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Multi-seasonal effects of warming and elevated CO_2 on the physiology, growth and production of mature, field grown, Shiraz grapevines

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Abstract

Industry concerns in Australia about the impacts of climate change have, to date, focused on the effects of warming, particularly shorter maturation periods. The effects of elevated CO_2 concentration (eCO_2) on C_3 plant physiology have been extensively studied and suggest that eCO_2 impacts on viticulture could affect grapevine shoot growth, fruit production and fruit composition. We previously used open top chambers (OTC) with an active heating system to study the effects of elevated air temperature (eTemp) on mature grapevines in the field. This system was augmented with the ability to elevate atmospheric CO_2 and established in a mature Shiraz vineyard in a factorial combination of eTemp and eCO_2. Three seasons of observations on the eTemp only treatment corroborated our previous study; all aspects of phenology were advanced, but leaf function was largely unaffected. In contrast, the effects of eCO_2 on phenology were small in the first season, but increased over the subsequent two seasons. Interactive effects of the treatments on gas exchange were observed; photosynthesis rates were significantly higher in the eCO_2+eTemp treatment, compared to eCO_2 alone, suggesting that the likely future climate will have a larger impact on viticulture than might be predicted from experiments examining only one of these factors.

Keywords: Shiraz, temperature, CO_2, phenology, leaf function

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Introduction

There is now a large body of literature suggesting that the emission of CO_2, and other gases of anthropogenic origin, is resulting in warming of the troposphere (summarised in IPCC 2014). This combination of higher CO_2 concentrations and warming of the atmosphere is of particular importance to viticulture, due to the longevity of plantings and a limited ability to change varieties or relocate to cooler areas due, to the cost and difficulty of doing so.

To date, industry focus has been on the potential effect of warming on vine phenology (e.g. Petrie and Sadras 2008, Webb *et al.*, 2012) and our previous work with open top chambers in the field has demonstrated that 2°C of atmospheric warming is indeed enough to cause a significant advancement of all major phenological stages (Sommer *et al.*, 2012).

However, the largest contributory factor to climate warming is CO_2 and atmospheric CO_2 concentrations are rising year on year at a rate that has been shown to affect photosynthetic rates in C_3 plants, relative to pre-industrial times, (Gerhart and Ward, 2010) and is expected to have an even larger effect in the future.

To date, no viticulture experiment has been able to address the combined effects of elevated atmospheric CO_2 (eCO_2) and elevated atmospheric temperature (eTemp) in the field. We have established an open top chamber (OTC) facility in a major Australian winegrape growing region using mature Shiraz vines, managed to current industry best practice, which is able to impose an eCO_2 treatment of 650 ppm and an eTemp treatment of +2°C relative to ambient, simulating the likely climate around 2075. The facility applies these treatments in a factorial design and is thus able to separate effects of eCO_2 and eTemp as well as be used to study their interaction. The facility was fully operational prior to the 2013/14 southern hemisphere growing season and has been running continuously since that time.

Materials and methods

The experiment was established in a block of mature Shiraz grapevines at the Department of Economic Development, Jobs, Transport and Resources (DEDJTR), Irymple, Australia,. Sixteen open top chambers (OTCs), 5.4x4.8x2.4 m (LxWxH), were erected, each enclosing a single panel of three vines. The OTC structure, heating system and fan-only system are described in Sommer *et al.* (2012). The CO_2 enrichment system (described in Edwards *et al.*, 2016) was designed to allow CO_2 to quickly mix with the chamber air and be transported in and around the grapevine canopy by air movement (with or without the heating system fan running). CO_2 was only supplied during daylight hours, with timing adjusted weekly. As grapevines are a deciduous woody perennial plant, requiring chilling for even budburst (Mullins *et al.*, 1992), the temperature treatments were maintained over each winter.

