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The Influence of Short-term Partial Shading on Photosynthesis and Stomatal Conductance in Relations to Water Status of Grapevines (*Vitis vinifera* L.)

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Abstract

This project was designed to investigate the impact of short term light intensity changes in relation to water status of grapevine (*Vitis vinifera* L.) cv. Pinot noir canopy. Shading caused a rapid increase in the net photosynthesis (A) and stomatal conductance (g_s) of the illuminated part of the canopy. Water-stress reduced A and g_s compared to well-watered vines. Inter-cellular CO_2 concentration (C_i) was unaffected by shading or crop loading. The overall response by vines to partial shading was similar across all water stress treatments. It is concluded that in grapevines, the rapid changes in A and g_s in the illuminated part of the canopy caused by partial shading elsewhere, are regulated by hydraulic processes. However, the mechanisms by which stomata sense those changes are still unknown.

Introduction

Evaporation of water from the leaves helps to maintain normal physiology by minimizing overheating. When water loss continues to exceed replacement from the roots, the stomata close. If the deficit persists, continued water loss through the cuticle results in cell plasmolysis and death. Reduced shoot growth is one of the most sensitive signs of grapevine water stress (Jackson, 1994). Jones *et al.* (1990) reported that the most marked effect of water stress was to induce stomatal closure in response to a light shock caused by briefly shading the leaves. Dry *et al.* (1996) results showed that the g_s and growth rate of the shoot of the unirrigated vines decreased to approximately 50 to 60% of that of the irrigated after 12 to 15 days of the soil drying. The rate of photosynthesis and stomatal conductance in Braeburn apple were reduced by withholding water (Killili *et al.*, 1996). Water deficit in the root zone caused stomatal closure as well as reduced synthesis and downward transport of carbohydrates and hormonal growth regulators (Kozlowski, 1969). Similarly Yoon (1995) concluded that water stress reduces stomatal conductance in 'Fuji' apple. Reynolds and Naylor (1994) also reported that in Pinot noir and Riesling grapevine, increasing water stress duration progressively reduced transpiration and stomatal conductance. The relative growth rate and net assimilation rate of cultivated mulberry were reduced by summer drought reported by Tazaki *et al.* (1980). Desiccation avoidance in deciduous species might also be achieved by developing plants that will shed leaves early during developing drought, but this also reduced photosynthesis (Kozlowski, 1973). Zavitkovski and Ferrell (1970) reported that when droughted trees were irrigated, photosynthesis did not always return to normal, but transpiration rates usually recovered faster than photosynthesis. According to Törökaly and Kriedemann (1977) if leaves are fully exposed, and the roots have an ample water supply for rapid transpiration, the increase in leaf temperature may be held to about 5 °C. However, if the leaves are water stressed, or there is little air movement, the temperature increase may be great and sufficient to suppress photosynthesis. For example, the rate of photosynthesis at 35 °C may be only 15% of that at 25 °C. Grapevine canopies with leaves mostly exposed resulted in

high stomatal conductance and generated moderate water stress, which increased water use efficiency (Carbonneau *et al.*, 1987). Kramer and Kozlowski (1979) reported that midday water deficits even in region of abundant and uniformly distributed rainfall can be caused by absorption lagging behind transpiration, as shown by midday decreases in leaf moisture content, leaf water potential, and stomatal closure. Reductions of both photosynthesis and stomatal conductance by water stress were mediated by abscisic acid (Bunce, 1987).

The effects of short-term shading in the irrigated and unirrigated plants and the recovery of the plant are less understood, especially how the exposed part of the canopy, responds to shading of another part under different water status in terms of photosynthesis and stomatal conductance. So, this project was designed to investigate the impact of short-term light intensity changes in relation to water status of grapevine canopy.

