

Effect of Girdling on Leaf Gas Exchange, Water Status, and Non-structural Carbohydrates of Field-grown *Vitis vinifera* L. (cv. Flame Seedless)

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Flame Seedless grapevines were girdled at fruit set to determine the effect of this practice on leaf net CO₂ assimilation rate (A), carbohydrate partitioning, and water potential. The treatments consisted of vines that were trunk girdled, cordon girdled (one of a vine's cordons were girdled), the non-girdled cordon from vines of the previous treatment, and a non-girdled control vine. Girdling reduced midday A and stomatal conductance (g_s) by approximately 50% for a period of four weeks after treatment imposition when compared to vines or cordons that were not girdled. Midday leaf water potential values were more negative for the two control treatments than those of the two girdled treatments during the same time period. Diurnal measurements of leaf non-structural carbohydrates did not differ among treatments. Both girdling treatments increased berry size compared to the controls. The data indicate that the reduction in g_s due to girdling resulted in less leaf transpiration and, therefore, a more favorable vine water status (as measured by leaf water potential) for those vines. In addition the reduction in A after girdling was probably due to a reduction in g_s and not to an accumulation of carbohydrates in the leaf.

KEYWORDS: table grapes, photosynthesis, water potential, berry growth, source/sink relationships

Trunk girdling has long been used commercially to increase the size of seedless grapes [11]. However, it has been shown to decrease net CO₂ assimilation rate [4,8,10,12,15,17] and stomatal conductance [4,10] and alter carbohydrate distribution [17] of grapevines. The reduction in photosynthesis due to girdling but increase in berry size and crop yield [8,9] would indicate that increased berry growth can occur despite a reduction in carbohydrate production by the leaves.

Presently, there is no information as to the effect of girdling on diurnal or season long measures of leaf water potential, net CO₂ assimilation rate and stomatal conductance for seedless grape cultivars grown in the field. Therefore, a study was initiated to measure the above-mentioned gas exchange parameters and vine water status on Flame Seedless grapevines. A companion paper on Thompson Seedless has been published elsewhere [23]. It is anticipated that the results obtained from these studies will further our understanding of the mechanism(s) by which girdling increases berry size of seedless cultivars and source sink relationships of grapevines.

Materials and Methods

Vitis vinifera L. (cv. Flame Seedless) used in this study were field-grown nine-year-old vines at the University of California, Kearney Agricultural Center near

Fresno, California. The vines were trained to bilateral cordons and spur-pruned. Vine and row spacings were 2.44 and 3.66 m, respectively. Field station personnel performed normal cultural practices. The vines were flood-irrigated at approximately two- to three-week intervals beginning 12 May. Vines were either trunk- or cordon-girdled with a double-bladed, 4.8-mm knife and rechecked for completeness. Berry size was 5 mm at the time treatments were imposed (19 May [Day of Year 140] 1992). In order for the treatments to have similar crop loads, clusters were removed on the trunk girdled vines to account for the increased berry size due to girdling which was found in a previous study [9].

Treatments consisted of a control, vines that were trunk-girdled, and vines in which one of the cordons was girdled and the other not girdled. Each treatment was replicated eight times using single vine replicates. Blocks were imposed down a single row. Data collected were analyzed by two-way analysis of variance (ANOVA).

Techniques used to measure A and g_s were as described elsewhere [16]. An ADC-LCA2 photosynthesis apparatus was used to measure A and g_s. Leaf water potential (Ψ) was measured with a pressure chamber as described by Grimes and Williams [6]. Leaves fully exposed to solar radiation prior to data collection were chosen for measurement. Leaf tissue used to determine non-structural carbohydrates was initially killed in liquid nitrogen and then lyophilized on 2 June (DOY 153). Extraction and quantification of soluble sugars (glucose, fructose, and sucrose) and starch was done according to the method of Roper and Williams [17]. Leaves used to determine non-structural carbohydrates were the same as those used in the gas exchange measurements. Ber-

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ries were sampled five times during the growing season using the procedure as described by Harrell and Williams [9]. Twenty-five berries from an individual replicate were collected on the first four measurement dates. On the last sample date, 100 berries comprised an individual sample. Berries were chosen at random from all clusters

Results

Measurements of midday leaf A began one day after imposition of treatments (Fig. 1). On this day, A of the girdled treatments were already lower than A measured on vines or cordons that were not girdled. Leaf A was significantly ($p < 0.05$) lower for the girdled treatments compared to the controls from Day of Year (DOY) 143 to 177. Stomatal conductance followed a similar pattern. Midday leaf water potential generally was more negative for the non-girdled treatments compared to the girdled treatments. Girdled and non-girdled treatments differed in Ψ_1 from DOY 143 to 161.

