Influence of Crop Load on Photosynthesis and Dry Matter Partitioning of Seyval Grapevines. II. Seasonal Changes in Single Leaf and Whole Vine Photosynthesis

C. E. EDSON[1]*, G. S. HOWELL[2], and J. A. FLORE[3]

Photosynthesis (Pn), leaf area/vine and dry matter partitioning were measured at four phenological stages of development on two-year-old, own-rooted Seyval grapevines adjusted to five different crop loads. Crop loads were 0, 1, 2, 4, or 6 clusters/vine with all laterals removed to eliminate intra-vine shading. Yield/vine was positively correlated and leaf area/vine negatively correlated with clusters/vine. Total dry weight/vine was similar for all crop loads, but increased at each phenophase. Whole vine Pn (WVPn) was measured in a whole plant chamber and expressed as WVPn per unit leaf area (WVPn/L) and WVPn per vine (WVPn/V). Single leaf Pn (SLPn) was also measured on leaves at four node positions. SLPn was highest at the basal node position (node four or five) at fruit set. SLPn at all other node positions was highest mid-season or veraison. WVPn increased through veraison, then declined. SLPn was positively correlated with crop load in at least one leaf position at each phenophase. WVPn/L was positively correlated with crop load only at harvest. WVPn/V was inversely correlated with crop load at mid-season, indicating that vegetative, as well as fruiting sinks, can strongly influence whole vine photosynthetic rates. Over the season, SLPn of the most recently fully expanded leaf was best correlated with WVPn/L. However, there was no general relationship between SLPn and WVPn/V.

KEY WORDS: photosynthesis, crop load, whole vine, dry matter partitioning, source-sink

Research has shown the influence of canopy design on light penetration and air movement within the canopy (26,37,39,40,43). Specific physiological responses to environmental influences (e.g., light, temperature) are discussed, but often how the interaction between vegetative and fruiting sinks affects morphological development and physiological response is not made clear. High crop loads are inversely related to shoot growth, leaf size, whole plant leaf area (3,13,15), and root growth (13). Crop load effects on vigor and their influence on canopy density are mediated through a competition for photoassimilates (15). Production of adequate amounts carbohydrates to meet both the daily metabolic and vine growth demands is necessary for adequate productivity and vine survival. There is evidence of compensation in photosynthetic efficiency (4,19), assimilate transport (32,36), leaf area development (5,13,28), and root system development (13,23) to adjustments in source-sink relationships.

The presence of fruiting sinks stimulates photosynthetic activity in grapevines (6,13,22) and tree crops (17,19) when measured at a single leaf position. However, the nature of this response is not fully understood. Chaves (6) found differences only late in the season, while Williams (42) found no difference in leaf photosynthesis between fruiting and non-fruiting vines. Gucci et al. (19) also pointed out the importance of vegetative sinks in stimulating single leaf photosynthesis (SLPn) following fruit removal in *Prunus domestica* trees. Recently, we reported an increase in SLPn as the relative source to sink ratio decreased and a concurrent increase in whole vine photosynthesis when expressed on a per unit leaf area basis (13). However, when whole vine photosynthesis was expressed on a per vine basis (WVPn/V), crop load had no effect at harvest. In fact, the presence of additional vegetative sinks, in the form of laterals, tended to stimulate rates of WVPn/V, especially following harvest (13).

In earlier work, we concluded that crop load does not have a direct effect on WVPn, *per se* (13). Rather, that the effect on WVPn is indirect, mediated initially through altered allocation of assimilates to meet carbon demands. The resulting morphological differences associated with different crop loads are linked to localized physiological responses, such as the photosynthetic activity of single leaves, i.e. if the vine grew fewer leaves because it was growing fruit, carbon assimilation by each leaf must increase if total vine demands for assimilate remain unchanged (13). Vines integrate metabolic and physiological processes to produce similar carbon gains (and WVPn/V) for both low and high crop loads (13). In fact, total dry matter accumulation was not influenced by crop load in earlier studies (13,16). Further, harvest measurements of

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SLPn and WVPn/V are not correlated (13).

Sink activity changes as the season progresses, and the cluster's ability to attract carbon gradually increases after fruit set (2,20). However, the nature of the relationship between changing sink activity and SLPn remains poorly understood and has not been fully investigated for WVPn. Chaves (6) found the fruiting effect stimulating SLPn to be greatest at harvest. In contrast, others (4,24,34) have shown greater SLPn activity mid-season with a gradual decline at harvest. Clearly, internal response to source-sink alterations changes as the growing season progresses.

