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Effects of post-bloom low light and girdling on fruit set of *Vitis vinifera* (L.) cv. 'Riesling' and *Vitis labruscana* (L.) cv. 'Concord'

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Abstract

Aim: In grapevines, similarly to many woody crops, berry set is a crucial determinant for vine productivity. We reduced vine carbohydrate supply through shading and preventing phloem flow by girdling to investigate the effects on fruit set and berry weight, in field-grown 'Concord' (*Vitis labruscana* L.) and 'Riesling' (*Vitis vinifera* L.) grapevines.

Methods and results: Carbon supply to the fruit was manipulated by shading (30 % light transmissivity) individual shoots or shading and girdling. Girdling isolated the shoot and its fruit from possible carbohydrate supply from the rest of the vine. Shading was accomplished by covering shoots with a woven strip of shade cloth for four consecutive days in the period between flowering and 28 ('Concord') or 16 ('Riesling') days after flowering. The percentage of fruit set was calculated from estimated flower numbers using a photographic method and actual berry counts.

Conclusions: In both 'Concord' and 'Riesling', short-time shading caused reductions in fruit set, although this effect was more severe in 'Concord'. Both species were most sensitive to reductions in carbon supply during the period between 5 and 12 days after flowering. In 'Concord' vines, the effects caused by shading were greater with girdling probably because 'Concord' vines had higher crop level.

Significance and impact of the study: The results can be used as basis for modelling fruit set in grapevines.

Key words: branch autonomy, carbon supply, flowering, girdling, shading

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Introduction

Poor fruit set may limit grapevine (*Vitis vinifera* L.) yield under certain environmental conditions, such as low temperature, overcast sky or rain, which seem to reduce fruit set, likely because they limit carbon assimilation (Caspari *et al.*, 1998). Moreover, fruit set in grapevines is source-limited, and, consequently, if leaf area decreases, fruit set and bud fertility may be reduced (Coombe, 1959; Candolfi-Vasconcelos and Koblet, 1990; Poni *et al.*, 2006a, 2008). In addition, treatments that increase carbohydrate availability, such as girdling and removal of competing sinks, usually improve fruit set (Coombe, 1959).

However, there is insufficient knowledge about the specific period of time shortly before and after bloom when grapevine is most sensitive to low carbohydrate supply and how this would affect the setting of fruits. For instance, this knowledge is important for modelling carbon balances in grapevines where fruit set routines have not been included (Poni *et al.*, 2006b). The current study aimed to determine with more precision the period around flowering and fruit set when a reduction in carbon supply due to artificial shading would have a large effect on fruit set. Shoot girdling was used in conjunction with the shading to differentiate within-shoot supply alone versus potential additional support from the vine.

Materials and Methods

1. Experimental plot and plant material

The experiment was carried out during the 2007 growing season at the Cornell University NY State Agricultural Experiment Station in Geneva, NY, USA (42N 77W). An own-rooted 'Concord' (*Vitis labruscana* L.) vineyard planted in 1997 at a spacing of 2.74 by 2.44 m (1496 vines ha^{-1}) and a 'Riesling' (*Vitis vinifera* L.) vineyard planted in 2005 on 101-14 rootstock at a spacing of 2.74 by 2.1 m (1738 vines ha^{-1}), both oriented in the North-South direction, were used in the current study. These cultivars represent two commercial *Vitis* species and one is grown to obtain lower yields for wine quality ('Riesling') whereas the other one is grown for obtaining high yields of acceptable maturity ('Concord').

'Concord' vines were trained to a high (1.6 m) bilateral cordon with short canes of 5-6 buds and a single pendant curtain pruned during the winter to retain about 80 nodes. 'Riesling' vines were pruned by leaving two canes; shoot thinning was performed pre-bloom in early June to retain an average of 24 shoots per vine (11 shoots m^{-1}). Yields of these vineyards were 14.4 and 20.8 tons per ha for 'Riesling' and 'Concord', respectively.