Diurnal measures of leaf A, g_s , and Ψ_1 were taken seven and 14 days after imposition of treatments (Fig. 2, 3). On both dates, A and g_s of the girdled treatments were significantly lower than either of the control treatments over the course of the day. However, Ψ_1 was more negative for both controls than those of the girdled vines or cordons. There were few differences in leaf non-structural carbohydrates among the treatments 14 days after the study was initiated except for starch concentration at 1200 hr (Fig. 4). Leaf soluble sugar concentrations in the leaves of all tended to be higher late in the afternoon than earlier in the day.

Berry weight was greater for the trunk and cordon girdled vines 40 days after girdling and remained so until the experiment was concluded (Fig. 5). Yield did not differ between the control and trunk girdled treatments (Fig. 6). Yield of the non-girdled cordons was less than that of the girdled cordons on the combination vines. Vegetative growth was not measured.

Discussion

Girdling depressed midday measures of leaf A anywhere from 25% to 50% over a 40-day period in this study. Previous studies [4,8,10,12,17] investigating the effects of girdling on leaf gas exchange have demonstrated that A was depressed to the same extent as shown here. Unfortunately, those studies did not extend the time their measurements were taken beyond four weeks. This study demonstrated that A can be depressed well beyond the time when the girdle heals (most girdled vines had callus formed across the girdles within 5 weeks). The data presented here and that obtained on Thompson Seedless [23] indicate that leaf

