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PJBS

ISSN 1028-8880

Pakistan Journal of Biological Sciences

ANSInet
Asian Network for Scientific Information
308 Lasani Town, Sargodha Road, Faisalabad - Pakistan

Pakistan Journal of Biological Sciences 3 (2): 279-283, 2000

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

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Abstract: The main objective of this study was to investigate the impact of short-term light intensity changes in relation to crop loading on the net photosynthesis (A) and stomatal conductance (g_s) of grapevine (*Vitis vinifera* L.) cv. Pinot noir. Shading caused a rapid increase in the net photosynthesis (A) and stomatal conductance (g_s) of the illuminated part of the canopy. Fruiting grapevines had a higher A and g_s (4.7 μmol CO_2 m^{-2} s^{-1} and 0.08 mol H_2O m^{-2} s^{-1}, respectively), than non-fruiting vines (2.9 μmol CO_2 m^{-2} s^{-1} and 0.05 mol H_2O m^{-2} s^{-1}, respectively). Intercellular CO_2 concentration (C_i) was unaffected by shading or crop loading, It is concluded that crop load has significant role in the rapid changes in A and g_s in the illuminated part of the canopy.

Key words: The influence of light intensity in relations to crop load on the physiology of grapevine

Introduction

Whitehead and Teskey (1995) reported that decrease in irradiance from 800 to 200 μmol m^{-2} s^{-1} between 5 and 60 minutes on needles of *Pinus taeda* trees under laboratory conditions reduced the rate of photosynthesis immediately by 58 percent but the rate of change was more rapid than the change in stomatal conductance. When shading was removed, this induced a 39 percent decrease in stomatal conductance, the conclusion was that the increase in photosynthesis during the induction phase after shading was limited by both stomatal and biochemical effects. Reductions in leaf area by transient shading a portion of the foliage of western redcedar (*Thuja plicata* Donn.) can immediately reduce the whole seedling transpiration and cause a concomitant increase in stomatal conductance, photosynthesis and transpiration in the remaining illuminated foliage. These compensatory effects were fully reversed after the shade was removed. When a portion of a seedling's foliage was shaded (by interposing an opaque screen between an overhead light and the cuvette), the reductions in whole-plant photosynthesis transpiration were proportionally less than the changes in the area of illuminated foliage.

The degree of crop loading in term of sink is also play an important role on the physiological activities of the plant. Hofstra and Nelson (1969) reported that after full expansion and under good environmental conditions for photosynthesis, leaves may export 60-80 percent of their assimilate to other part of the plant Carbon export from grapevine shoots starts when 10-12 leaves have expanded. The early cessation of the shoot growth allowed a more rapid export (Lakso and Grappadelli, 1992).

Several management factors can influence the source (where carbohydrates are synthesized): sink (where carbohydrates are utilized) ratio. For example, fruit can stimulate the individual leaf photosynthesis rate in grapevine leaves (Edson *et al.,* 1993). When the source or sink size has been manipulated by fruit removal (Hofacker, 1978), defoliation (Hofacker, 1978; Hunter and Visser, 1988), topping (Kaps and Cahoon, 1989) or girdling (Kriedemann and Lenz, 1972) this usually results in by increasing photosynthesis rate as the relative source: sink ratios decrease. However, this response does not appear consistently and the mechanism behind it is not fully understood. In the absence of fruit when there are other large sinks present (such as rapidly growing shoots) photosynthesis rates may be elevated (Edson *et al*., 1993). The diurnal response of leaves is also influenced by different crop loadings. The depression of photosynthesis during the afternoon are decreased and delayed by the presence of fruit (Downton *et al*., 1987).

Increased crop loading increased the net photosynthesis per unit leaf area but, it did not increase the total net photosynthesis of the whole vine (Edson *et al*., 1993). Fruiting increased photosynthesis, dark respiration and the drought sensitivity of the apple trees (Wibbe and Blanke, 1997). Vines with a higher crop load partition more carbon to the fruit, resulting in a reduced leaf area. This means that the remaining leaves need to photosynthesis at a higher rate to maintain the total vine photosynthesis level. This relationship is confirmed when the total dry weight of the vines is considered. The different levels of crop have no effect on the total dry weight produced by the vine (Edson *et al*., 1993; Petrie, 1997), although the dry matter production per unit of leaf area is increased by higher crop levels. In contrast Koblet *et al*. (1996) reported that crop load had no significant effect on photosynthesis in Muller-Thurgau vines, yet there was a marked interaction between rootstock and N fertilization with respect to the photosynthesis rate. The sink: source ratio can also be influenced by the relative proportions of the canopy illuminated, which will vary throughout the day and season. The effects of short-term shading and the recovery of the plant are less well understood, particularly how the exposed part of the canopy, responds to shading of another part in the presence of different degree of crop load.