The soil within the vineyards corresponds to the Lima series (fine-loamy, mixed, active, mesic Oxyaquic Hapludalf) and it is very deep (> 2 m), moderately well drained, with a fine loamy structure (Soil Survey Staff, 2018). In both vineyards, cultural practices of irrigation, fertilization and pest management were appropriate to maintain healthy vines with minimal stress. Rainfall was 317 mm over the growing season (May to October), as recorded by a weather station located close to the 'Concord' vineyard. Data on temperature, rainfall, solar radiation and wind speed were collected from this weather station (available at http://weather.nysaes.cals.cornell.edu/) during the study period (Figure 1).

2. Treatments

Within the vineyard, 9 'Concord' vines were selected for their uniformity (assessed visually). In each single vine (block), 9 uniform canes with 4 to 5 shoots each were selected and randomly assigned to each of the following treatments (Table 1):

Similarly, 10 'Riesling' vines were selected and 2 adjacent shoots were randomly chosen and assigned to the first five treatments mentioned before (S0 to S13-16), due to the fact that 'Riesling' vines have 10 shoots on average and, as done for 'Concord', each single vine carried all treatments. In both 'Riesling' and 'Concord' experiments flowering was considered

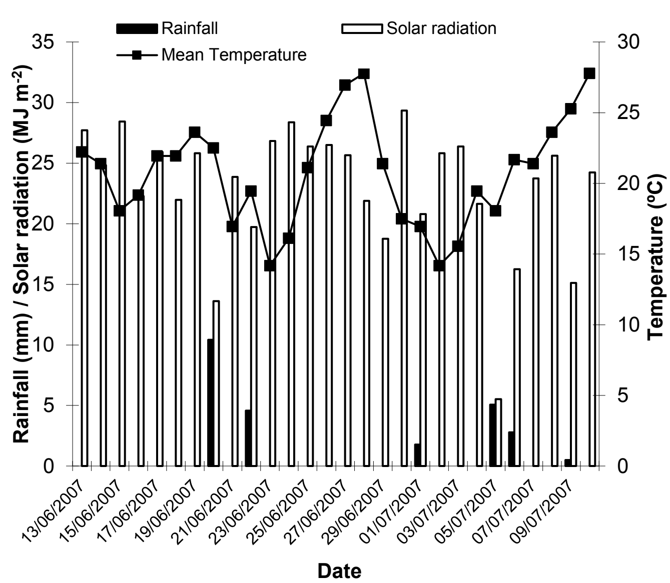

Figure 1 - Weather conditions during the study period (13th June – 10th July 2007): daily rainfall, solar radiation and mean air temperature.

when, at the whole vine level, around 50 % of the flowers were opened.

In both species, heavy shading was achieved by covering entire shoots with woven strips with a photosynthetically active radiation (PAR) transmissivity of 30 %. Shading cloths were moved between treated shoots every four days. Moreover, control shoots were always ungirdled; however, for 'Concord', in each of the shading treatments, 2 shoots per cane were girdled in order to avoid the buffer capacity of the rest of the vine, while the other 2 shoots of each cane were ungirdled. In 'Riesling', half the shaded shoots were girdled. Girdling was carried out by performing a circular incision, with a razor blade, below the basal cluster at the beginning of the treatment in each specific case to isolate the shoot and cluster from potential carbohydrate import from the rest of the vine.

3. Determinations

At the beginning of the experiment, the length of each shoot was measured. Fruit set was determined following the procedures described by Poni *et al.* (2006a). At flowering, photographs of the basal cluster of all the shaded shoots were taken. For both species, a relationship between the flowers counted in the printed photograph and the real number of flowers was established ('Concord': Flower number = 1.29 * Flowers in image; $r^2 = 0.95$, $n = 27$; 'Riesling': Flower number = 2.13 * Flowers in image; $r^2 = 0.94$, $n = 19$). These relationships were performed using entire clusters and all the pollinated berries in each of these clusters. Very few berries without seeds were present and they were not measured. At harvest, all the berries in a cluster were counted and berry weight was determined. Fruit set was calculated as the number of set fruit x 100 divided by the number of flowers.