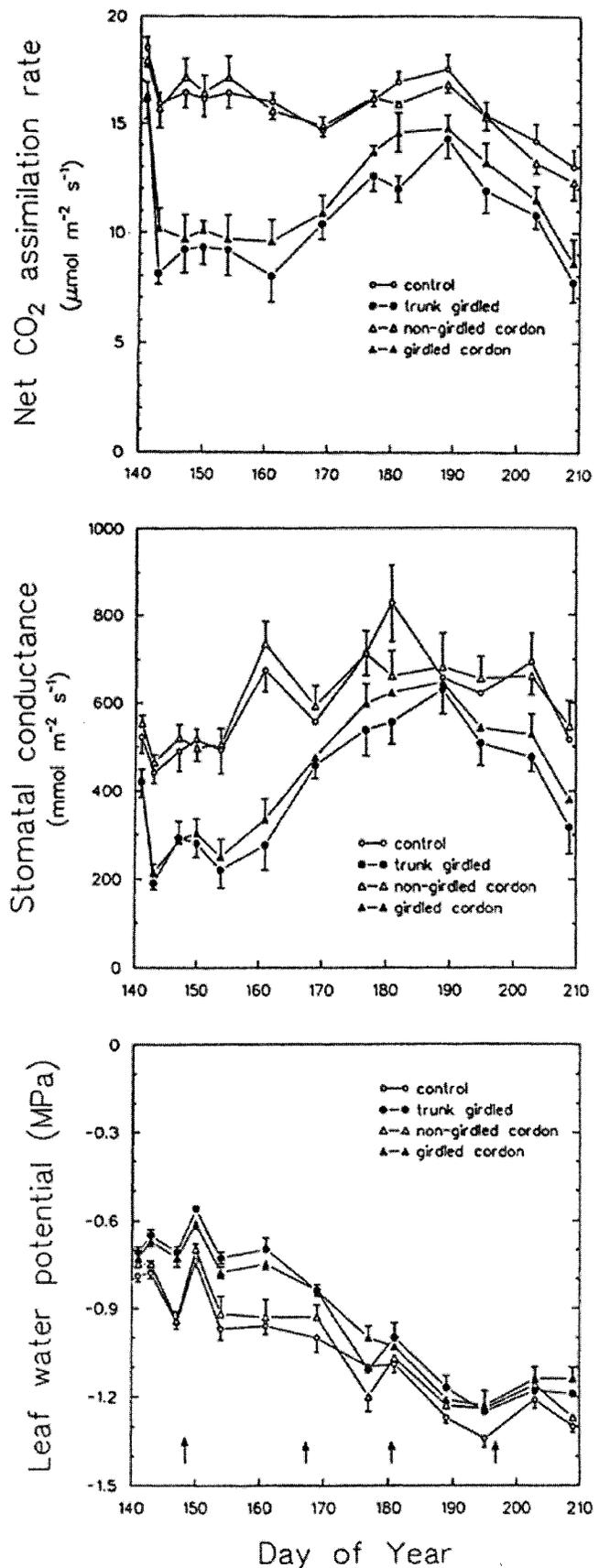


Fig. 1 (right). The effect of girdling on midday measurements of net CO₂ assimilation rate, stomatal conductance and leaf water potential of Flame Seedless grapevines. Treatments were imposed on day of year 140 (19 May). Measurements were made between 1200 and 1400 hr each day. Each point is the mean of 8 individual leaf measurements (bars equal \pm one standard error). The vertical arrows at the bottom of the graph indicate days on which the vines were flood-irrigated.

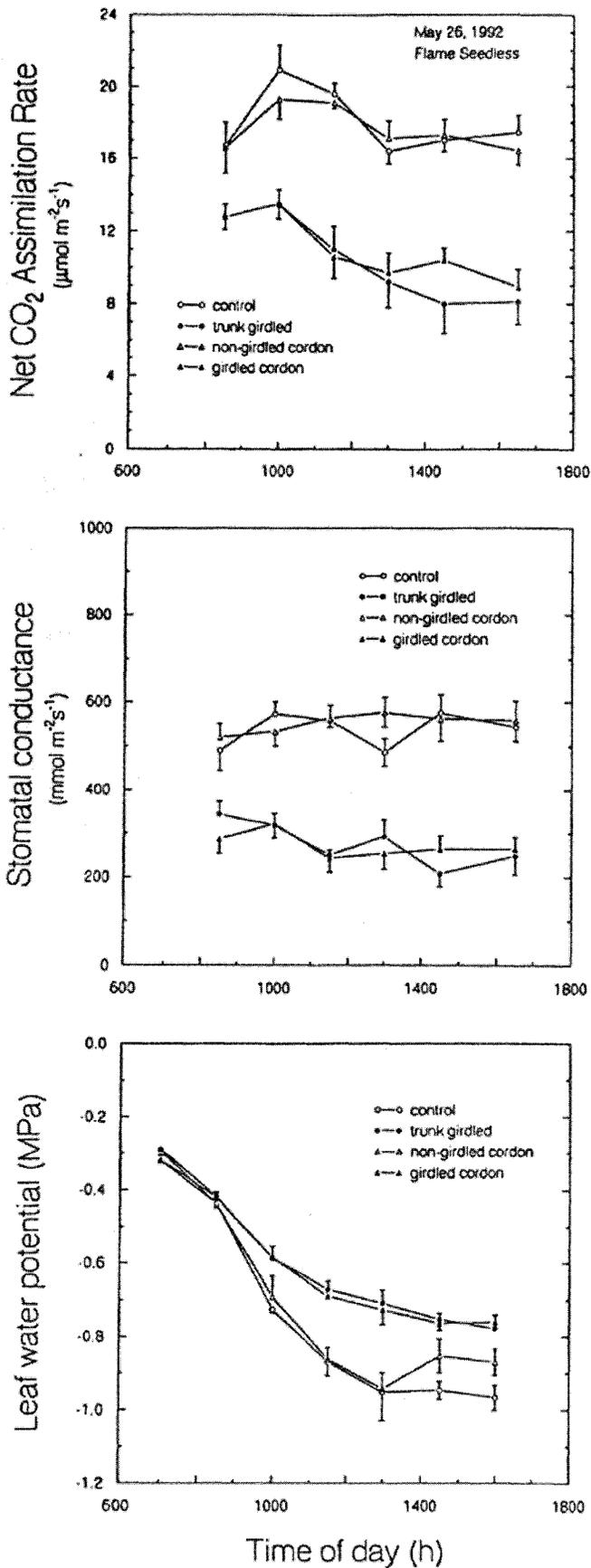


Fig. 2. The diurnal time course of net CO₂ assimilation rate, stomatal conductance and leaf water potential of Flame Seedless grapevines as a function of girdling on 26 May. Other information as given in Fig. 1.