Materials and Methods

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 80 mm 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 15 cm 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% 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 were placed over the potting mix in each pot. The fertility was supplemented with a fertilizer application of Osmocote at 2 g/pot fortnightly. Vines were trained in such a way that each had two shoots, which were grown in opposite directions.

Short term shading of part of the canopy was studied in green house condition on the potted grapevines (*Vitis vinifera* L.) cv. Pinot noir during 1998. 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. Fruiting with shade
2. No-fruiting with shade
3. No-fruiting with no-shade
4. Fruiting with no-shade vines

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 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). 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 in 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 progressive decline in A and g_s measured in the previous experiment was also observed in this experiment (Fig. 1, 2). The presence of fruit resulted in significantly ($p<0.001$) higher A and g_s when compared non-fruiting vines (Table 1) which was maintained throughout the day and during the shading treatment period (Fig. 1, 2).

Shading part of the canopy caused a significant increase in A and g_s in the illuminated part of the canopy (Table 2) very rapidly, within 15 minutes of imposing the treatment (Fig. 1 and 2). Shading caused A and g_s to increase in the illuminated part of the vine by 55 and 20 percent respectively of control values for the fruiting vines and 68 and 73 percent respectively for non-fruiting vines (Table 2). However, the instantaneous increase over the 20 minutes between measurements when the treatment was imposed caused g_s of the fruiting vines to almost double (Fig. 2). During the shading period, g_s of the illuminated part of the canopy returned to a value similar to the control vine, while A was still noticeably higher, only returning to values similar to those of the control vine once the shade was removed. The A:g_s ratio was not significant in all treatments and time (Table 3). C_i was unaffected by crop load or shading (Table 2 and 1).

Despite the higher g, of the fruited vines, overall vine transpiration rates were lower (Fig. 3), reflecting the lower total leaf area. When measured using the heat pulse logger, shading did not appear to have a marked effect on the xylem flow of the whole vine, although the relatively low rates of xylem flow and considerable technical problems encountered using the logger means these data need further investigation.

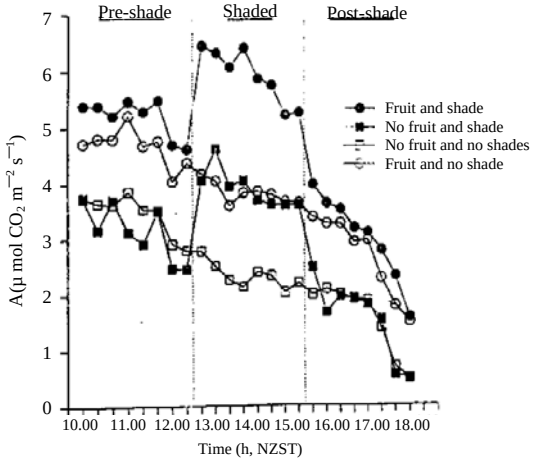

Fig. 1: Influence of short term changes of light intensity on the net photosynthesis (A) in pre-shaded, shaded and post-shaded canopies of Pinot noir grapevine (*Vitis vinifera* L.)

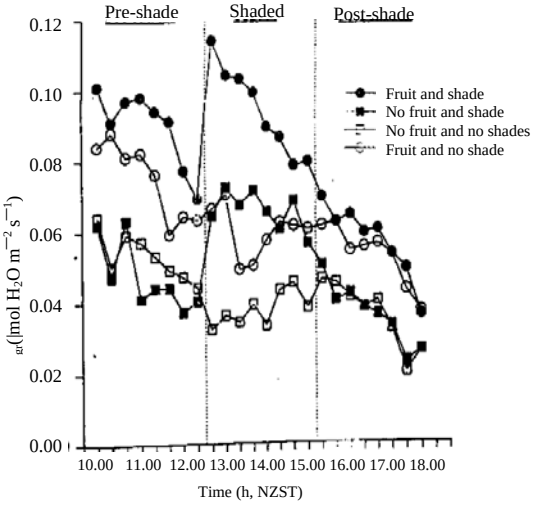

Fig. 2: Influence of short-term changes of light intensity on the stomatal conductance (g_s) in pre-shaded, shaded and shaded and post canopies of pinot noir grapevine (*Vitis vinifera* L.)

There was no difference in the slope of the A and g, throughout the treatments (Fig. 4) Regression analysis of A against g_s suggested that the higher photosynthetic rate occurred largely in relation to higher stomatal conductance in the fruiting vines (Fig. 4). 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, when this vine was compared to the control vine (Fig. 4), when the shaded vines were compared with the control vine (Fig. 5). Similarly, there was no effect of fruiting on the relationship between A and g_s (Fig. 6).