Materials and Methods

The effect of partial shading of part of the canopy was studied in grapevines (*Vitis vinifera* L.) cv. Pinot noir in greenhouse at Lincoln University, Canterbury, New Zealand during the year 1998. Grapevine (*Vitis vinifera* L.) cv. Pinot noir fruiting plants were grown from winter dormant, six node cuttings using the method as described by Mullins and Rakasekaran (1981). Cuttings were planted in trays filled with 80mm fine sand in last week of June 1997. Trays were placed in a hot bed in a shade house for six weeks. At this time well-rooted grapevines having two sprouted shoots per cutting were transplanted in 1 litre plastic pots each 15cm diameter. Pots were filled with potting mix, consisting of 80:20 bark:sand mix, 5kg m⁻³ of 16:3.5:10 slow (9 month) release Osmocote® fertilizer and 4kg m⁻³ Dolomite. Vines were then placed in a shaded (87% light transmittance) glasshouse (day/night temperatures 24/15 °C) in the Lincoln University Horticultural nursery complex. Lighting was supplemented by using 400 Watt high pressure sodium lamps (Philips Son-T Agro 400®). Vines were irrigated (300 mL/day) by trickle irrigation twice a day using an automatic timer. To ensure even spread of water, 5 mm fine sand was placed over the potting mix in each pot. The fertility was supplemented with a fertilizer

Table 1: The influence of treatments, and time on the photosynthesis (A), stomatal conductance (g_s) and intercellular CO₂ concentration (C_i): main effects.

Treatment	A (μmol CO ₂ m ⁻² s ⁻¹)	g _s (mol H ₂ O m ⁻² s ⁻¹)	C _i (μmol CO ₂ mol ⁻¹ air)
+W+S	4.350 a1	0.061 a	165.583 a
-W+S	2.800 b	0.030 b	131.696 b
+W-S	3.579 d	0.045 c	149.292 ab
-W-S	1.888 c	0.022 b	135.870 b
Significance	***	***	*
Time			
Pre-shaded	3.032 a	0.037 a	142.039 a
Shaded	3.810 b	0.046 b	141.004 a
Post-shaded	2.621 a	0.035 a	153.788 a
Significance	***	**	ns
Interaction			
Time vs treatment	*	**	ns
Branch vs treatment	ns	ns	***

Mean showing a common letter are not significantly different at P<0.05 (Fisher LSD test). +W water, -W water stress, + shaded, and -S unshaded vines; Interaction significant at (P<0.05), (P<0.01) and (P<0.001) denoted by *, ** and *** ns is not significant.

Table 2: The influence of treatments, and time on the net photosynthesis, stomatal conductance, and intercellular CO₂ Concentration of Pinot noir grapevine: interaction effects.

Treatment	Time 1 (Pre-shaded)	Time 2 (Shaded)	Time 3 (Post-shaded)	Ratio of Time 3: Time 1
(A) Net photosynthesis (μmol CO₂ m⁻²s⁻¹)				
+W+S	3.45 a	5.76 a	3.84 a	111.3
-W+S	2.73 ab	3.53 b	2.14 b	078.4
+W-S	3.63 a	3.90 b	3.21 a	088.4
-W-S	2.33 b	2.05 c	1.29 b	055.4
(B) Stomatal conductance (mol H₂O m⁻²s⁻¹)				
+W+S	0.045 a	0.083 a	0.054 a	120.0
-W+S	0.033 ab	0.033 b	0.024 b	072.7
+W-S	0.042 a	0.048 c	0.043 a	102.4
-W-S	0.028 b	0.022 b	0.018 b	064.3
C Intercellular CO₂ Concentration (μmol CO₂ mol⁻¹ air)				
+W+S	154.8 a	172.0 a	170.0 a	109.8
-W+S	130.8 a	123.8 b	140.6 a	107.5
+W-S	142.1 a	146.3 ab	159.5 a	112.3
-W-S	140.5 a	122.0 b	145.1 a	103.3

Means follow by the same letter are not significantly different at P<0.05 (Fisher LSD test).. Letters refer to comparison between treatments for each time combination.. +W water, -W water stress, + S shaded, and -S unshaded vines.

application of Osmocote at 2g /pot fortnightly. Vines were trained in such a way that each had two shoots, which were grown in opposite directions.

Four vines i.e. two fruited and two un-fruited were chosen and were placed under artificial light sources a week before of the start of experiment. The four treatments were: 1. Water with shade, 2. Water-stress with shade, 3. Water-stress with no-shade and 4. Water with no-shade vines. The water-stressed vines were supplied with 50% of their daily water consumption. The pots were irrigated and covered with silver foil in order to avoid evaporation from the soil surface.