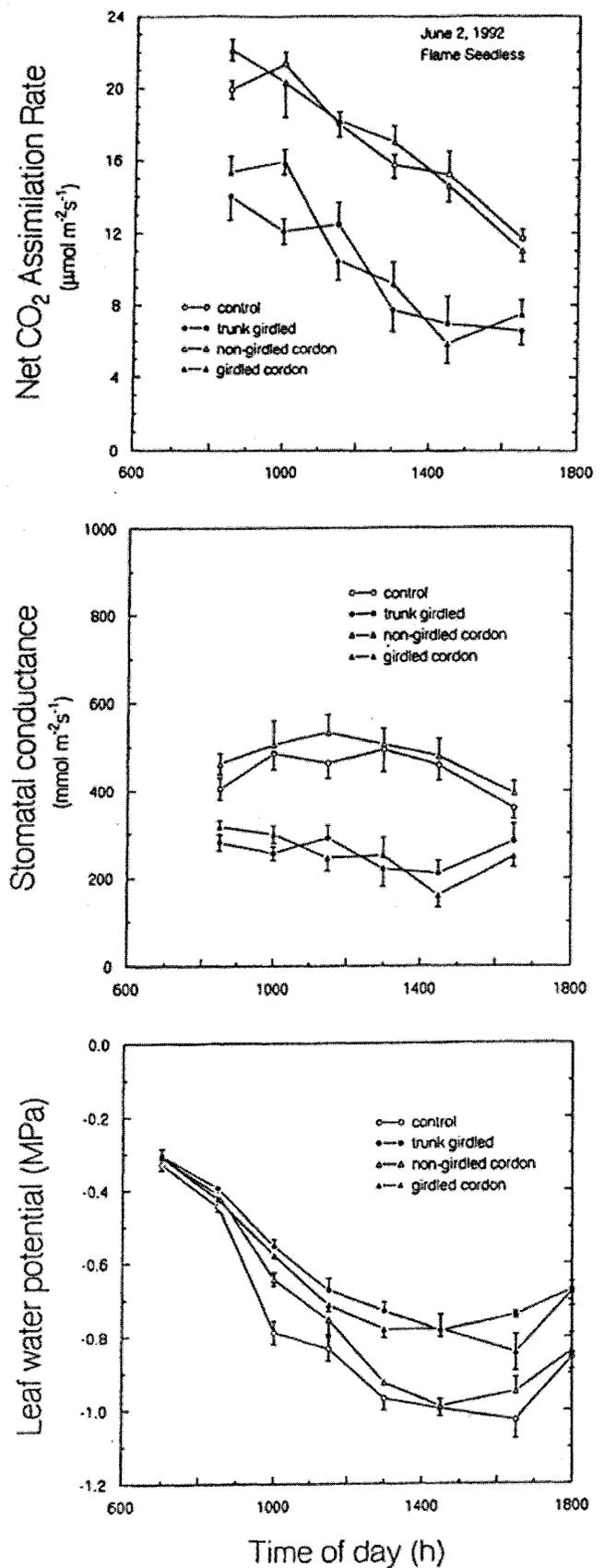


Fig. 3. The diurnal time course of leaf gas exchange and water potential of Flame Seedless grapevines on 2 June. Other information as given in Fig. 1 and 2.