This study was undertaken to investigate the seasonal changes in whole vine photosynthesis and dry matter partitioning as influenced by crop load in potted Seyval grapevines. The objectives were to determine: *(1)* whether our previous conclusions concerning whole vine response and the relationships with SLPn at harvest were consistent over the entire growing season; *(2)* at what phenophase the whole vine responses we had observed at harvest became evident and significant; and *(3)* whether seasonal whole vine data would suggest modification of cultural practices or recommended cropping levels for Seyval. This paper will be primarily concerned with the photosynthetic response of Seyval to crop load. A companion paper reports the partitioning, vine morphology, yield, and fruit composition results of this study (14).

Materials and Methods

Plant material: Seyval (S.V. 5276) is a large clustered, hybrid direct producer widely grown in the eastern United States. Seyval was chosen for this study because of its inherent tendency to overcrop and its sensitivity to these effects. Two-year-old, own-rooted, Seyval grapevines grown in 20-L pots were used for this study. Soil was an equal loam, sand, and peat mix with good water holding and aeration properties. Pots were never allowed to dry out and were fertilized using a Peter's 20-20-20 solution. They were maintained on a gravel pad at the Horticulture Research and Teaching Center, Michigan State University, East Lansing, Michigan. The pots were painted white to reflect light and reduce soil temperature. Vines were spaced 0.9 m × 1.5 m. Vines were netted near harvest to prevent bird predation on fruit.

Vine training: A special vine architecture system was devised for this study so that high cluster numbers per vine could be produced while retaining only two vegetative shoots per vine. Vines were pruned to eight shoots following bud burst and were allowed to grow for three weeks (*i.e.*, two weeks prior to bloom). Two shoots were retained as vegetative shoots, and all flower clusters were removed from these shoots. All laterals were removed weekly from these shoots to eliminate variation in intra-vine shading which could have been created by differential lateral shoot growth due to crop load (5) and the subsequent potential effects on Pn due to the presence of variable vegetative sinks (13,19). The vegetative terminals on those shoots

were never cut. Flower clusters were retained on separate shoots to provide crop load treatments of 0, 1, 2, 4, or 6 clusters per vine. These fruiting spurs were cut two to three nodes beyond the clusters and defoliated. The fruiting spurs were maintained in this condition (*i.e.*, without vegetative growth) throughout the growing season. The validity of this unique experimental approach was tested in a separate study (12).

Whole vine photosynthesis: WVPn was measured using an open gas exchange system and a chamber designed to enclose the entire vine described previously (13). Measurements were made at 25°C ± 0.5°C which falls within the optimum range for grapevine photosynthesis (30). All measurements were taken at a minimum of 1000 μmol m^{-2}s^{-1} ambient light within the chamber, considered to be above saturating light levels (30,39). Flow rate in the chamber was a minimum of 84 L/min for measurements at fruit set, 117 L/min at mid-season, 124 L/min at veraison, and 182 L/min at harvest. Gas exchange measurements were made using a LCA-2 portable gas analyzer manufactured by Analytical Development Corporation (ADC), Hoddesdon, Herts, England, adapted for use with this chamber. Photosynthesis was calculated using a Basic computer program developed and written by Moon and Flore (31). The WVPn measurements were expressed on both a per unit leaf area basis (WVPn/L) and a per vine basis (WVPn/V).

Diurnal adjustments: We have previously discussed using a midday time window of 1100 hr to 1400 hr for whole vine measurements of Pn to reduce intra-vine variability associated with the diurnal effect (13). Partly cloudy days are common in Michigan, and procuring Pn data at a specific phenophase under cloudless conditions can be difficult. As a result, it was necessary to make some whole vine measurements up to 1600 hr. Since reductions in Pn have been demonstrated after 1400 hr (10,13) this presented the possibility that WVPn measured 1400 hr to 1600 hr might be comparatively lower than WVPn measured earlier (1100 hr to 1400 hr), due to the diurnal, rather than the treatment effect alone. Further, Downton *et al.* (10) observed that fruiting White Riesling maintains a higher Pn rate and exhibits a later decline than non-fruiting vines during the day. We used two separate approaches to deal with this problem. First, the replications were blocked over time. No adjustments were made to these measurements; they are reported in the WVPn data as observed values (OBS). Alternatively, we used diurnal response curves measured at variable crop loads (data not shown) to help normalize WVPn measurements taken from 1400 hr to 1600 hr to reflect midday values. These values are reported in the WVPn data as adjusted values (ADJ).