In mid-October, all the shoots of the selected canes were individually harvested to determine individual shoot yield and the number of clusters per shoot. Average berry weight was estimated on each individual shoot in a sample of 30 berries collected from the intact clusters; then, cluster weight was divided by the average berry weight to estimate the number of berries per cluster. The shoot harvesting operation was performed during the same day. The rest of the vine was harvested three days later in order to obtain the overall vine yield and the number of clusters per vine.

4. Statistical analyses

Analysis of variance was performed using the 'aov' function of the R statistical package (version 3.2.3; R Core Team, 2015). The effects of vine, shading treatment and girdling and the interactions between vine and shading and vine and girdling were assessed independently for each of the species studied using a completely randomized design for the ANOVA. The assumptions of normality (Shapiro-Wilks) and homoscedasticity (Bartlett's test) were checked. Data on fruit set percentage were used in the ANOVA after an arcsine square root transformation. Means were separated ($p < 0.05$) using the Tukey Honest Significant Difference (HSD) test. Pearson's correlation coefficient was used for assessing significant relations of these variables with shoot length and yield.

Table 1 - Shading treatments applied to 'Concord' and 'Riesling' grapevines.

Abbreviation	Treatment
S0	Control unshaded during the entire season
S0-4	Heavy shaded from flowering to 4 days after flowering
S5-8	Heavy shaded from 5 to 8 days after flowering
S9-12	Heavy shaded from 9 to 12 days after flowering
S13-16	Heavy shaded from 13 to 16 days after flowering
S17-20	Heavy shaded from 17 to 20 days after flowering
S21-24	Heavy shaded from 21 to 24 days after flowering
S25-28	Heavy shaded from 25 to 28 days after flowering

Results

In the 'Concord' control vines, the position of the clusters within the shoot affected the number of flowers and berries per cluster and berry weight, decreasing with the upper clusters, but not the percentage of fruit set (Table 2). Basal and second clusters had more flowers and berries than third clusters. Berry weight changed similarly in this species.

In 'Riesling' control vines, basal and second clusters showed a greater number of flowers than the third cluster. In contrast, berry weight was greater in the second and third than in the basal clusters. Moreover, no differences in the number of berries per cluster were detected as well as in the percentage of fruit set (Table 2). We looked for other internal correlations that may have had effects, but found no significant correlations among number of flowers and fruits, fruit set and berry weight with shoot length and yield for any of the two species (data not shown).

The effect of the individual vine was significant for 'Concord' (Table 3). In this species, berries per cluster and fruit set were significantly altered by shading treatments. Girdling exerted a significant effect on all the variables measured in 'Concord', except for the number of flowers, which was determined before the treatments. The interaction between vine and shading was significant for fruit set and berry weight in 'Concord' (Table 3).

The effect of the individual vine was not significant for 'Riesling' (Table 3). Berries per cluster and fruit set were significantly altered by shading treatments. Girdling exerted a significant effect on berry weight but not on berry set in 'Riesling'. Finally, the interaction between vine and shading was not significant (Table 3).

The influence of shading and girdling was expressed as the percentage of fruit set with respect to that of the control treatment (Figure 2). In the case of 'Concord', shading of girdled shoots (i. e. only support from within the shoot) had the strongest reduction of fruit set by about 30-40 % when applied in the first 12 days after bloom, while having less effect after that period. When the shoots were not girdled, allowing import from other exposed shoots, shading reduced the fruit set by about 40 % at 9-12 days after bloom, while having less effect immediately after bloom or after about 2 weeks. The difference between the girdled and ungirdled shoots

Table 2 - Number of flowers and berries per cluster, percentage of fruit set and berry fresh weight of 'Concord' and 'Riesling' control vines as a function of the position on the cluster. Data are averages ± standard errors per position within the shoot.

