three- and six-shoot vines had a higher water content than did one-shoot vines (59.2%, 60.0% and 56.3%, respectively). This reflects the lower percentage of lignified nodes on three- and six-shoot vines compared to one-shoot vines. Fresh weight of whole three- and six-shoot vines was greater than that of one-shoot vines at $p \leq 0.05$ (298g, 293g and 238g, respectively).

A regression of whole vine dry weight on leaf area shows that leaves of one-shoot vines were more efficient at dry weight assimilation than were leaves of three- and six-shoot vines (Figure 6). Leaves of one-shoot vines assimilated 0.040g of dry weight per cm^2 leaf area, whereas three- and six-shoot vines assimilated only 0.035 g dry weight per cm^2.

Photosynthesis

Single leaf assimilation rates were not different among treatments on any of the four measurement dates (Figure 7a). Stomatal conductance and transpiration rate were higher, and vapor pressure deficit lower for one-shoot vines than for three- and six-shoot vines only at harvest (data not shown).

Whole vine CO_2 assimilation increased linearly with shoot number at 5mm berry size and veraison ($r^2 = 0.966$ and 0.918, respectively) (Figure 7b). Vines of all treatments were assimilating at nearly the same rate prior to bloom.

DISCUSSION

Rate of leaf area development increased as shoot numbers increased, apparently due to greater leaf numbers as shoot number per vine increased. A grapevine has the potential to assimilate a finite amount of carbon during a given growing season (6). However, the amount of carbon assimilated is dependent on environmental conditions, and the balance of carbohydrate sources and sinks. If the number of shoot apical meristems is limited (e.g. by severe pruning), they will grow rapidly and the leaf blades will expand to their maximum possible size but canopy development may be slowed by the low number of shoots and points of leaf initiation (i.e. canopy development is "sink" limited) (22,23). In this situation, there are adequate carbohydrate reserves and root-supplied substances to support the maximum rate of growth per shoot. As shoot numbers increase, they begin to compete with one another for available carbohydrates, water, nutrients and root-supplied resources such as cytokinins. At this point, the actual amount of growth per shoot is reduced but canopy development potential and shoot length per vine are maximized.

Changes in leaf and shoot morphology with increasing vegetative competition are similar to those caused by water stress (8). This result would be expected if the demand for water by apical meristems and leaf blades was greater than the supply of water provide by the roots and xylem. There appears to be a point at which shoot numbers are in optimum balance with the vine's growth potential (in our experiment it was when three shoots were present). In "small" field-grown Concord vines, yields were similar when pruned to either 90 or 120 nodes (11). By contrast, "large" vines had higher yields with 120 nodes compared to 90 nodes. Beyond the point of maximized growth, there is no obvious benefit of having additional shoots but there is a morphological effect; the additional shoots are shorter with fewer, smaller and less efficient leaves. In this case, shoot growth is source limited (22).

There apparently is an upper limit to the number of shoots a vine can support above which the vine becomes source limited. In this experiment, six shoots were originally retained from 12 or more swelling buds on the six-shoot vines. As growth began, some shoots ceased growth and some buds never burst. Of the shoots which remained, two or three often grew at a higher rate than did others, suggesting that a competition was occurring for available resources. Clingeleffer (3) demonstrated that as the node number retained at pruning increases, the percentage of nodes producing shoots decreased; 48 nodes produced 59 shoots (123%) and 336 nodes produced 204 shoots (61%).

Shoot length, leaf size, leaf area and flower cluster length on a given shoot are linearly related. Flower cluster length and the number of florets per cluster are also linearly related (data not shown), so shorter shoots have fewer flower clusters and fewer flowers per cluster. In itself this would result in reduced fruitfulness. However, fruitfulness may be further reduced if the carbohydrates available at bloom are reduced relative to severely pruned vines (1). The combination of smaller flower clusters, fewer flower clusters per shoot and lower carbohydrate production per unit leaf area on lightly pruned vines would explain in part the large reduction in shoot fruitfulness observed with increasing shoot numbers in field studies (3,4,5,10). As shoot number and shoot length per vine increase, total flower number per vine increases as well. It is thus possible to increase the total number of berries per vine even as the fruitfulness of individual shoots declines.

The greater leaf area of three- and six-shoot vines was responsible for greater whole vine Pn and slightly greater dry weight at harvest. Further research will determine how both potted and mature vines will respond in the presence of fruit. Whole vine Pn was similar for all treatments prior to bloom. The small additional dry matter production was apparently the result of greater carbohydrate sink activity and greater exposed leaf area from bloom through harvest. These data indicate that canopy surface area at bloom influences annual carbohydrate assimilation only slightly in potted vines under the conditions imposed in this study.

More research using mature vines is necessary to find the optimum number of shoots which will maximize annual dry matter production and produce sufficient berry numbers to maximize the vines production of high quality fruit while building reserves in preparation for the subsequent growing season. This concept was first outlined by Partridge in 1926 as "balanced pruning" (13). Since current approaches will likely employ both pruning and crop reduction to achieve the desired crop load, a more accurate name might be "balanced cropping" (16).

CONCLUSION

In young, potted vines with no fruit, increasing shoot number results in an alteration of canopy morphology. Vines with a relatively large number of shoots present a larger leaf surface for a greater portion of the growing season, but one that is less productive per unit leaf area, than vines with fewer shoots. The result is a small increase in dry matter production with increasing shoot number, that occurs between bloom and harvest in the absence of fruit. The effect of shoot competition on canopy morphology may explain the reduction in shoot fruitfulness observed in minimally pruned vines in commercial vineyards. Shoot competition results in shorter shoots with smaller flower clusters and fewer flowers per cluster. This phenomenon may be utilized to produce less compact clusters in tight-clustered varieties by reducing fruit set and berry size, and be useful as a tool in an integrated approach to viticulture.

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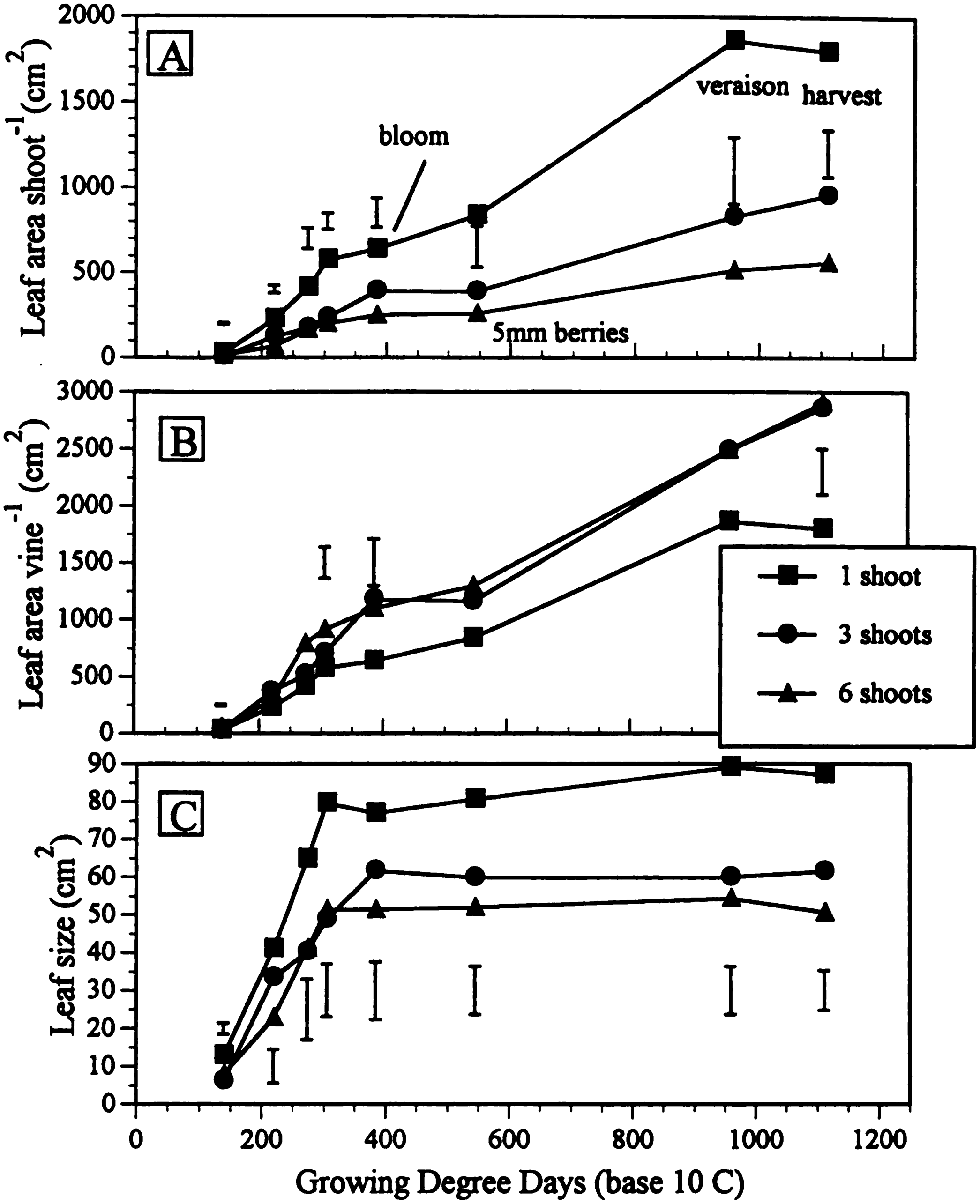

Figure 1. Leaf area (cm^2) for individual shoots (A), whole vines (B) and leaves (C) of potted Chambourcin grapevines with 1 shoot (■), 3 shoots (●), or 6 shoots (▲). Bars represent the LSD at $p = 0.05$.

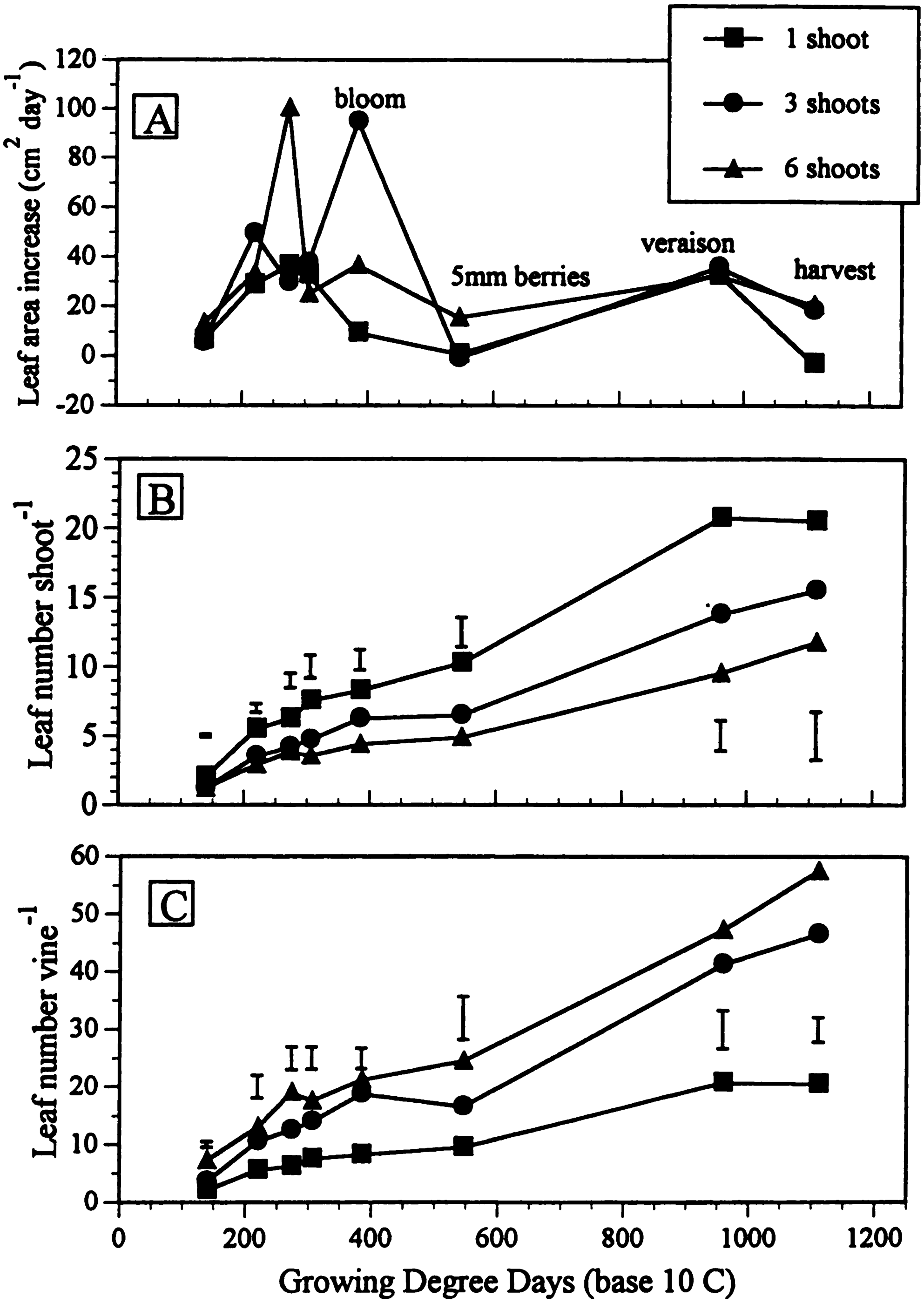

Figure 2. Rate of leaf area increase (cm^2 day^{-1}) (A) and leaf number of individual shoots (B) and whole (C) Chambourcin grapevines with 1 shoot (■), 3 (●) shoots, or 6 (▲) shoots. Bars represent the LSD at $p=0.05$.

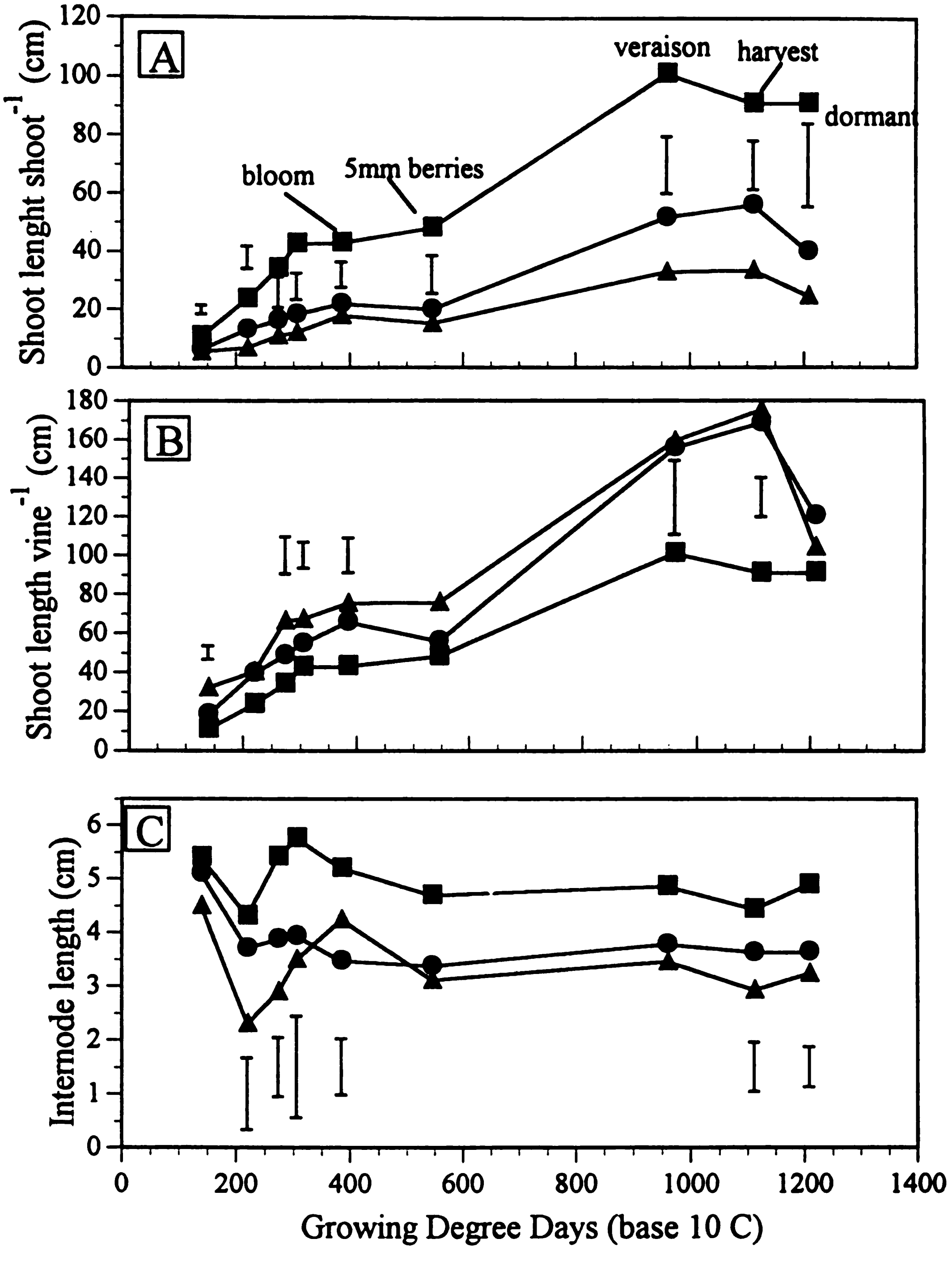

Figure 3. Length (cm) of individual shoots (A), entire vines (B) and internodes (C) of potted Chambourcin grapevines with 1 shoot (■), 3 (●) shoots, or 6 (▲) shoots. Bars represent the LSD at p=.05.