Single leaf photosynthesis: Single leaf determinations were made using a Parkinson broad leaf chamber and air supply unit (both manufactured by ADC) on leaves at four node positions along the shoot: *(1)* basal position, node four or five (BAS); *(2)* one to two nodes above BAS at fruit set and veraison, and three to

five nodes above BAS at harvest (BAS+2); *(3)* mid-shoot leaf (MID); and *(4)* most recently fully expanded leaf (MRFE). Ambient environmental conditions were: photon flux density $\geq$ 1000 μmol m^{-2}s^{-1}; leaf temperature 24°C to 30°C; inlet humidity 0 to 5%. Single leaf measurements were timed to correspond with WVPn measurements: at fruit set, mid-season, veraison, and harvest. SLPn was calculated using a Basic computer program previously described (31).

Yield, vine morphology, and dry matter partitioning: The fruit was harvested 18 September 1989. Shoot length was measured at harvest. Leaf area was measured at four phenophases: fruit set, mid-season, veraison and harvest. Leaf area was determined using a LiCor leaf area meter (Model LI 3000, LiCor Inc., Lincoln, Nebraska, U.S.A.). Total vine dry weight was determined at fruit set, veraison and harvest. Vines were oven-dried at 66°C and dry weight determined. Additional yield, vine morphology, and dry matter partitioning data are reported in a companion paper (14).

Experimental design and statistical analysis: The experimental design was a randomized complete block design with vines blocked on initial vine fresh weight as an estimate of vine size. Crop load was the main plot factor. Four replicates were measured. Regression analysis was most appropriate for comparisons between crop loads at the individual dates (7). Crop load can be expressed as clusters or berries per vine, both of which may also be considered as components of total fruit yield per vine. Linear and polynomial regressions were calculated using clusters per vine, berries per vine, and yield per vine as the independent variables for dependent variables of interest. For comparisons over time (at different phenophases) analysis was by ANOVA with phenophase split on crop load. Mean separation was calculated using Duncan's multiple range test. Statistics were calculated using the MSTAT-C (Michigan State University, East Lansing, MI) and PLOTIT (Scientific Programming Enterprises, Haslett, MI) statistical computer packages.

Results and Discussion

Yield and vine growth parameters: Crop load had a significant effect on both yield and vegetative vine growth. Yield per vine and berries per vine were significantly higher for those vines having greater cluster numbers, with berries per vine and yield being strongly correlated (Table 1). Reduced fruit set, evident when greater cluster numbers per vine were present (data not shown) may have occurred due to intra-vine competition for carbohydrates and growth substances (41). Shoot length for the six-cluster vines was nearly 40% less than defruited vines at harvest (Table 1). In a companion paper we reported that shoot growth, nodes per vine, and internode length were inversely correlated with crop load as early as mid-season (14).

Source size (leaf area) is an important morphological component related to photosynthetic activity.

Edson and Howell (12) considered the interactions of the yield components: total yield, clusters per vine, and berries per vine and how these reproductive components might influence source-sink relationships. They hypothesized that early in the season clusters per vine was likely to be the dominant reproductive sink, the strength of which was increasingly mediated by berries per cluster as the season progressed; and finally, driven primarily by total berries per vine. Leaf area is negatively correlated with clusters per vine as early as fruit set, a difference that could be measured just 16 days following crop load adjustments (14). While the flower cluster is reported to be a weak sink for attracting labelled carbon (2,20), this suggests that the vine does, in fact, perceive the flower clusters sometime prior to fruit set and that allocation patterns respond at that time to the number of fruit sinks.

Previously, we concluded that the increase in Pn per unit leaf area associated with higher crop loads (4,6,24,27) was part of an integrated physiological and morphological response by the whole vine to produce net carbon gains (or losses) (13). The effect appears to be mediated through allocation of assimilates resulting from changes in sink demands.

The concept of a shift or a 'balancing' of vine resources is supported by the total dry weight data. There were no significant differences in total dry weight accumulated at any phenophase (Table 2), suggesting that differences in morphological response and dry weight partitioning were the result of differences in allocation of resources (13,14). Other studies have shown that total vine dry weight at harvest is similar between fruiting and non-fruiting vines (13,16) across a range of leaf area to crop ratios (13). How the vine establishes and senses sink strength is unknown.

