

Effects of the whole vine versus single shoot-crop level on fruit growth in *Vitis labruscana* 'Concord'

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Summary

The fruit growth response to the whole vine and single shoot crop level was studied in *Vitis labruscana* 'Concord' grown in the North-Eastern United States. In vines thinned to lower and higher yields (equivalent to 12 and 21 t·ha⁻¹), different number of clusters per shoot were retained after cluster thinning one week after set. Results showed that the seasonal accumulation of berry dry weight, fruit fresh weight, and the berry total soluble solids at harvest were only affected by the whole vine crop level. This suggests that under the conditions of this experiment shoots are not autonomous in terms of carbon partitioning to the fruit. Hence, crop level effects on fruit development can be considered and modelled on a whole vine basis.

Key words: carbon partitioning, shoot autonomy theory, sink-source relationship.

Introduction

Modeling plant productivity requires an understanding of source-sink relations. It is not clear if the growth of sinks such as fruits and their related leaves on shoots behave as independent units or if the sink development responds to the whole plant source-sink status (KOBLET and PERRET 1972, CARBONNEAU 1976, SPRUGEL *et al.* 1991). The term autonomy for carbohydrates is used to refer to a high degree of independence of a shoot or a branch from the parental plant. For carbon balance modeling, autonomy of shoots would require detailed submodeling of individual shoots or multiple shoots groups, while lack of autonomy would allow a much simpler “big leaf” “big fruit” modeling approach (LAKSO *et al.* 2001).

In peach trees, large old branches were considered autonomous (MARSAL *et al.* 2003) because fruit weight responded to certain patterns of fruit distribution within a tree. However, other research on peach has shown that fruit dry mass was better explained when the whole plant carbon balance was considered (WALCROFT *et al.* 2004). In apple, PALMER *et al.* (1991), modified sink-source ratios of different branches shortly after bloom, and found little autonomy in terms of fruit development (*i.e.* final fruit size was explained by whole tree leaf area fruit ratio regard-

less of spatial distribution patterns). In grapevine WOLPERT *et al.* (1983) observed that clusters on shoots that were more exposed to sun had clusters of similar weight than those that were shaded but had higher total soluble solids and lower acidity.

The autonomous behaviour of a shoot is certainly in part genetically determined by the sink strength of the organ and the resistance to carbon flow in the pathway. However, the timing of the organ growth, in relation to source supply, and the whole plant carbon balance might determine the final expression of organ autonomy. The crop level is known to interact and determine the final response to several physiological or practical cultures such as shoot or branch light exposure (LAKSO *et al.* 1989). The fruit on a shoot, for instance, may only be able to attract carbohydrates from the rest of the plant if there is a low crop load. On a heavily-cropped plant, shoots may appear to behave more autonomously if carbon is preferentially partitioned to fruit on the same shoots.

The objective of this work was to study the effects of the whole vine and single shoots-crop level on fruit growth as a way to test the shoot autonomy theory in 'Concord' grapes. In vines with two yield levels, different number of clusters per shoots were left by cluster thinning (lightly-cropped shoots on heavily-cropped vines and vice-versa). If berry growth and sugar accumulation depended on the shoot crop level, it would suggest an autonomous behaviour of shoots. In the case that berry growth was a function of the whole vine crop level, regardless of the number of clusters left in a shoot, it would indicate non-autonomous behaviour of shoots in terms of carbon partitioning to the fruit.

Material and Methods

Experimental plot and plant material: The experiment was carried out during 2006 in an own rooted 'Concord' (*Vitis labruscana*) vineyard planted in 1997 at a spacing of 2.74 m between rows and 2.44 m between vines. The vineyard was located at Cornell University NY State Agricultural Experiment Station in Geneva, NY, USA (42N 77W) and consisted of four rows with 31 vines per row. Vines were trained to a 1.6 m high bilateral cordon with single pendant curtain, oriented North-South, and short-cane pruned during the

winter to retain about 80 nodes. Non-count shoots were not removed, however there were relatively few. Each cane left after pruning had 3 to 5 nodes, giving approximately 20 canes per vine. During the previous seasons vines were similarly pruned and no differential treatments were applied. The soil within the vineyard was a Lima series, moderately deep, moderately well-drained, with a fine silt loam structure. Cultural practices of fertilization and pest management were those common for 'Concord' grapes in the area. Irrigation was not applied due to adequate rainfall during the growing season (May to October rainfall was 675 mm).