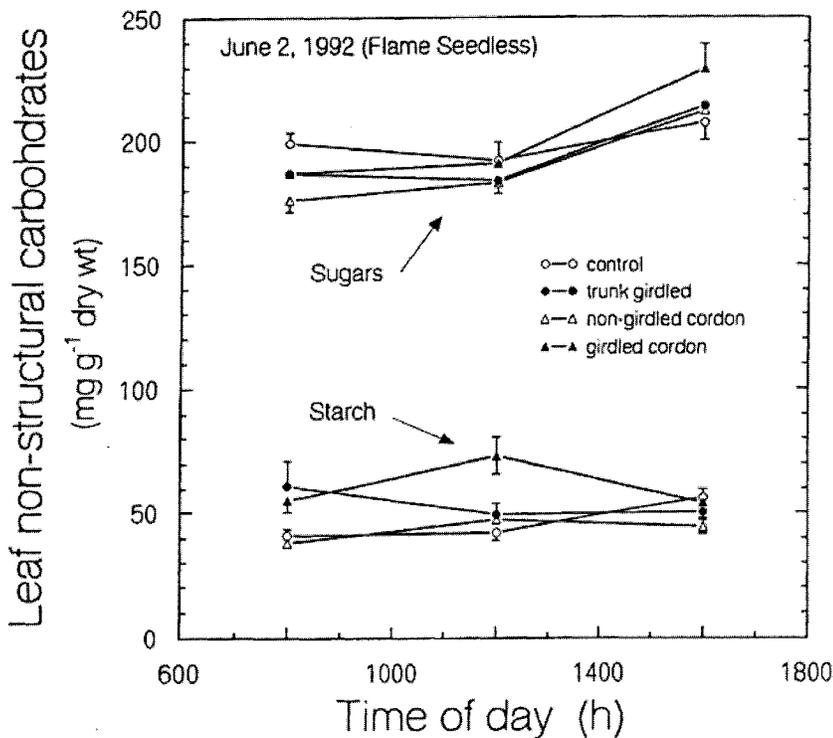


Fig. 4. Non-structural carbohydrates of Flame Seedless leaves collected three times during the day on 2 June. These leaves are the same ones used to measure photosynthesis at that specific time of the day.

photosynthesis never fully recovers after girdling.

The diurnal measurements of leaf gas exchange indicate that during most of the day A and g_s of girdled vines is depressed relative to the controls. The reduction in g_s resulted in a concomitant reduction in leaf transpiration [unpublished data]. It has been demonstrated that whole-vine water use will decrease after girdling and not recover until 40 days later [1, L. E. Williams unpublished data]. Reduced transpiration of the girdled vines is the probable cause for their more favorable vine water status (*i.e.*, less negative Ψ_1) compared to the controls. Girdling increases berry size by making more carbohydrates available for fruit as translocation to the root system is interrupted [17,20] or that there is a promotion of endogenous phytohormones after girdling [18]. Results from this study indicated that girdling may also increase berry size via a more favorable vine water status. It was reported that the berry set stage of fruit growth is very sensitive to soil water deficits [22]. Therefore, even a small increase in vine water status at this time in conjunction with any other mechanism involved may prove most beneficial to increasing berry size.

The reduction in grapevine leaf A due to girdling has been attributed to end-product inhibition of photosynthesis [12]. However, end-product inhibition of A is reported to be minimal as long as the starch concentration remains below 200 mg g⁻¹ dry weight [7]. Differences in leaf non-structural carbohydrates among the treatments found in this study throughout the day were not as great as one would expect based upon the significant reduction in A due to girdling. Therefore, the results from this and a previous study [17] would indicate that the reduction in A of girdled, field-grown grapevines is probably not due to end-product inhibition.

ABA causes stomatal closure, which in turn reduces A of grapevine [3]. Accumulation of ABA in the leaves of girdled grapevines [4,15] and other plants [19] would indicate that the reduction in A brought about by girdling is probably the result of stomatal closure. However, it is unclear as to the exact origin of ABA in the grapevine. Studies on other

