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Influence of shoot number and crop load on potted Chambourcin grapevines. II: Whole-vine vs. single-leaf photosynthesis

by

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S u m m a r y : Two-year-old potted Chambourcin grapevines were trained to one shoot with 0 or 1 cluster (1/0 and 1/1 respectively) or four shoots with 0 or 4 clusters (4/0 and 4/4 respectively) to determine the effects of canopy development rate, canopy morphology, and crop load on whole-vine photosynthesis. Significant differences in canopy development rate, canopy morphology and dry matter partitioning occurred among treatments but whole-vine net photosynthesis (Pn) and dry matter production were not affected. Photosynthetic compensation by leaves of severely pruned vines enabled them to produce quantities of dry matter similar to vines with greater leaf area. Vines bearing crop supported the development of berries by partitioning carbohydrate to fruit at the expense of vegetative tissues so overall vine dry weight was not different among cropped and non-cropped treatments. Whole-vine Pn determinations were linearly related to vine dry mass. By contrast, single leaf measurements used to estimate whole-vine Pn were not related to dry mass. If a similar relationship can be demonstrated in field vines, it may be possible to quantify the influence of biotic and abiotic stresses on vine biomass production and subsequent yields.

K e y w o r d s : leaf area, whole-vine photosynthesis, shoot number, crop load, canopy, dry matter partitioning.

Introduction

Measurement of leaf gas exchange is an important technique used to estimate net photosynthesis (Pn). Individual-leaf photosynthetic determinations, however, have limitations when used to estimate whole-plant CO_2 exchange. Leaf Pn can vary due to differences in leaf age (PONI *et al.* 1994 a), chlorophyll content (CANDOLFI-VASCONCELLOS and KOBLET 1991), angle of incident radiation (FLORE and LAKSO 1989), leaf shading (FLORE 1994), respiration of vegetative and reproductive tissues (CORELLI-GRAPPADELLI and MAGNANINI 1993), or biotic or abiotic stress. Further, 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). Consequently, although individual leaf measurements estimate the relative carbon uptake per unit leaf area, it is problematic to extrapolate to whole-plant assimilation from these values.

An accurate assessment of the net carbon uptake by whole-plants is essential if plant production per unit land area is to be maximized. One approach is the employment of a whole-plant gas exchange system (KATERJI *et al.* 1994). HEINECKE and CHILDERS (1937) first devised a whole-tree gas-exchange 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). Recently, whole-plant systems have been reported for use on apple trees (CORELLI-GRAPPADELLI and MAGNANINI 1993) and grapevines (KATERJI *et al.* 1994; MILLER *et al.* 1996 a).

EDSON *et al.* (1991) demonstrated that grapevines with a wide range of crop loads had similar whole-vine Pn and dry matter production per vine. Varying fruit quantity caused a change in dry matter partitioning but had no effect on whole-vine dry matter production. Researchers working with minimally pruned (MP) grapevines (vines which were not pruned but had only low-hanging canes removed) reported large increases in fruit yields relative to spur-pruned control vines (DOWNTON and GRANT 1992). The researchers attributed the increased yield to an increase in "vine capacity", thought to result from the more rapid canopy development of MP vines ("vine capacity" is the total dry matter production of a vine during a given growing season and directly influences the quantity of fruit the vine can produce and mature). Research reported from potted vine studies did not support this conclusion (MILLER *et al.* 1996 c and d). When shoot numbers (and early season leaf area) varied, dry matter was not affected. It is difficult, however, to determine the dry matter production of entire vines under vineyard conditions over the course of the growing season. A simple and direct method is required for comparing the dry matter production of various treatments.

The objectives of this study were to: a) compare whole-plant and single-leaf Pn determinations and examine their efficacy as a means of estimating whole-vine dry matter production and b) determine if the methodology works over a wide range of canopy morphology and crop load conditions.

Materials and methods

P l a n t m a t e r i a l : Two-year-old Chambourcin (J.S. 26-205) grapevines grafted to 5 C rootstock were planted in 19-l plastic pots with a 45 % sand, 45 % loam and 10 % peat sterile potting mix on May 11, 1994. Potted vines were

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placed on pea-gravel in full sun and watered regularly. Fertilizer was applied as a balanced N,P,K solution monthly. Pesticides were applied as needed based on recommendations by the cooperative extension service spray calendar.