One FEN leaf was selected on each vine for the measurement of A and g_s. An alternative shoot was selected on each of the four days of the experiment, to make sure that data represented the responses of both shoots of each vine. Shading treatments consisted of covering one shoot with black polythene covered in silver foil and the shoots of the vines became the exposed and shaded treatments. Control data were measured on the uncovered vines. A different shoot was selected on each of

the days of the experiment. Leaves were measured before the shading treatments were imposed (pre-shade), during shading (shade) and after the shading treatment was removed (post-shade). Three measurements were done on each time period. The block temperature of the photosynthesis chamber was set at 28°C, which is within the range that maximum photosynthesis is believed to occur (Honjo *et al.*, 1989). No measurements were recorded on the shaded shoot. A, g_s and C_i were measured from 10.00 to 18.00 (NZST). Measurements were taken 8 times each treatment period (pre-shade, shade and post-shade). The experiment was designed as a split plot, having branch and treatment main plots and time as a sub plots. Analysis of the data was undertaken using the Systat® statistical package and graphs were made by using graphic package SigmaPlot® version 2.0.

Results

The water-stress treatment resulted in a significant decrease in A, g_s and C_i (Table 1 and Fig. 1,2). When comparing the water-stress and non-stress treatments

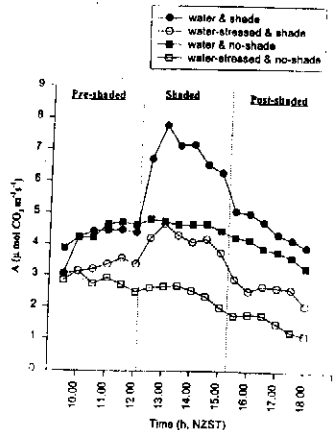


Fig. 1: Influence of short term changes of light intensity and the degree of water status on the net photosynthesis (A) in pre-shaded, shaded and post shaded canopies of Pinot noir grapevine (*Vitis vinifera* L.)

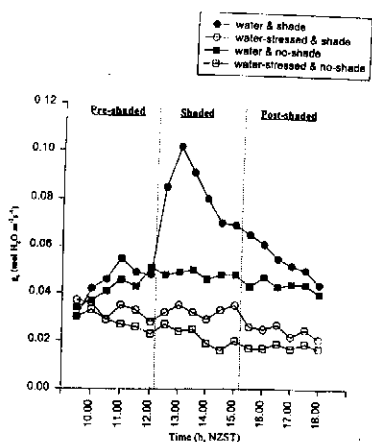


Fig. 2: Influence of short term changes of light intensity and degree of water status on the stomatal conductance (g_s) in pre-shaded, shaded and post-shaded canopies of Pinot noir grapevine (*Vitis vinifera* L.)

Table 3: The influence of treatments, and time on the ratio of net photosynthesis : stomatal conductance of Pinot noir grapevine.

Treatment	Time 1 (Pre-shaded)	Time 2 (Shaded)	Time 3 (Post-shaded)
+W+S	79.57 a	69.28 a	71.63 a
-W+S	93.90 a	108.62 b	92.77 a
+W-S	86.64 a	81.54 ac	73.97 a
-W-S	96.44 a	100.2 bc	91.33 a

Means follow by the same letter are not significantly different at $P < 0.05$ (Fisher LSD test). Letters refer to comparison between treatments for each time combination.. +W water, -W water stress, +S shaded and -S unshaded vines.

There were no significant differences in water potential measurements compared with the pre-shading period, although significant differences developed from mid-way through the shade period, and continued into the post-shade period (Fig. 3). The shading treatment had no

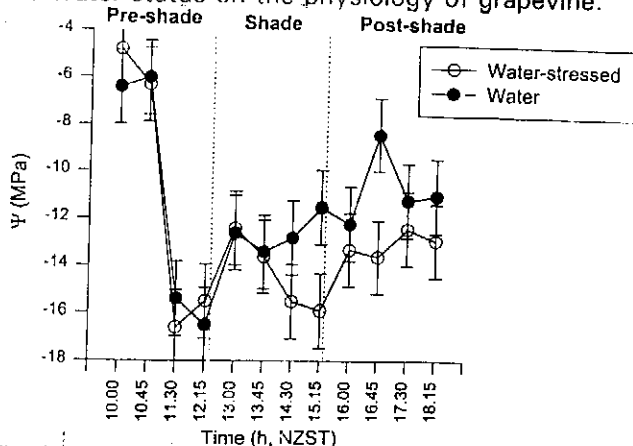


Fig. 3: Influence of short term changes of light intensity and degree of water status on the water potential (Ψ) of Pinot noir grapevine (*Vitis vinifera* L.) Bars represent the LSD at the 5 % lever of significance.