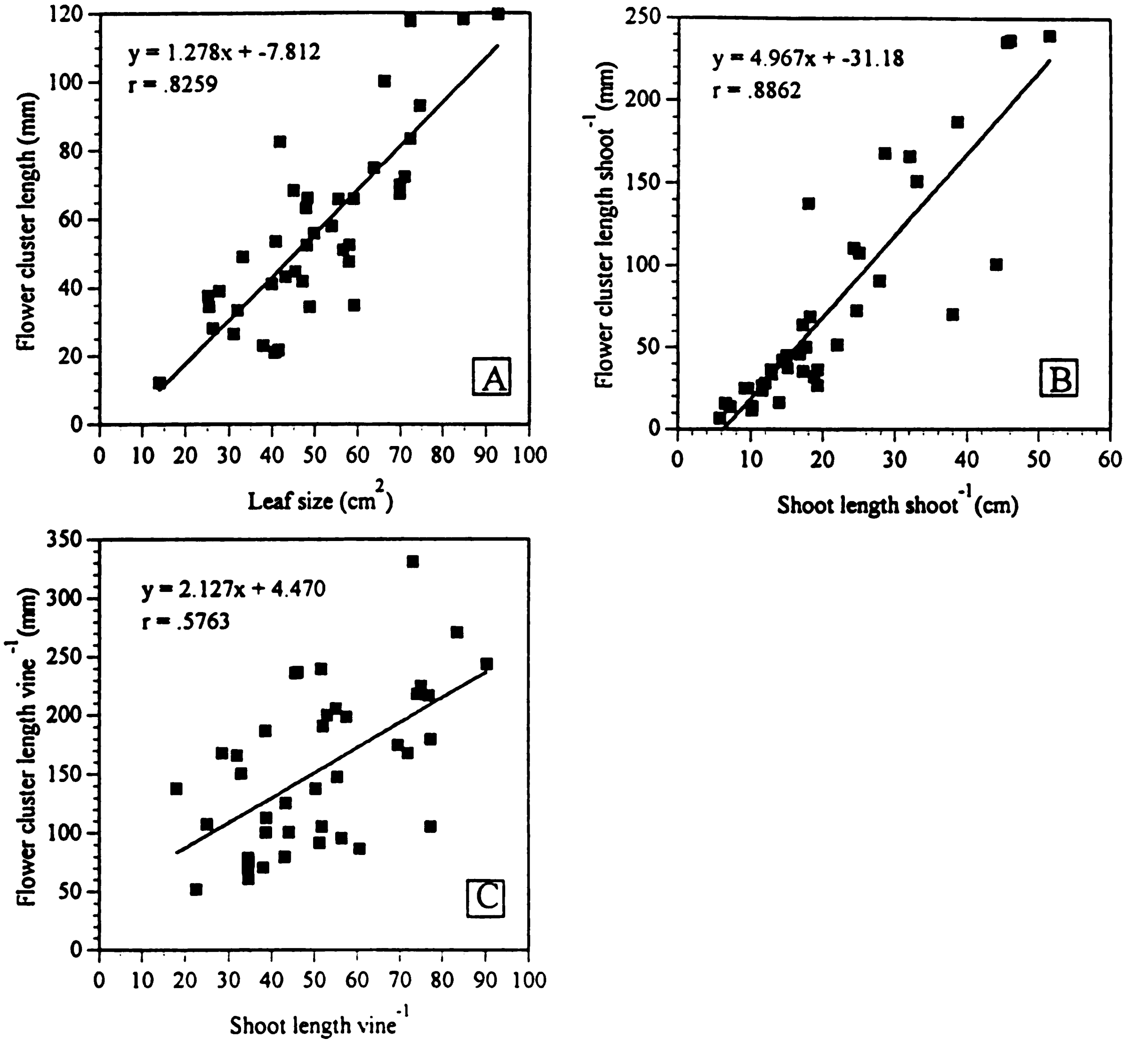

Figure 4. Relationship between individual cluster length and leaf size (A); flower cluster length per shoot and shoot length per shoot (B), and, flower cluster length per vine and shoot length per vine (C) from bud burst to bloom in potted Chambourcin grapevines.

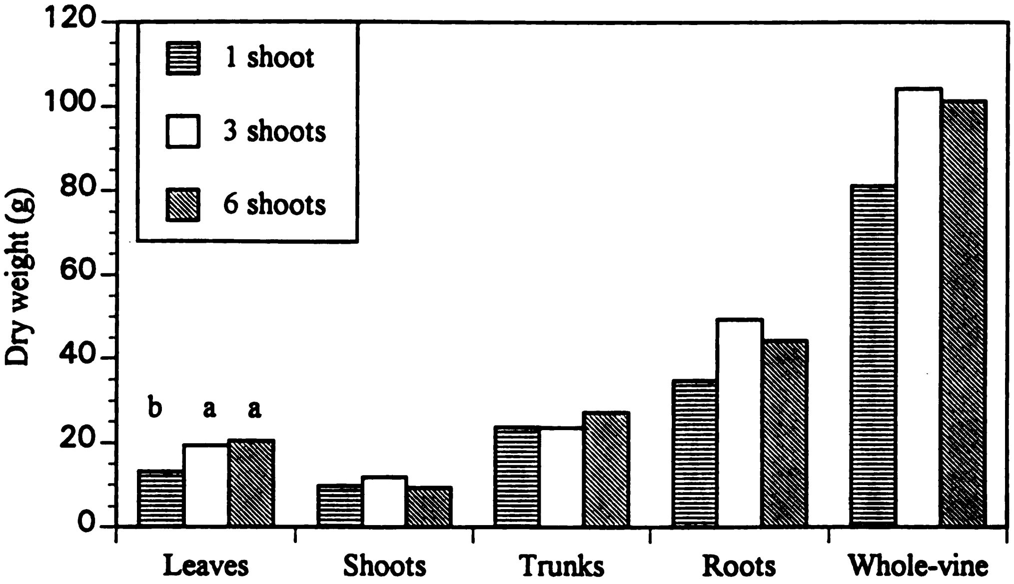

Figure 5. Dry weight of vine organs at harvest of potted Chambourcin grapevines with 1, 3 or 6 shoots. Bars followed by different letters are different at $p = 0.05$.

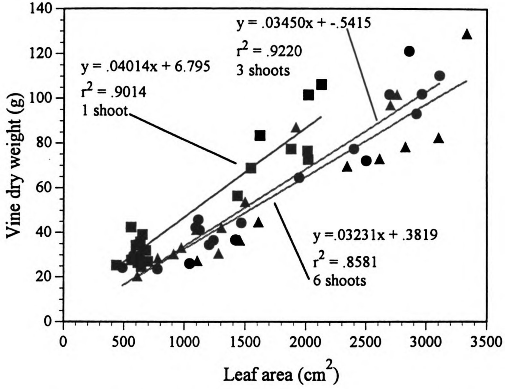

Figure 6. Relationship between leaf area and vine dry weight (g) of potted Chambourcin grapevines with 1(■), 3 (●) or 6(▲) shoots.

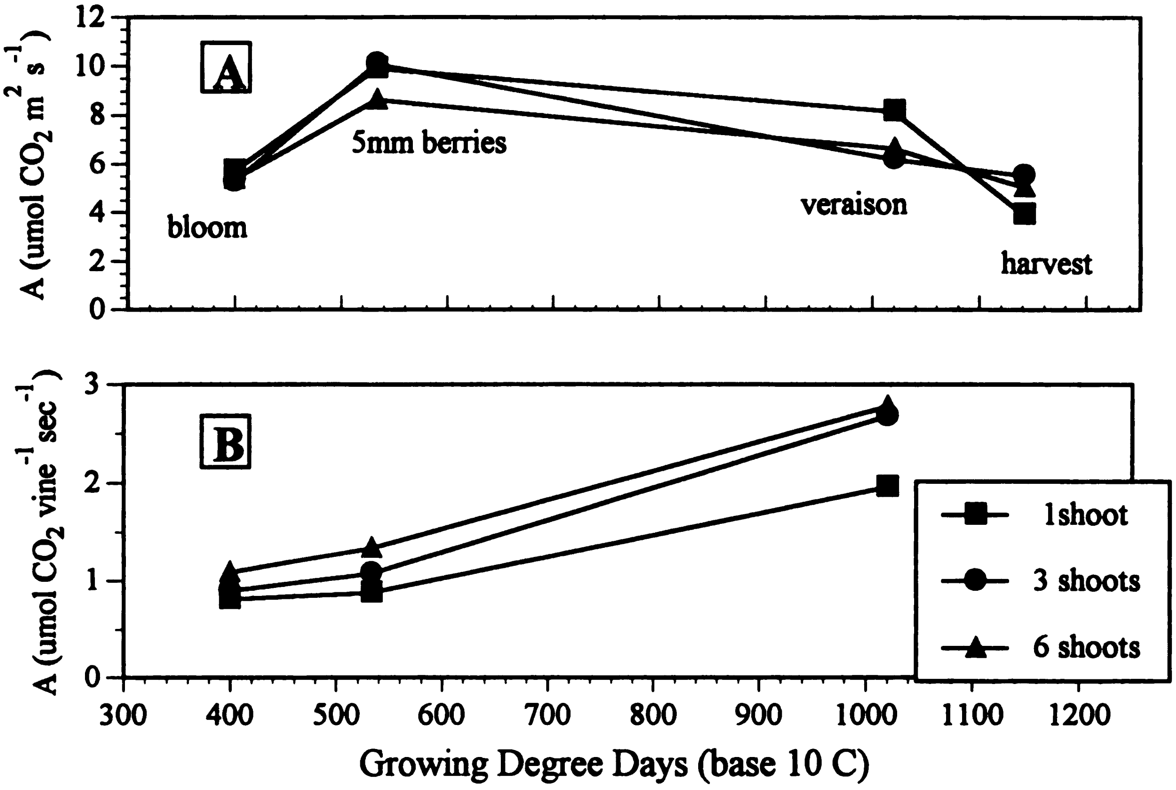

Figure 7. A) Single leaf CO_2 assimilation rate (A) (μmol CO_2 m^2 s^{-1}); B) whole vine A (μmol CO_2 $vine^{-1}$ sec^{-1}), measured with whole-plant chambers using potted Chambourcin grapevines with 1 (■), 3 (●) or 6 (▲) shoots.

III. EFFECT OF SHOOT NUMBER ON POTTED GRAPEVINES: II. DRY MATTER ACCUMULATION AND PARTITIONING

ABSTRACT

Potted, one-year old Chambourcin grapevines were grown with one, three or six shoots in the absence of fruit to determine the impact of increasing early-season leaf area on dry weight accumulation throughout the growing season. No fruit was retained so the role of vegetative sinks could be more carefully studied. Very few differences in dry weight were found for vegetative organs (roots, trunks, shoots and leaves) among the three treatments. Six-shoot vines had greater shoot weight just after bud burst, but at veraison and harvest, there was an inverse, linear relationship between shoot number and shoot dry weight. Three- and six-shoot vines had greater leaf and total canopy dry weights (leaves + shoots) at harvest only. Total plant dry weight was slightly greater with increasing shoot number at harvest only. No other differences were detected in vine dry weight during the growing season. While dry weight differences were not large, increasing shoot numbers affected canopy morphology. Specific leaf and shoot weights decreased as shoot numbers increased, but leaf area per unit shoot weight increased. Additionally, the ratio of cane fresh weight to storage tissues (roots + trunks) was inversely related to shoot number. These results support the hypothesis that cane fresh weights are of questionable value when used to estimate the cropping capacity of minimally pruned vines.

INTRODUCTION

A goal of grape growers is to maximize the yield of fruit of a desired composition per unit land area while keeping production costs low. Since the limits of acceptable fruit composition differ among processors, each grower must decide between increasing yields or better fruit composition. When machines are used to prune or "hedge" a dormant vineyard, there is a cost savings over the use of hand labor (16). Dramatic yield increases have been reported in both cool climate and semi-arid vineyards when vines were subjected to minimal pruning (MP) or "skirting" (removing only low hanging canes by machine) as compared to hand-pruned controls (3,4,5,17,23). MP vines, it is thought, assimilate more carbon over a growing season than do spur pruned vines, because of the rapid canopy development caused by the growth of many shoots. It is suggested that this enables MP vines to produce and ripen larger crops (3,4,12,23). MP vines, however, bear many more clusters and berries than do spur pruned vines. Without vine dry weight data, it is unclear if the larger canopy is solely responsible for the larger yields of MP vines (5,12,15,17,23). It is possible that redirection of carbohydrates to fruit at the expense of vegetative tissues supports fruit development with no net change in canopy dry weight. Substantial effort has been invested to understand the effects of canopy microclimate on fruit quality (19,20,21,22), but little effort has been expended to investigate canopy development during the spring growth flush and whole-vine carbon assimilation over the course of the growing season with varying early-season canopy area.

Whole vine CO_2 assimilation (A) increased with shoot number in potted vines with no fruit (15). The differences were greatest between bloom and veraison; the time between bud burst and bloom was a period of relatively low carbon uptake. Vine dry weight was only slightly greater at harvest in vines with greater shoot numbers. In addition, the relationship between increasing shoot numbers and photosynthesis is asymptotic: carbohydrate assimilation increases with shoot number to a point, and then plateaus. There is an effect, however, on shoot, leaf and cluster morphology with increasing shoot numbers which resembles a drought response (8,26). Water availability to "sinks" may be limited if demand outstrips the water supply from the roots and xylem, even under well-watered conditions. The influence that early-season (bud burst through bloom) canopy area has on carbon assimilation at various times throughout the growing season remains in question, however.

The objective of this research was to monitor the dry weight accumulation and partitioning of potted grapevines with increasing numbers of shoots to determine; (1) the rate at which reserves are utilized during the growth flush when different numbers of vegetative sinks are present; (2) if and at what periods during the growing season greater dry matter production occurs with increasing shoot numbers; and (3) the relationship between the dry weights of various organs with increasing numbers of vegetative sinks.

MATERIALS AND METHODS

Plant Material

On May 26, 1993, one-year old Chambourcin grapevines grafted to 5-C rootstock were planted in 19-liter plastic pots with a 45% sand, 45% loam and 10%

peat sterile potting mix. Potted vines were placed on pea-gravel in full sun and watered regularly. Fertilizer was applied as a balanced N,P,K solution once per month. Pesticides were applied occasionally, as conditions warranted.

When buds were at the swell-2 stage (9) of development (elongated sphere prior to burst), their numbers were adjusted to give either 1, 3 or 6 developing buds. As the vines grew, all laterals were removed once per week. Flower clusters were retained for measurement until bloom at which time they were removed. Fruit was retained on several "monitor" vines not in the experiment but selected from the same group as the experimental vines so fruit phenology could be followed and described as the season progressed. Phenological stages used in the study were: bloom (50% of flowers in bloom); 5mm berries; veraison (30% of berries showing coloration); harvest (fruit at 20°brix and pH 3.45); and dormancy (all leaves fallen).