Photosynthesis: To date, Pn research on grapes has relied primarily on single-leaf measurements. However, Edson *et al.* (13) reported recently that while WVPn/L was significantly correlated with yield, crop load did not directly affect WVPn/V when measured at harvest. During the present study, we were interested

Table 1. Influence of crop load on shoot length and yield response of Seyval grapevines harvested 18 September 1989.

Clusters/ vine	Yield/ vine (g)	Shoot length (cm)	Berries/ vine
6	507.2	239.6	262
4	520.7	265.6	271
2	384.1	292.7	198
1	288.2	308.2	150
0	0	380.7	0
Independent variables^z		r^2	
Linear			
Clusters	0.63***	-0.53**	0.61***
Berries	0.95***	-0.61***	—
Yield	—	-0.61***	0.95***

^{z}r^2 significant at the 1% (**) or 0.1% (***) level.

Table 2. Influence of crop load on total dry weight at several phenophases in Seyval grapevines, 1989.

Clusters/ vine	Total dry weight/vine (g)			
	Fruit set[z] 1 July	Veraison[y] 18 August	Harvest 18 September	
6	54	207	277	
4	50	201	307	
2	48	193	299	
1	53	209	289	
0	—	—	286	
Independent variables[z]		r^2		
Linear and Quadratic				
Clusters	ns	ns	ns	
Berries	ns	ns	ns	
Yield	ns	ns	ns	

[z]Fruit set data collected five days post full bloom date.

[y]Berry soluble solids at 10° Brix.

[x]r^2 not significant (ns).

Table 3. Influence of crop load and phenophase on single leaf photosynthesis at several leaf positions of Seyval grapevines, 1989.

Treatment (clusters/vine)	SLPn (μmol m^{-2}s^{-1})			
	BAS[z]	BAS + 2	MID	MRFE
6	12.8 a[y]	13.9 a	15.9 a	14.3 a
4	11.9 ab	13.0 a	15.1 a	14.2 a
2	10.5 ab	11.9 ab	14.5 a	13.1 ab
1	8.7 bc	10.9 ab	11.1 b	9.8 b
0	6.4 c	8.4 b	11.5 b	9.9 b
	**	**	**	**
Independent variables[x]		r^2		
Linear				
Clusters	0.26***	0.30***	0.24***	0.13**
Berries	0.17**	0.28***	0.18**	0.13*
Yield	0.16**	0.30***	0.19**	0.17*
Phenophase				
Fruit set	14.7 a	N.A.	13.2 b	7.2 c
Mid-season	11.8 b	12.8 a	16.6 a	15.2 a
Veraison	10.2 b	12.8 a	14.8 ab	15.5 a
Harvest	5.3 c	9.2 b	9.8 c	11.1 b
	***	***	***	***
Independent variables[x]		r^2		
Linear				
Clusters	0.26***	0.30***	0.24***	0.13*
Berries	0.17*	0.24**	0.18**	0.12*
Yield	0.16**	0.30***	0.19**	0.17**

[z](BAS) basal position leaf, node four or five; (BAS + 2) leaf one to two nodes above the BAS leaf at fruit set and veraison, and three to five nodes above BAS at harvest; (MID) mid-shoot leaf; (MRFE) most recently fully expanded leaf. Cluster/ vine values are means across phenophase. Phenophase values are means across crop load.

[y]Mean separation for clusters/vine and phenophase by Duncan's multiple range test, significant F at the 1% (**) or 0.1% (***) levels. Same letter within each column and group not significantly different.