	'Concord'			'Riesling'		
	Basal cluster	Second cluster	Third cluster	Basal cluster	Second cluster	Third cluster
# Flowers per cluster	84 ± 5 b	69 ± 6 b	45 ± 6 a	197 ± 13 b	188 ± 12 b	137 ± 21 a
# Berries per cluster	26 ± 2 b	22 ± 2 b	15 ± 2 a	97 ± 10 a	102 ± 10 a	87 ± 13 a
Fruit set (%)	33 ± 2 a	35 ± 3 a	34 ± 4 a	50 ± 4 a	55 ± 5 a	67 ± 4 a
Berry weight (g)	3.0 ± 0.1 b	2.9 ± 0.1 b	2.4 ± 0.1 a	0.9 ± 0.1 a	1.0 ± 0.1 ab	1.2 ± 0.1 b

Within each species, different letters in the row indicate significant differences at $p < 0.05$, according to Tukey HSD test.

Table 3 - Effects of vine, shading and girdling on number of flowers and berries, fruit set and berry fresh weight in 'Concord' and 'Riesling' vines. Data shown are p-values.

	# Flowers per cluster	# Berries per cluster	Fruit set (%)	Berry weight (g)	# Flowers per cluster	# Berries per cluster	Fruit set (%)	Berry weight (g)
Vine	**4.59×10^{-7}**	**0.041**^{y}	**1.69×10^{-8}**	**0.002**	0.317	0.379	0.998	0.512
Shading	0.071	**4.42×10^{-5}**	**3.88×10^{-7}**	0.139	0.198	**0.041**	**0.048**	0.121
Girdling	0.078	**0.037**	**1.09×10^{-4}**	**0.021**	0.204	0.304	0.680	**0.003**
Vine x Shading	0.076	0.525	**0.017**	**3.18×10^{-4}**	0.179	0.737	0.716	0.749
Vine x Girdling	0.735	0.845	0.948	0.231	0.053	0.556	0.372	0.130
Shading x Girdling	0.420	0.181	0.065	0.999	0.805	0.994	0.854	0.346

Bold values indicate significant ($p < 0.05$) effects.

was greatest just after bloom and then later at 21-24 days after bloom.

In ‘Riesling’, the reduction of fruit set was significant when shading was applied starting 5 and 13 days after flowering. However, the shade effect was very mild, 10-15 % (Figure 2). Girdling did not significantly change the effect of shade on fruit set in ‘Riesling’.

Shading combined with girdling produced different results in ‘Concord’ (Table 4). The number of berries

Table 4 - Effect of shading date on the number of flowers and berries, percentage of fruit set and berry weight in ‘Concord’. Ambient solar radiation accumulated over the four-day period when each treatment was imposed is also shown for the S0 treatment and, between parentheses, for the shaded treatment.

Treatment	Accumulated solar radiation (MJ m^{-2})	Girdling	# Flowers per cluster	# Berries per cluster	Fruit set (%)	Berry weight (g)
S0	634.4	No	71	22 b	34 b	2.84 b
S0-4	101.4	No	77	21 b	31 b	2.81 b
	(30.4)	Yes	88	17 a	22 a	2.63 a
S5-8	85.3	No	68	16 a	28 a	2.77 b
	(25.6)	Yes	77	18 a	24 a	2.71 ab
S9-12	101.3	No	82	18 a	23 a	2.70 ab
	(30.4)	Yes	77	15 a	21 a	2.60 a
S13-16	92.9	No	61	22 b	38 b	2.71 ab
	(27.9)	Yes	82	17 a	23 a	2.46 a
S17-20	102.4	No	72	22 b	37 b	2.74 b
	(30.7)	Yes	70	19 ab	29 ab	2.64 a
S21-24	67.0	No	62	18 a	30 b	2.74 b
	(20.1)	Yes	66	16 a	26 a	2.57 a
S25-28	84.1	No	73	20 b	30 b	2.65 a
	(25.2)	Yes	76	22 b	31 b	2.50 a

[a]Different letters in the column indicate significant differences among treatments at $p < 0.05$, according to Tukey HSD test.