Vines were blocked according to their fresh weight prior to planting, producing four blocks. Treatments were randomly assigned to 12 vines for each treatment in each block. At various intervals (described below), one vine of each treatment within each block was selected for destructive harvest. The experimental design was a randomized complete block with three treatments, four replicates and nine harvest dates for a total of 108 vines.

Vine Dry Weight

Vines were destructively harvested at approximately five-day intervals (reported as growing degree days (GDD) base 10°C) during the period from bud burst through bloom, at 5mm berry diameter, veraison, harvest and when vines were dormant. One group of vines was also destructively harvested prior to planting to provide baseline weight data. Short time intervals were used between bud burst and anthesis to determine the rate of reserve utilization during the storage-dependent growth flush. Dry weight was determined at each destructive harvest by partitioning the vine into its various organs and recording the fresh weight of each. The tissues were then placed into paper bags in a drying oven at 60 °C until no further weight reduction occurred, generally about four days. After drying, tissue weights were recorded and percentage water content was calculated.

Leaf Area

Leaf area was determined using a Li-Cor LI-3000 portable leaf area meter (Lambda Instrument Corp., Lincoln, Nebraska) at each destructive harvest date.

Non-Structural Carbohydrate Analysis

Samples for non-structural carbohydrate analyses were collected at the time of vine partitioning. Tissue samples were selected as follows: (a) 2 or 3 leaves from the mid-shoot; (b) approximately a 2 cm long segment from the basal five node region of the shoot; (c) approximately a 2 cm long complete cross-section from the mid-trunk; (d) old, suberized roots (2.5-4 mm dia.); and (e) young non-suberized (1-2 mm dia.) roots in roughly equal quantities, which were then combined. Samples were weighed and immediately frozen in liquid N. Within 24 hours of collection, the tissues were lyophilized for approximately 72 hours and were then placed in a freezer at -20 °C where they remained until analyzed. Samples were ground to pass through a 40 mesh screen and 100 mg used for extraction. Sugars were extracted by suspending the tissue in 80% ethanol three times and then combining the three aliquots. After removing sugars, the starch was digested using α-amylase and amyloglucosidase. The tissue starch content was then assayed spectrophotometrically as described previously (13).

Data Analysis

Data were analyzed with the MSTATC statistical package (MSTATC, Michigan State University, East Lansing, MI) using a two-way Analysis of Variance and orthogonal contrasts, or where appropriate, by regression analyses using DeltaGraph (Delta Point Inc., Monterey, CA).

RESULTS

Leaf and Shoot Dry Weight

A positive relationship existed between leaf dry weight and shoot number ($p \leq 0.05$) at harvest only (Figure 1a). Leaf weight increased rapidly during the spring growth flush, slowed for about 10 days around bloom and then increased until veraison at roughly the same rate as before bloom. After veraison, leaf dry weight of three- and six-shoot vines continued to increase while that of one-shoot vines decreased slightly.

Shoot dry weight accumulation followed a pattern similar to that of leaves, slowing slightly around bloom. There was an inverse, linear relationship between shoot number and total shoot dry weight in dormant vines ($y = 13.36x - 0.80$; $r^2 = 0.98$) only (Figure 1b).

Leaf and shoot dry weight were combined to give "canopy dry weight" (Figure 1c). A positive relationship existed between canopy dry weight and shoot number on the first sampling date and at harvest. The pattern of dry weight accumulation in the vegetative tissues of the canopy resembles that described for many types of fruit; it forms a roughly double-sigmoid shaped curve (11). The first increase occurred immediately after bud burst, followed by a lag phase around bloom and a second increase from bloom until veraison. After veraison, the rate of dry weight accumulation in the canopy decreased in one-shoot vines but three- and six-shoot vines continued to accumulate dry matter at approximately the same rate as they had from bloom through veraison. As vines entered dormancy, canopy dry weight dropped precipitously due to loss of non-hardy vegetative tissues (i.e. leaves and the non-lignified portion of shoots) after a freeze of -2 °C.

Root and Trunk Dry Weight

Trunk dry weight decreased during bud burst and through the spring growth flush (the first 350 GDD) (Figure 2a). It then stabilized around bloom (about 400 GDD) before increasing. Trunk dry weight increased from bloom through harvest for all treatments. The only exception was that three-shoot vine trunk weight changed little between veraison and harvest. The period from harvest until the vines became dormant found little change in trunk dry weight for any treatment.

Treatment did not affect root dry weight at any time (Figure 2b). Root weight increased for all treatments from bloom through harvest. Root weight increased slightly between harvest and dormancy in one-shoot vines but decreased in three- and six-shoot vines during the same period.

Total Vine Dry Weight

There was a positive relationship ($p \leq 0.10$) between shoot number and vine dry weight at harvest only (Figure 2d inset). Dry weight differences among treatments were small relative to leaf area differences, however. No net dry matter production occurred from bud burst through bloom (the first 400 GDD or 25 days post-burst). After anthesis, vine dry weight increased through harvest and then decreased going into dormancy as non-hardy tissues abscised.

Specific Leaf and Shoot Weights

An inverse relationship existed between specific leaf weight (SLW) and shoot number at similar leaf area (Figure 3a). SLW increased with leaf area for all treatments from bud burst through harvest. At harvest (maximum LA in Figure 3a), SLW was similar in all treatments.

Specific shoot weight (SSW) was inversely related to shoot number at similar shoot length (Figure 3b). SSW increased in all treatments as the season progressed (Figure 3b inset), but the magnitude of the difference among treatments was greater late in the season due to a more rapid increase of SSW in one-shoot vines than in three- and six-shoot vines (Figure 3b).

Leaf area per gram shoot dry weight was positively related to shoot number particularly after shoot weight exceeded about 2 grams (around bloom) (Figure 3c). The difference was greatest from 5 mm berries through harvest (530 GDD to 1110 GDD).

Root Dry Weight cm^{-2} Leaf Area

Root dry weight per cm2 leaf are varied from bud burst through bloom (Figure 4). An inverse relationship existed between root dry weight per cm^2 leaf and shoot number at 220 GDD, at bloom and again at veraison (Figure 4). The initial root dry weight per cm^2 leaf area at bud burst was quite high due to the small amount of leaf area, so it was omitted from Figure 4. As leaf area increased post-burst, root dry weight changed little, resulting in decreasing root dry weight per unit leaf area. This reached its lowest value at bloom and then increased slowly through harvest for all treatments.

Weight Ratios of Canes (Vine Size) to Storage Organs

There was an inverse, linear relationship between the ratio of cane fresh weight and the weights of perennial tissues, and the number of shoots (Figure 5). Differences in cane weight were responsible for the decreasing ratio of lignified, one-year wood to perennial storage tissues as shoot number increased.

Starch Data

Tissue starch content showed few differences among treatments when the data were expressed either as a concentration or as total starch weight (Appendix A). Starch content of roots and trunks declined as shoots began growth and did not begin to increase until bloom. After bloom, starch concentration and total starch of all vine organs increased through harvest. Shoot number had no influence on starch reserve mobilization rate during the spring growth flush or on tissue contentration throughout the growing season.

DISCUSSION

Vine capacity is defined by Winkler (28) as, "...the quantity of action with respect to the total growth and total crop of which the vine is capable". To paraphrase, it is a vines capacity for dry matter production under a given set of environmental conditions. In this experiment, vines of similar fresh weight produced similar quantities of dry matter regardless of canopy morphology. This suggests that vine capacity is based on the quantity of reserves available to support the spring growth flush, and the size of the root system to support the canopy. Since canopy development is supported by reserves and reserves were similar among treatments at the end of the experiment, it is likely that vine capacity was also similar among treatments as vines entered dormancy.

It has been suggested that cane fresh weight is an estimate of leaf area and vine capacity (4). Increasing the leaf area and/or storage tissue mass per gram shoot weight (as occurred here with increasing shoot number) indicates an increase in vine capacity per unit cane weight with increasing shoot numbers. This observation is in agreement with results from studies using mature vines and suggests the need to find an alternative method for estimating vine capacity in MP vines.

Measurements of root dry weight during the spring growth flush showed no change in any of the treatments from bud burst through bloom. Starch determinations, however, showed a sharp drop in the tissues of all treatments while observations of vine roots during destructive harvests indicated that the roots were actively growing during this time. Thus, a large portion of root growth during the spring growth flush is likely dependent upon the carbohydrate reserve pool available in the roots themselves.

A loss of trunk weight was detected in all treatments as starch levels declined with the onset of growth. A nearly equal amount of weight was found as new shoot and leaf growth. Clearly, there is not a 100% conversion from storage into new tissue and several studies have shown that basal leaves begin to export photosynthate once the fifth leaf is beginning to expand, which would add to the dry weight of the canopy (29,30). The data herein, however, provide evidence that trunk (above ground) reserves of one-year-old vines are responsible for a large portion of canopy growth during the spring flush. Koblet et al. (10) reported similar conclusions from studies using mature vines. They found a positive correlation between the volume of perennial, above ground tissue (i.e. trunks and cordons) and bud fruitfulness, total and lateral leaf area, yield, cluster weight, berries per cluster and must soluble solids. Since no differences were found among treatments in the present study from bud burst through bloom in dry weight or starch content of roots or trunks, I conclude that the numbers of vegetative sinks employed did not cause differences in the rate of carbohydrate reserve mobilization or in the absolute quantity of carbohydrate reserves utilized during the spring growth flush. In addition, the size of the canopy which can be generated by reserves during the growth flush appears to be indicative of the vines capacity. Further work is necessary to confirm this.

Three- and six-shoot vines had nearly identical root dry weight/unit leaf area throughout the season but always less than one-shoot vines. The similarity between values for three- and six-shoot vines suggests that available root mass may ultimately limit canopy development becasue of a functional equilibrium between roots and tops (6,18). This conclusion is supported by the fact that canopies of three- and six-shoot vines were quite similar in their morphologies but differed from one-shoot vines (15). The morphological changes closely resemble those associated with water stress e.g. shorter shoots, smaller leaves and lower specific leaf and shoot weights (8,14,26) as would be expected if water availability were limiting growth. Additionally, no further decline in root weight/leaf area occurred when shoot numbers were increased from three to six. In fact, some shoots either failed to develop beyond a single leaf or grew very slowly on six-shoot vines suggesting that availability of water, nitrogen, cytokinins or some combination of these was limiting development.

Dry weight of whole vines was different only at harvest. Leaf area differences between one-shoot and three- or six-shoot vines were about 2x at bloom. This difference, however, did not result in increased dry weight production during the early growing season. Dry weight production is driven not by the supply of photosynthetically produced sugars; rather, it is driven by sink activity (13,24,25). In one-shoot vines where less leaf area had developed by the end of the spring growth flush, the leaves had a higher SLW and were more effective at carbon assimilation per unit leaf area (15). Photosynthetic compensation in leaves has been demonstrated in *Vitis* (1,2) and *Prunus* (13) when leaf area is reduced relative to the carbohydrate sinks present. Photosynthetic compensation occurs in response to the carbohydrate source/sink relationship. As carbohydrate sources (leaves) are removed, the supply of photosynthate is reduced. Because the reduced supply is utilized more rapidly by the sinks, there are fewer end products of photosynthesis (hexose phosphates) in leaf cells to inhibit the rate of photosynthesis (12). It also possible that the increase in the available transpiration stream to leaves as leaf surface decreases relative to root mass, causes an increase in photosynthetic activity in leaves (7) concomitant with increasing sink demand.

The strength of carbohydrate sinks was apparently the limiting factor for dry matter accumulation in this study since vines with greater leaf area did not assimilate greater amounts of carbohydrates between bud burst and veraison. By contrast, between veraison and harvest continuing carbohydrate sink activity in three- and six-shoot vines resulted in their continuing accumulation of dry matter. The dry weight of one-shoot vines changed very little during the same period. Sink strength is defined as the sink's size times its activity (27) and this can be estimated by the rate of dry weight accumulation (24). By this definition, all tissues of three- and six-shoot vines continued as active carbohydrate sinks between veraison and harvest (with the exception of roots in three-shoot vines). Organs of one-shoot vines were very weak sinks during the same period. The cause of the continuing sink activity in three- and six-shoot vines is not clear.

Generally, vine productivity will be determined by (a) the amount of leaf canopy exposed to the sun; (b) the length of time the canopy is exposed; (c) the temperature during this exposure; and (d) the amount of sunlight the canopy receives during its exposure. The variable that is vine-dependent is the leaf surface area that can be generated. The amount of canopy that will be produced by the vine is dependent on (a) the quantity of reserves available to support the spring growth flush; (b) the number of growing points able to utilize those reserves; and (c) the quantity of roots available to support the canopy once it is developed. This listing is a great simplification since it ignores many biotic and abiotic factors influencing plant growth. It addresses however, the interrelationship between roots and canopy that results in a relatively constant root to shoot ratio (6,11).

CONCLUSION

For small, potted vines without fruit, I conclude that: (a) the rate at which reserves are utilized was not different with increasing numbers of vegetative sinks; (b) dry weight accumulation was only slightly greater for vines with greater leaf area and

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only between veraison and harvest; and (c) the ratio of mature cane fresh weight to perennial tissues (trunk and roots) was less in six-shoot vines than in one-shoot vines, supporting the observation that the use of pruning weights as an indicator of vine capacity in MP vines must be reevaluated. Vine capacity is defined by Winkler (28) as "the quantity of action with respect to total growth. The term refers to a vine's ability for total production rather than to rate of activity". Estimates of vine capacity may be possible by measuring trunk diameter or leaf area per vine at the end of the growth flush.

Developing a better understanding of the dynamics of grapevine canopy development and dry weight accumulation should allow fine tuning of vineyard management programs to maximize yields on a sustainable basis. Displaying greater leaf area early in the growing season does not necessarily lead to greater carbon assimilation in young, potted vines, and competition between vegetative sinks for available resources can alter canopy morphology and physiology.

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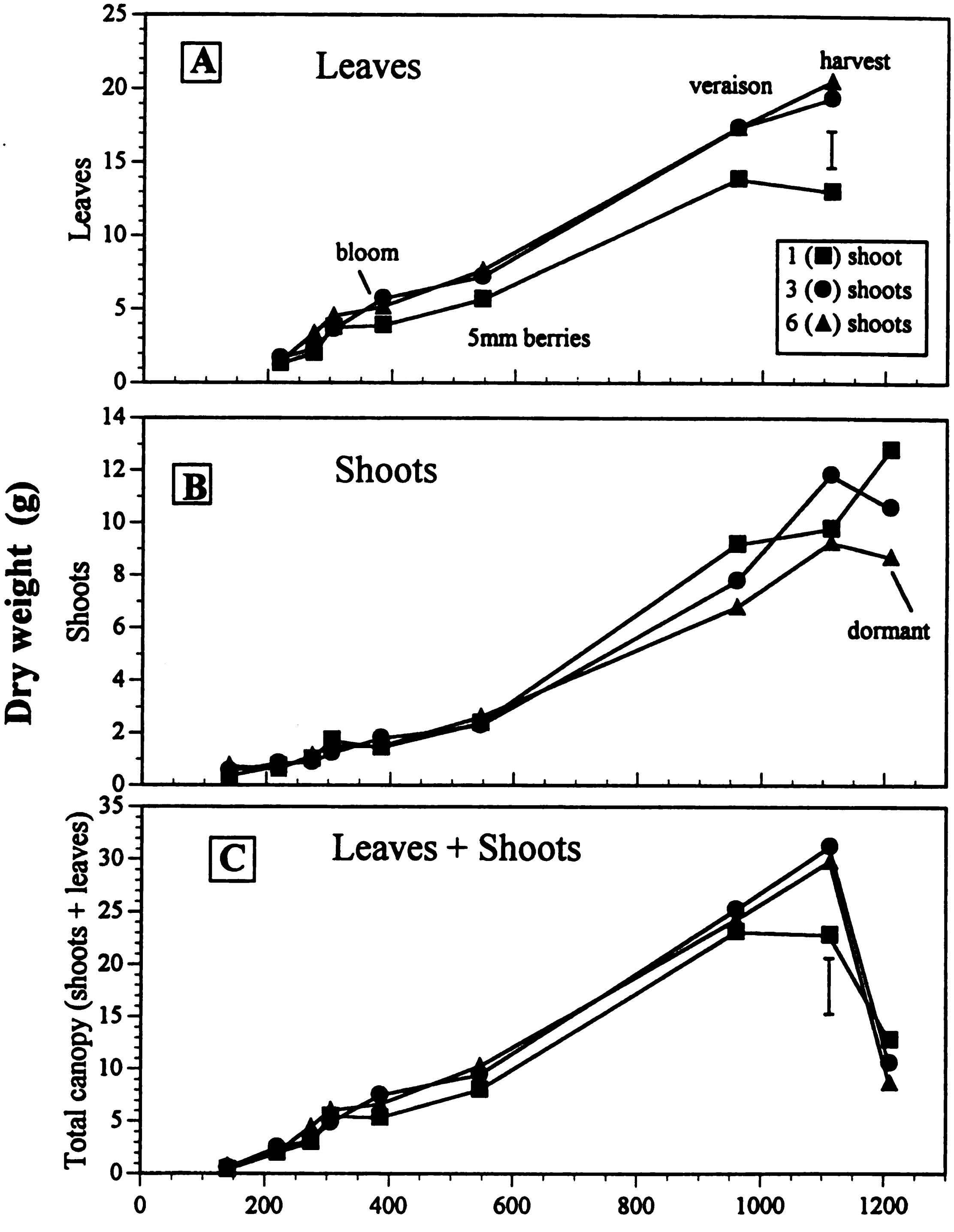

Figure1. Dry weight (g) of A) leaves; B) shoots; and C) shoots and leaves combined of potted Chambourcin grapevines with 1(■), 3(●) or 6(▲) shoots. Bars represent the LSD at p = 0.05.