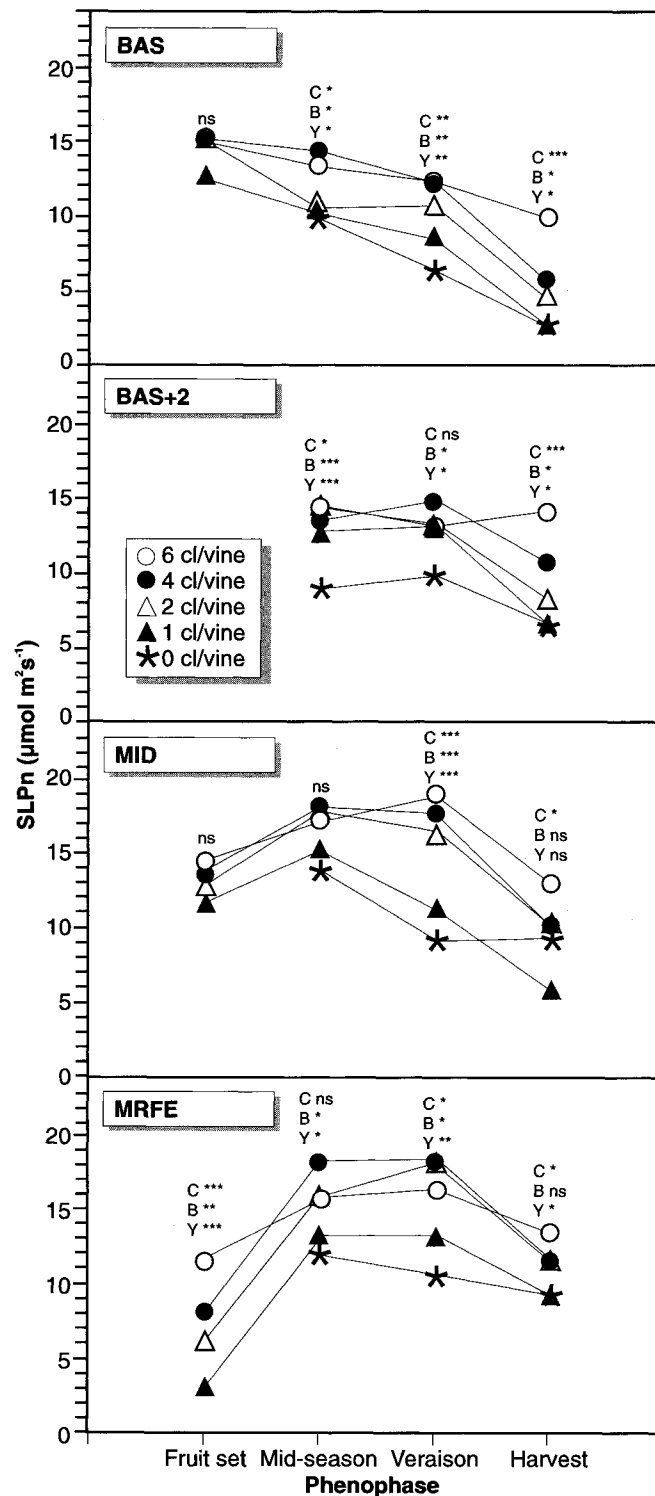[x]Independent variables; r^2 significant at 5% (*), 1% (**), or 0.1% (***).

Fig. 1. Influence of crop load and leaf position on single leaf photosynthesis of Seyval grapevines at several phenophases, 1989. Fruit set = four days post full bloom date; Mid-season = 29 July; Veraison = berry soluble solids at 10° Brix on 18 August; Harvest = 18 September. (BAS) basal node position, node four or five; (BAS + 2) one to two nodes above BAS at mid-season and veraison, and three to five nodes above BAS at harvest; (MID) mid-shoot leaf; (MRFE) most recent fully expanded leaf. Significance of linear regression analysis is shown for the independent variables: clusters per vine (C), berries per vine (B), and yield per vine (Y); with r^2 significant at 5% (*), 1% (**), 0.1 % (***), or not significant (ns).

in determining both the WVPn and SLPn response to crop load at four phenophases during the season.

Single leaf photosynthesis: Single leaf Pn increased with crop load although clear differences were usually only evident between the highest (4 to 6 clusters per vine) and lowest (0 to 1 cluster per vine) treatments (Fig. 1, Table 3). The effect of crop load on SLPn became evident as early as fruit set, with a significant positive correlation at the MRFE leaf position and comparative trends at the BAS and MID leaf positions (Fig. 1). By veraison, there were significant positive correlations between crop load parameters and SLPn at every leaf position (Fig. 1). Previously, we had concluded that either the MID or MRFE node positions might be acceptable for showing SLPn response to crop load at harvest (13). However, there was a significant correlation for each date only at the MRFE leaf position in this study (Fig. 1).

Since vines with high crop load produce fewer, smaller leaves (13,14), each individual leaf must assimilate carbon at a higher rate if total vine sink demands remain unchanged (13). While the mechanism behind this relationship is unknown, Candolfi-Vasconcelos and Koblet (4) have shown that partially defoliated vines compensate for the reduction in leaf area by increasing stomatal and mesophyll conductance, chlorophyll content, and water use efficiency. They concluded that compensation due to the mesophyll component was primarily responsible for increased Pn and suggested that enhanced carboxylation efficiency of ribulose-1,5-bisphosphate carboxylase/oxygenase was likely involved. This interpretation was based on the relationship between internal CO_2 concentration (C_i) and Pn, which assumes a homogenous stomatal response (9). If stomatal response to crop load is heterogenous, as shown for water stress (11) and for exogenous abscisic acid (ABA) applications (9), then leaf compensation to reductions in leaf area may be due, in greater part, to increased stomatal conductance.