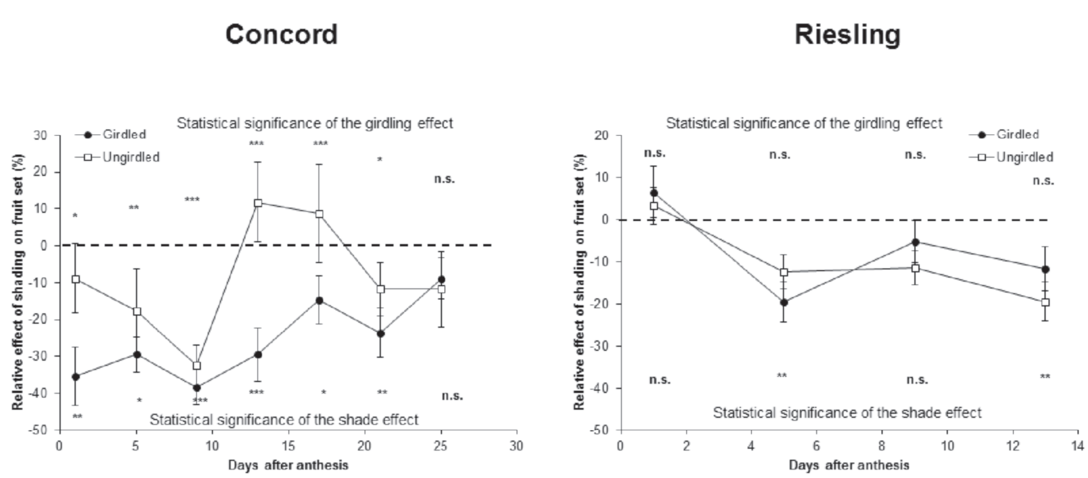

Figure 2 - Relative effect of shading and girdling on fruit set for ‘Concord’ and ‘Riesling’ as a function of the days after flowering. The points are situated on the first day of the shade period. The significance of the shade effect refers to the shading versus the unshaded control, whereas the significance of the girdling effect refers to the girdled treatment versus the ungirdled control.

Asterisks indicate significant differences: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. not significant. Bars indicate standard errors.

Table 5 - Effect of shading date on the number of flowers and berries, percentage of fruit set and berry weight in 'Riesling'. Ambient solar radiation accumulated over the four-day period when each treatment was applied is also shown for the S0 treatment and, between parentheses, for the shaded treatment.

Treatment	Accumulated solar radiation (MJ m^{-2})	# Flowers per cluster	# Berries per cluster	Fruit set (%)	Berry weight (g)
S0	380.9	181	97 ab	56 b	1.02
S0-4	101.4 (30.4)	191	105 b	58 b	1.06
S5-8	85.3 (25.6)	165	77 a	47 a	1.18
S9-12	101.3 (30.4)	182	87 ab	51 ab	1.10
S13-16	92.9 (27.9)	195	84 ab	47 a	1.08

and the percentage of fruit set were significantly lower in the treatments shaded between 5 and 8 days (S5-8) and between 9 and 12 days after bloom (S9-12). However, when shading from day 13 after flowering onwards, ungirdled shoots showed numbers of fruits and fruit set percentages similar to those recorded in the control treatment. In general, berry weight was lower in girdled shoots.

In the case of 'Riesling', girdling had no significant effects on any of the variables considered. Moreover, neither the number of flowers nor fruit set have been significantly affected by the shading treatment (Table 5). However, a slight trend to lower fruit set percentages was observed from 5 days after bloom (S5-8). Moreover, the number of berries was lower for the treatment shaded between 5 and 8 days after bloom (S5-8). In addition, this treatment presented the highest value of berry weight.

Discussion

The current study confirmed that basal and second clusters appeared to show a better differentiation capacity, namely produce more flowers, than third clusters, as previously reported for 'Concord' by Goffinet (2004). This finding was suggested by the significantly lower values of flowers and berries observed on third clusters of both species. The lower size and weight of these third clusters and their later development might be a feasible explanation for their weaker action as sinks.

The experiment was not specifically designed to explore different responses between the two studied species, considering the fact that different vineyards were used. Because of this, the different response to the applied treatments among the two species cannot be explained simply by the genetic material employed. Furthermore, 'Concord' vines had 50 % higher crop level than 'Riesling' vines, suggesting a stronger carbon limitation that may partly explain the stronger response to shading in 'Concord'.

