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The response of vine leaf photosynthesis to shoot tip excision and stem cincturing

by

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Der Einfluß des Gipfelns und Ringelns auf die Photosynthese des Rebenlaubes

Z u s a m m e n f a s s u n g . — Um den Assimilatbedarf von Reben zu verändern, wurden die Triebspitzen von Gewächshauspflanzen gegipfelt, die Triebe geringelt oder beide Eingriffe kombiniert vorgenommen. 7—8 Tage danach wurde die Photosynthese-aktivität reifer Blätter im Labor gemessen. Die Ausschaltung der Wurzeln als wichtiges „sink" führte zur Anhäufung von Assimilaten in den Blättern und verursachte in Über-einstimmung damit einen Rückgang der Photosynthese gegenüber den unbehandelten Reben, unabhängig davon, ob die Triebspitzen vorher entfernt worden waren oder nicht. Eine entsprechende Wirkung auf die Photosynthese der verbliebenen Blätter wurde durch das Gipfeln nicht hervorgerufen.

Introduction

Leaf photosynthesis depends upon demand for assimilates, and CO_2 fixation per unit leaf area responds positively to either increased intensity of sinks, or number of sinks; conversely, reduced demand for assimilate produces lowered photosynthetic rates which are related to carbohydrate accumulation in leaves. These effects have been reviewed by Neales and Incoll (1968) and while we presumed grape vines would respond similarly, their photosynthetic response to accumulation of assimilates is undocumented.

Rapidly growing grapevines combine vigorous shoot development with growth and starch accumulation in their roots. In this system, young tips derive assimilates from adjacent mature leaves (Hale and Weaver 1962) but this requirement is quantitatively small. Young leaves photosynthesize (Kriedemann, Kliewer and Harris 1970) and contribute towards their own growth, but they also act as sinks for photosynthetic products until they are one third to one half full size (Hale and Weaver 1962). Shoot tips could therefore be largely self sufficient, photosynthetically, and tip removal (a widespread viticultural practice) might have no immediate consequences for remaining leaves. By contrast, the root system is wholly dependent and its elimination should lead to accumulation of photosynthate.

To test this proposition we applied stem cincturing (i. e. ring barking) singly, or in combination with shoot tip excision to potted grapevines, and then measured photosynthesis some days later. In this way we could demonstrate whether vine leaf photosynthesis was sensitive to the assimilate accumulation that almost inevitably occurs with ringbarking (Neales and Incoll 1968).

Materials and Methods

Vines established in Berlin from hardwood cuttings of *Vitis vinifera* (L) cultivars Müller Thurgau and Alicante (wine and table varieties respectively) were used in two successive experiments. The material was grown in sand culture in a glasshouse and supplied daily with Hoagland's nutrient solution. The vines had achieved
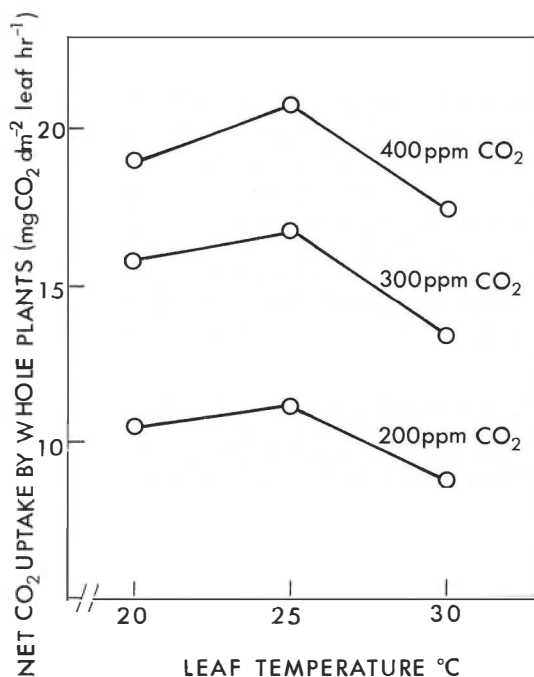
Fig. 1: Response of vine leaf photosynthesis to CO_2 concentration and temperature.

Table 1

The effect of "sink" removal on photosynthetic rate and other leaf parameters in grape vines

	1 (Control) Tips present stem intact	2 Tips removed stem intact	3 Tips present stem cinctured	4 Tips absent stem cinctured
Experiment 1 (Müller-Thurgau)				
Net photosynthesis (mg CO_2 dm^{-2}hr^{-1})	19.9	18.9	13.1	12.1
Leaf "density" (mg dry wt cm^{-2})	4.45	5.38	6.57	7.80
Moisture content (% fresh wt)	76.5	73.8	67.8	68.8
Experiment 2 (Alicante)				
Net photosynthesis (mg CO_2 dm^{-2}hr^{-1})	14.6	15.0	10.8	13.8
Leaf "density" (mg dry wt cm^{-2})	3.52	4.32	4.50	5.92
Moisture content (% fresh wt)	76.1	72.5	73.1	66.7

vigorous growth by the time treatments were imposed (in the month of May, 1971); shoots were 80—100 cm long with 15—20 primary leaves. The plants were ranked according to size and a total of 16 were then distributed evenly over each of 4 treatments, giving 4 vines per treatment.

The potted vines were then manipulated as follows:

T r e a t m e n t 1 : Control, no excision or cincturing.

T r e a t m e n t 2 : Distal portion of shoot excised, removing that portion with leaves less than ⅔—¾ full size. In treatment 2 (and 4) we took the added precaution of removing axillary buds to eliminate development of lateral shoots following tip removal. Such shoots would otherwise have represented alternative sinks.