Herold (21) points out that artificial manipulations of source-sink relationships may affect hormone synthesis and availability (i.e., increases in root:shoot ratios may increase the availability of cytokinins to the remaining sinks). Root:shoot ratios in the current study were 85 percent higher for the six-cluster vines compared to the defruited vines at harvest (data not shown), implying the possibility for higher cytokinin concentrations in the leaves of those vines. Exogenously applied cytokinins act rapidly to open stomates (25), suggesting a possible role in mediating the compensatory effect measured in this and other studies (4,12,13). Other plant growth substances may also be involved in mediating this response. Roper and Williams (38) have suggested that ABA and gibberellin (GA) may be involved in regulating photosynthetic rate adjustments to source-sink modifications. They hypothesized that accumulations of ABA in the leaves following girdling may have been responsible for reductions in Pn, and further, that exogenously applied

GA could partially negate the effects of ABA. However, they did not discuss how this response might be integrated with the stimulatory effect that GA can have on vegetative growth. As Herold (21) concludes, the integration between sink activity, hormones and photosynthetic rate has not been conclusively demonstrated.

Leaf age effects were also observed in this study. Leaves in the BAS position were the greatest contributors to Pn at fruit set, but later, from mid-season to harvest, MID and MRFE leaves had higher rates of SLPn (Table 3). Our data are consistent with the leaf age effects observed by Koblet (28) and Kriedemann et al. (29) (e.g., once leaves become fully expanded, they are maximally productive, gradually decreasing towards senescence). Chaves (6) observed that gross photosynthetic rates always increased from the basal leaf to the mid-shoot leaf and then decreased to the apical leaf, which was not yet fully expanded. Our measurements of leaves at various stages of leaf expansion indicated that variation in Pn was high when using young, not yet fully expanded leaves (data not shown).

Photosynthesis increased over time from fruit set to mid-season and veraison and then declined following veraison to harvest (Fig. 1, Table 3). The exception was SLPn at the BAS node position, which was maximal at fruit set. Although Pn at the MID node position tended to decline after mid-season (Fig. 1), there were no significant differences between Pn measured at mid-season and veraison at any node position (Table 3). These results are similar to those reported by Pandy and Farmahan (34) who observed a gradual reduction in photosynthesis following the lag phase in berry development. The relatively high SLPn rates observed mid-season and veraison for both MID and MRFE leaves (Table 3) would appear to accurately reflect the high metabolic sink demands of the vine at those times. During mid-season, vegetative growth is usually strong. At veraison, vegetative growth normally continues (at varying rates depending on vine vigor), the fruit accumulates sugar at a rapid rate, and root sinks are active (44).

Considering SLPn values measured on the MRFE leaf at various crop loads provides additional insight into how vine metabolic demands shift throughout the growing season. MRFE SLPn was maximal at mid-season for vines without crop (Fig. 1), reflecting the importance of the vegetative sinks in those vines. This concurs with Candolfi-Vasconcelos and Koblet (4) and Chaves (6). However, MRFE SLPn was equivalent to or higher than mid-season rates at veraison when crop was present (Fig. 1).

Comparison of SLPn and WVPn: Photosynthesis determined on a whole vine basis leads to somewhat different conclusions than those formulated from SLPn data for several reasons (13). Among these are: *(1)* whole plant measurements represent the mean activity of the entire continuum of leaves; neither the variation in leaf age, nor the influence of phyllotaxy are necessarily considered for single leaf measurements; *(2)* angle of inclination to the sun can be opti-

Table 4. Influence of crop load on whole vine photosynthesis expressed on a leaf area basis in Seyval grapevines, 1989.