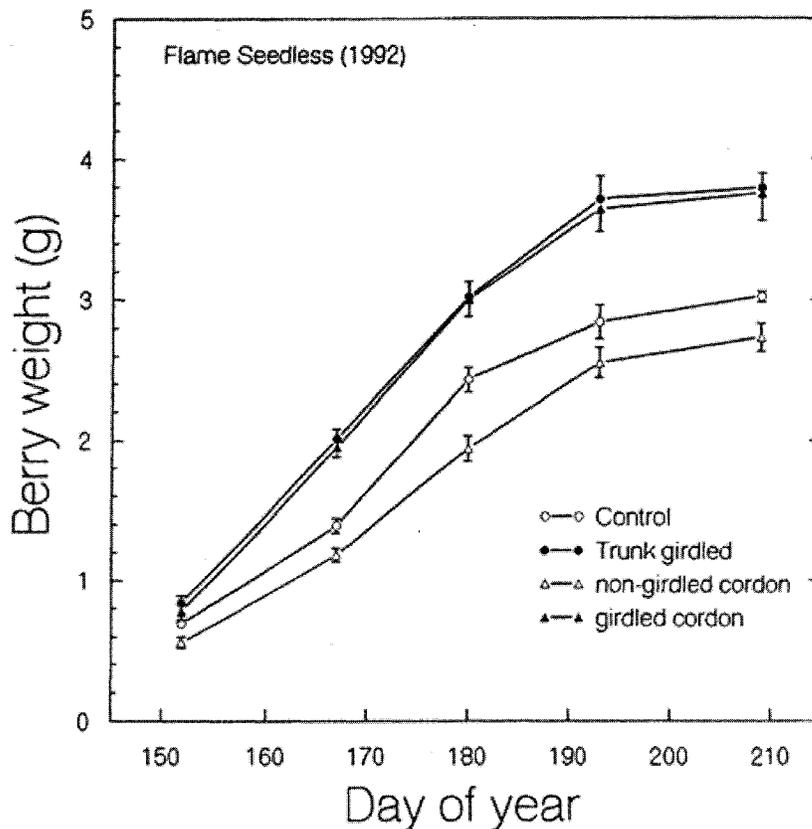


Fig. 5. Weight of Flame Seedless berries sampled subsequent to the imposition of the girdling treatments. Each value is the mean of eight individual vine replicates (\pm one standard error).

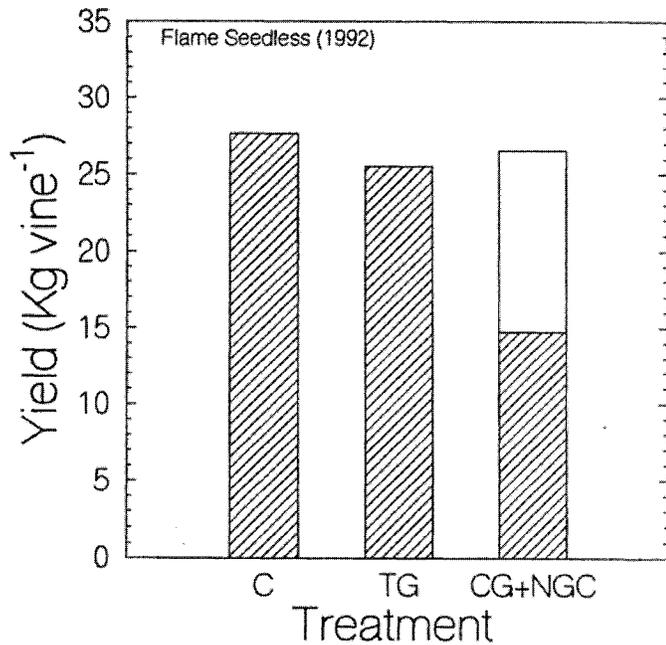


Fig. 6. Fruit yield of Flame Seedless grapevines as a function of girdling treatments. Vines were harvested on 11 August. The CG + NGC bar represents yield from the vine with both girdled and non-girdled cordons. Yield for the cordon girdled (shaded) and non-girdled cordon (clear) portions of the vine were 14.8 and 11.8 kg vine⁻¹ respectively. Standard errors for the C, TG, and CG + NGC were 1.8, 1.7, and 2.2 kg vine⁻¹, respectively.

plant species indicate a 'root signal' (possibly ABA) may cause a reduction in stomatal conductance under water stress [21]. However, it is unknown how girdling would put the grapevine root system under stress (in this case a carbohydrate stress) as rapidly as observed in this study. In addition, if a signal from the root system was involved in reducing A of girdled grapevines, one might have expected A of the non-girdled cordons on the split-treatment vines to be somewhat reduced. This was not observed in the present study. Under non-stress conditions, Loveys [14] has suggested that ABA is exported from the leaves to the roots and then transported back to the leaves via the xylem. The ABA would be used to control stomatal aperture and optimize water use efficiency [13]. As girdling would effectively disrupt the movement of ABA from the leaves via the phloem to the root system, ABA would accumulate in the leaves as long as the girdle remained open.