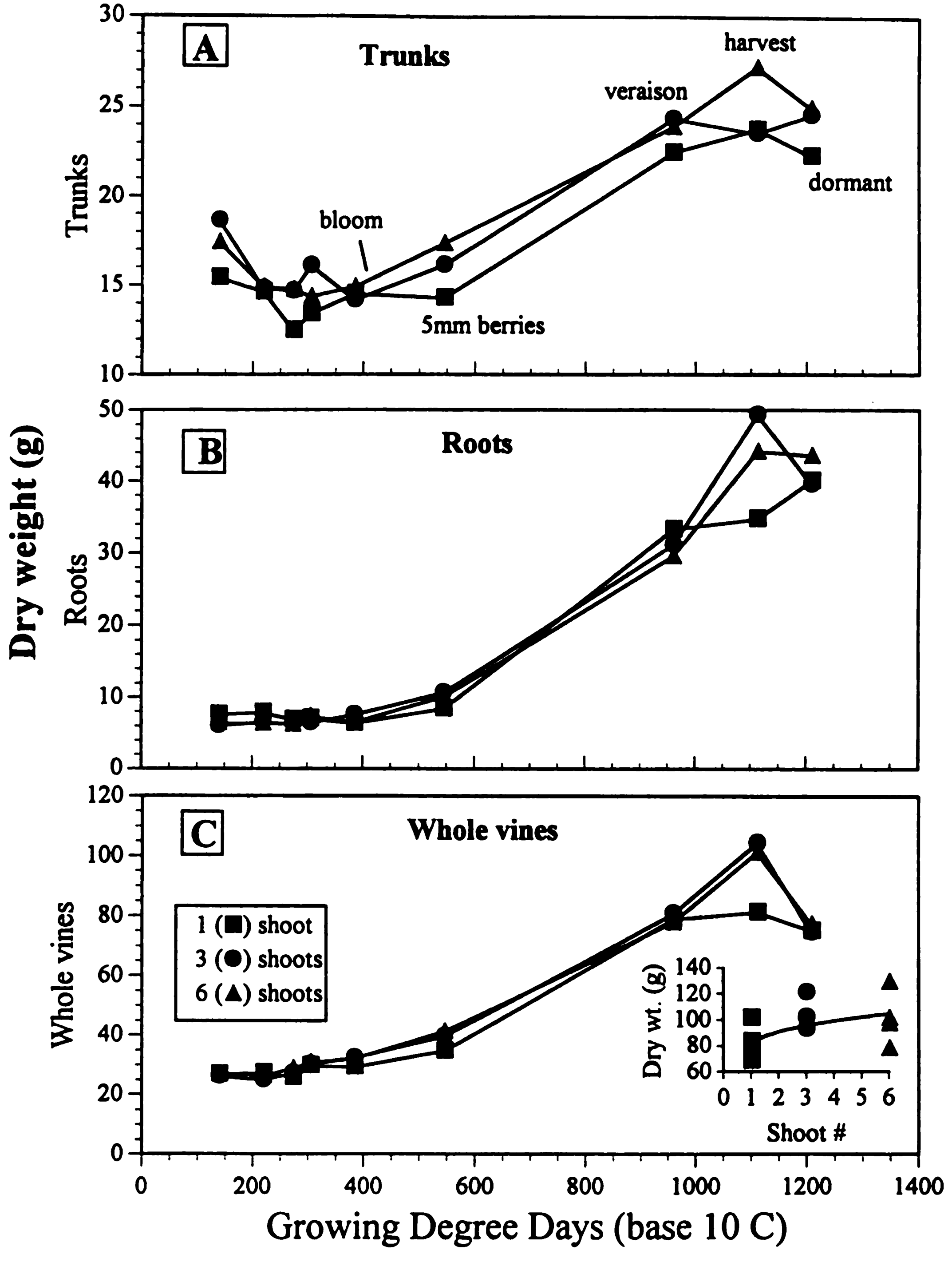

Figure 2. Dry weight (g) of A) trunks; B) roots, and; C) whole Chambourcin grapevines with 1(■), 3(●), or 6(▲) shoots. Inset in "C" shows the relationship between whole vine dry weight (g) and shoot number at harvest (y = 82.85 (x^0.1303) $r^2 = 0.2724$. p=0.10).

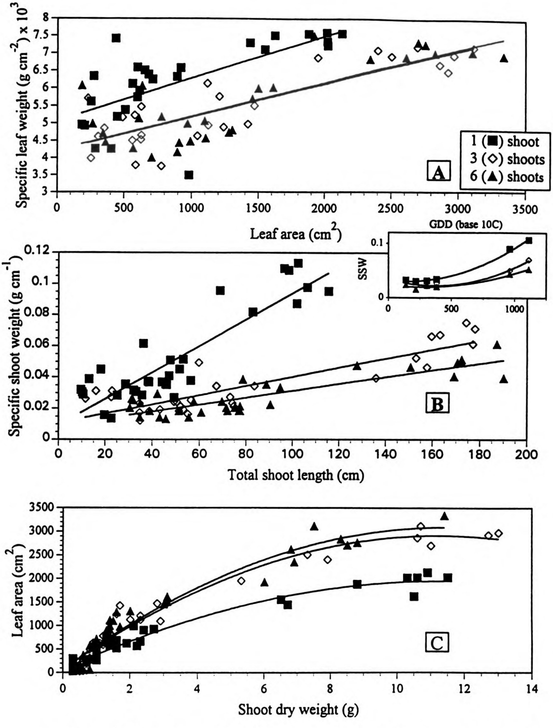

Figure 3. Relationship between A) leaf area and specific leaf weight; B) shoot length and specific shoot weight; and C) leaf area and shoot dry mass for Chambourcin grapevines with 1(■), 3(◇) or 6(▲) shoots. Inset in "B" shows change in specific shoot weight over the growing season.

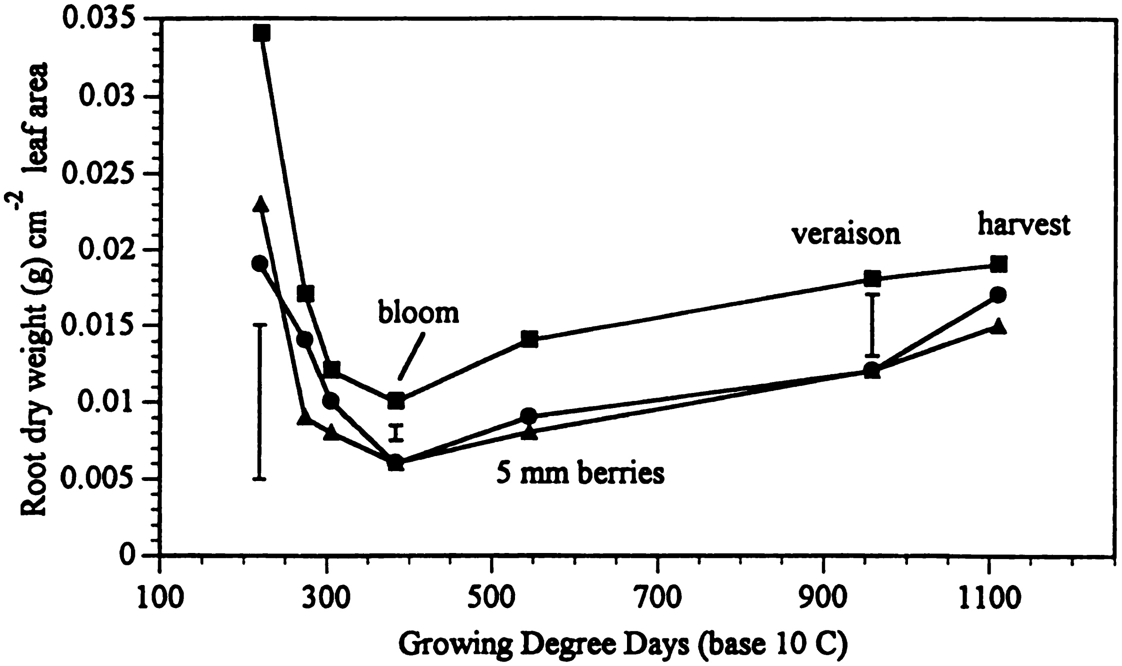

Figure 4. The relationship between root dry weight (g) and leaf area (cm^2) of potted Chambourcin grapevines with 1 (■), 3 (●) or 6 (▲) shoots. Bars represent the LSD at $p = 0.05$.

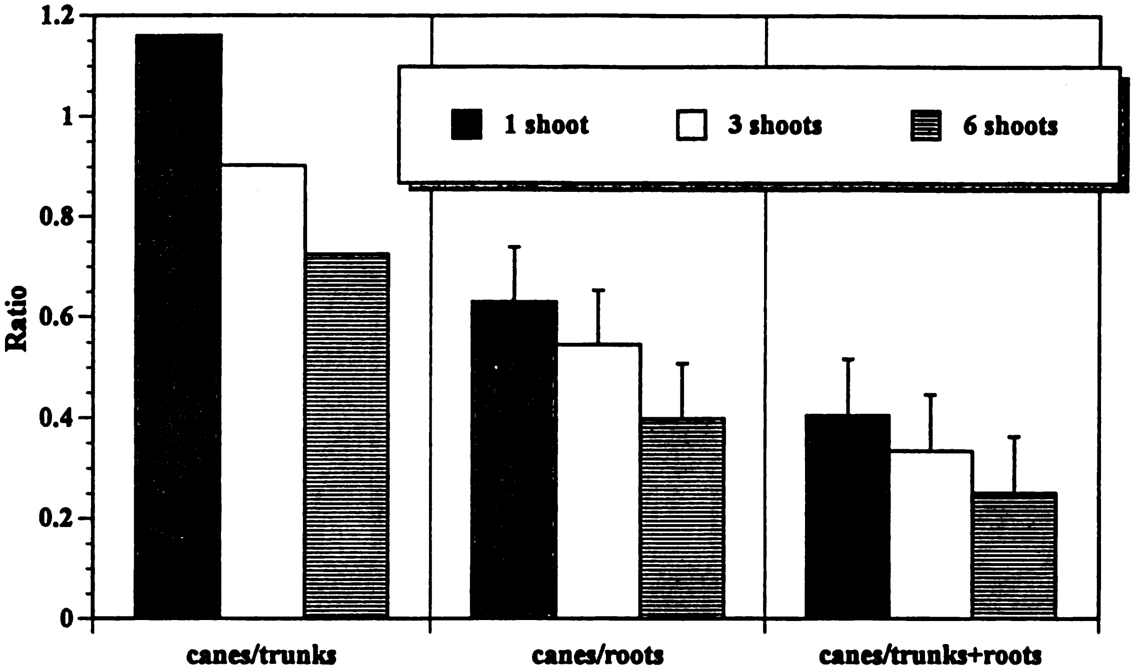

Figure 5. Relationship between cane fresh weight in grams (vine size) and the dry weight (g) of trunks, roots, or trunks + roots (total storage), of Chambourcin grapevines with 1-, 3- or 6-shoots. Bars represent the LSD value at p = 0.05.

IV. INFLUENCE OF SHOOT NUMBER AND CROP LOAD ON POTTED CHAMBOURCIN GRAPEVINES. I: MORPHOLOGY AND DRY MATTER PARTITIONING

ABSTRACT

Two-year-old Chambourcin grapevines were grown in 19-liter pots with the following treatments: one- or four-shoots and no clusters (1/0 and 4/0 respectively); one-shoot and one-cluster (1/1), and; four-shoots with one (4/1), two (4/2), three (4/3) or four (4/4) clusters. Four-shoot vines had greater leaf area, shoot length and leaf numbers per vine but 1-shoot vines had longer shoots, larger leaves, and greater leaf area and leaf number per shoot. Crop load effects on canopy morphology were relatively small. Berry number per cluster, berry weight and fruit soluble solids were not different among treatments but 4/2, 4/3, and 4/4 vines had two to three times greater fruit fresh weight than did 1/1 and 4/1 vines. Whole vine dry weight was never different among treatments, but there was a positive linear relationship between berry number and vine dry weight at harvest. More dry weight was partitioned to the fruit at the expense of roots, shoots and leaves in cropped vines vs. non-cropped vines. Dry weight differences of vegetative organs were small among crop load treatments. The combination of differences in individual organ weights, when partitioned to fruit rather than to vegetative tissues, resulted in increased in fruit dry weight with increasing berry numbers. Since fruit is approximately 75% H_2O by weight at harvest, small differences in dry weight result in large increases in yield. These data indicate that: (a) vegetative sinks have a greater impact than fruit on canopy morphology; and (b) carbohydrates used in fruit production are derived primarily from greater partitioning to fruit at the expense of vegetative tissues, and to

a lesser degree, greater dry matter production between veraison and harvest in vines with increasing fruiting sink strength.

INTRODUCTION

Reducing the cost of dormant pruning is very important as competition increases in global grape and wine markets (16). Researchers have shown that the use of mechanical or "minimal" pruning (MP) has resulted in greater yields than traditionally pruned controls (6,8,18,20). Winkler demonstrated that controling crop load on unpruned vines by removing clusters gave higher yields and fruit quality than did crop control by traditional, severe pruning, but was uneconomical (25,26). Thus, crop control by dormant pruning has been the method of choice due to economic considerations. Research conducted in cool climates has supported Winkler's conclusions (18,26), but recent investigations into crop thinning on mechanically pruned vines have focused on the use of mechanized thinning (6,7,8,12,18,20). If perfected, mechanized thinning could allow producers to maximize yield and fruit quality per unit land area on a sustainable basis.

To thin to the desired level, it is essential to first have an estimate of: (a) the vines' cropping potential or "capacity" (defined by Winkler (18) as "..the quantity of action with respect to the total growth and total crop of which the vine is capable"); and (b) the amount of fruit that is on the vine before thinning. Partridge suggested that a vine's crop be "balanced" with its capacity (17). Shaulis (19) followed this suggestion with a formula that increased the number of buds (and thereby crop) as the amount of mature, one-year old canes (and presumably capacity) increased.

It has been suggested that MP vines produce yields as much as two times greater than traditionally pruned vines because the capacity of MP vines is greater (6,8,12,20). Rapid canopy development by MP vines during the spring growth flush is thought to cause greater annual dry matter production (6,12). However, while some research has shown large, season-long differences in leaf area between spur and MP vines (20), other research showed that leaf area differences disappear by mid-season and spur vines actually had greater leaf area by harvest (8). In addition, when canopy dry weight was determined (including vegetative and reproductive growth), there was no difference among treatments. These data suggest that the greater yields of minimally pruned vines may be due to greater carbohydrate partitioning to fruit at the expense of vegetative tissues as opposed to increased vine capacity. The physiological basis for higher yields of minimally pruned vines remains unclear.