Treatments: Sixteen vines were selected from the two central rows of the vineyard. Eight vines were chosen in the north end and another eight vines in the south end of the vineyard. On each side, four consecutive vines were selected from the two central rows and were respectively assigned to each crop level treatment (high or low). Crop level treatments were based exclusively on the number of clusters retained after thinning, regardless of vine pruning weight.

In the eight vines assigned for the low crop level, approximately 16 out of a total of 20 canes, were fruit thinned to about half of the shoots with only the basal cluster and the other half with no cluster (low crop level). Two out of these 16 canes were randomly selected as representative of the thinned-shoot population. The remaining 4 canes were selected for differential thinning treatment. Two canes were left unthinned for the unthinned treatment (Fig. 1). In the other two canes shoots were unevenly thinned in order to have two un-thinned shoots and one shoot without clusters and the remaining shoot with one cluster as depicted in Fig. 1. Hence, the shoots with either no cluster or one cluster could potentially export to the unthinned shoots on the same cane. Instead, in the unthinned canes, the expected larger dry matter demand of these shoots had to be satisfied by shoots located on different canes (Fig. 1)

In the other eight vines selected for the high crop level approximately 18 canes out of 20 were left unthinned (high crop level). Two of these 18 canes were randomly selected as representative of the entire population. The remaining two canes were assigned to the thinned treatment and were thinned similarly to the thinned treatments in the low crop level (e.g. approximately half of the shoots with only the basal cluster and the other half with no cluster, Fig. 1).

For the whole vine as well as single cane treatments, fruit thinning was performed 18 d after flowering in order to avoid fruit set compensation effects. Average whole vine yield was 7.9 and 14.0 kg·vine⁻¹ equivalent, on a hectare basis, to 11.8 and 20.8 tn.

Measurements taken: At bloom, the cane diameter was measured on all canes selected to represent the treatments using electronic caliper at the base, close to the junction with the older wood, across the longest axis. Shoot length was measured in all the shoots arising from the selected canes. This was done in order to ensure uniformity in the initial shoot size selected for comparisons. Only in the canes representative for the whole vine crop levels shoot lengths were measured at the end of the season. Every seven to ten days throughout the season, berry equatorial diameter was determined in four individual marked berries in each experimental cane, for a total of 64 berries per cane type treatment. In each cane, two berries per shoot were randomly selected from the basal cluster. Berry diameters were determined in the same berries during all the season. Berry diameter was converted into berry dry weight by means of allometric relationships obtained from a randomly collected sample of 20 berries. Dry weights were calculated after drying the samples at 65 °C until constant weight. Before veraison, berries were only randomly collected from shoots thinned as the entire vine (thinned shoots in the low crop level and unthinned shoots in the high crop level). After veraison, specific allometric relationships were obtained for all the cane types. There were however only differences in the allometric relationship between berry diameter and dry weight on the last measurement day between high and low crop level, but not between cane types within a crop level at any sampling time.

In mid-October, the vines were harvested and all the shoots of the selected canes were separated to determine total shoot fruit yield, number of clusters per shoot, average cluster weight, berry weight, and berries per cluster. Total soluble solids (TSS) were estimated on each individual shoot in a random sample of 30 berries with a temperature compensated digital refractometer (Sper Scientific, USA). The selected treatment shoots were harvested three days before the rest of the vine. A sample of 100 berries per vine was also collected randomly to obtain the average berry weight and berry TSS for the whole vine.