When buds were at the swell-two stage of development (elongated sphere prior to burst; JOHNSON and HOWELL 1981), their numbers were adjusted to give either 1 or 4 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 resulting in the following treatments: 1- or 4-shoots with 0 clusters (1/0 and 4/0, respectively); 1-shoot with 1 cluster (1/1); or 4-shoots and 4 clusters (4/4). Basal clusters were retained and each cluster was retained on a separate shoot.

Vines were blocked according to their initial fresh weight prior to planting, producing 4 blocks. Treatments were randomly assigned to 5 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 randomly selected from each treatment block for destructive harvest. The experimental design was a randomized complete block with 7 treatments, 4 replicates (blocks) and 5 partitioning dates for a total of 140 vines.

Vine dry weight: Vines were destructively harvested at 5 phenological stages: (1) pre-bloom (ca. 5 d before any flowers opened) at 330 growing degree days base 10 °C (GDD); (2) post-anthesis (5 mm berry diameter; 512 GDD); (3) veraison (30 % of berries showing coloration; 1018 GDD); (4) fruit ripeness (soluble solids >20 °Brix;1089 GDD); and (5) dormancy (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 (leaves, shoots, fruit, trunks, and roots) and recording the fresh weight of each. Tissues were then placed in paper bags in a drying oven at 60 °C until no further weight reduction occurred (ca. 4 d; 7-10 d for fruit). After drying, tissue weights were recorded and percentage water content calculated. Whole-vine dry weight was determined by combining the weights of individual tissues.

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 composition: Ten-berry samples, collected from vines partitioned at harvest, were weighed and placed in sealed plastic bags at -20 °C until analyzed. Berries were

Table 1

Canopy morphology parameters of Chambourcin grapevines with 1 shoot and 0 (1/0) or 1 (1/1) cluster, or 4 shoots with 0 (4/0) or 4 (4/4) clusters

Phenological[1] stages	Treatment	Total shoot length (cm)	Total leaf area (cm^2)	Total leaf number	Single shoot length (cm)	Leaf area per shoot (cm^2)	Leaf size (cm^2)	Leaf number per shoot
Pre-bloom	1/0	31.3 b	409.0 b	7.0 b	31.3 a	409.0 ab	57.4 ab	7.0 a
330 GDD	4/0	57.4 a	687.0 ab	20.0 a	14.4 b	171.8 b	35.2 c	5.0 b
	1/1	34.4 b	495.7 b	7.5 b	34.4 a	495.7 a	65.0 a	7.5 a
	4/4	65.4 a	872.7 a	20.5 a	16.4 b	218.1 b	42.7 bc	5.2 b
	F sig.	***	***	***	***	**	**	**
5 mm berries	1/0	62.4	1131.5 b	14.0 b	62.4 a	1131.5 a	80.7 a	14.0 a
512 GDD	4/0	64.8	1580.1 a	32.8 a	22.9 b	395.0 b	48.3 b	8.2 b
	1/1	65.0	1111.3 b	13.5 b	65.0 a	1111.3 a	81.5 a	13.5 a
	4/4	89.3	1482.3 a	30.5 a	22.3 b	370.6 b	48.8 b	7.7 b
	F sig.	n.s.	*	***	***	***	***	***
Veraison	1/0	114.5 b	2016.0 ab	26.3 c	114.5 a	2016.0 a	76.7 a	26.3 a
018 GDD	4/0	163.4 a	2574.0 a	61.5 a	40.9 b	643.5 b	42.0 b	15.4 b
	1/1	110.8 b	1912.8 b	26.0 c	110.8 a	1912.8 a	73.5 a	26.0 a
	4/4	139.8 ab	2544.4 a	47.8 b	38.8 b	636.1 b	53.6 b	12.0 c
	F sig.	**	*	***	***	***	***	***
Fruit ripeness	1/0	142.9 b	2602.0 b	31.0 b	142.9 a	2602.0 a	84.0 a	31.0 a
1089 GDD	4/0	192.0 a	3224.5 a	63.0 a	51.8 c	806.2 c	51.4 b	15.8 b
	1/1	116.5 b	2242.3 b	28.8 b	116.5 b	2242.3 b	78.0 a	28.8 a
	4/4	143.5 b	2613.0 b	52.0 a	41.9 c	653.3 c	50.8 b	13.0 b
	F sig.	***	**	***	***	***	***	***