The purpose of this experiment was to: (a) study carbohydrate assimilation and partitioning in vines with differing canopy structure and crop load; (b) develop a better understanding of how changing carbohydrate source/sink relationships affect vine capacity; and (c) determine the physiological difference between severely and lightly pruned vines in terms of intravine carbohydrate relations. Specifically, the following were addressed: (1) which sink (vegetative or reproductive) has the greatest effect on canopy morphology; and (2) what is the source of carbohydrate used to sustain additional fruit as crop load is increased?

MATERIALS AND METHODS

Plant Material

Two-year old Chambourcin (J.S. 26-205) grapevines grafted to 5-C rootstock were planted in 19-liter plastic pots with a 45% sand, 45% loam and 10% peat sterile potting mix on May 11, 1994. Potted vines were placed on pea-gravel in full sun and watered regularly. Fertilizer was applied as a balanced N,P,K solution once per month. Pesticides were applied as necessary.

When buds were at the swell-two stage (10) of development (elongated sphere prior to burst), their numbers were adjusted to give either one or four buds which would be allowed to develop. As the vines grew, all laterals were removed once per week. Flower cluster numbers were adjusted about one week before anthesis to give the following treatments: one- or four-shoots with zero clusters (1/0 and 4/0, respectively); one-shoot with one-cluster (1/1); or four-shoots with one, two, three or four clusters (4/1, 4/2, 4/3 and 4/4, respectively) (Table 1).

Vines were blocked according to their fresh weight prior to planting, producing four blocks. Treatments were randomly assigned to five vines for each treatment in each block; one vine for each treatment-block to be used at each destructive harvest. At various intervals (described below), vines were selected for destructive harvest. The experimental design was a randomized complete block with seven treatments, four replicates and five partitioning dates for a total of 140 vines.

Vine Dry Weight

Vines were destructively harvested at five phenological stages: (1) pre-bloom (about five days before any flowers opened); (2) post-anthesis (5-mm berry diameter);

(3) veraison (30% of berries showing coloration); (4) harvest; and (5) dormant (all leaves abscised). Shoot length, leaf number and dry weight were determined at each destructive harvest. Dry weights were determined by partitioning the vine into its various organs and recording the fresh weight of each. Tissues were then placed into paper bags in a drying oven at 60°C until no further weight reduction occurred (about four days; seven to ten days for fruit). After drying, tissue weights were recorded and percentage water content calculated.

Leaf Area

Leaf area was determined using a Li-Cor LI-3000 portable leaf area meter (Lambda Instrument Corp., Lincoln, Nebraska) at each destructive harvest date.

Fruit Chemistry

Ten-berry samples, collected from vines partitioned at harvest, were weighed and placed in sealed plastic bags at -20°C until analyzed. Berries were crushed and the juice strained through cheese cloth in preparation for analysis. Sugar content, expressed as °Brix, was determined with a bench top, temperature compensating refractometer, and titratable acidity and pH were determined using previously described methods (2).

Data Analysis

Data were analyzed with the MSTATC statistical package (MSTATC, Michigan State University, East Lansing, MI) using a two-way Analysis of Variance and orthogonal contrasts and, where appropriate, by regression analyses using DeltaGraph (Delta Point Inc., Monterey, CA).

RESULTS AND DISCUSSION

Canopy Morphology

The number of shoots on vines had the greatest influence on whole vine leaf area until veraison (Figure 1a.). Four-shoot vines had 200% more leaf area than one-shoot vines pre-bloom. At that time, 4/0, 4/1 and 4/2 vines had leaf area intermediate to 1/0 and 1/1, and 4/3 and 4/4 vines. No leaf area differences existed at 5mm berry diameter. At veraison, 1/1 and 1/0 vines had the least and four-shoot vines the greatest leaf area. The only exception was 4/3 vines which had leaf area intermediate to the remaining four-shoot and one-shoot treatments. Leaf area increased between veraison and harvest in non-fruited and 1/1 vines only. Leaf area and shoot length were shown to be closely related (14) and this was true in the present study. Leaf area per shoot (Figure 1b) and shoot length per shoot (Figure 2b) were always greatest on one-shoot vines, and each increased faster on one-shoot vines throughout the growing season as compared to four-shoot vines. Crop load did not effect leaf area per shoot or shoot length per shoot at any date. Leaf area per vine (Figure 1a) and shoot length per vine (Figure 2a) were related. Shoot length per vine was effected both by shoot number and crop load from anthesis through leaf abscission. Pre-bloom and at 5mm berries, treatments were grouped by shoot number with one-shoot vines having the least and four shoot vines the greatest shoot length per vine (Figure 4a). By veraison, crop load had caused a reduction in the rate of shoot elongation of 4/3 and 4/4 vines so they had shoot length per vine intermediate to one-shoot vines and 4/0, 4/1 and 4/2 vines. Shoot growth stopped after veraison in all cropped treatments but continued in non-cropped vines. At harvest, 4/0 vines had the greatest shoot length per vine and 1/1 vines the least. The remaining treatments (1/0, 4/1, 4/2, 4/3 and 4/4) were intermediate.

Leaf size was always greater in one-shoot vines (Figure 1c). Crop load had no effect on leaf size in either one- or four-shooted vines. Four-shoot vines had a greater number of leaves per vine, but fewer leaves per shoot than one-shoot vines (Figures 3a and 3b, respectively). Increasing the crop load caused 4/3 and 4/4 vines to have lower leaf numbers than 4/0 and 4/1 vines at veraison and harvest.

Canopy morphology is clearly affected more by competing vegetative sinks than by competition from reproductive sinks from bud burst through veraison. Similar observations have been made in minimally pruned grapevines in the field (6,7,8). However, the relative effects of vegetative and reproductive sinks on canopy morphology at different phenological stages have not been clear from past studies. The data presented here demonstrate that shorter shoots and smaller, thinner (data not shown) leaves are the result of competing vegetative sinks. It is the presence of many vegetative sinks (shoot tips and expanding leaf blades) that produce the rapid canopy deployment and morphology characteristic of minimally pruned vines (12,20)

Dry Weight Partitioning

One-shoot vines had lower leaf dry weights at veraison only (Figure 4a). At veraison, the higher crop load of 4/3 and 4/4 vines caused them to have leaf dry weight intermediate between 1/0 and 1/1 vines and 4/0, 4/1 and 4/2 vines. Between veraison and harvest, leaf dry weight declined in all vines with fruit, possibly due to a retranslocation of carbohydrates to ripening fruit. Leaf dry weight increased in non-cropped vines during the same interval, however, but at a slower rate than the period from bud burst through veraison suggesting that the relative sink strengths of leaves and storage tissues had changed. At harvest, 4/0 vines had the greatest leaf dry weight, 1/0 vines were intermediate and all other treatments were similar with the least amount of leaf dry weight.

Shoot dry weight increased from pre-bloom through veraison, but was similar in all treatments (Figure 4b). Treatment had no effect on shoot dry weight until veraison. At harvest, 1/1 vines had the greatest, 4/0 and 1/1 vines intermediate and 4/1, 4/2 and 4/3 vines the least shoot weight. By contrast, in dormant vines, 1/0, 1/1 and 4/0 vines had the greatest shoot weights. Even though heat accumulation was low, the post-harvest period was a time of rapid increase in shoot dry weight. The percentage of lignified nodes also increased during this time in all treatments (data not shown). The percentage of lignified nodes of 1/1 vines increased the most (50.8% to 87.75%) and of 4/4 vines the least (44.5% to 57.7%) between harvest and leaf fall.

Shoot dry weight decreased rapidly between veraison and harvest in four-shoot vines with crop. The observed change may be due to a retranslocation of carbohydrates from shoots to fruit during fruit loading (5,14). Differences in dry weight loss from shoots of fruiting one-and four-shoot vines may be due to differences in shoot structure. Specific shoot weights were always greater in one-shoot vines indicating a greater amount of structural tissue (data not shown). Since shoots of four-shoot vines contained less structural tissue, a greater percentage of the total dry weight may have been available for retranslocation as non-structural carbohydrates.

Fruit dry weight was not different among treatments until harvest (Figure 4c). However, the rate of carbon allocation to fruit was greater in vines with higher crop loads from bloom through harvest reflecting the greater sink strength represented by higher crop loads. At harvest, fruit dry weight was greatest in 4/2, 4/3, and 4/4 vines and least in 1/1 vines. Dry weight accumulation by fruit of 4/2, 4/3 and 4/4 vines occurred at a much higher rate between veraison and harvest as compared to fruit of 1/1 and 4/1 vines.

Root dry weights were similar for all treatments from bud burst until veraison (Figure 5a). Root dry weights were greater for non-fruiting vines at harvest and in dormancy only. Vines with a high crop load (4/3 and 4/4) and 1/1 vines had the least root dry weight in dormancy in contrast to 1/0, 4/0 and 4/1 which had the greatest. Root weight was nearly static between veraison and harvest in cropped vines indicating that the strength of roots as a carbohydrate sink had virtually ceased while fruit was ripening. By contrast, roots of non-cropped vines accumulated dry weight between veraison and harvest faster than any other organ.

Trunk dry weight was similar among treatments until veraison (Figure 5b). At veraison, trunk weight was least in 4/0 vines and greatest in 4/4 vines. All other treatments were intermediate and their was no relationship between crop load or shoot number and trunk dry weight. Trunk dry weights declined slightly on all fruit-bearing vines between veraison and harvest. These data again indicate a strong possibility that carbohydrates were retranslocated from trunks as well as shoots and leaves to promote fruit maturation. The post-harvest period was again marked by an increase root and trunk dry weights, demonstrating the importance of even short recovery periods following harvest for the replenishment of storage reserves.

The dry weight of current-season canopy tissues was nearly identical for non-cropped one- and four-shoot vines (Figure 6a). Carbohydrates were allocated differently however, so that four-shoot vines had greater leaf weight and one-shoot vines had greater shoot weight at veraison (Figures 4a and 4b). Canopy dry weight of 4/3 vines was greater than non-fruiting vines at both veraison and harvest due to the weight of fruit. The 1/1, 4/1, 4/2 and 4/4 vine canopy weights were intermediate between 4/3 and 1/0 and 4/0 vines at veraison. By contrast, at harvest, canopy dry weights of 4/2, 4/3 and 4/4 vines were greatest, 1/1 and 4/1 vines intermediate, and non-fruited vines least. Trunk + root weights were similar in all treatments until harvest when non-fruited vines had more storage mass (Figure 6b). The ratio of root dry weight to shoot + leaf dry weight was not different among treatments at any time (data not shown).

Differences in canopy dry weights account for most of the dry weight difference among crop-bearing treatments. A comparison of vine organ dry weights among treatments for evidence of differential carbon partitioning to fruit is shown in Table 2. The presence of fruiting sinks caused a large amount of the total vine dry weight (approximately 25% depending on crop load) to be partitioned to fruit at the expense of vegetative tissues (1/1 - 1/0 and 4/1 - 4/0 comparison). The roots were most affected by reallocation of carbohydrates to the fruit. The addition of increasing numbers of berries (fruiting sinks) caused small additional amounts of dry matter partitioning to the fruit (4/4-4/1; 4/3-4/1; 4/2-4/1 comparisons). There was evidence that vines with larger fruiting sinks assimilated as much as 10% additional carbohydrate over the growing season relative to non-cropped controls. Remarkably, there was no difference in the weight of whole, dormant vines suggesting similar vine capacity during the following season. However, root weight of 1/1, 4/3 and 4/4 vines was less than 1/0, 4/0 and 4/1 vines and 4/2 vines were intermediate. It is likely that a reduction in root mass would have detrimental effect on the following seasons vine capacity (26,27), but it is not clear from these data if a mature vine would maintain the same capacity as in the current growing season. The root mass of vines in all treatments increased during the course of this experiment. In an established vineyard the goal would be to simply reutrn to the same status that existed at the beginning of the growing season, assuming that condition was acceptable.

Whole vine dry weight differed among treatments at veraison only (Figure 6c). At that time, 4/1, 4/2, 4/3 and 4/4 vines had greater dry weight than 1/0 and 4/0 vines, and 1/1 vines were intermediate. Vine dry weight was linearly related to berry number in fruiting vines at harvest ($y=0.52x + 9.37$, $r=.691$. Figure 6c inset). These data indicate that greater reproductive sink strength caused greater carbon assimilation, and the additional carbon was responsible for a portion of the increased yield of 4/2 and 4/3 vines. When vine dry weight was regressed against leaf area (Figure 7), 4/3 vines showed a higher rate of assimilation per unit leaf area than 4/1 vines (.065 g cm^{-2} and .045 g cm^{-2}, respectively) which would be expected with a decreasing carbohydrate source/sink ratio (8,22). Unlike earlier work (15), the presence of more leaf area at bloom in 4/0 vines did not result in greater seasonal carbon assimilation than in 1/0 vines. The 4/0 vines had an average of 5% more dry weight at harvest than 1/0 vines. The reason for the discrepancy between these and earlier data is not known. It may be due to variation between seasons and/or vines.

Yield

Components of yield data appear in Table 3. Fruit yields were greater in 4/2 and 4/3 vines. The 1/1 and 4/1 vines had similar, low yields and 4/4 vines were intermediate. The 4/2 and 4/3 vines had 2.4 and 2.9 times greater yield (respectively) than 1/1 vines. Yield differences were due to cluster and berry number. Treatment did not effect berry weight but there was an inverse, linear relationship between cluster number and berries per cluster in four-shoot vines ($y = -5.92x + 48.60$;

$r = .941$). Cluster weight was greatest in 4/1, 4/2 and 4/3 vines, intermediate in 1/1 vines, and least in 4/4 vines. The difference in cluster weights is the result of varying numbers of berries per cluster. The lower number of berries per cluster observed in four-shoot vines with increasing cluster numbers may be caused by one, or a combination of two factors. First, less leaf area (and carbohydrate) per cluster available at bloom (data not shown) results in a lower percentage of flowers that will set fruit (4). Second, as competition among vegetative sinks increases, cluster length and flower number per cluster decrease (15). Calculations showed that the leaf area per flower on 4/1 vines was the highest of any treatment (Appendix C) because of pre-bloom flower cluster thinning, and these vines had the highest percentage fruit set. By contrast, 4/4 vines had the least leaf area per flower and the lowest percentage fruit set.

Total soluble solids, pH and total acidity were not different among treatments (Table 4). Total sugar accumulation, however, was much greater in the fruit of 4/2, 4/3 and 4/4 vines by comparison with fruit of 1/1 and 4/1 vines (Figure 8).

Crop load (weight of fruit/weight of dormant cane prunings) is considered to be an effective indicator of the carbohydrate source/reproductive sink relationship in grapevines (3). Because leaves are borne on canes, greater cane weight is thought to equal more leaves and a larger canopy. The efficacy of this approach has recently been questioned (6). Crop load calculated for the various treatments appears in Table 5. The 1/1 vines had the lowest crop load and 4/3 vines the greatest. The observed range of crop load would indicate that 4/3 vines were overcropped and 1/1 and 4/1 vines undercropped. Yet fruit quality was not different among treatments (Table 4). A careful examination however, indicates that there is a difference between the highest and lowest crop loads in the quantity of root tissue. This indicates that there may be an effect of high crop loads resulting in a reduced capacity for canopy development and growth the following season.

Leaf area per gram fruit fresh weight was greater in 1/1 and 4/1 vines than in the remaining treatments which were similar (Table 5). However, even the 4/3 vines with the highest crop load had over 15 cm^2 of leaf area per gram fruit and this is considered more than adequate (11,25). These data support the suggestion that cane pruning weight (vine size) does not have the same meaning in a vine system where vegetative competition leads to short shoots with low specific weights (6,7,15,20). The higher leaf area per gram shoot weight found under these circumstances (15) coupled with the higher yields associated with this type of vine system (6,8,18) lead to crop load estimates that are not indicative of the true carbohydrate source:reproductive sink relationship. Crop load assessments, therefore, must be based on actual leaf area per unit fruit weight measurements.