T r e a t m e n t 3 : Shoot tip intact. Stem cinctured thereby interrupting the phloem.

T r e a t m e n t 4 : Vines were tipped as well as cinctured.

The response of photosynthesis (Phs) to an absence of sinks in tips or roots (with or without alternate sink) could be gauged as follows:

Phs in Tr 1 — Phs in Tr 3 = Root effect in presence of tip,
Phs in Tr 2 — Phs in Tr 4 = Root effect in absence of tip,
Phs in Tr 1 — Phs in Tr 2 = Tip effect in presence of roots,
Phs in Tr 3 — Phs in Tr 4 = Tip effect in absence of roots.

A total of 16 vines in each of 2 successive experiments was treated as described and taking the 4 vines of each treatment collectively, their photosynthetic rates were compared one week later. Tip leaves were removed immediately prior to photosynthetic measurements on treatments 1 and 3 to restore their total leaf number to that for treatments 2 and 4, thus rendering all measurements comparable with respect to leaf age and eliminating the complication of terminal foliage.

Net photosynthesis was determined by the CO_2 compensation method described previously (Lenz and Daunicht 1970). Briefly, the entire vines (including pots) were hermetically sealed into a cubic plexiglass chamber (almost 1 m³) which comfortably accomodated the 4 potted vines. The turbulent atmosphere of the chamber was recirculated through a URAS 2 which monitored CO_2 concentration and drove a servo system maintaining atmospheric tension at 300 ($\pm$0.5) ppm CO_2 (or any other set value). The volume of CO_2 injected to replace photosynthetic consumption was automatically monitored, and this rate of replenishment served as our index of net photosynthesis. The plants were irradiated with 4 HPLR 400 W lamps providing 33,500 lux at the top of the foliage. Leaf temperature was held at 25⁰ ($\pm$.05⁰) C, relative humidity was 70%.

Following gas exchange measurements, plants were harvested and leaf area recorded photometrically. Fresh and dry weights were subsequently determined.

Results

(a) O p t i m u m p h o t o s y n t h e s i s

To obtain full expression of experimental treatments on leaf photosynthesis, we provided the maximum available light (35,000 lux) and maintained a favourable leaf temperature (25⁰ C) (see Fig. 1).

(b) P h o t o s y n t h e t i c r e s p o n s e t o t r e a t m e n t s

In both experiments (data summary in Table 1) the photosynthetic activity of mature leaves depended on the presence of sinks. The root system exerted greater effect, and its elimination caused an identical reduction (6.8 units) in photosynthesis

irrespective of shoot tip condition in Experiment 1. This root effect was again demonstrated in Experiment 2, but to a reduced degree.

By contrast to the root influence, elimination of shoot tips in Experiment 1 elicited only a minor decrease in photosynthesis (1.0—1.1 units). This small effect was inconsistent in Experiment 2.

(c) Leaf Characteristics

While removal of major sinks led to reduced photosynthesis, net CO_2 fixation by the leaf was still well in excess of respiratory losses as measured by CO_2 exchange. Consequently a substantial accumulation of photosynthate should have resulted. This effect is evident in Table 1 as increased leaf "density" and reduced moisture content. The elimination of both major sinks in treatment 4 resulted in the highest leaf "density". These leaves corresponding to treatment 4 were also characterised by a more resilient, or leathery texture, probably a further expression of their carbohydrate accumulation. The absence of tip or root sinks in this treatment was also associated with marked stem swellings above the cincture.

Discussion

Assimilate flow is arrested in vine shoots following ringbarking (Hardy and Possingham 1969) hence the stem swelling observed on our vines. Nevertheless, by utilising xylem elements, some solutes can move past such a discontinuity in the bark. The root system might therefore derive substrate to a limited degree, although in a different chemical form (Hardy 1969). This limited supply is apparently not enough to counter the cincturing effect because leaf photosynthesis was still reduced. In fact, photosynthesis showed greater response to the apparent substrate demands of the root system compared to shoot tips. Moreover when shoot tips were missing, roots and perhaps additional stem deposition, represented an adequate alternate sink. The data on leaf density support this view and imply greater photosynthate accumulation in the absence of shoot tips.

Our contention that young tips are largely self-sufficient, photosynthetically, gains further support from observations during gas exchange measurements on control vines. We measured photosynthesis on intact plants, and then repeated the measurements immediately following removal of shoot tips. The rate was virtually unchanged.

The reduction in photosynthesis following ringbarking is most likely due to assimilate build-up, but this response might be more complicated than a "simple" source sink effect (see review of Neales and Incoll 1968). For example, if root derived hormones (cytokinins) exert a major control on photosynthesis via stomatal action or by altering internal resistances, the effect of cincturing could result from a change in the level of cytokinin present in leaves. This alternate viewpoint gains force from the demonstration of cytokinin synthesis in vine roots (Skene and Kerridge 1967) plus related data showing a reduction in cytokinin level of xylem sap after ringbarking (Skene 1972).

Summary

The photosynthetic activity of mature leaves on glasshouse grown vines was measured in the laboratory 7—8 days after applying 4 treatments designed to vary the plant's demand for assimilates. These comprised shoot tip excision, stem cincturing and a combination of the two. The elimination of roots as an effective sink for

assimilate led to assimilate build-up in leaves and caused a consistent reduction in photosynthesis, compared to control vines, regardless of whether shoot tips had been retained or previously excised. Excision of shoot tips did not elicit a consistent, photosynthetic response in remaining leaves.

Acknowledgement

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