Table 1: Influence of treatments and time on the net photosynthesis (A), stomata! conductance (g_s) and intercellular CO_2 concentration (C_i): main effects

Treatments	A (μmol CO, $m^{-2}s^{-1}$)	g_s (mol H_2O m^{-2} s^{-1})	C_i (μmol CO_2 mor^{-1}air)
+F+S	4.699 a[1]	0.080 a	227.802 a
+F-S	3.716 c	0.068 c	269.958 a
-F+S	2.853 b	0.050 b	247.177 a
-F-S	2.436 b	0.042 b	261.534 a ns
Significance	***	***	ns
Time			
Pre-shaded	4.108 a	0.066 a	244.752 a
Shaded	3.982 a	0.069 b	229.977 a
Post-shaded	2.187 b	0.045 b	280.125 a
Significance	***	***	ns
Interaction			
Time vs treatment	*	ns	ns
Branch vs treatment	ns	*	ns

Mean[1] showing a common letter are not significantly different at $p<0.05$ (Fisher LSD test) + F fruit, F no-ftuit, +S shaded and -S unshaded vines; Interaction significant at ($p<0.05$) and ($p<0.001$) denoted by* and***, respectively. ns is not significant

Table 2: Influence of treatments and time on the net photosynthesis, stomatal conductance and intercellular CO_2 concentration of Pinot noir grapevine: interaction effects

Treatments	Time 1 (Pre-shaded)	Time 2 (Shaded)	Time 3 (Post-shaded)	Percent Ratio of Time 3: Time) (A)
Net photosynthesis (μmol CO_2 $m^{-2}s^{-1}$)				
+F-FS	5.19 a	5.91 a	3.00 a	57.8
4-F-S	4.67 a	3.81 b	2.70 a	57.8
-F + S	3.13 b	3.89 b	1.54 b	49.2
-F-S	3.45 b	2.32 c	1.55 b	44.9
Stomata! conductance (mol H_2O $m^{-2}s^{-1}$)				
+F+S	0.090 a	0.094 a	0.057 a	63.33
+F-S	0.075 a	0.078 ab	0.053 a	70.67
-F + S	0.047 b	0.066 b	0.036 b	76.60
-F-S	0.053 b	0.038 c	G.036 b	67.92
Intercellular CO_2 Concentration (μmol) CO_2 mol^{-1} air)				
+F+S	245.0 a	201.0 a	237.5 a	096.9
+F-S	251.5 a	231.7 a	326.7 a	130.0
-F + S	236.4 a	230.0 a	275.2 a	116.4
-F-S	246.2 a	257.2 a	281.2 a	114.2

Means follow by the same letter are not significantly different ($p<0.05$). Letters refer to comparison between treatments for each time combination. +F fruit, -F no-fruit, +S shaded and -S unshaded vines

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

Treatments	Time 1 (Pre-shaded)	Time 2 (Shaded)	Time 3 (Post-shaded)
+F+S	59.23 a	64.06 a	54.13 a
-F+S	71.19 a	59.58 a	44.10 a
1-F-S	64.38 a	53.38 a	51.03 a
-F-S	65.01 a	65.47 a	44.74 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. +F fruit, -F no-fruit, +S shaded and -S unshaded vines

Discussion

A and g_s were higher in fruited vines compared to non-fruiting vines. The presence of fruit stimulated A in grapevine leaves (Chaves, 1984; Edson *et al.,* 1993; Hofacker, 1978; Kaps and Cahoon, 1989). Once fruit set has occurred, the fruit becomes the largest sink in the grapevine (Mullins *et al.*, 1992). In the non-fruiting (limiting sink) situation the demand for photo assimilate was less. Therefore, this is a possible reason for the lower A and g_s rates in the non-fruiting vines compared to fruiting vines. Flore and Lakso (1989) also reported that A was decreased by high levels of assimilate in the leaves, caused by low sink demand. Leaves act as a source for photo assimilate production, while, fruit and other growing parts of vines act as a sink. When the source or sink sizes were manipulated by fruit removal (Hofacker, 1978), defoliation (Hofacker, 1978), topping (Kaps and Cahoon, 1989), or girdling (Hofacker, 1978; Kriedemann and Lenz, 1972) A was increased in the remaining as the relative source:sink ratio decreased. It is very noticeable that A and g_s increased in the illuminated part of the shaded vines. This means that shading part of the canopy resulted