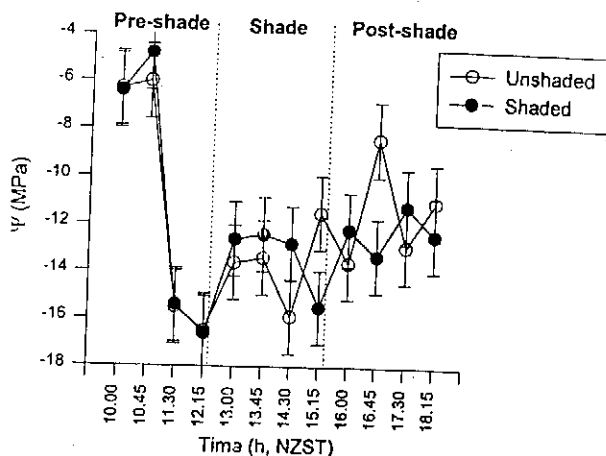


Fig. 4: Influence of short term changes of light intensity on the water potential (Ψ) of Pinot noir grapevine (*Vitis vinifera* L.) Bars represent the LSD at the 5 % lever of significance.

consistent effect on vine water potential (Fig. 4).

As in the previous experiment, where vines were not water-stressed, shading caused a marked increase in the A and g_s of the illuminated half of the vine (Fig. 1, 2). However, under water-stressed conditions while A increased above pre-shading values, and 72 above the control values, g_s was little affected.

The A: g_s relationship of the water stressed and shaded treatments at pre-shading and post-shading was not significant, but during shading water-stressed vines showed a significantly higher A: g_s ratio than that on the non-stressed vines (Table 3).

Regression analysis of A against g_s suggested that the higher photosynthetic rate occurred largely in relation to higher stomatal conductance in the watered vines $R^2 = 0.90$, (Fig. 5). The higher photosynthetic rate by the illuminated half of the canopy observed during the shading treatment did not cause a significant change in the A: g_s relationship, when either the pre- and post-shading measurements were compared to the shaded period, or

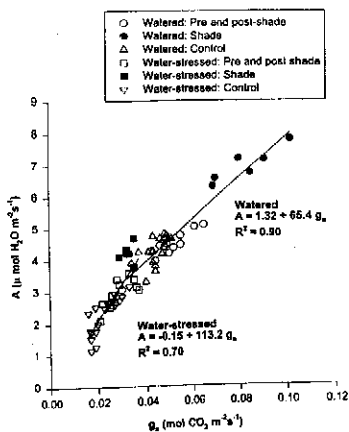


Fig. 5: The influence of short term changes of light intensity on the relationship between net photosynthesis (A) and stomatal conductance (g_s) in water and water stressed Pinot noir grapevine (*Vitis vinifera* L.)

when this vine was compared to the control vine (Fig. 5), or when the shaded vines were compared with the control vine (Fig. 5). Regression analysis of A and g_s suggested that the relationship of photosynthesis and stomatal conductance trend in water-stressed vines was same ($R^2 = 0.70$) as watered vines although the A and g_s values were lower in water-stressed vines compared to watered vines (Fig. 5).

Discussion

The reductions in A, g_s and C_i caused by the water-stress treatment in the experiment reported here were similar to those observed elsewhere (Kozłowski, 1973; Tazaki *et al.*, 1980; Bunce, 1987; Jones *et al.*, 1990; Reynolds and Naylor, 1994; Dry *et al.*, 1996; Kilili *et al.*, 1996).

The original hypothesis was that a reduction in exposed leaf area would reduce the transpiration rate by the vine, (the sink for water, while not affecting the source) and thus any water-stress being experienced by the plant. At the same time, the reduction in photosynthetic area caused by shading, would increase the sink:source ratio for photosynthates. It was anticipated therefore, that the shading treatment would have a proportionally greater effect on the water-stressed treatment, when compared to the well-watered control. However, while A of the illuminated part of the vine did increase during shading, the effect was less (a 44% increase) where vines were water-stressed compared to 57% for the non-stressed vines. The g_s stressed and non-stressed vines increased by 13 and 66% respectively, and g_s did not increase above the early pre-shade values. These results had a similar effect on A of the illuminated part of the vine, while the water-stress imposed here had a proportionally greater influence on stomatal conductance than light intensity. This apparent difference in response may be explained by the lower C_i values of the water-stressed vines, similarly to those reported by Johnson *et al.* (1987).

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