Carbohydrate Source/Sink Relationships

Increasing shoot numbers caused an alteration of canopy morphology in four-shoot vines, but it is not clear from the data presented how this occurs. However, shorter shoots and reduced specific leaf weight are characteristic responses to water stress (13,24). More research is necessary to determine if the size of the root or xylem systems ultimately limit water supply, whether the supply of growth regulators is limiting, or if some combination of the two cause the observed changes in canopy morphology. On a whole vine scale, the additional buds allow for early canopy development as observed earlier (6,8,12,25). By bloom, four-shoot vines had nearly twice the leaf area of one-shoot vines, although this difference was nearly gone by veraison. An additional benefit of retaining more buds is the production of more flower clusters which give the vine the potential to set more fruit.

In the absence of fruit or with a small number of berries, a vine's carbon assimilation appears to be sink limited. In this situation, end-product inhibition of photosynthesis occurs when sugars are not utilized as rapidly as they are synthesized in the leaf (9,23). If that condition continues, there is a down-regulation of production of photosynthetically active proteins, the net result being a decrease in photosynthetic efficiency per unit leaf area (1,21). The addition of more fruiting sinks within the range used in this study resulted in greater total carbon assimilation and a greater portion of the total carbohydrate being budgeted to fruit at no cost to the perennial parts of the vine (i.e. tissues not lost to frost or pruning) as compared to vines with lower crop loads. In other words, yield was brought into balance with the vines capacity. By contrast, a comparison of fruiting and non-fruiting vines shows that the presence of fruit results in less carbon allocation to vegetative tissues, especially roots, after veraison. Root mass increased in low crop-load vines between harvest and leaf fall but not in high crop-load or 1/1 vines. More research is necessary to determine the long-term effects of this phenomeno.

Sink strength can be estimated by the rate of dry weight accumulation in a given organ (22). Root weight increased at the highest rate between veraison and harvest on non-fruiting vines, so roots are the strongest carbohydrate sink during this period in the abscence of fruit. When fruit is present, it becomes the strongest carbohydrate sink between veraison and harvest. The results of the present study suggest that a benefit of minimal pruning in field vines is that fruit production is in closer balance with the vines capacity, and the vines are neither sink limited nor source limited. Pool (18) suggested that crop load could be adjusted on minimally pruned field vines after danger of spring frost and after an assessment of bud fruitfulness to more fully utilize vine capacity. It appears that within limits, small amounts of additional carbon allocated to fruit or assimilated due to the presence of fruit translate into large additional yields of fresh fruit. This is due to the fact that fruit is nearly 75% water at harvest when fully ripe (21°Brix in this study). For each gram of carbon allocated to fruit, there is a return of about four grams of fresh fruit.

CONCLUSION

Retaining large numbers of buds at pruning insures that the maximum amount of leaf area (i.e. carbohydrate sources) is expressed at the earliest possible time. This large source is then available to supply a strong fruiting sink while at the same time maintaining the vines vegetative structure. The large number of shoots resulting from light pruning produce many flower clusters which usually produce sufficient crop so that it can be balanced with the vines capacity. Yet it is obvious that vines can be overcropped. So we must develop methods to determine when sources and sinks are in balance at a time sufficiently early during the growing season to allow adjustments to be made.

Data presented in this and previous chapters support the hypothesis that the quantity of leaf area that a lightly-pruned vine can generate during the spring growth flush is indicative of that vine's relative capacity for dry matter production under a given set of environmental conditions. More research is necessary to determine how the genotype of scion and rootstock interacting under varying environmental conditions will affect vine capacity as determined by the canopy size at the end of the growth flush.

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Table 1. Shoot and cluster number treatments used on potted Chambourcin grapevines

Treatment	Shoot #	Cluster #
1/0	1	0
4/0	4	0
1/1	1	1
4/1	4	1
4/2	4	2
4/3	4	3
4/4	4	4

Table 2. Dry weight differences of vine organs between selected crop load treatments of Chambourcin grapevines. Values for vines with lower crop loads were subtracted from those of vines with higher crop loads. A negative value indicates that the organ was of greater size in vines with a lower crop load.

	Dry weight difference in grams				Sub total	Cluster	Total vine weight
Comparison	**Leaves**	**Shoots**	**Trunks**	**Roots**	**organs z**	**dry weight (g)**	**(g) y**
Crop x control							
1,1 - 1,0	-3.3	-4.6	0.3	-16.3	-24.0	17.4	-6.6
4,1 - 4,0	-5.5	-4.5	3.7	-23.6	-29.8	20.7	-9.1
4,2 - 4,0	-5.7	-4.4	3.8	-25.2	-31.6	41.3	9.7
4,3 - 4,0	-7.2	-6.1	6.5	-25.7	-32.5	47.2	14.8
4,4 - 4,0	-7.1	-5.0	3.3	-29.7	-38.5	38.4	-0.1
Crop Load							
4,2 - 4,1	-0.2	0.1	0.0	-1.7	-1.8	20.5	18.8
4,3 - 4,1	-1.7	-1.6	2.8	-2.1	-2.6	26.5	23.9
4,4 - 4,1	-1.6	-0.5	-0.4	-6.2	-8.7	17.7	9.0

z Represents the sum of dry weight differences in leaf, shoot, trunk and root tissues.

y Calculated by subtracting the summed differences in vegetative tissue weights from fruit weight

Table 3. Components of yield for potted Chambourcin grapevines with 1 shoot and 1 cluster (1/1) or, 4 shoots and 1(4/1), 2 (4/2), 3 (4/3) or 4 (4/4) clusters.

Treatment	Yield (g)	Cluster weight (g)	fruitfulness (g shoot-1)	Berry number vine-1	Berry number cluster-1	Berry fresh weight grams
1/1	66.7	66.7	66.7	31.5	31.5	2.1
4/1	81.2	81.2	20.3	41.3	41.3	2.0
4/2	162.1	82.5	41.3	76.0	38.0	2.2
4/3	190.6	74.8	47.6	89.0	36.0	2.1
4/4	145.5	46.1	36.4	84.3	27.3	1.7
F sig.	**	*	**	**	n.s.	n.s.
LSD .05	77.5	24.6	22.6	35.8		

Table 4. Fruit chemistry of Chambourcin grapes from vines with 1 shoot and 1 cluster (1/1) or, 4 shoots and 1 (4/1) 2 (4/2), 3 (4/3) or 4 (4/4) clusters.

	Berry Chemistry		
Treatment	SS	pH	TA
1/1	21.5	3.23	7.9
4/1	20.6	3.34	7.4
4/2	21.5	3.32	7.8
4/3	21.1	3.31	7.2
4/4	21.8	3.31	7.3
F sig.	n.s.	n.s.	n.s.
LSD .05			

SS = soluble solids (brix)
TA = total acidity (g/l)

Table 5. Crop load and leaf area gram-1fruit fresh weight for Chambourcin grapevines with 1 shoot and 1 cluster (1/1) or, 4 shoots and 1 (4/1), 2 (4/2), 3 (4/3) or 4 (4/4) clusters.

Treatment	Crop Load (yield/ vine size)	Leaf area (cm2) g-1 uit wt (fresh)
1/1	2.89	36.8
4/1	5.03	32.1
4/2	10.97	15.3
4/3	20.16	15.6
4/4	13.41	19.4
F sig.	*	**
LSD .05	10.35	13.0

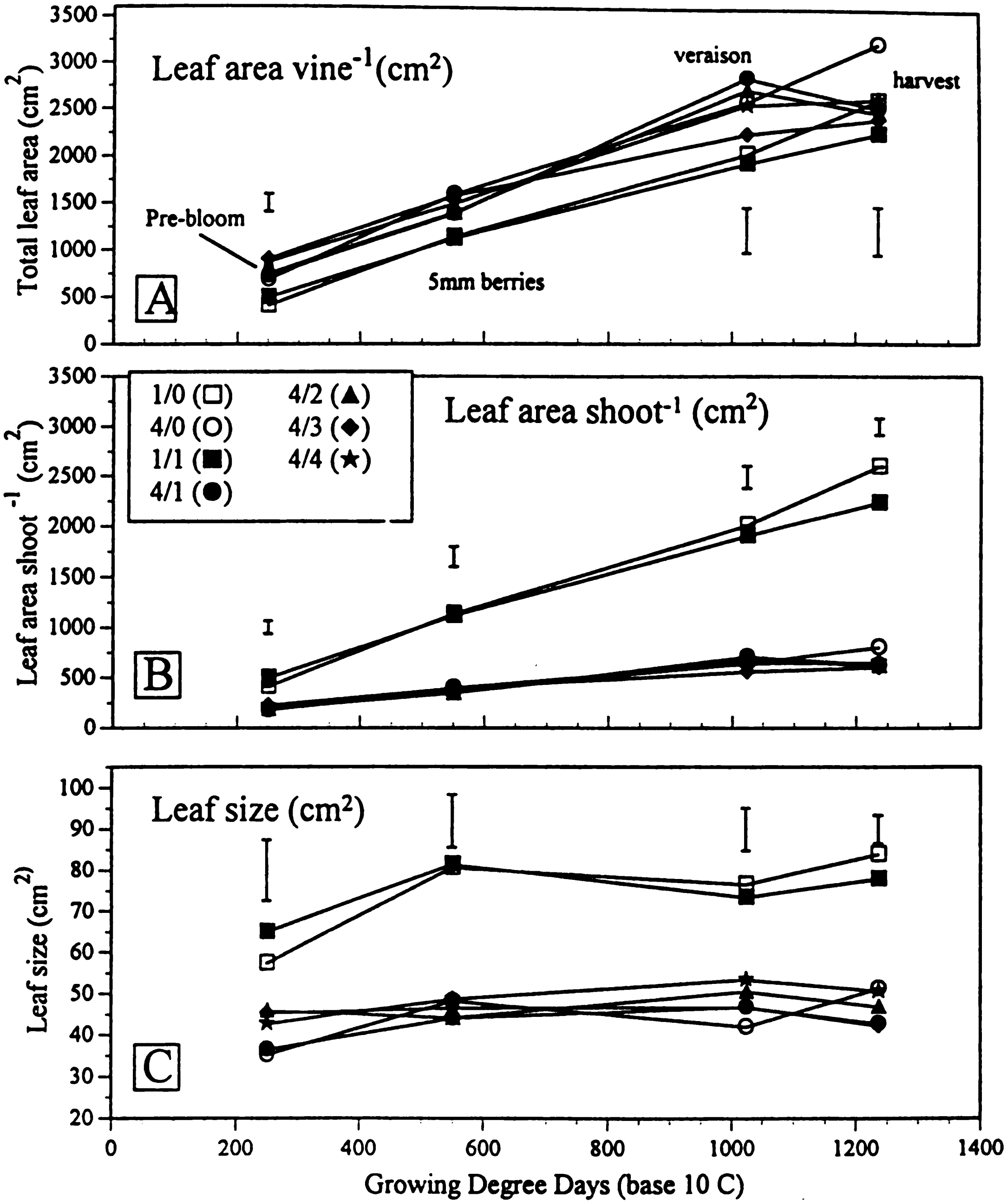

Figure 1.Leaf area vine^{-1} (A), shoot^{-1} (B) and leaf size (C) of potted Chambourcin grapevines with 1(□) or 4(○) shoots and no clusters: 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at $p = 0.05$.

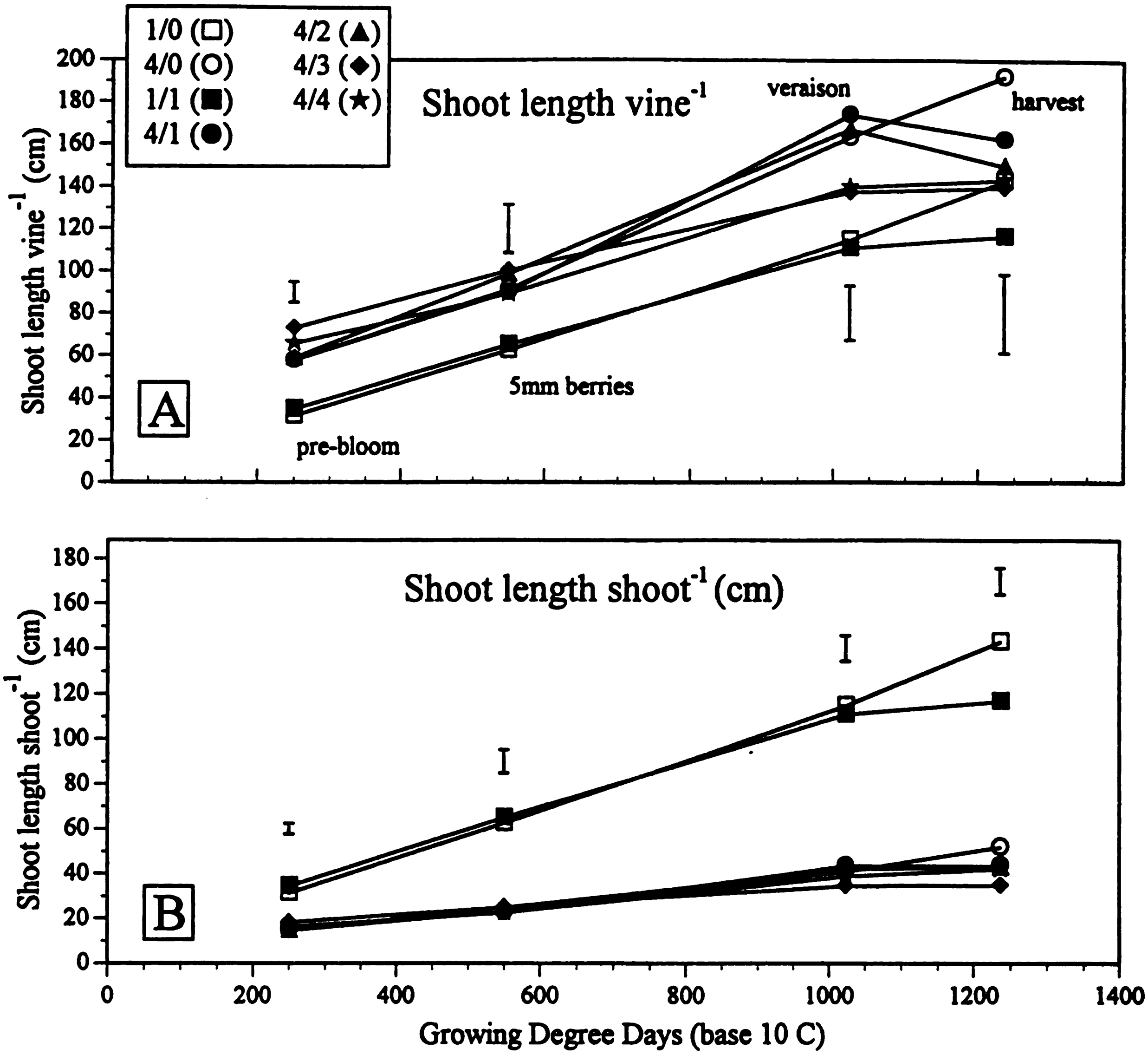

Figure 2. Shoot length vine^{-1} (A) and shoot^{-1} (B) of potted Chambourcin grapevines with 1(□) or 4(○) shoots and no clusters: 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at $p = 0.05$.