[1] See text for a detailed description of phenological stages.
Means separated by a different letter within a column are significantly different at p=0.05 (*), 0.01 (**), 0.001 (***) or not significant different (n.s.). Means separated using Duncan's new multiple range test.
GDD: Growing Degree Days, base 10 °C.

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 (AMERINE and OUGH 1988).

Whole-vine Pn measurement: Whole-vine net photosynthesis (Pn) was determined using a Mylar „balloon" chamber as described previously (MILLER *et al.* 1996 a). At the outset of the experiment, a vine was selected at random from each treatment replicate to be used for whole-vine Pn measurements. Those vines were utilized for the whole-vine and single-leaf Pn measurements for the remainder of the experiment. Pn was determined by placing a balloon over the vine canopy and monitoring the change in CO_2 concentration in the air stream passing over the vine. Air flow rates were monitored with a thermal anemometer (Model 3700; Cole Parmer, Chicago) and CO_2 concentration was determined using an infrared gas analyzer (IRGA) (ADC LCA-2; Analytical Development Co., Hoddesdon, U.K.). Whole-vine and single-leaf Pn were determined at the same phenological stages as vine partitioning with additional measurements at 631 and 884 GDD (between fruit set and veraison).

Single-leaf Pn measurement: Pn was determined for single leaves at the same physiological stage of development as for whole-vines. Pn determinations were made on a recently, fully expanded leaf using an ADC LCA-2 portable, open gas exchange system equipped with a Parkinson broadleaf chamber and an air-supply unit (Analytical Development Co., Hoddesdon, U.K.). The data were used to calculate whole-vine Pn which was then compared to measurements made with whole-vines.

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: As we reported earlier, the number of shoots had the greatest influence on canopy morphology (MILLER *et al.* 1996 d). Shoot length, leaf area per shoot, and leaf size were greatest on one-shoot vines at every partitioning date (Tab. 1). Shoot length per vine was greatest in four-shoot vines at the pre-bloom partitioning and similar among treatments at 5 mm berries. At veraison, 4/4 vines were intermediate to one-shoot and 4/0 vines and at harvest, shoot length was greatest in 4/0 vines. Leaf area per vine increased more rapidly in 4-shoot vines than 1-shoot vines during the spring growth flush. At 5 mm berries, four-shoot vines had the greatest leaf area. At veraison, 1/0 vines had leaf area intermediate to 1/1 and four-shoot vines but at harvest, 4/0 vines had the greatest leaf area.

Fruit yield and composition: Fruit yield was greater on 4/4 vines than 1/1 vines (145.5 and 66.7 g, respectively) but there were no differences in fruit composition among the treatments. Vines with 4 shoots and 4 clusters had fruit compositional values of 21.5 °Brix, 3.23 pH and 8.0 $g \cdot l^{-1}$ total acidity while the values for 1/1 vines were 21.8, 3.31 and 7.0, respectively.

Dry matter production and partitioning: Dry weights of shoots, trunks, and roots was similar among treatments from bud burst through veraison (Tab. 2). Four-shoot vines had greater leaf dry weights both pre-bloom and at 5 mm berries than had one-shoot vines, reflecting the more rapid canopy development associated with greater shoot numbers. Between veraison and harvest, partitioning of dry matter differed among cropped vs. non-cropped treatments. Vines with fruit diverted carbohydrates away from vegetative tissue production to fruit production. The net result was a reduction in leaf, shoot, and root weights in vines which bore fruit relative to non-fruiting vines. However, whole-vine dry weight was not different among treatments at any time during the study. These data support the hypothesis that vines beginning the growing season in a given condition (e.g. quantity of carbohydrate reserves, root system size) have the capacity for a fixed amount of growth under a given set of environmental conditions. The vine itself is very "plastic" and is able to adapt to conditions imposed upon it (e.g. pruning severity, crop load) with little influence on the total dry matter production but with potentially significant influences on vine morphology and dry matter partitioning.