	WVPn/L (μmol m⁻²s⁻¹)							
	Observed				Adjusted[z]			
Clusters/ vine	Fruit Set[y] 30 June	Mid-season 29 July	Veraison 19 Aug.	Harvest 18 Sept.	Fruit set 30 June	Mid-season 29 July	Veraison 19 Aug.	Harvest 18 Sept.
6	5.9	11.7	11.8	8.0	6.9	13.7	13.3	8.5
4	7.7	11.2	10.7	7.3	8.3	11.2	12.1	7.3
2	6.6	10.4	11.8	5.8	6.6	10.9	11.8	6.1
1	5.9	10.5	10.8	5.5	5.9	10.8	11.5	5.7
Independent variables[x]				r²				
Linear								
Clusters	ns	ns	ns	0.41*	ns	0.47*	ns	0.38*
Berries	ns	ns	ns	ns	ns	ns	ns	ns
Yield	ns	ns	ns	ns	ns	ns	ns	ns
Quadratic								
Clusters	ns	ns	ns	ns	ns	0.59*	ns	ns
Berries	ns	ns	0.73**	ns	ns	ns	0.53*	ns
Yield	ns	ns	ns	ns	ns	ns	ns	ns

[z]Adjusted to account for the diurnal response where appropriate (see text).
[y]Fruit set= four days post full bloom date; Veraison soluble solids = 10° Brix on 18 August.
[x]r² significant at 5% (*), 1% (**), or not significant (ns).

mized for single leaf determinations, but is restricted to the normal leaf orientation on the vine for whole vine determinations; and *(3)* photosynthesis and respiration of plant tissues other than the leaf being measured (*i.e.*, fruit) are not considered during single leaf measurements. These issues are discussed further in Edson *et al.* (13).

Single leaf Pn of the MRFE leaf was best correlated with WVPn/L at harvest in an earlier study (13). However, under the conditions of the present study, if we considered individual leaf positions at several phenophases, correlation between SLPn and WVPn/L was almost nonexistent and certainly inconsistent (data not shown). In contrast, when we considered correlations made across the season for the individual leaf positions, SLPn at both the MID and MRFE leaf positions were highly correlated with WVPn/L (r² = 0.43, signif. *** and r² = 0.44, signif. ***, respectively). In no cases were correlations between SLPn and WVPn/V significant. It would appear that although

Table 5. Influence of crop load on whole vine photosynthesis expressed on a per vine basis at several phenophases for Seyval grapevines, 1989.

	WVPn/V (μmol vine⁻¹s⁻¹)							
Clusters/vine	Fruit Set[z]		Mid-season		Veraison		Harvest	
	OBS[y]	ADJ	OBS	ADJ	OBS	ADJ	OBS	ADJ
6	0.6	0.7	3.0	3.5	4.6	5.3	2.9	3.1
4	0.9	0.9	3.9	3.9	4.6	5.2	3.3	3.3
2	0.9	0.9	4.0	4.2	5.5	5.5	2.9	3.0
1	0.8	0.8	4.2	4.3	5.1	5.4	2.7	2.9
Independent variables[x]				r²				
Linear								
Clusters	ns	ns	-0.55**	-0.35*	ns	ns	ns	ns
Berries	ns	ns	ns	ns	-0.35*	ns	ns	ns
Yield	ns	ns	ns	ns	-0.36*	ns	ns	ns
Quadratic								
Clusters	ns	ns	-0.62*	ns	ns	ns	ns	ns
Berries	ns	ns	ns	ns	-0.72**	ns	ns	ns
Yield	ns	ns	ns	ns	-0.73**	ns	ns	ns

[z]Fruit set = four days post full bloom date; Veraison berry soluble solids = 10° Brix on 18 August; Harvest date = 18 September.
[y]OBS: measured values; ADJ: values adjusted for diurnal response (see text).
[x]r² significant at 5% (*), 1% (**), or not significant (ns).

SLPn measurements accurately reflect the localized metabolic response of the vine to varying crop load, and in fact, that the general nature of the SLPn and WVPn/L response is similar, SLPn determinations cannot be used to extrapolate WVPn/V response to crop load.

Whole vine photosynthesis: Several metabolic and physiological processes and morphological differences are integrated by the whole plant as it responds to different crop loads. As observed in our earlier work (13), WVPn response to crop load was different, depending whether WVPn/L (Table 4) or WVPn/V (Table 5) was considered. The highest photosynthetic rates were observed at mid-season and veraison, irrespective if WVPn was calculated on a leaf area or whole plant basis (Tables 4 and 5). When considered on a per unit leaf area basis WVPn tended to be positively correlated with crop load, as the season progressed. However, this relationship was not strong. Conversely, crop load had no significant effect on WVPn/V at harvest (Table 5), supporting our previous conclusions to that effect (13).

