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# The Influence of Short-term Partial Shading on Photosynthesis and Stomatal Conductance in Different Leaf Position of Grapevines (*Vitis vinifera* L.)

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**Abstract:** The fully expanded new (FEN) leaves of grapevines (*Vitis vinifera* L.) appeared to be most sensitive to shading and A and gs increased by 55 and 20 percent respectively, with in 30 minutes. This response was reversed when the shading was removed. Old and new leaves showed similar responses to change in light intensity. The progressive declines in gs and A was observed during the day in all leaf positions. The A:gs ratio was lager and Intercellular $CO_2$ concentration (Ci) lower in the FEN leaves than in either the new or old leaves on the canopy.

**Key words:** Grapevine; photosynthesis; stomatal conductance; intercellular CO, concentration; leaf position; illuminated

## Introduction

The consequence of leaf position can be considered in two ways. First the sequential development of leaves along a shoot results in basal leaves being chronologically older than those closer to the shoot apex. At the same time, approximately 95-98 percent of photosynthetically active radiation (PAR) is absorbed by leaves as light passes through (Smart and Robinson, 1991; Blanke and Notton, 1992). Thus the basal leaves on a shoot will generally be more shaded and the light intensity within canopies of more than 1-2 leaf layers will be low. About 80 to 90 percent of the photosynthate fixed by perennial plants is by the outer leaves of the canopy (Smart, 1985). However, the outer leaf canopy is not a total continuum and interior leaves may be exposed to intermittent direct exposure to light for different duration.

**Leaf position on shoot:** Leaf age or position along the shoot has a significant effect on individual leaf photosynthesis rates (Alleweldt *et al.*, 1982). Pon and Intrien (1996) found that photosynthesis reached a maximum at 30 days after unfolding and then declined with leaf age. Pon and Intrien (1996) measured photosynthesis in grapevine leaves and found a small but non-significant increase on day 135 that appears to coincide with the time that the berries were passing through veraison. Petrie (1997) proposed that this increase in photosynthesis was the result of an additional demand for photosynthates placed on leaves by the ripening fruit. Hunter *et al*. (1994) reported that the photosynthesis rate of basal leaves of cv. Cabernet Sauvignon vines, increased until the berries reached pea-size, but declined to low rates during grape ripening and after harvest. Apical leaves, on the other hand, showed a more or less uniform pattern of photosynthesis during the whole season with higher assimilation rates than basal leaves after veraison. High photosynthetic rates in young leaves are likely to be sustained by a continuous demand for assimilates from local or adjacent sinks. Inner canopy leaves eventually turn yellow and drop prematurely (Smart, 1985).

**Leaf position and shading effects on stomatal conductance (gs):** Shading effects on the stomatal conductance of grapevine leaves have been extensively studied (eg. Smart *et al*., 1988). They reported that a 44 percent decrease in photosynthetically active radiation (PAR) reduced stomata' conductance. Similar responses have been observed in a wide range of species. For example Dhopte *et al*. (1991) observed that reductions in light intensity markedly reduced stomatal conductance of cotton genotypes. In contrast Valenzuela *et al*. (1991) reported that stomatal conductance and transpiration *Xanthosoma sagittifolium* cv. South Dade White plants were not significantly affected by (50 or 70 percent shading when compared to unshaded control and Palanisamy and Yadukumar (1994) observed stomatal conductance did not vary significantly with leaf direction or time of day in the field grown cashew.

Part of the discrepancy in these observations may have been the results of the intensity of the fully illuminated treatment. The stomatal conductance: photosynthetic active radiation relationship is frequently described as a non-rectangular hyperbole and stomata are fully open at a light intensity 200 $\mu$mol $m^{-2}$ $s^{-1}$ (Smart and Robinson, 1991). As this light intensity is potentially less than 50 percent of full intensity on a bright day, 50 percent shading on such a day would be expected to have little effect on stomatal conductance. However, 50 percent shading on a dull day could be expected to have a proportionally greater effect on stomata! conductance. Species selection and even cultivars within species can have an influence on stomatal conductance responses.

## Materials and Methods

Two defruited vines were chosen, having about 140-150 cm long branches with 35-40 leaves on each shoot. On each shoot three leaves, (i) new, (ii) fully expanded new (FEN) and (iii) old were chosen at different positions. "New" was the 3-4 leaf, "FEN" was the 11-14 leaf position from the shoot apex and "old" was the 3-4 leaf position from the base of the shoot. Stomatal conductance (gs), net photosynthesis (A) were measured and interacellular $CO_2$ concentration (Ci) was calculated using a portable photosynthesis system (Li-cor model 6400) at each of the leaf positions at approximate hourly intervals from 10.00 to 17.00 (NZST). 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 in 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).

