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## **Low morning temperature limits photosynthesis and growth in cool climate grapevines**

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### **Introduction**

Chilling temperatures, between 0-15 °C, are common in temperate climates and can severely limit photosynthesis and productivity in plants that have a tropical or sub-tropical evolutionary history. Chilling effects on photosynthesis include restriction of carbon reduction, photo-phosphorylation, sucrose synthesis and CO<sub>2</sub> supply through the stomata (Allen & Ort, 2001). All these factors combine to limit carboxylation in the stroma. This can dramatically reduce thylakoid electron transport, inducing down regulation of photosystem II (PSII) and increasing dependence on non-photochemical dissipation of excess light energy (Huner *et al*, 1993; Chaumont *et al*, 1995). When light intensity is high, chronic photoinhibition of PSII can result under chilling conditions since low temperature reduces the reaction rates of not only carboxylation but also photorespiration, another important energy sink in plants (Park *et al*, 1996; Takeba & Kozaki, 1998; Sonoike, 1999). Grapevines, which are grown in cool climates for the production of premium quality wine, are often exposed to the combination of low temperatures and high light. This study was aimed at determining the effects of light and sub-optimal temperature on the photosynthesis of field-grown grapevines and whether this limits growth in cool-climate vineyards.

### **Materials and methods**

*Plant material* Photosynthesis and growth of grapevines (*Vitis vinifera* cv Riesling) was studied in a vineyard near Murrumbateman, NSW. The grapevines were planted in rows oriented north-south on a 15 ° north-west facing slope such that eastern and western halves of the canopy were exposed to direct sunlight in the morning and the afternoon, respectively. Two sub-populations of vines were chosen on 'upper' and 'lower' sites with respect to their position on the slope. A total of 10 vines per site were chosen randomly for study. Grapevines were irrigated every 2 days and given supplemental watering when required.

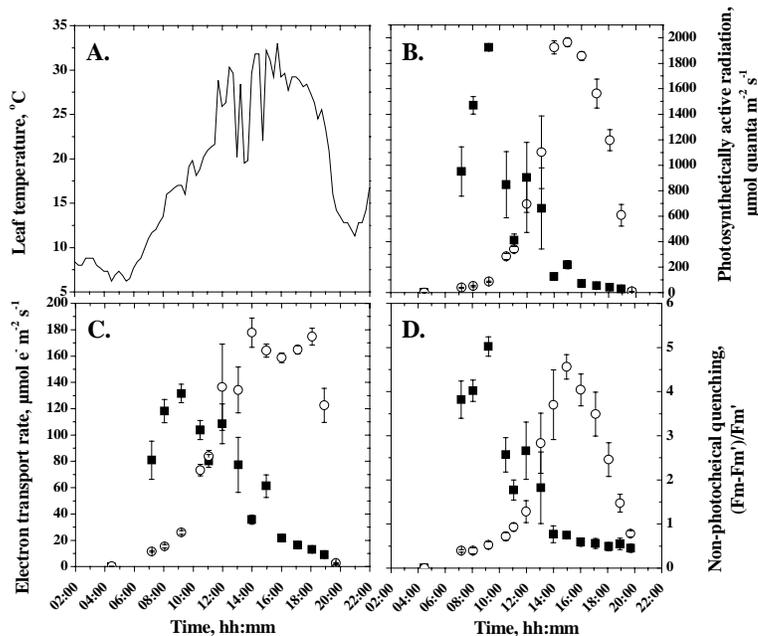
*Photosynthesis measurements* Diurnal rates of photosynthetically-active radiation (PAR), photosynthesis (as estimated by electron transport rate (ETR:  $([Fm' - Fs]/Fm') * 0.5 * PAR * 0.85$ ) and non-photochemical dissipation (NPQ:  $[Fm/Fm'] - 1$ ) was measured simultaneously with pulse-modulated chlorophyll fluorescence (Mini-PAM, Walz, Effeltrich, Germany). On select days, diurnal rates of carbon assimilation were measured with an infrared gas analyzer (LI-

6400, LI-COR, Nebraska, USA) and integrated over time. Photosynthetic rates were measured for both east- and west-facing leaves at the upper and lower sites.