Damage to the xylem upon girdling could also have been the cause for the reduction in A of girdled grapevines. Such damage would probably mimic the effects of water stress on vine gas exchange and Ψ_1 . Water stress will reduce A and g_s of grapevines [21], similar to the response measured here on girdled vines. However, water stressed grapevines will have Ψ_1 values more negative than well-watered vines. Diurnal measures of Ψ_1 in this study demonstrated that the stressed (girdled) vines had values less negative than the controls. Therefore, it is doubtful that damage to the xylem of girdled vines was the cause for the reduction in A reported here and elsewhere.

The diurnal pattern of A differed between 26 May and 2 June. Leaf A of all treatments on 2 June decreased throughout the day, a pattern similar to what one would expect for water stressed vines [21] or a high light stress effect [2]. Vines in this vineyard were irrigated on 28 May (DOY 148) and, additionally, the Ψ_1 values indicated that the vines were not under water stress [6,22]. Solar radiation measurements at this location on both dates were similar; however, ambient temperature and vapor pressure deficit were much greater on 2 June than 26 May. Maximum temperature on 26 May was 30°C compared to 37°C on 2 June. It has been demonstrated that photoinhibition in *V. californica* will occur under a combination of high light and high leaf temperatures [5].

Results obtained from this study demonstrate several interesting points with regard to source/sink relationships in the grapevine. Berry size can be increased by girdling even though photosynthesis is reduced anywhere from 25% to 50% over a 40-day period (*i.e.*, a decrease in the source did not adversely affect sink strength). It also has been shown that yield can be increased by girdling [9] even though A is reduced [8]. The elimination of the root system as a sink for carbohydrates on girdled vines would be one reason for this apparent anomaly. Berry size was smallest for the fruit obtained from the non-girdled cordons on the combination treatment vines (Fig. 5). A similar result was observed for Thompson Seedless vines in which half of the canes had been girdled [23]. This may be the result of competition for carbohydrates between the fruit and the root system of the vine (the roots of the combination treatment vines were being supported with only half of the vine's leaf area). It should be pointed out, though, that the increased sink demand on leaves of the non-girdled canes did not enhance leaf A above those on the control vines (*i.e.*, sink demand did not regulate the rate of leaf photosynthesis).

Conclusions

Photosynthesis of Flame Seedless grapevines can be reduced significantly for a period of up to 40 days after being trunk- or cordon-girdled. However, the reduction in leaf A does not adversely affect the ability of girdled vines to increase berry size. The reduction in stomatal conductance due to girdling results in leaf water potential values that are greater than the controls. This more favorable vine water status may be another mechanism by which girdling is able to increase the size of seedless grapes.

Literature Cited

1. Bucks, D. A., O. F. French, *et al.* Trickle irrigation management for grape production. *In: Proceedings 3rd International Drip/Trickle Irrigation Congress*. Fresno, California. ASAE Publ. 10-85 Vol. 1. pp 204-211, ASAE, St. Joseph, MO (1985).
2. Correia, M. J., M. M. C. Chaves, and J. S. Pereira. Afternoon depression of photosynthesis in grapevine leaves - evidence for a high light stress effect. *J. Exp. Bot.* 41:417-426(1990).
3. Downton, W. J. S., B. R. Loveys, and W. J. R. Grant. Stomatal closure fully accounts for the inhibition of photosynthesis by abscisic acid. *New Phytol.* 108:263-266 (1988).