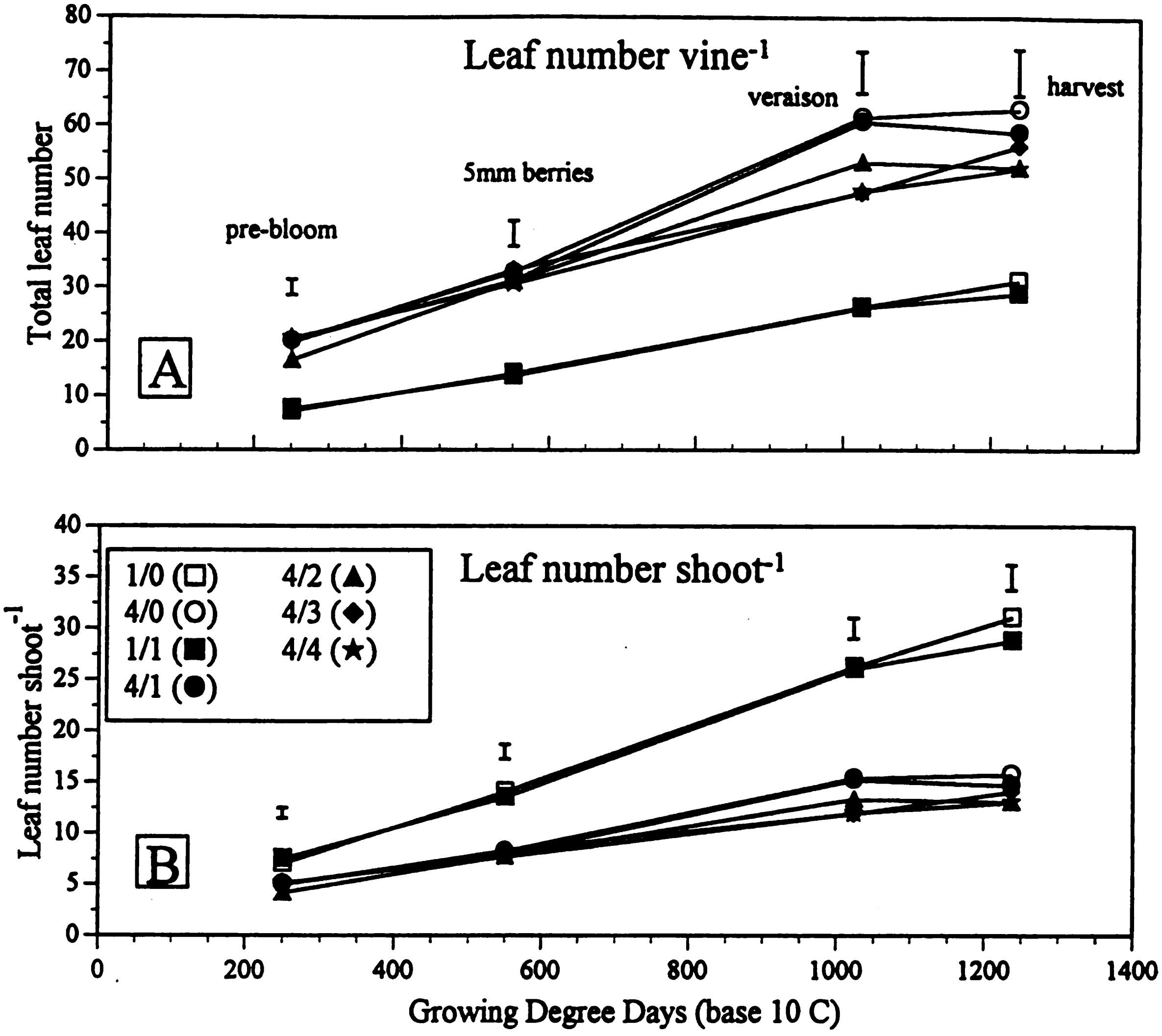

Figure 3. Leaf number vine^{-1} (A) and shoot^{-1} (B) of potted Chambourcin grapevines with 1(□) or 4(○) shoots and no clusters: 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at $p = 0.05$.

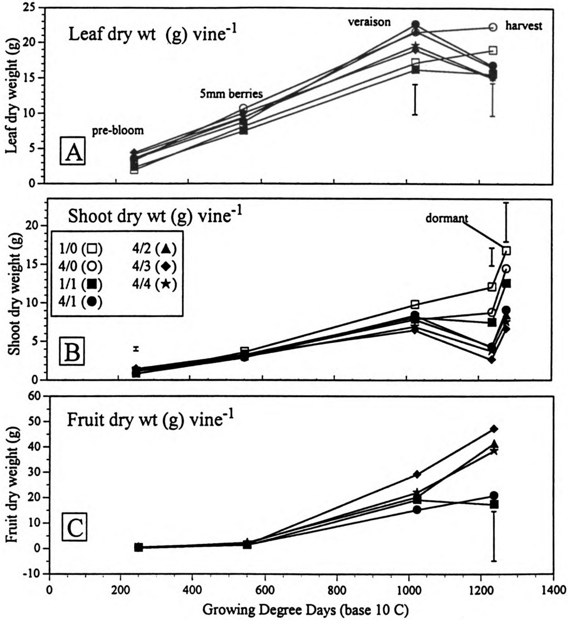

Figure 4. Dry weight (g) of leaves (A), shoots (B) and fruit (C) of Chambourcin grapevines with: 1(□) or 4(○) shoots and no clusters; 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at p = 0.05.

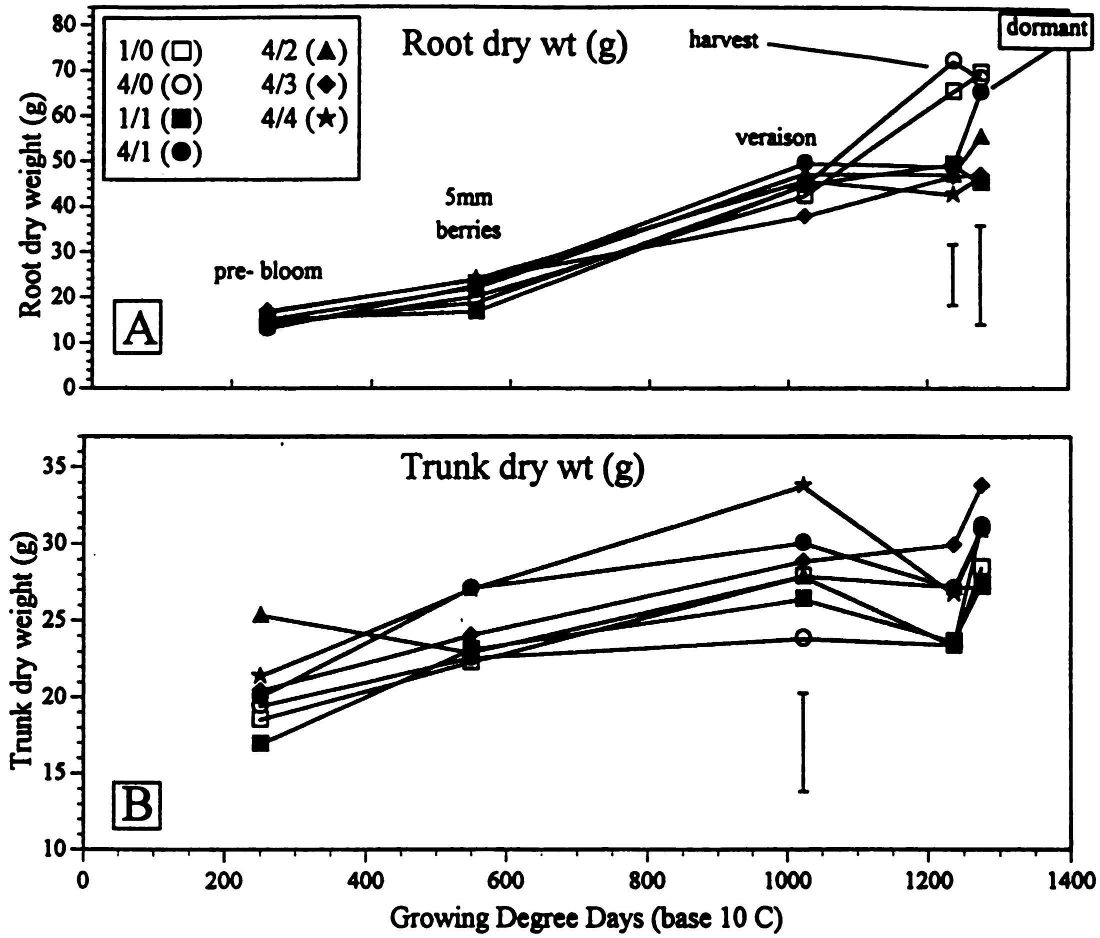

Figure 5. Dry weight (g) of roots (A) and trunks (B) of Chambourcin grapevines with: 1(□) or 4(○) shoots and no clusters; 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at p=0.05.

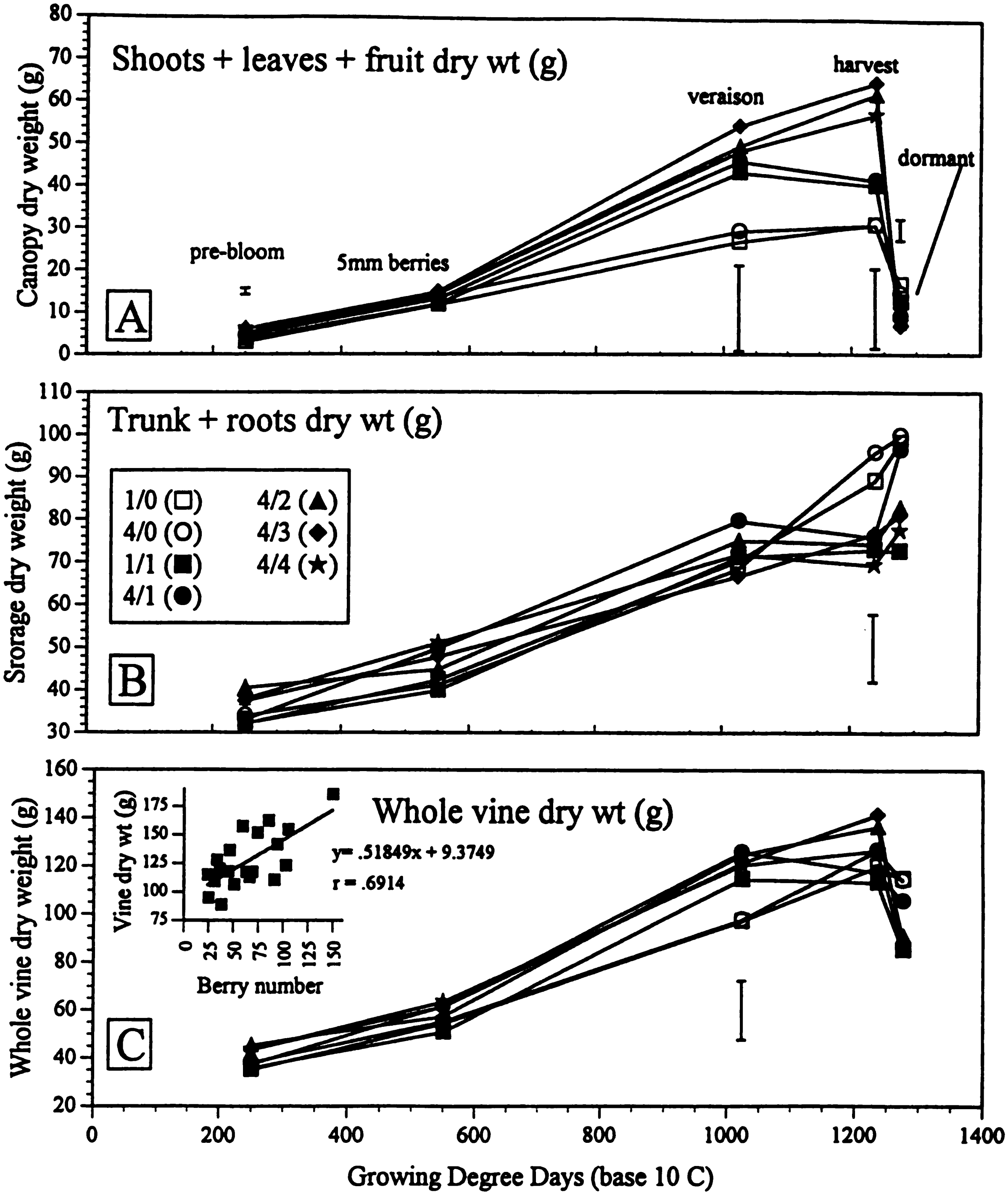

Figure 6. Dry weight (g) of canopies (A); trunks + roots (B); and whole vines (C) of Chambourcin grapevines with: 1(□) or 4(○) shoots and no clusters; 1shoot, 1cluster (■) and; 4 shoots with 1(●), 2(▲), 3(◆) or 4(★) clusters. Bars represent the LSD at p = 0.05. Inset in C shows the relationship between vine dry weight at harvest and berry number.

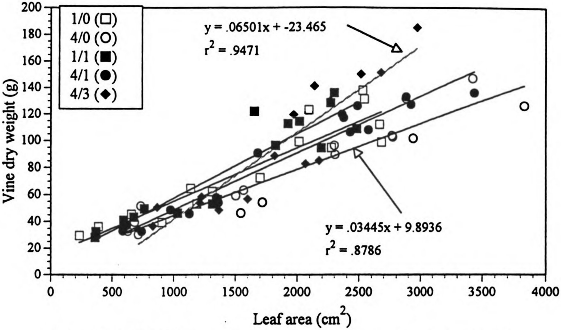

Figure 7. Relationship between vine dry weight and leaf area of potted Chambourcin vines with 1(□) or 4 (○) shoots and no clusters; 1 shoot, 1cluster (■), and; 4 shoots with 1(●) or 3 (◆) clusters.

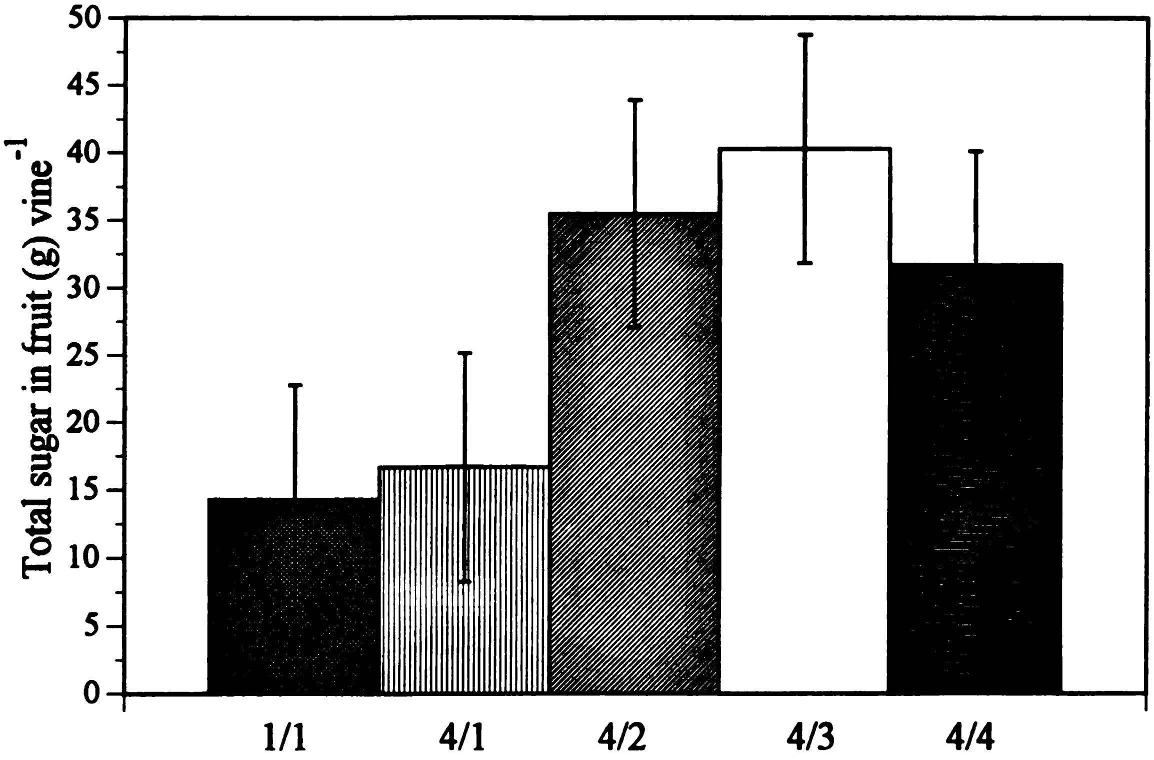

Figure 8. Mean total sugar content of fruit vine^{-1} at harvest in potted Chambourcin grapevines with 1 or 4 shoots and 1 cluster (1/1 and 4/1 respectively) or, 4 shoots and 2 (4/2), 3 (4/3) or 4 (4/4) clusters. Bars represent the LSD at $p = 0.05$.