**Growth and Temperature measurements** Leaf temperature was measured with thermistors every 15 minutes and was recorded with a data logger (Tinytalk, Gemini Data Loggers, West Sussex UK). Temperature was logged throughout the growing season (01/09/00-30/04/01) for both the upper and lower sites. An index of temperature sum over the growing season was calculated as the sum of daily maximum and minimum temperature for both sites. Vine productivity was measured as total shoot length for east- and west-facing shoots at both the upper and lower sites.

## Results and Discussion

**Photosynthesis measurements** Maximum diurnal ETR under full sunlight was 35% higher for west-facing leaves compared with east-facing leaves which experienced peak PAR earlier in the day when leaf temperature was 12.6 °C lower (Fig. 1). The difference between NPQ (10% higher for east-facing leaves) was more marginal on this day compared to other days. A similar observation was made for the upper site (data not shown).

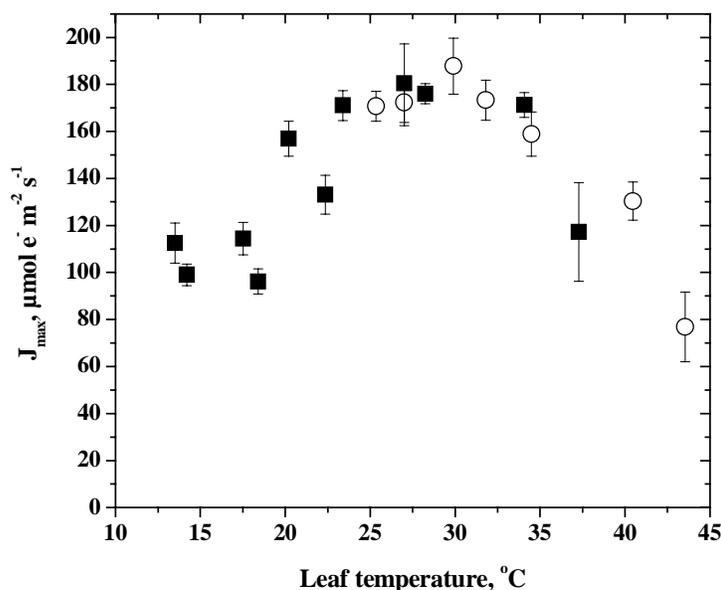


**Fig. 1.** Diurnal leaf temperature, (A), PAR (B), electron transport rate (C) and NPQ (D) for lower site east-facing (closed squares) and west-facing (open circles) leaves for a spring day. Each point is the mean  $\pm$  s.e. of 6-10 leaves.

Interestingly, there was no evidence of chronic photoinhibition, as measured by predawn dark-adapted  $F_v/F_m$  (data not shown). The lack of slowly reversible photoinhibition in grapevine has been noted in previous studies and suggests a strong photoprotective capacity (Demmig-Adams et al, 1989; Bilger & Björkman, 1991; Chaumont *et al*, 1995; Iacono & Sommer, 1996).

East-facing leaves experience a wide range of temperatures during illumination but the lower temperatures (Fig. 2) frequently limit electron transport rates. Alternatively west-facing leaves attain higher rates of electron transport because temperatures are more favourable during afternoon peak illumination. However, ETR declines with increases in leaf temperature

above 30 °C (Fig. 2). This pattern is consistent with an optimum photosynthetic temperature of 27-30 °C as reported by Kriedemann (1968). Variance components analysis supports the hypothesis of a significant difference between east- and west-facing leaf ETR that is the result of an interaction with temperature (REML, *Wald/d.f.*>34, *p*<0.001). A comparison of upper and lower sites revealed that the upper site attained higher rates of light-saturated electron transport rate (REML, *ald/d.f.*>8, *p*<0.003).



**Fig. 2.** Summary of light-saturated electron transport rates ( $J_{\max}$ ) against leaf temperature during respective morning and afternoon peak daily PAR for both east-facing (closed squares) and west-facing (open circles) leaves. Each point is the mean  $\pm$  s.e. of 5-10 leaves; measurements were made for 8 days as in Fig 1

Integrated diurnal carbon assimilation (Table 1) shows that on this particular day, the lower site leaves fix approximately 13% less  $\text{CO}_2 \text{ m}^{-2}$  than the upper site leaves despite intercepting similar amounts of light. The majority of this difference is attributable to lower rates of photosynthesis in east-facing leaves that were subject to lower temperatures. If generalisable, higher overall temperature, especially morning temperature, would presumably contribute to enhanced growth of upper site vines