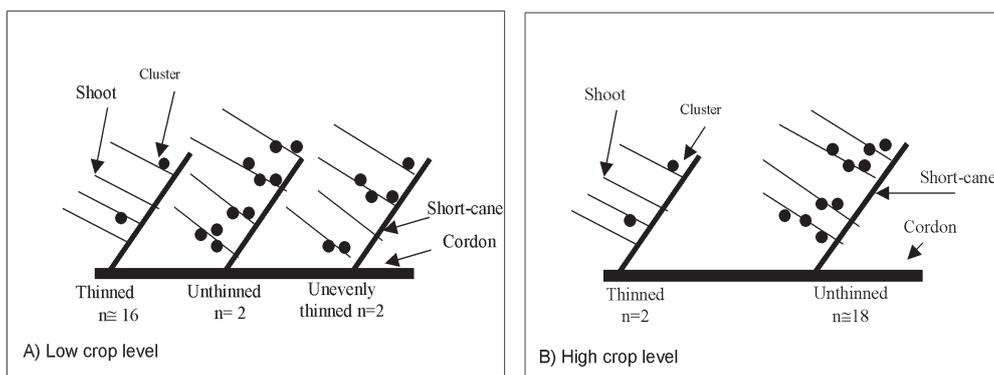


Fig. 1: Schematic representation of the cluster left after thinning in the shoots for the different cane types in **A)** low crop level vines and **B)** high crop level vines. In each cane type the number of canes per vine (n) is also indicated.

Statistical analysis: Analysis of variance was performed using the 'mixed' procedure of the SAS statistical package (version 9.0; SAS Institute, Cary, NC). Differences between treatment means were assessed by designed contrasts among treatments. Analysis of variance was performed considering each individual vine as unit, so there were eight repetitions per treatment. Mean values were weighted for the number of data that were entered for the average. Individual data of berry weight and TSS from each shoot were used to perform multiple linear regression with the following independent variables: whole vine yield, shoot yield, cane diameter and shoot length both measured at the beginning of the experiment. The multiple regression analysis of berry weight and berry total soluble solids versus vine and shoot parameters was performed using the 'reg' procedure with a stepwise independent variables selection criterion (SAS version 9.0; SAS Institute, Cary, NC).

Results and Discussions

This study focused on the fruit growth responses to the whole vine and single shoot crop levels. The lengths of each shoot were estimated at bloom and showed that selected canes were uniform among crop level and shoot types (Tab. 1). Therefore, at the beginning of fruit growth, the source capacity of the selected shoots were similar. The final shoot dimensions were measured in the canes representative of the whole vine treatments, and showed that there were not significant differences between whole vine high and low crop levels (Tab. 1).

Throughout berry growth, berry dry weight was mainly influenced by whole-vine crop yield (Fig. 2). In each whole vine crop level, the thinning to different number of clusters did not have any significant ($P < 0.05$) effect on berry dry weight development (Fig. 2).

This suggests that in the low crop level vines there was carbon available to be shared that was apparently utilized by the un-thinned shoots, suggesting that there was some carbon translocation between shoots. This is in agreement with other reports that showed that carbon translocation between shoots can occur (KOBLET and PERRET 1972) particularly if the sink-source ratio of shoots is manipulated by defoliation (Quinlair and WEAVER 1970) or shading (VANDEN HEUVEL *et al.* 2002) of individual shoots.

In the lightly cropped vines, there were not significant differences ($P < 0.05$) in berry growth between the unevenly thinned and the unthinned treatments (Fig. 2 and Tab. 1). In the unevenly-thinned canes the un-thinned shoots might have imported photosynthates from the thinned shoots located in the same cane. Instead, in the unthinned treatment shoots had to import carbon from other shoots located on different canes and thus at a larger distance (see Fig. 1). In this experiment then the distance and vascular connection between organs were not a significant factor for the autonomy behaviour of shoots. Horizontally divided canopies often have bottom cordons or canes that produce fruit with lower sugars than the upper canes (WOLF *et al.* 2003, BORDELON *et al.* 2008). This might be because of differences in cluster microclimate or altered physiology of downward-oriented shoots (SCHUBERT *et al.* 1995). However, it may be that the whole vine crop level can be subdivided into large zones that consist of individ-