A previous study by Caspari *et al.* (1998) showed that girdling without leaf removal apparently raised the source : sink ratio (by eliminating the woody stem and roots as sinks). In our case, girdling reduced fruit set because of the assumed limitation on carbohydrate availability due to shading and the absence of photo-assimilate transport from unshaded shoots. Fruit abscission occurs shortly after bloom and determines the amount of crop, which in turn affects carbon distribution between clusters and vegetation for the rest of the season. Previous findings (Intrigliolo and Lakso, 2009) showed that fruit drop in 'Concord' mainly occurred during the first 10 days after flowering, whereas in 'Riesling' it was closer to 14.

The current study clearly indicated that, for both species, the period from 5 to 12 days after flowering is when they are most sensitive to suffer reductions in fruit set caused by factors that reduce the carbohydrate supply. This sensitivity could have been caused by a coincidence of this time-span with the period when most flowers were going through pollination and fertilization. In the case of 'Concord' vines, final berries per cluster were also reduced at 21-24 days after bloom, likely due to the approximately 30 % reduction in ambient radiation in combination with shading lowering the total light.

Nevertheless, compensation by photo-assimilates transported from the whole vine can overcome an eventual reduction in carbohydrate supply of a single shoot, as suggested by our observations and previous studies (Vanden Heuvel *et al.*, 2002).

Isolating shoots from the rest of the vine through girdling modified the behaviour of the shoots with respect to the shading treatments. Specifically, on girdled shoots in 'Concord', reductions in fruit set caused by shading were evident even when shoots were shaded three weeks after flowering, whereas ungirdled shoots were only sensitive until two weeks after flowering. The number of berries and their weight followed a similar behaviour in this species. These findings suggest that translocation and partitioning of photo-assimilates from unshaded to shaded shoots occurred in 'Concord' and were able to partially or fully counteract the negative effects of shading in fruit set. Previous research on potted grapevines was able to identify these translocation patterns (Vanden Heuvel *et al.*, 2002). In field-grown grapevines, Hunter and Ruffner (2001) observed that translocation of photo-assimilates among vine organs was highly dependent on girdling, as early as at berry set.

Girdling did not significantly alter the behaviour of shaded shoots in 'Riesling' and the effects of the shading treatments on fruit set were similar for both girdled and ungirdled shoots in this species. As observed by Goffinet (2004), carbon reserves in 'Concord' vines tend to decline until bloom or two weeks after bloom, then stop declining and begin to recover. In this sense, the difference between girdled shoots and the ungirdled control at bloom until 9-12 days after bloom may represent the declining availability of reserves to import for the fruit. Then, the increasing difference in the 2-3 week period may reflect the opposite, namely, stopping carbon export from the shoot to other organs thus retaining more carbon for the fruit. This decay in carbon reserves at flowering has been observed in *Vitis vinifera* (L.) varieties such as 'Chasselas' (Zufferey *et al.*, 2015).

Furthermore, although the shading and girdling were constant, the weather and varying development imply that there is a variable baseline of carbon relations that we superimposed to our treatments. Therefore, solar radiation and temperature over the period when each treatment was applied likely had a strong influence on the results, making data interpretation more difficult. For instance, solar radiation and temperature were much lower 9-12 days after bloom than 13-16 days after bloom; consequently, the effect of shading was different because the amount of total radiation received by shaded clusters was much lower for the 9-12 days after bloom treatment. Previous research (Holzapfel and Smith, 2012) proved that developmental stage or climatic factors had a stronger influence on carbohydrate mobilization and storage than the manipulation of reserve accumulation through cultural practices. In the current study, the combined effect of lower solar radiation and lower temperatures on certain days, added to the shading treatment, seemed to reduce flowers and berries per cluster, and fruit set.

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 (Sprugel *et al.*, 1991). The results from the current study were dependent on the vine, suggesting that a low level of branch autonomy is reached in 'Concord' and 'Riesling', which might have implications for modelling plant productivity. In fact, this lack of autonomy would allow for simpler "big leaf" or "big fruit" modelling approaches (Lakso *et al.*, 2001). Nevertheless, this does not exclude the possibility of local effects within a vine because different light microclimates between portions of a vine affect fruit composition (Friedel *et al.*, 2015).

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