The data were analysed in a number of ways. The experiment was designed as a split-split plot, having branch and treatment as main plots and leaf age and time as sub and sub-sub plots respectively.

**Experimental Protocol:** 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 Rajasekaran (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, 5 kg m$^{-3}$ of 16:3.5:10 slow (9 month) release Osmocote® fertiliser and 4 kg m$^{-3}$ Dolomite. Vines were then placed in a shaded (87 percent light transmittance) glasshouse (day/night temperatures 24/15°C) in the Lincoln University Horticultural nursery complex. Lighting was supplemented by using 40.0 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 ensue even spread of water, 5 mm fine sand were placed put over the potting mix in each pot. The fertility was supplemented with a fertilizer application of Osmocote at 2 g pot$^{-1}$ fortnightly. Vines were trained in such a way that each had two shoots, which were grown in opposite directions.

## Results

Average net photosynthesis (A) and stomatal conductance (gs) were 8.27 ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) and 0.126 (mol H$_2$0 m$^{-2}$ s$^{-1}$) in the pre- and 4.86 ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) and 0.07

Table 1: The influence of treatments, time and leaf age on the net photosynthesis, stomatal conductance and intercellular CO$_2$ concentration of Pinot noir grapevine: interaction effects

| Leaf age | Treatment | Time 1 (Pre-shaded) | Time 2 (Shaded) | Time 3 (Post-shaded) | Percent Ratio of Time 3: Time 1 |
|---|---|---|---|---|---|
| (A) | | | Net photosynthesis ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$) | | |
| Old | Control | 6.94 a | 4.93 a | 4.22 a | 63.3 |
| | Exposed | 7.83 a | 6.36 a | 4.96 a | 65.5 |
| | Shaded | 6.56 a | -1.21 b | 4.30 a | 60.8 |
| FEN | Control | 10.79 a | 8.35 a | 5.65 a | 49.7 |
| | Exposed | 12.05 a | 8.58 a | 6.00 a | 59.0 |
| | Shaded | 10.06 b | -1.96 b | 5.94 a | 52.4 |
| New | Control | 7.18 a | 5.46 a | 4.07 a | 63.3 |
| | Exposed | 6.68 a | 6.02 a | 4.23 a | 63.4 |
| | Shaded | 6.94 a | -2.86 b | 4.40 a | 56.7 |
| (B) | | | Stomatal conductance (mol H$_2$0 m$^{-2}$ s$^{-1}$) | | |
| Old | Control | 0.11 a | 0.07 a | 0.06 a | 53.8 |
| | Exposed | 0.13 a | 0.10 a | 0.07 a | 63.4 |
| | Shaded | 0.11 a | 0.02 b | 0.07 a | 54.5 |
| FEN | Control | 0.14 a | 0.09 a | 0.07 a | 50.0 |
| | Exposed | 0.14 a | 0.10 a | 0.07 a | 50.0 |
| | Shaded | 0.13 a | 0.01 b | 0.07 a | 50.0 |
| New | Control | 0.13 a | 0.08 a | 0.07 a | 61.5 |
| | Exposed | 0.13 a | 0.10 a | 0.08 a | 53.8 |
| | Shaded | 0.13 a | 0.04 b | 0.07 a | 53.8 |
| (C) | | | Intercellular CO$_2$ Concentration ($\mu$mol CO$_2$ mol$^{-1}$ air) | | |
| Old | Control | 231.42 a | 221.28 a | 229.19 a | 099.0 |
| | Exposed | 233.00 a | 228.75 a | 221.52 a | 095.1 |
| | Shaded | 232.42 a | NA | 239.00 a | |
| FEN | Control | 201.92 a | 211.49 a | 203.83 a | 101.0 |
| | Exposed | 184.34 a | 207.67 a | 195.58 a | 106.1 |
| | Shaded | 210.08 a | NA | 207.50 a | 099.0 |
| New | Control | 240.29 a | 252.71 a | 250.58 a | 104.3 |
| | Exposed | 247.42 a | 239.75 a | 245.25 a | 099.1 |
| | Shaded | 257.33 a | NA | 237.00 a | 092.1 |