CONCLUSION

Shoot number was varied by a factor of six in the first experiment reported in this dissertation with no apparent effect on the rate of starch utilization from reserves during the spring growth flush. The canopies of three- and six-shoot vines developed leaf area more rapidly, however, than did one-shoot vines leading to the conclusion that the rapid leaf area development was due to greater numbers of leaf development sites with larger numbers of apical meristems. Secondly, the mere presence of a larger leaf area during the growth flush and during the growing season did not result in greater dry matter production by three- and six-shoot vines. Between veraison and harvest, three- and six-shoot vines continued to produce dry matter, apparently in response to continued sink demand, while the dry matter content of one-shoot vines was essentially unchanged during the same period. The result was greater dry weight of three- and six-shoot vines at harvest, but only at harvest. This leads to the conclusion that greater leaf area by itself does not cause greater dry matter production; CO_2 assimilation and dry matter production are equally dependent on sink activity.

Canopy morphology was profoundly altered by varying shoot numbers. The changes that occurred resembled morphological changes associated with water stress, suggesting that the ability of the roots and/or vascular system to supply water to the growing shoot tips may ultimately limit shoot elongation and leaf expansion in vines with a relatively large number of shoots. The morphological changes led to fewer flowers per cluster and less leaf area per flower which would result in reduced shoot fruitfulness. This appears to be a means by which vines regulate the amount of fruit they produce.

The final experiment demonstrated that competition among shoots for root supplied growth factors (e.g. water, nutrients and growth hormones) has a much greater influence on canopy morphology than does competition for carbohydrates by fruit. Shoot length per shoot, leaf area per shoot and leaf size were inversely related to shoot number but were not significantly affected by crop load.

Carbon utilized for fruit production was derived from preferential partitioning to fruit at the expense of vegetative organs. Dry weight of non-fruited control and low-crop-load vines was not different but the relative dry weights of vegetative tissues were altered as carbon was used for fruit production. In addition to changes in dry matter partitioning, there was an increase in the amount of dry matter production all of which was used for fruit production at high crop loads. Because fruit is about 75% water, a one gram increase in dry weight results in a four gram increase in fresh weight.

Roots were the vegetative tissue most negatively affected by the redirection of carbon to fruit between veraison and harvest. In the absence of fruit, roots appear to be the strongest carbohydrate sink during the veraison-harvest period. When fruit is present, it is the strongest sink during that time. Root weights recovered in low crop-load vines between harvest and dormancy but not in high crop-load or one-shoot vines with crop. This may result in reduced vine capacity in the latter treatments during the following growing season.

The data presented in this dissertation indicate that vines will be most efficient at sustained fruit production when the fruiting sink is in balance with the carbohydrate source, leaves. The higher yields observed in minimally pruned vines result from crop loads which are in balance with vine capacity. It appears that the control vines in many studies, which are pruned to a standard node level, are not cropped to their capacity.

Data collected on cane fresh weight (typically referred to as "vine size") support the hypothesis that this variable does not accurately reflect vine capacity. An inverse relationship exists between shoot number and cane fresh weight in the absence of crop. The presence of crop causes a further decrease in cane fresh weight. However, the traditional use of "vine size" is to represent vine leaf area. The hypothesis is that a given weight of canes will support some fixed amount of leaf area. If cane weight increases, then leaf area must also increase. Because the amount of fruit which a vine can ripen is directly related to the amount of exposed leaf area which that vine can produce, an indication of greater leaf area is also an indication of the capacity for more fruit production. The assumption that a given weight of canes will support some fixed amount of leaf area, however, is in error. The data presented here show that a given cane weight can support varying amounts of leaf area depending on shoot number and crop load. This means that some other method must be employed to estimate vine capacity of minimally pruned grapevines.

The term "vine vigor" is related to vine capacity. It is used in reference to the growth *rate* of individual shoots. However, it is apparent that individual shoots may grow slowly while a vine still maintains a high capacity for dry matter production. In this context a vine may have two or three rapidly growing (vigorous) shoots but low capacity. It would be more appropriate to speak in terms of *shoot* vigor in this circumstance. By contrast, a vine may have 150 slowly growing shoots but high capacity (vigor) for dry matter production. The *total* amount of shoot growth a vine can produce appears to be an indicator of "*vine* vigor" or vine capacity. Shoot length is directly related to leaf area, so it is possible to integrate the concepts of vine vigor and vine capacity with measurements of leaf area and shoot length. The concepts of vine vigor and vine capacity were first identified by Winkler et al.(1974) and it seems appropriate in light of the information contained herein, to reiterate them here.

Results from this study indicate that the total amount of leaf area (or shoot length) a vine can produce during the growth flush may be related to the total dry matter production (i.e. vine capacity) for that season. Further work is necessary to confirm these results and develop the appropriate mathematical models which will allow for a precise adjustment of crop load to maximize sustained yields of high quality fruit. It is likely the results obtained with Chambourcin grafted to 5-C rootstock will not apply directly to other rootstock/scion combinations and under different environmental conditions (e.g. growing season length, water and nutrient availability, and soil type). Thus it is necessary to test the hypotheses developed in this dissertation under various conditions and with various plant materials.

Appendix A

Starch content

Appendix A

Table 1. Starch concentration (mg g-1 dry weight) of vegetative tissues of Chambourcin grapevines with one-, three- or six-shoots.

			Mean concentration (mg/g dry weight)				
Date, 1993	GDD (base 10 C)	Shoot #	Trunk	Root	Leaf	Shoot	Cane
6-16	139	1	55.77	91.34	n.a.	3.24	n.a.
		3	37.40	109.93	n.a.	11.52	n.a.
		6	40.55	95.99	n.a.	11.86	n.a.
	F sig.		n.s.	n.s.		n.s.	
	LSD .05						
6-28	273	1	18.05	45.07	18.13	12.08	10.38
		3	35.44	60.51	14.18	15.68	20.89
		6	19.75	41.48	22.45	17.12	9.24
	F sig.		**	n.s.	n.s.	n.s.	**
	LSD .05		8.93				8.67
7-7	384	1	30.42	64.02	5.89	36.53	15.19
		3	23.81	25.33	6.38	38.76	18.82
		6	23.70	52.78	7.70	53.27	27.19
	F sig.		n.s.	n.s.	n.s.	*	n.s.
	LSD .05					15.64	
7-20	545	1	40.75	57.36	16.10	52.37	39.88
		3	49.22	76.39	26.24	48.87	42.48
		6	52.58	74.88	17.53	45.81	53.32
	F sig.		n.s.	n.s.	n.s.	n.s.	n.s.
	LSD .05						
8-26	959	1	66.94	80.83	25.49	52.72	n.a
		3	71.77	93.41	21.28	54.09	n.a
		6	75.23	75.41	29.94	55.61	n.a
	F sig.		n.s.	n.s.	n.s.	n.s.	
	LSD .05						
9-16	1111	1	96.60	131.71	13.42	0.84	n.a.
		3	89.90	141.93	6.55	1.25	n.a.
		6	100.86	123.97	19.08	1.25	n.a.
	F sig.		n.s.	n.s.	n.s.	n.s.	
	LSD .05						

Table 2. Total starch content (mg) of vegetative tissues of Chambourcin grapevines with one-, three-, or six-shoots.

			Mean total starch content of tissues (mg)				
Date, 1993	GDD (base 10 C)	number of shoots	Trunk	Root	Leaf	Shoot	Cane
6-16	139	1	566.10	637.40	n.a.	1.17	n.a.
		3	692.50	420.20	n.a.	5.95	n.a.
		6	685.30	436.80	n.a.	9.49	n.a.
	F sig.		n.s.	n.s.		n.s.	
	LSD .05						
6-28	273	1	223.10	297.07	35.95	10.95	36.03
		3	525.60	388.80	38.85	13.22	58.72
		6	335.30	259.50	64.09	20.25	27.58
	F sig.		n.s.	n.s.	n.s.	n.s.	n.s.
	LSD .05						
7-7	384	1	426.10	416.90	21.80	53.02	49.09
		3	329.90	179.30	34.56	69.47	55.93
		6	352.20	331.30	39.28	78.89	110.68
	F sig.		n.s.	n.s.	n.s.	n.s.	n.s.
	LSD .05						
7-20	545	1	556.50	505.50	66.80	123.20	167.09
		3	802.10	825.40	195.70	112.60	141.95
		6	901.90	738.10	125.60	117.80	189.83
	F sig.		n.s.	n.s.	**	n.s.	n.s.
	LSD .05				65.68		
8-26	959	1	1521.60	2703.40	249.20	487.20	n.a
		3	1753.30	2854.80	379.00	427.80	n.a
		6	1815.90	1569.20	512.90	377.80	n.a
	F sig.		n.s.	n.s.	n.s.	n.s.	
9-16	1111	1	2292.60	4570.20	176.90	8.30	n.a.
		3	2113.10	6907.30	128.90	14.20	n.a.
		6	2828.50	5663.90	386.80	1.25	n.a.
	F sig.		n.s.	*	n.s.	n.s.	
	LSD .05			1870.10			

Appendix B

Photosynthesis

Appendix B

Table 1. Photosynthesis data obtained from measuring individual leaves of Chambourcin grapevines with 1 or 4 shoots and no fruit (1/0 and 4/0 respectively); 1 shoot and 1 cluster (1/1) or 4 shoots with 1 (4/1), 2 (4/2), 3 (4/3), or 4 (4/4) clusters. VPD = vapor pressure deficit (kpa); A = net CO2 assimilation rate (umol m-2 sec-1); Gs = stomatal conductance (mmol CO2 m-2 sec-1); E = transpiration rate (mmol H2O m-2 sec-1); WUE = water use efficiency (mol CO2 / mol H2O); Ci = intracellular CO2 concentration (umol CO2 / mol CO2) and; Gm = mesophyll conductance (mmol CO2 m-2 sec-1).

Treatment	GDD base 10 C	VPD	A	Gs	E	WUE	Ci	Gm
				Pre-bloom				
1/0	250	4.66	7.42	68.11	4.19	0.002	153.09	56.40
1/1	250	5.38	4.89	29.45	2.61	0.002	92.53	11.36
4/0	250	5.31	3.59	28.05	2.23	0.004	13.83	27.75
4/1	250	5.14	4.70	25.71	2.10	0.003	68.63	27.57
4/2	250	4.90	5.28	40.84	2.64	0.003	57.66	24.32
4/3	250	6.00	3.24	10.88	1.04	0.005	221.93	3.73
4/4	250	4.85	4.61	42.09	3.26	0.001	201.00	23.81
F sig		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LSD .05								
				5mm berries				
1/0	497	2.48	15.21	187.87	7.72	0.002	253.64	60.25
1/1	497	2.46	13.74	185.89	7.48	0.002	259.94	52.75
4/0	497	2.45	13.52	209.42	8.50	0.002	268.85	50.55
4/1	497	2.56	12.24	184.35	7.75	0.002	266.06	46.27
4/2	497	2.42	12.96	206.84	8.31	0.002	271.51	47.77
4/3	497	2.43	13.65	204.84	8.07	0.002	268.01	50.90
4/4	497	2.55	13.17	204.66	8.06	0.002	260.12	50.37
F sig		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LSD .05								
				mid-season				
1/0	619	1.94	11.40	139.29	4.32	0.003	233.97	48.67
1/1	619	2.39	10.54	98.49	3.55	0.003	200.78	51.73
4/0	619	2.21	7.96	97.81	3.31	0.003	219.42	36.39
4/1	619	2.17	10.34	113.73	3.84	0.003	196.92	56.81
4/2	619	2.06	11.33	135.57	4.11	0.003	211.50	53.76
4/3	619	1.99	11.11	119.78	3.63	0.003	211.37	52.46
4/4	619	2.19	9.10	98.37	3.26	0.003	205.02	43.74
F sig		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LSD .05								
				veraison				
1/0	961	3.10	5.48	55.78	2.41	0.004	181.39	29.32
1/1	961	2.64	8.86	127.00	4.91	0.002	226.39	43.16
4/0	961	3.40	6.30	59.55	3.10	0.003	164.42	48.11
4/1	961	3.55	5.05	44.61	2.44	0.003	170.69	48.85
4/2	961	3.56	3.12	47.87	2.80	0.001	249.37	13.00
4/3	961	3.11	6.35	71.44	3.36	0.002	227.64	29.66
4/4	961	3.37	4.46	48.40	2.61	0.002	198.91	19.49
F sig		*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
LSD .05		0.55						
				harvest				
1/0	1065	1.68	7.91	131.06	3.53	0.002	250.42	31.48
1/1	1065	1.51	9.09	157.83	3.84	0.002	255.81	35.82
4/0	1065	1.60	8.95	148.92	3.90	0.002	253.14	35.53
4/1	1065	1.51	9.26	154.33	3.77	0.002	253.22	36.61
4/2	1065	1.34	10.04	205.02	4.42	0.002	264.43	38.35
4/3	1065	1.50	8.55	191.75	4.19	0.002	269.91	31.78
4/4	1065	1.52	9.66	163.22	3.99	0.002	254.67	37.95
F sig		**	n.s.	**	*	n.s.	n.s.	n.s.
LSD .05		0.16		35.08	0.48			

Table 2. CO2 assimilation by Chambourcin grapevines with 1 shoot with 0 (1/0) or 1 (1/1) cluster or, 4 shoots and 0 (4/0) or 4 (4/4) clusters. Data were collected using either the whole-plant gas-exchange system described in chapter 1 or a Parkinson broad leaf chamber.

		bloom			
		Whole-vine chamber		Parkinson broad-leaf chamber	
Treatment	GDD base 10 C	A (umol CO2 vine-1 sec-1)	A (umol CO2 m-2 sec-1)	A (umol CO2 vine-1 sec-1)	A (umol CO2 m-2 sec-1)
1/0	330	0.72	10.85	0.33	7.42
1/1	330	1.26	17.50	0.34	4.89
4/0	330	0.82	8.18	0.19	4.7
4/4	330	0.99	11.00	0.41	4.61
F sig		n.s.	n.s.	n.s.	n.s.
LSD .05					
		5mm berries			
1/0	512	1.17	12.51	1.69	15.21
1/1	512	1.64	19.98	2.15	13.74
4/0	512	1.47	10.86	1.47	12.24
4/4	512	1.56	16.21	1.97	13.17
F sig		n.s.	*	n.s.	n.s.
LSD .05			6.97		
		mid summer			
1/0	631	1.53	15.00		
1/1	631	1.23	13.42	N.A	N.A.
4/0	631	1.50	11.05		
4/4	631	1.48	14.88		
F sig		n.s.	n.s.	n.s.	n.s.
LSD .05					
		late summer			
1/0	884	2.68	17.07	1.78	11.40
1/1	884	3.08	23.36	2.16	10.54
4/0	884	2.70	12.74	1.20	7.96
4/4	884	2.73	16.76	1.88	9.10
F sig		n.s.	**	n.s.	n.s.
LSD .05			4.05		
		veraison			
1/0	1018	4.29	21.32	1.04	5.48
1/1	1018	3.29	19.94	2.34	8.86
4/0	1018	4.39	15.78	1.20	6.30
4/4	1018	3.53	16.76	1.10	4.46
F sig		n.s.	n.s.	n.s.	n.s.
LSD .05					
		harvest			
1/0	1089	1.75	6.67	2.05	7.91
1/1	1089	1.99	8.72	2.98	9.08
4/0	1089	1.77	5.83	2.01	8.95
4/4	1089	1.05	4.07	2.52	9.66
F sig		n.s.	n.s.	n.s.	n.s.
LSD .05					

Appendix C

Fruitfulness

Appendix C

Table 1. Parameters affecting fruitfulness of potted Chambourcin grapevines with 1 shoot and 1 cluster (1/1) or. 4 shoots and 1 (4/1), 2 (4/2), 3 (4/3) or 4 (4/4) clusters.

					Leaf area (cm2)				
Tmt	Cluster Length shoot-1	cluster-1	Total Cluster Length (mm)	flower number	per mm rachis length	per flower	Berry number	Berry number cluster-1	% Berry set
1/1	88.5	59.6	88.5	300.7	7.18	2.17	31.5	31.5	14.50
4/1	30.0	37.8	119.8	414.4	14.46	4.61	41.3	41.3	26.01
4/2	39.3	31.9	157.3	550.9	9.15	2.76	76.0	38.0	32.97
4/3	34.9	41.6	139.5	486.3	8.21	2.40	89.0	36.0	25.16
4/4	60.7	47.2	242.8	862.2	4.95	1.41	84.3	27.3	13.08
F sig.	**	n.s.	n.s.	n.s.	**	**	**	n.s.	n.s.
LSD .05	30.6				5.01	1.66	35.8		