Pn per unit leaf area: Net CO_2 assimilation rates per unit leaf area were not different among treatments at any date when determined using the Parkinson broadleaf chamber (Fig. 1 A). The Pn rate increased from pre-bloom to a

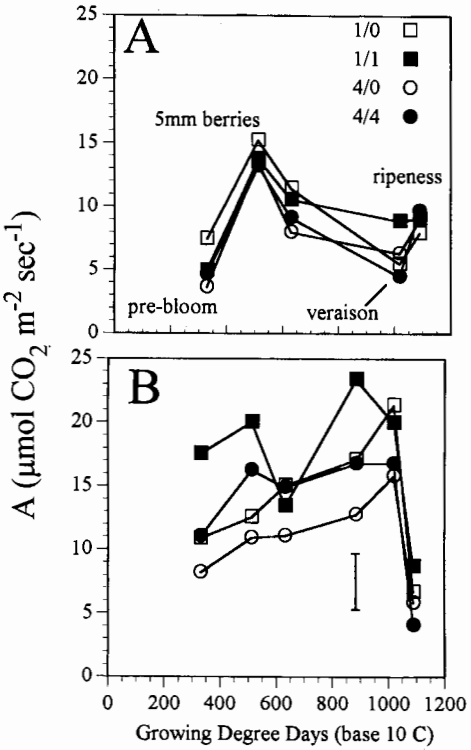

Fig. 1: CO_2 assimilation per unit leaf area (µmol m^{-2} s^{-1}) of Chambourcin grapevines with one shoot and 0 (1/0) or 1 (1/1) cluster, or 4 shoots and 0 (4/0) or 4 (4/4) clusters as determined with the Parkinson broadleaf chamber (**A**) or the whole-vine chamber (**B**). Bar shows the standard error where means are significantly different at p = 0.05.

Table 2

Tissue dry weight (g) for Chambourcin grapevines with 1 shoot and 0 (1/0) or 1 cluster (1/1), or 4 shoots with 0 (4/0) or 4 (4/4) clusters

Phenological stages[1)]	Treatment	Leaves	Shoots	Clusters	Trunks	Roots	Total plant
Pre-bloom	1/0	1.9 b	0.8	0.2	18.5	13.6	34.8
330 GDD	4/0	3.2 ab	0.8	0.4	19.4	14.6	38.0
	1/1	2.3 b	1.1	0.2	16.9	15.3	35.6
	4/4	4.1 a	1.4	0.6	21.4	16.6	43.4
	F sig.	**	n.s.	n.s.	n.s.	n.s.	n.s.
5 mm berries	1/0	8.1 b	3.6	n.a.	22.5	20.2	54.1
512 GDD	4/0	10.6 a	3.2	n.a.	22.5	18.7	55.0
	1/1	7.5 b	3.3	1.3	23.1	16.8	50.6
	4/4	9.4 ab	3.0	2.0	27.0	24.0	63.4
	F sig.	*	n.s.	n.s.	n.s.	n.s.	n.s.
Veraison	1/0	17.2	9.8	n.a.	27.8	42.4	97.1
1018 GDD	4/0	21.5	7.9	n.a.	23.8	44.6	97.8
	1/1	16.2	8.1	19.2	26.4	44.8	114.6
	4/4	19.6	6.9	20.0	33.8	45.6	120.3
	F sig.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Fruit ripeness	1/0	18.9 ab	12.1 a	n.a.	23.4	65.7 ab	120.0
1089 GDD	4/0	22.3 a	8.8 b	n.a.	23.4	72.4 a	126.8
	1/1	15.6 b	7.5 c	17.4 b	23.6	49.4 bc	113.4
	4/4	15.2 b	3.8 d	38.4 a	26.7	42.7 c	126.7
	F sig.	**	***	**	n.s.	**	n.s.