Table 1

Effects of the vine crop level and cane type on: cane diameter and shoot length at bloom and at the end of the season; single shoot average yield and number of cluster; and berry weight and berry total soluble solids (TSS) in the whole vine and in the single shoots

Crop yield Cane Type treatments	Cane diameter (mm)	Shoot length at bloom (cm)	Shoot length at the end season (cm)	Shoot yield (g)	#Cluster per shoot	Berry weight (g)	#Berries per cluster	TSS (°Brix)
Low crop (LC)						3.5	33	16.3
Thinned (T)	9.5	93	244	118	0.7	3.5	34	16.1
Unthinned (UT)	9.8	103		259	2.2	3.5	32	16.3
Unevenly thinned (UVT) ¹	10.1	96		279	2.3	3.5	34	16.3
High crop (HC)						3.0	32	15.2
Thinned (T)	9.5	98		96	0.5	2.9	32	15.2
Unthinned (UT)	9.1	108	234	231	2.2	3.0	33	15.2
ANOVA								
Crop level effects								
LC vs HC			n.s.			**	n.s.	**
Cane type effects								
T vs UT in Low crop	n.s.	n.s.		***	***	n.s.	n.s.	n.s.
T vs UVT in Low crop	n.s.	n.s.		***	***	n.s.	n.s.	n.s.
UT vs UVT in Low crop	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.	n.s.
UT vs T in High crop	n.s.	n.s.		***	***	n.s.	n.s.	n.s.
T in LC-T in High crop	n.s.	n.s.		*	n.s.	*	n.s.	**
UT in LC-UT in High crop	n.s.	n.s.		n.s.	n.s.	*	n.s.	***
UVT in LC-UT in High crop	n.s.	n.s.		*	n.s.	**	n.s.	***

***, ** and n.s. indicate significant differences at $P < 0.001$, $P < 0.01$, $P < 0.05$ or non significant, respectively.

⁽¹⁾ Data are those from the shoots with either two or three clusters.

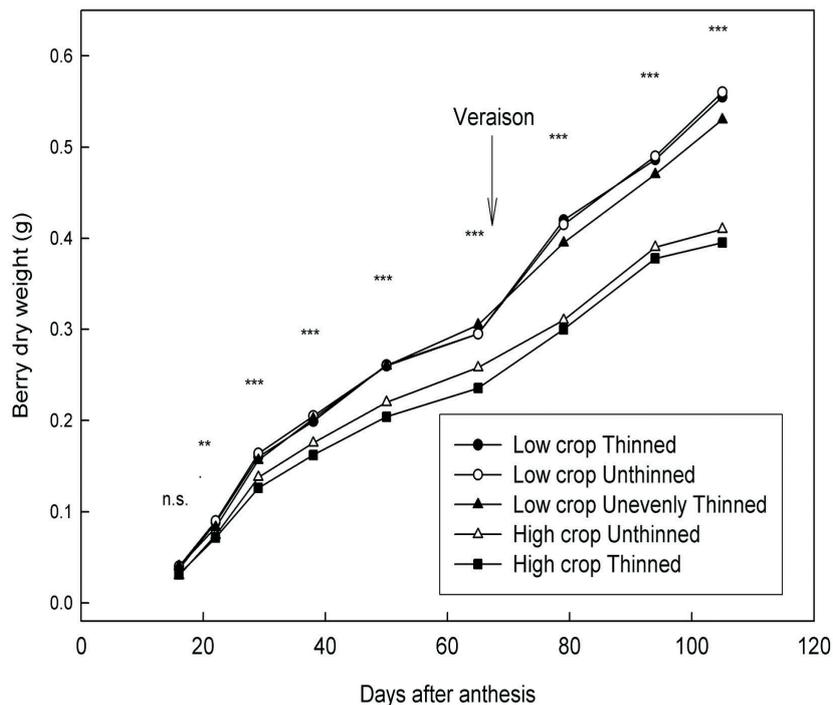


Fig. 2: Seasonal pattern of the cumulative berry dry weight. Data are means of 64 berries per cane type. ***, **: indicate significant differences at $P < 0.001$, $P < 0.01$ for the vine crop level. Cane thinning effects were never significant.