Means follow by the same letter are not significantly different ($p<0.05$). Letters refer to comparison between treatments for each time, leaf age combination. FEN (Fully Expanded new leaf). NA = The calculated Ci under the shaded conditions was outside values that could be handled by the equation and is probably a reflection of the faster response time of the photosynthetic process compared to stomatal conductance

Table 2: The influence of treatments, leaf age and time on the net photosynthesis (A) and stomatal conductance ($g_s$): main effects.

| Treatment | A ($\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$) | ($g_s$) (mol $H_2O$ $m^{-2}$ $s^{-1}$) |
|---|---|---|
| Exposed | 6.967 a1 | 0.102 a |
| Shaded | 3.506 b | 0.071 b |
| Control | 6.398 a | 0.090 a |
| Significance | *** | *** |
| **Leaf age** | | |
| New | 4.987 a | 0.080 a |
| FEN2 | 7.273 b | 0.091 a |
| Old | 4.611 a | 0.092 a |
| Significance | *** | ns |
| **Time** | | |
| Pre-shaded | 8.267 a | 0.126 a |
| Shaded | 3.740 b | 0.069 b |
| Post-shaded | 4.864 c | 0.068 a |
| Significance | *** | *** |
| **Interaction** | | |
| Leaf age vs treatment | ns | ns |
| Time vs leaf age | ** | ** |
| Time vs treatment | *** | *** |
| Time vs treatment vs leaf age | ns | ns |

Mean showing a common letter are not significantly different at $p<0.05$ (Fisher LW test).

FEN Fully Expanded new leaf. Interaction significant at ($p<0.000$), ($p<0.001$) and ($p<0.05$) denoted by ***, **, *respectively; ns is not significant

(mol $H_2O$ $m^{-2}$ $s^{-1}$) in the post-shading periods respectively (Table 1). Progressive declines in gs and A were observed during the day (Fig. 1 and 2). The fully expanded new leaves (FEN) had a significantly ($p<0.001$) higher A in the pre-shade period when compared to new or old leaves (Table 1). There was little difference between the leaves later in the day, in the post shade period. There was no significant difference between the old or new leaves. The proportional decline in A was greatest in the FEN leaves, mainly as these leaves had the mean highest pre-shading 10.8 $\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$ from 10.00 to 12.00 NZST (Fig. 1). In contrast gs was not significantly affected by leaf age (Table 1). The A:gs ratio was larger and intercellular carbon dioxide concentrations (Ci) lower in the FEN leaves than in either the new or old leaves on the canopy (Fig. 7 and 8) (Table 2 and 3) suggesting that stomatal limitation of photosynthesis for the FEN leaves was greater than that for either the old or new leaves. The A and gs in the exposed parts of the vines showed no significant variation during shade period (Fig. 5 and 6).

The post-shading values of gs and A were 54.5 and 59.3 percent of the pre-shading time respectively (Tables 1 a and b), while the Ci values were 226 and 225 $\mu$mol $CO_2$/mol air (Table 3) suggesting that gs and A were decreasing proportionally during the day.

A rapid decline in A and gs was observed on the shaded leaves within 30 minutes of applying the shading treatment (Fig. 3 and 4). During the shading period the carbon dioxide balance was negative (leaves were respiring $CO_2$ at a faster rate Than it was being fixed). The rate of leaf respiration, during shading was higher in the newer leaves compared to older leaves (Table 1). Once the shading had been removed leaf A and gs returned to similar levels to those of the leaves that had been continuously exposed to light within 30 minutes (Fig. 3 and 4).

The impact of shading half the canopy on the rate of photosynthesis by the remaining exposed leaves resulted in a small, but non-significant increase in the photosynthetic rate by the old and hew leaves measured (Table 1).

Table 3: Influence of treatments, time and leaf age on ratio of A ($\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$): gs (mol $H_2O$ $m^{-2}$ $s^{-1}$) of Pinot noir grapevine

| Leaf age | Treatment | Time 1 (Pre-shaded) | Time 2 (Shaded) | Time 3 (Post-shaded) |
|---|---|---|---|---|
| | Control | 64.38 a | 75.26 a | 70.22 a |
| Old | Exposed | 64.10 a | 66.43 a | 77.85 a |
| | Shaded | 63.72 a | -89.31 b | 65.03 a |
| | Control | 80.92 a | 90.20 a | 86.06 a |
| FEN | Exposed | 93.63 a | 83.71 a | 92.69 a |
| | Shaded | 76.55 a | -240.78 b | 90.43 a |
| | Control | 57.54 a | 70.57 a | 58.42 a |
| New | Exposed | 56.80a | 61.14 a | 55.67 a |
| | Shaded | 48.98 a | -99.40 b | 66.95 a |