[1)] See text for a detailed description of phenological stages.
Means separated by a different letter within a column are significantly different at p=0.05 (*), 0.01 (**), 0.001 (***) or not significant different (n.s.). Means separated using Duncan's new multiple range test.
n.a.: not available (0-cluster vines). GDD: Growing Degree Days, base 10 °C.

maximum at 5 mm berries, gradually declined through veraison and remained unchanged in 1/1 vines from veraison through harvest while increasing slightly in the remaining treatments.

In contrast to the data obtained with the Parkinson broadleaf chamber, data collected using the whole-vine chamber showed 1/1 vine leaves to have the highest Pn rate from pre-bloom through late summer, just prior to veraison (Fig. 1 B). Leaves of 4/0 vines had the lowest assimilation rates per unit leaf area during the same period. The only exception was the determination made at 5 mm berries during which 1/0, 1/1 and 4/4 vines were similar. At veraison no differences among treatments were detected in Pn per unit leaf area. The Pn rate dropped rapidly from veraison through harvest when measured with the whole-vine chamber, in sharp contrast to the broadleaf chamber data which showed no change in Pn rate per unit leaf area over the same period. The disparity between the two measurement techniques between veraison and harvest could be due to the fact that the whole-vine chamber detected respiration from the fruit. A high rate of respiration during fruit ripening would greatly reduce whole-vine Pn but would not be detected using the broadleaf chamber.

In contrast to earlier reports (EDSON *et al.* 1991; PONI *et al.* 1997) we found higher rates of Pn per unit leaf area when using the whole-vine chambers as compared to the broadleaf chamber except at harvest. We speculate that this could be due to: a) the leaves used in the broadleaf chamber may not have reached maximum photosynthetic rates when measured or b) vines used in this study had less leaf area then vines reported in the other studies so more of the leaves may have been in full sunlight during the Pn determinations of whole-vines. Further research is required to resolve this issue.

P n p e r v i n e : Using the Parkinson broadleaf chamber, net CO_2 assimilation rates per vine increased rapidly from very low pre-bloom levels until vines reached the 5 mm berry stage (Fig. 2 A). From 5 mm berries through late summer, whole-vine Pn did not change and there were no differences detected among treatments at any date. At veraison, whole-vine Pn declined in 1/0 and 4/4 vines but remained stable in 4/0 and 1/1 vines. Whole-vine Pn increased slightly from veraison through harvest in all treatments.

Whole-vine Pn determined using the whole-vine chambers gave lower values during the pre-bloom period but the

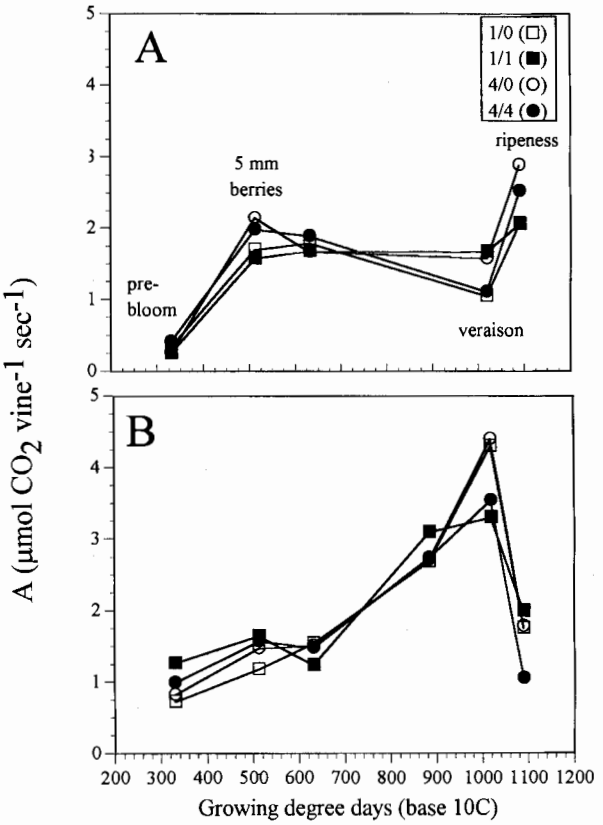

Fig. 2: Whole-vine photosynthesis A (μmol CO_2 $vine^{-1}$ sec^{-1}) of potted Chambourcin grapevines with 1-shoot and 0 (□) or 1 (■) cluster, or 4-shoots and 0 (○) or 4 (●) clusters. **A**: measured using single leaf determinations extrapolated to whole-vine; **B**: measured using whole-vine Pn chamber. No differences existed among treatments on any date using either measurement technique.