ual cordons dependant on the training system used. In the high-crop vines berries grew at a same rate all season despite the thinned shoots having only one cluster compared to two to three clusters for unthinned shoots (Fig. 2). At the beginning of the season, grapevine shoot development and growth is highly dependent on the reserves (WILLIAMS 1997). However, when fruit set is reached, a shoot seems to be able to provide photoassimilates for berry growth (HALE and WEAVER 1962). This feature might potentially allow some apparent autonomy of the shoot particularly in terms of berry growth. However, our results suggest that even just before harvest, berry growth was mainly affected by the whole vine crop level (Fig. 2).

At harvest, berry weight and berry TSS were only affected by crop level and not by the individual shoot crop level (Tab. 1). Multiple regressions of berry weight as a function of several variables (Tab. 2) showed that vine yield was the only variable that explained some of the vari-

ability of the data. Fruit yield/shoot and initial shoot length were significant at $P < 0.05$ but their inclusion provided little increase in the r^2 value. Initial cane diameter did not meet the 0.150 significance level required for entry into the model. Similarly, for berry TSS the only variable that met the 0.150 threshold level to enter into the model was vine yield, which explained 26 % of the variation in the data. However, since the r^2 was low (Tab. 2) other factors affecting early fruit growth before treatments were established played an important role.

Overall, these results indicate that fruit growth and sugar accumulation was primarily dependent on the whole vine crop level. This does not exclude the possibility of local effects within a vine. Differences in light microclimates between portions of a vine are for instance well known to affect fruit composition (KLIOWER and SMART 1989, WOLPERT 1983) or shoot to shoot variations in yield (SMART *et al.* 1982).

Table 2

Summary of the stepwise selection for the berry weight and total soluble solids (TSS) multiple regression analysis

Independent variables	Dependent variable							
	Parameter estimate	Berry weight (g)			TSS (°Brix)			
		Prob	Partial r^2	Model r^2	Parameter estimate	Prob	Partial r^2	Model r^2
Vine yield ($t\ ha^{-1}$)	-0.043	<0.001	0.204	0.204	-0.100	<0.0001	0.260	0.260
Shoot yield (g)	-6.7 E ⁻⁴	0.001	0.039	0.244		n.s.		
Shoot length (cm)	0.0022	0.034	0.017	0.261		n.s.		
Cane diameter (mm)		n.s.				n.s.		
Berry weight (g) ¹	--	--	--	--		n.s.		

¹)Berry weight was included as independent variable only in the TSS regression, n.s. non significant at $P > 0.150$.

Conclusions

Results reported here indicate that shoots do not behave very autonomously in *Vitis labruscana* 'Concord'. This suggests that under the conditions of this experiment crop level effects on fruit development can be considered on a whole vine basis. These results have relevance for carbon balance modelling and canopy management because models can be greatly simplified by treating fruit as a "big fruit" organ. Our results also imply that the use of individual shoots as the unit level for carbon partitioning studies requires isolation from the parental vine to avoid the buffer capacity of the rest of the vine.