Means follow by the same letter are not significantly different ($p<0.05$) Letters refer to comparison between treatments for each time, leaf age combination. FEN (Fully Expanded new leal)

## Discussion

Leaf position on the shoot has been reported to have a significant effect on the rate of photosynthesis (Alleweldt *et al.*, 1982; Kriedemann *et al.*, 1970; Pon and Intrien, 1996).

The effect of leaf position on A was most noticeable early in the day, in the pre-shading period, with FEN having a higher A compared to that for new or old leaves. The lack of a leaf age effect later in the day may have been associated with the progressive decline in A and gs

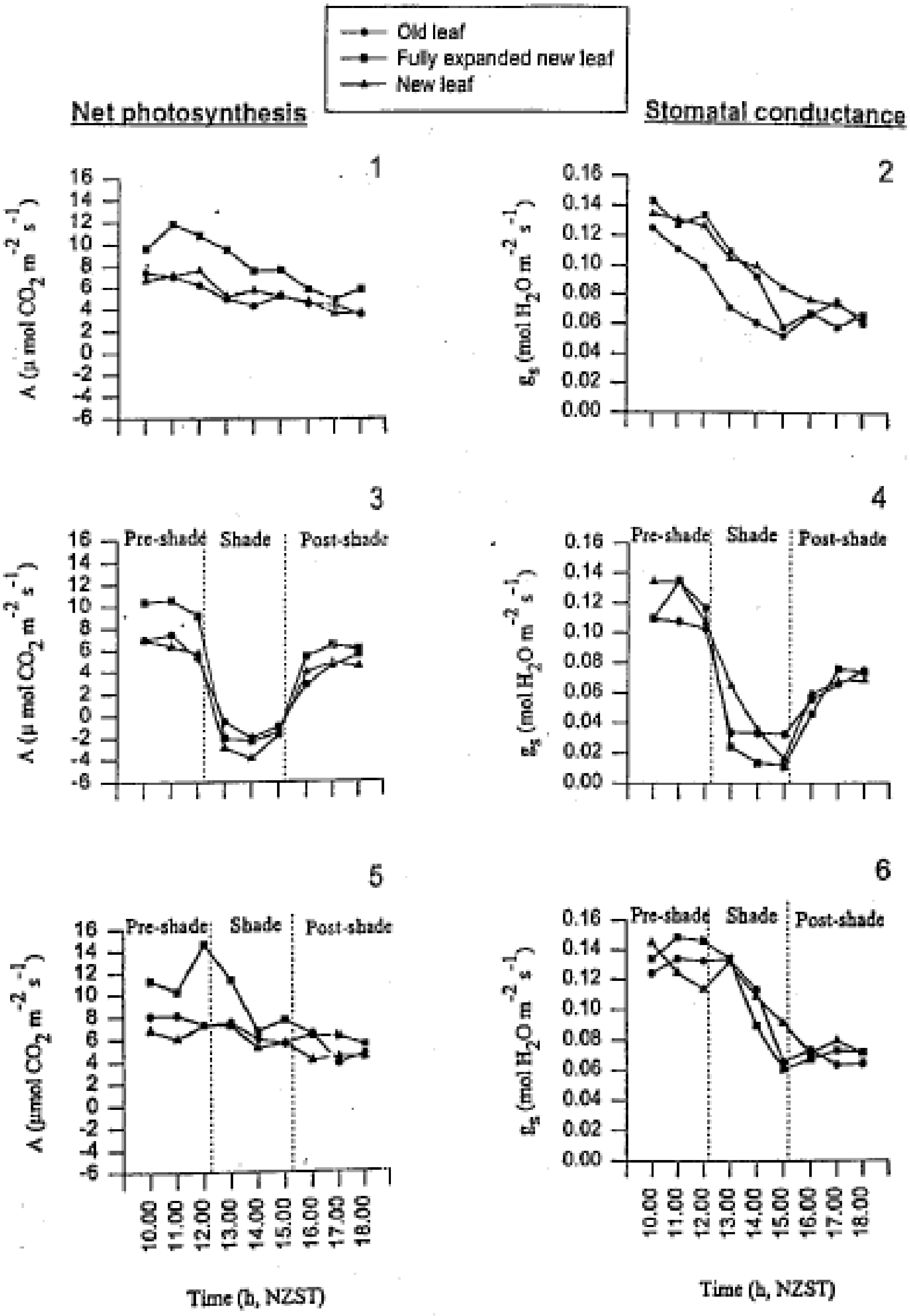

Fig. 1-6: Influence of leaf age and short term changes of light intensity on the net photosynthesis (A) and stomatal conductnace (gs) in different leaf position in control (1 and 2) shaded (3 and 4) and illuminated (5 and 6) canopies of piont nior grapenive (*Vitis vinifera* L.)

observed from 12.00 to 18.00 (NZST) hours. This decline may have been the result of an accumulation of photosynthates in the leaves (Flore and Lakso, 1989) or the progressive development of a mild water stress caused by the relatively small pots drying out or an increase in the vapour pressure deficit and has been observed by others (Correia *et al.*, 1990; Chaves *et al.*, 1987).

It was hypothesised that shading part of the canopy would decrease the overall canopy transpiration rate and thereby increase the water potential (decrease water stress) of the vine, at the same time, the reduction in canopy area would reduce the source:sink ratio, possibly causing an increase in demand for photosynthates from the exposed portion of the canopy. Shading and the