relationship among treatments was similar to that obtained with the single leaf measurements (Fig. 2 B). In contrast to the single leaf measurements, the period from 5 mm berries through veraison was a period of increasing whole-vine assimilation. Whole-vine photosynthesis (A) peaked at veraison and then declined through harvest. No differences were detected among treatments at any date which agrees with the single leaf determinations.

Since both methods of measuring Pn showed similarity among treatments, it was not clear which gave the most precise and accurate assessment of whole-vine CO_2 assimilation. Prior work indicated that there was a positive linear relationship between whole-vine A and dry matter production using whole-plant chambers (Miller *et al.* 1996 a) and the same was found to be true in this study. Fig. 3 A shows the relationship between vine dry mass and whole-vine CO_2 uptake determined with the whole-vine chamber between bud burst and veraison. In contrast, Fig. 3 B shows the same relationship using the Parkinson broadleaf chamber. From these graphics it is clear that the determination of CO_2 uptake using a whole-plant chamber gives a more accurate and precise measurement of dry matter production.

This is of considerable importance in plant physiology research. If the same relationship is true in mature plants in the field, it will be possible to begin to quantify the effect of environmental stresses on plant biomass production without destructively harvesting those plants.

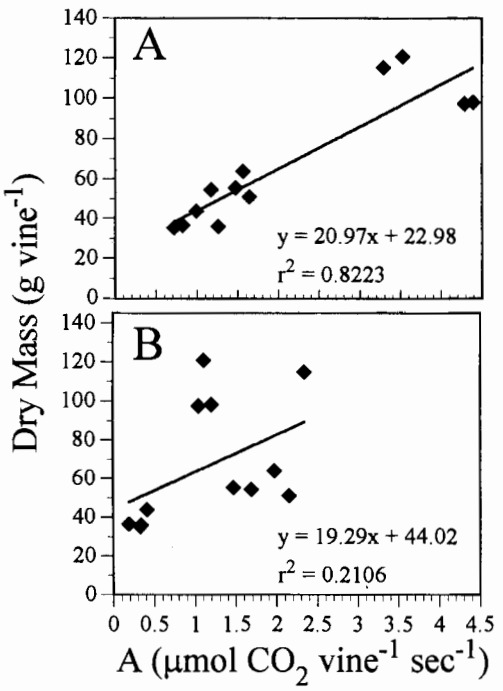

Fig. 3: Relationship between whole-vine Pn and vine dry mass. **A**: whole-vine Pn measured using a whole-plant chamber; **B**: whole-vine Pn measured using single leaf determinations extrapolated to whole-vines. Each point is the mean of 4 measurements. Data represent measurements made June 15 (bloom), July 11 (5 mm berries), and August 30 (veraison).

Leaf area ratio: Leaf area ratio (LAR) [leaf area (cm^2) per plant dry mass (g)] was greatest in 4-shoot vines throughout the growing season (Fig. 4). Since LAR is an estimate of carbohydrate source:sink relations, the 4-shoot vines had the highest source:sink ratio and the 1-shoot vines the lowest. Within a shoot number treatment, vines with crop had a lower source:sink ratio than non-cropped vines as expected. As stated earlier in the discussion of whole-vine Pn, there were no differences among treatments in whole-vine Pn or dry matter production. This indicates that photosynthetic compensation buffered the differences in leaf area among the treatments.