Also, in our previous study, vines having the greatest number of vegetative sinks had the highest (albeit, not significant) photosynthetic rate per vine. In the current study, a similar pattern of response was apparent. Mid-season and veraison, WVPn/V was negatively correlated with crop load (Table 5). Differences in WVPn/V between high crop load vines (6 clusters per vine) and low crop load vines (1 cluster per vine) were greatest at mid-season when the grapevines were in an active vegetative growth phase. The relationship weakens at veraison and is absent by harvest (Table 5). Choma et al. (8) reported that whole plant photosynthesis of deblossomed strawberry plants was higher than that for fruiting plants during the last half of the fruiting cycle, so this response does not appear to be limited to grapevines.

Carbon dioxide fixed/g total dry weight was calculated as an estimate of midday total vine productivity at three phenophases during the season (Table 6). Consider that total dry weight accumulation per vine was not different among crop load treatments at any time during the season (Table 2). Edson et al. (14) have, however, shown differences in the pattern of distribution between the various vine tissues due to crop load. For example, vines with a high crop load partition a greater percentage of their total dry weight to fruit clusters than do low crop load vines (14). Although WVPn/V at mid-season was inversely related to crop load (Table 5), there were essentially no differences in carbon fixed per unit of total dry weight at any time during the season (Table 6). This implies a higher metabolic cost for producing vegetative rather than fruiting structures. Several factors support this suggestion. Cell structure for the fruit is produced early, with remaining fruit growth being the result of cell expansion as water and sugars move into pre-existing cells (35). Vegetative growth, by comparison, involves a process of constantly generating new cells, and on a

Table 6. Influence of crop load on carbon assimilated per vine per gram of total vine dry weight at several phenophases in Seyval grapevines, 1989.

	CO$_2$ Fixed/Total Vine Dry Weight[z]					
	Fruit set[y]		Veraison		Harvest	
Clusters/	1 July		19 August		18 September	
vine	OBS[x]	ADJ	OBS	ADJ	OBS	ADJ
6	1.1	1.3	2.3	2.6	1.1	1.1
4	1.9	2.1	2.4	2.6	1.1	1.1
2	1.8	1.8	2.9	2.9	1.0	1.0
1	1.5	1.6	2.5	2.7	0.9	1.0
Independent variables[w]				r^2		
Linear						
Clusters	ns	ns	ns	ns	ns	ns
Berries	ns	ns	ns	ns	ns	ns
Yield	ns	ns	ns	ns	ns	ns
Quadratic						
Clusters	ns	ns	ns	ns	ns	ns
Berries	ns	ns	0.57*	ns	ns	ns
Yield	ns	ns	ns	ns	ns	ns

[z](μmol vine^{-1}s^{-1}/g dry weight) X 10^{-2}
[y]Fruit set data collected five days post full bloom date; Veraison berry soluble solids = 10° Brix on 18 August.
[x]OBS = measured value; ADJ = values adjusted for diurnal response (see text).
[w]r^2 significant at 5% (*) or not significant (ns).

whole vine basis may require greater metabolic energy.

Additionally, the WVPn/V response we observed may, in part, be explained if one considers: (a) that crop load affects the distribution of vine morphology (i.e. leaves, fruit, shoots, roots, old wood) (14); and (b) that there are differences in respiration among these vine tissues (1,33,34). For example, respiration on a fresh weight basis is considerably higher for leaf tissue than berry tissue (34). However, when calculated on a dry weight basis, the respiration rate of mature leaves is two to three times lower and 25% lower than that of the flower cluster and berries (post set), respectively (33). Meristematic and actively expanding tissues respire at a relatively high rate compared to mature leaf tissue (1) and dramatic reductions in berry respiration (on a dry weight basis) occur after Stage I (33). Additionally, patterns of specific rates of respiration vary at different leaf positions and may not be the same at similar leaf age (1).

Conclusions

Under the conditions of this study single leaf determinations of Pn appear useful only to elaborate localized treatment effects on Pn. If we restrict our inquires to the localized treatment response, the data indicate that SLPn measured at the MRFE leaf position most consistently correlated with crop load parameters. One must interpret SLPn data carefully. Inference of whole vine photosynthetic response to treatment may be in error regardless of the phenophase at the time of mea-

surement. Further, even whole vine trends in Pn calculated on a leaf area basis may not correlate with SLPn given the differences in correlation observed at different phenophases in this study.

We conclude from this study that the vine possesses a balanced system of assimilate allocation based on a ranking of sink priority. Sink demand changes as the season progresses and localized photosynthetic rates may increase with sink stimulus (vegetative or reproductive). However, this may occur as a secondary (or integrated) physiological response to metabolic changes (*e.g.*, leaf area increases as crop load decreases), which are then balanced by internal mechanisms, leaving total Pn per vine relatively unaffected by crop load.

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