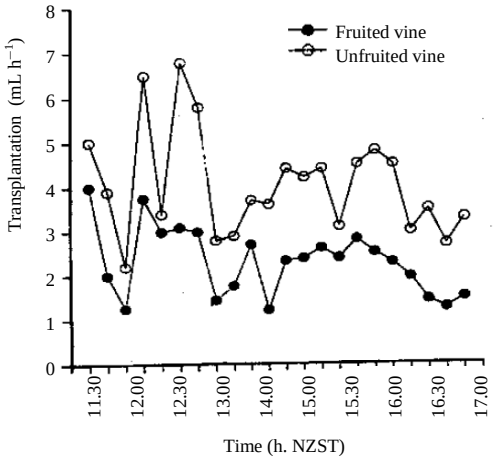

Fig. 3: Influence of degree of crop load on the transpiration in Pinot noir grapevine (*Vitis vinifera* L.) during a day under uniform climatic condition in the greenhouse

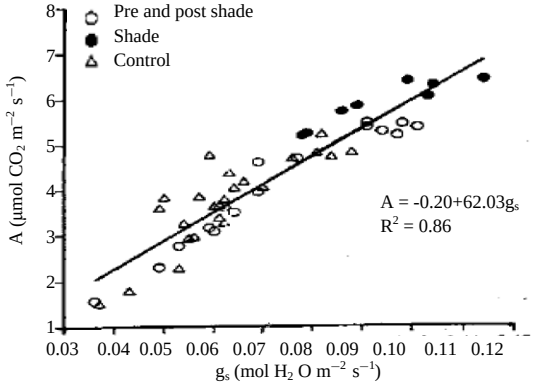

Fig. 4: The influence of short-term changes of light intensity on the relationship between net photosynthesis (A) and stomatal conductance (g_s) in fruited (pre and post shade, shade and control) Pinot noir grapevine (*Vitis vinifera* L.)

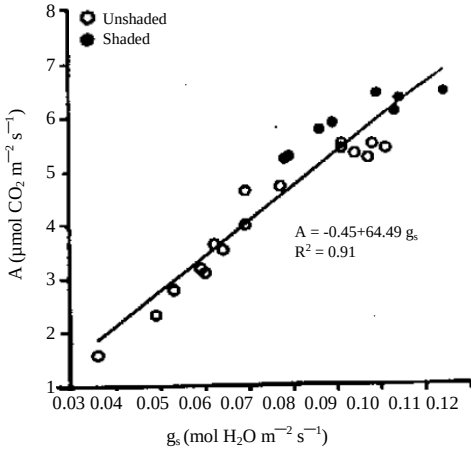

Fig. 5: The influence of short-term changes of light intensity on the relationship between net photosynthesis (A) and stomatal conductance (g_s) in the fruited pinot noir grapevine (*Vitis vinifera* L.)

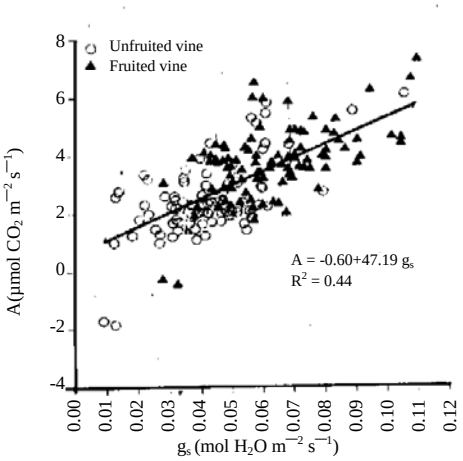

Fig. 6: Relationship between met photosynthesis (A) and stomatal conductance (g_s) in the control pinot noir grapevine (*Vitis vinifera* L.)

in the physiological processes of the illuminated part to increase to maintain total A for the vine. The g_s did not decline in the fruited unshaded vines but did decline in the unshaded non-fruiting vines. This means that the presence of fruit may keep physiological processes active to fulfil the sink demand. Most important, C_i in the illuminated part of the vine was not affected by the shading treatment, in agreement with others (Cartechini and Palliotti, 1995; Whitehead *et al*., 1996). This confirms that the hypothesis that photosynthesis and stomatal conductance ar responding in a similar manner and that the enhancement of photosynthesis results from increased stomatal conductance in the illuminated part of the shaded vine. A and water use efficienc increased as light intensity increased (Shiraishi *et al.,* 1996). This means that at high light intensities when A increases, the CO_2 utilization also increases, which may cause a decline in C_i. Leaf temperature had no influence on the A and g_s. The transpiration rate was more in the unshaded non-fruiting vines compared to fruiting vines. The presence of fruit may result in reduced transpiration rate. There was a continuous decline in the transpiration rate during the day from morning to after noon in all canopies.

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