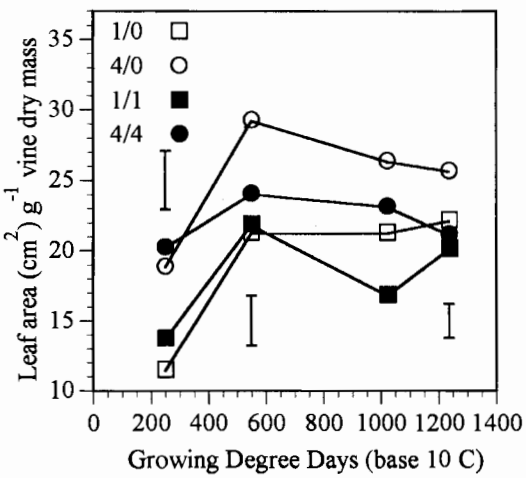

Fig. 4: Influence of shoot and cluster number on the leaf area ratio [LAR (cm^2 g^{-1})]. Bars represent the standard error at $p < 0.05$.

Studying the LAR it is possible to see at least part of the mechanism by which vines compensate for differences in leaf area imposed by pruning and differences in crop load. When a relatively large number of shoots are retained at pruning the canopy develops rapidly and there is a high LAR. In that case photosynthesis is sink-limited. By contrast, severely pruning of vines reduces the rate of canopy development by limiting the number of sites of leaf initiation thereby reducing the LAR. The leaves respond to the relatively greater sink strength by producing more dry matter per unit surface area (MILLER *et al.* 1996 d).

Retaining fruit has a similar effect. The presence of fruit represents a carbohydrate sink that reduces the LAR in two ways. First, shoot elongation and subsequent leaf area development are slowed relative to non-fruiting vines when fruit is present. With less leaf area development, there is a decrease in the LAR. Second, the fruit adds to the weight of tissues which must be maintained via photosynthesis, further decreasing the LAR. Both mechanisms lead to increased net photosynthesis per unit leaf area. Previous research has shown similar photosynthetic compensation when leaf area is artificially reduced (CANDOLFI-VASCONCELOS 1991). It was proposed that reductions in leaf area lead to an increase in the transpiration stream supplying the remaining leaves in addition to the increased demand for carbohydrates which occurs (FLORE and LAKSO 1989). In this study, the data indicate that the root mass available to support a given quantity of leaf area increases as the LAR decreases (Fig. 5). This supports the hypothesis that photosynthetic compensation may be due in part to an increase in the availability of water, nutrients and root-supplied growth factors for the remaining leaf area when a reduction occurs in the LAR.

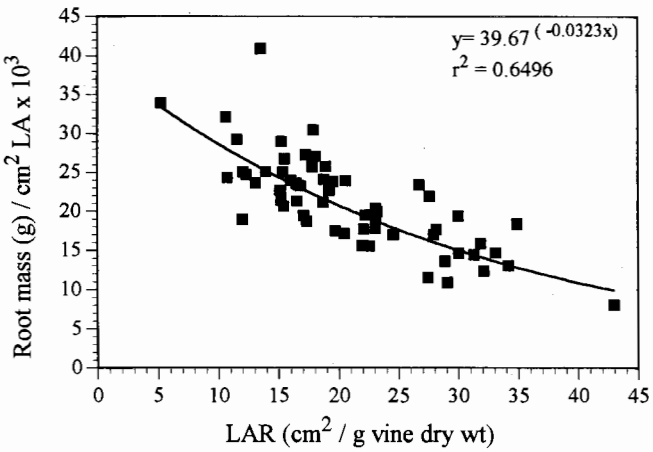

Fig. 5: Relationship between leaf area ratio (LAR) and root mass (g)/leaf area (cm^2) of potted, two-year-old Chambourcin grapevines.

It appears that through the mechanisms described above a grapevine is able to maintain a balance between roots and leaves and, whole-vine weight and LAR such that vines of similar fresh weight at the onset of growth will produce similar quantities of dry matter during the growing season despite varying crop loads and canopy morphologies. The distribution of dry matter among various organs may vary greatly but the total biomass will be similar.

Conclusion

The net CO_2 uptake by whole-vines is positively related to the whole-vine dry mass. Even though canopy morphology, crop load, and carbon partitioning varied greatly among treatments, whole-vine Pn accurately reflected whole-vine dry mass. If a similar relationship can be demonstrated in mature, field vines the whole-vine Pn chambers will be a powerful tool for demonstrating the influence of biotic and environmental stresses on vine dry mass production, and ultimately, on vineyard productivity.

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