associated decrease in light intensity had the expected effect on the shaded half of the canopy, causing a rapid closure of the stomata and decline in net photosynthesis, similar to that observed by others (Grant and Ryugo, 1984; Kappel, 1980; Rom and Ferree, 1986). A small, but generally non-significant increase in A was observed on the illuminated half of the vine during the shading period, when compared to the control vine.

In general, the effect of shading and time of day on gs reflected A and similar to results reported by Chaves *et al.* (1987) and Jacobs *et al.* (1996). Leaf age had no significant effect on gs and this was in contrast to Schubert *et al.* (1996), who reported significant differences in gs. The lack of a leaf age effect may have been the result of cloudy conditions and the relatively low light intensities (400-800 µmol $m^{-2}$ $s^{-1}$) recorded during the experiment. Ci was unaffected by time of day. On the basis of these results, the fully expanded leaf appeared to be the most sensitive to environmental conditions and shading. So, this leaf was used in further experiments to investigate the effect of crop load and water stress on the shading response.

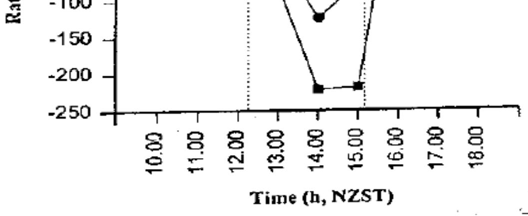

Fig. 7: Influence of short term changes of light intensity on the ratio of net photosynthesis (A) and Stomatal conductance (gs) on different leaf positions in shaded canopy of Pinot Noir grapevine (*Vitis vinifera* L.)

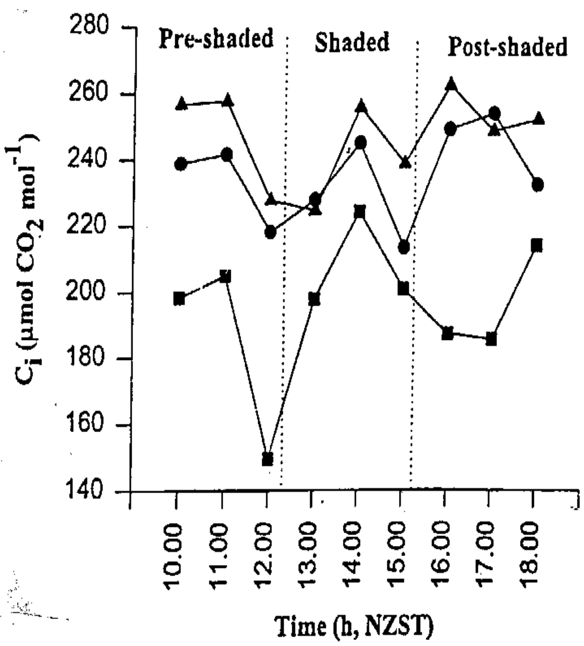

Fig. 8: Influence of short term changes of light intensity on the intercellular $CO_2$ concentration ($C_i$) on different leaf positions in shaded canopy of Pinot Noir grapenine (*Vitis vinifera* L.)

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