4. During, H. Studies on the environmentally controlled stomatal transpiration in grape vines. II. Effects of girdling and temperature. *Vitis* 17:1-9 (1978).
5. Gamon, J. A., and R. W. Pearcy. Photoinhibition in *Vitis californica*: The role of temperature during high-light treatment. *Plant Physiol.* 92:487-494 (1990).
6. Grimes, D. W., and L. E. Williams. Irrigation effects on plant water relations and productivity of 'Thompson Seedless' grapevines. *Crop Sci.* 30:255-260 (1990).
7. Guinn, G., and J. R. Mauney. Analysis of CO₂ exchange assumptions: Feedback control. *In: Predicting Photosynthesis for Ecosystem Models, Vol. 2.* J. D. Hesketh and J. W. Jones (Eds.). pp 1-16 CRC Press, Boca Raton, FL (1980).
8. Harrell, D. C. and L. E. Williams. Net CO₂ assimilation rate of grapevine leaves in response to trunk girdling and gibberellic acid application. *Plant Physiol.* 83:457-459 (1987).
9. Harrell, D. C., and L. E. Williams. The influence of girdling and gibberellic acid application at fruitset on Ruby Seedless and Thompson Seedless grapes. *Am. J. Enol. Vitic.* 38:83-88(1987).
10. Hofacker, W. Investigation on the photosynthesis of vines. Influence of defoliation, girdling and removal of grapes. *Vitis* 17:10-22 (1978).
11. Jacob, H. E. Girdling grapevines. *Calif. Agric. Ext. Ser. Circ.* 56: 1-18 (1931).
12. Kriedemann, P. E., and F. Lenz. The response of vine leaf photosynthesis to shoot tip excision and stem cincturing. *Vitis* 11:197-197 (1972).
13. Loveys, B. R. Diurnal changes in water relations and abscisic acid in field-grown *Vitis vinifera* cultivars. III. The influence of xylem-derived abscisic acid on leaf gas exchange. *New Phytol.* 98:563-73 (1984).
14. Loveys, B. R. Abscisic acid transport and metabolism in grapevine (*Vitis vinifera* L.). *New Phytol.* 98: 575-582 (1984).
15. Loveys, B. R., and P. E. Kriedemann. Internal control of stomatal physiology and photosynthesis. I. Stomatal regulation and associated changes in endogenous levels of abscisic and phasic acids. *Austral. J. Plant Physiol.* 1:407-415 (1974).
16. Retzlaff, W. A., L. E. Williams, and T. M. DeJong. Photosynthesis, growth, and yield response of 'Casselman' plum to various ozone partial pressures during orchard establishment. *J. Am. Soc. Hortic. Sci.* 117:703-710 (1992).
17. Roper, T. R., and L. E. Williams. Net CO₂ assimilation and carbohydrate partitioning of grapevine leaves in response to trunk girdling and gibberellic acid application. *Plant Physiol.* 89:1136-1140 (1989).
18. Sachs, R. M., and R. J. Weaver. Gibberellin and auxin-induced berry enlargement in *Vitis vinifera*. *J. Hortic. Sci.* 43:185-195 (1968).
19. Setter, T. L., W. A. Brun, and M. L. Brenner. Effect of obstructed translocation on leaf abscisic acid, and associated stomatal closure and photosynthesis decline. *Plant Physiol.* 65:1111-1115 (1980).
20. Weaver, R. J., and S. B. McCune. Girdling: its relation to carbohydrate nutrition and development of Thompson Seedless, Red Malaga, and Ribier grapes. *Hilgardia* 28:421-456 (1959).
21. Williams, L.E., N.K. Dokoozlian, and R. Wample. Grape. *In: Handbook of Environmental Physiology of Fruit Crops.* B. Schaffer and P. C. Anderson. (Eds.) pp 85-133. CRC Press, Boca Raton, FL (1994).
22. Williams, L. E., and M. A. Matthews. Grapevine. *In: Irrigation of Agricultural Crops - Agronomy Monograph No. 30.* B. A. Stewart and D. R. Nielson (Eds.). pp 1019-1059. ASA-CSSA-SSSA, Madison, WI (1990).
23. Williams, L. E., W. A. Retzlaff, *et al.* The effect of girdling on leaf net CO₂ assimilation, water potential and non-structural carbohydrates of Thompson Seedless. *In: Proceedings International Symposium on Table Grape Production, Anaheim, California.* pp 142-146. Am. Soc. Enol. Vitic., Davis, CA (1994).