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References

- BORDELON, B. P.; SKINKIS, P. A.; HOWARD, P. H.; 2008: Impact of training system on vine performance and fruit composition of Traminette. *Am. J. Enol. Vitic.* **59**, 39-46.
- CARBONNEAU, A.; 1976: Mise au point bibliographique sur la photosynthèse chez la Vigne. *Connaiss. Vigne Vin* **3**, 249-267.
- HALE, C. R.; WEAVER, R. J.; 1962: The effect of developmental stage on direction of translocation of photosynthate in *Vitis vinifera*. *Hilgardia* **33**, 89-131.
- KOBLET, W.; PERRET, P.; 1972: Wanderung von Assimilaten innerhalb der Rebe. *Die Weinwissenschaft* **27**, 146-154.
- KLIEWER, W. M.; SMART, R. E.; 1989: Canopy manipulation for optimizing vine microclimate, crop yield and composition of grapes. In: C. J. WRIGHT (Ed.): *Manipulation of fruiting*, 275-291. Butterworths & Co., London.
- LAKSO, A. N.; ROBINSON, T. L.; POOL, R. M.; 1989: Canopy microclimate effects on patterns of fruiting and fruit development in apple and grapes. In: C. J. Wright (Ed.): *Manipulation of fruiting*, 263-274. Butterworths & Co., London.
- LAKSO, A. N.; WHITE, M. D.; TUSTIN, D. S.; 2001: Simulation modeling of the effects of short and long-term climatic variations on carbon balance of apple trees. *Acta Hort.* **557**, 473-480.
- MARSAL, J.; BASILE, B.; DEJONG, T. M.; 2003: Influence of branch autonomy on fruit, scaffold, trunk and root growth during stage III of peach fruit development. *Tree Physiol.* **23**, 313-323.
- PALMER, J. W.; CAI, Y. L.; EDJAMO, Y.; 1991: Effect of part-tree flower thinning on fruiting, vegetative growth and leaf photosynthesis in 'Cox's Orange Pippin' apple. *J. Hort. Sci.* **66**, 319-325.
- QUINLAIN, J. D.; WEAVER, R. J.; 1970: Modification of pattern of photosynthate movement within and between shoots of *Vitis vinifera* L. *Plant Physiol.* **46**, 527-530.
- SCHUBERT, A.; RESTAGNO, M.; NOVELLO, V.; PETERLUNGER, E.; 1995: Effects of shoot orientation on growth, net photosynthesis, and hydraulic conductivity of *Vitis vinifera* L. cv. Cortese. *Am. J. Enol. Vitic.* **46**, 324-328.
- SMART, R. E.; SHAULIS, N. J.; LEMON, E. R.; 1982: The effect of concord vineyard microclimate on yield. II. The interrelations between microclimate and yield expression. *Am. J. Enol. Vitic.* **33**, 109-116.
- SPRUGEL, D. G.; HINKLEY, T. M.; SCHAAP, W.; 1991: The theory and practice of branch autonomy. *Ann. Rev. Ecol. System* **22**, 309-334.
- VANDEN HEUVEL, J. E.; LEONARDOS, E. D.; PROCTOR, J. T. A.; FISHER, K. H.; SULLIVAN, J. A.; 2002: Translocation and partitioning of ¹⁴C photoassimilate from light- and shaded- adapted shoots in greenhouse-grown 'Chardonnay' grapevines (*Vitis vinifera* L.). *J. Am. Soc. Hort. Sci.* **127**, 912-918.
- WALCROFT, A. S.; LESCOURRET, F.; GÉNARD, M.; SINOQUET, H.; LE ROUX, X.; DONÉS, N.; 2004: Does variability in shoot carbon assimilation within the tree crown explain variability in peach fruit growth? *Tree Physiol.* **24**, 313-322.
- WOLF, T. K.; DRY, P. R.; ILAND, P. G.; BOTTING, D.; DICK, J.; KENNEDY, U.; RISTIC, R.; 2003: Response of shiraz grapevines to five different training systems in the Barrosa Valley, Australia. *Aust. J. Grape Wine Res.* **9**, 82-95.
- WILLIAMS, L. E.; 1997: Grape. In: E. ZAMSKI, A. A. SCHAFFER (Eds): *Photoassimilate distribution in plants and crops: Source-sink relationships*, 851-881. Marcel Dekker Inc., New York.
- WOLPERT, J. A.; HOWELL, G. S.; MANSFIELD, T. K.; 1983: Sampling Vidal blanc grapes. I. Effect of training system, pruning severity, shoot exposure, shoot origin and cluster thinning on cluster weight and fruit quality. *Am. J. Enol. Vitic.* **34**, 72-76.

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