*Growth and temperature measurements* Regression analysis of upper and lower site temperature measurements revealed that minimum leaf temperatures at the lower site average 2 °C cooler than the upper site ( $r^2=0.95$ , s.d. =1.0, data not shown). Growth analysis of vine shoots at both the upper and lower site showed no difference between growth of east- and west-facing shoots (ANOVA,  $F=0.2$ ,  $p=0.65$ ). The upper site shoots had growth rates higher than the lower site as shown in Fig. 3.A (ANOVA,  $F>6$ ,  $p<0.01$ ). However, when stem elongation is plotted against the cumulative temperature sum (Fig. 3.B), differences in shoot growth between upper and lower sites disappear (ANOVA,  $F=0.867$ ,  $p=0.87$ ). This shows that the differences in final stem length in Fig 3.A are attributable to cumulative effects of small scale variation in temperature between the two sites, with growth being greater at the warmer, upper site.

**Table 1.** Integrated net carbon assimilation for a clear spring day

	Leaf aspect		Total mol CO <sub>2</sub> m <sup>-2</sup>
	East mol CO <sub>2</sub> m <sup>-2</sup>	West mol CO <sub>2</sub> m <sup>-2</sup>	
Lower site	0.239	0.256	0.495
Upper site	0.290	0.271	0.561

## Conclusions

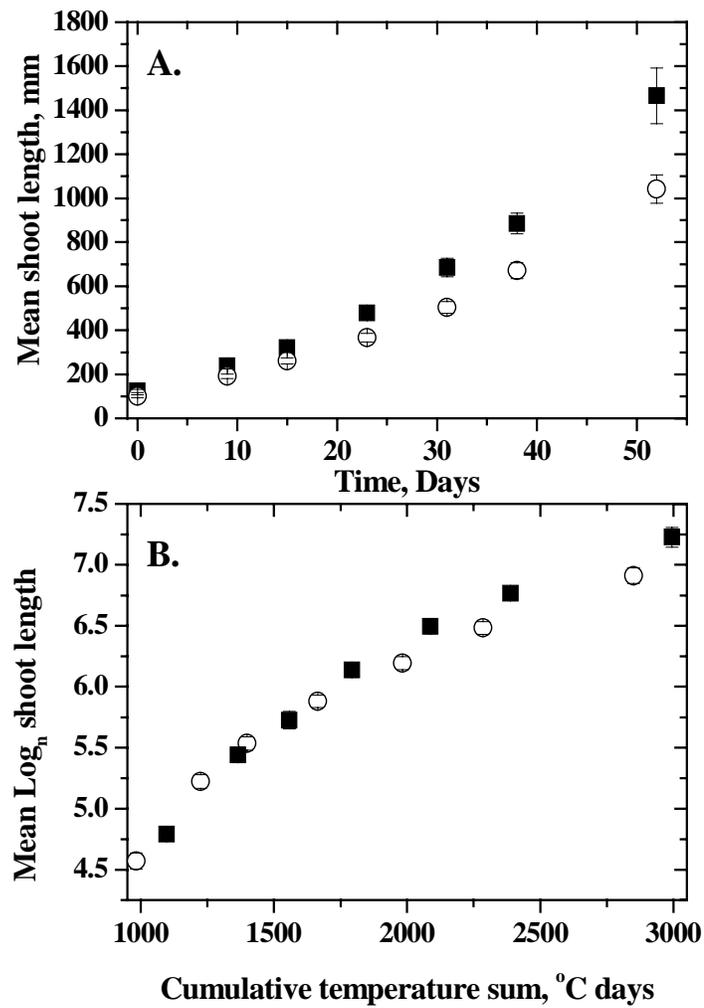
Low morning temperature limits the capacity of light-saturated photosynthesis of grapevines. This study has shown that even a 2°C warmer site can contribute to greater carbon gain and growth throughout the season. The frequency of both cool mornings and hot afternoons would be an important factor in determining productivity of grapevines in a climate with wide diurnal temperature ranges. Effects of small-scale variation in temperature on light-saturated photosynthesis can become manifest in the growth of grapevines. This has direct implications for the effects of vine canopy orientation on productivity.

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**Fig. 3.** Scatter plot of mean stem length against time and mean natural logarithm of stem length against cumulative temperature sum for both upper (closed squares) and lower (open circles) site vines. Each point is the mean  $\pm$  s.e. of 20 shoots.