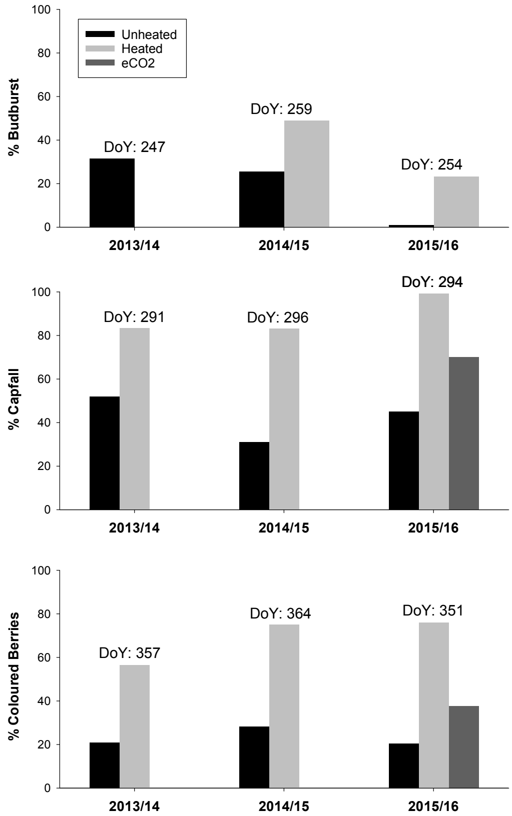

Figure 1 - Proportion of buds burst (a), capfall (b) and coloured berries (c) at a time point chosen to demonstrate the effect of 2 °C of warming (light grey) and elevated CO_2 (dark grey), compared to controls (black), in each of three growing seasons of treatment (only significant effects shown)

Four chambers were assigned to each of the treatment combinations: elevated temperature (eTemp), elevated CO_2 (eCO_2), elevated temperature and elevated CO_2 (eCO_2 +eTemp). The remaining four chambers were assigned as controls (chamber control) and were provided with a fan-only system to replicate the air movement generated by the heating system, without providing heating. Finally, a further four panels of vines were assigned to be non-chambered controls (chamberless control). The OTCs and chamberless control panels were distributed in a randomised design. The trial therefore consisted of 20 plots, with four replicates per treatment.

Air temperature and relative humidity were logged at 15 minute intervals in each of the 20 plots using a HOBO Micro Station Datalogger (One Temp Pty Ltd, Adelaide, SA, Australia), CO_2 concentration measured 5 times per second in each of the OTCs provided with eCO_2, and every second in the control chambers, using Li-Cor (Lincoln, NB, USA) and PP Systems (Amesbury, MA, USA) CO_2 sensors, respectively.

Treatments were applied immediately prior to budburst in the 2013/14 season, and maintained from that point onwards, including during winter. The data presented here represent three seasons of treatment; namely the 2013/14, 2014/15 and 2015/16 southern hemisphere growing seasons.

Vine water use was monitored at 15 minute intervals from September 2013 to June 2015 using a single SFM sap flow logging system (ICT International, Armidale, NSW) in the central vine of all 20 replicates, providing two full growing seasons of data.

The phenological stage of each replicate was determined at regular intervals according to the modified E-L system (data not shown). In addition, weekly photographs were taken and used to establish the onset of key phenological stages.

Leaf gas exchange was measured on four occasions per season on dates roughly equivalent to anthesis, canopy closure and veraison, with a final measurement after harvest. Each measurement was made on a single fully expanded sun-exposed leaf per replicate and consisted of a determination of assimilation under saturating light (A_{sat}) at the chamber/atmospheric CO_2 concentration over the course of one minute, following an equilibration period. The leaves used to measure photosynthesis were harvested at the end of the day, with leaf fresh weight, leaf area and leaf dry weight determined. For the 2013/14 and 2014/15 seasons, the dried leaves were then ground and used to determine the concentration of non-structural carbohydrates (NSC) according to Edwards *et al.*, (2011).

Harvest of all the bunches from the central vine was undertaken once sampling on the adjacent vines indicated that the juice had reached a total soluble sugar (TSS) level of 24°Brix. The total fruit weight was measured and a sub-sample of 100 berries used to determine TSS.

Results and discussion

The experimental system was effective in providing 2 °C of warming above ambient and in raising the CO_2 concentration of the air in the OTCs to an average of 650 ppm (data not shown, but see Edwards *et al.*, 2016). Both values are predicted to occur around 2060-2070 (IPCC, 2014).

Comparison of the environmental results from the control OTCs and the chamberless control plots indicated a small impact of the chamber infrastructure, for example an average air temperature increase close to 0.5 °C. There were also small differences between the control OTCs and chamberless controls in other measured parameters,

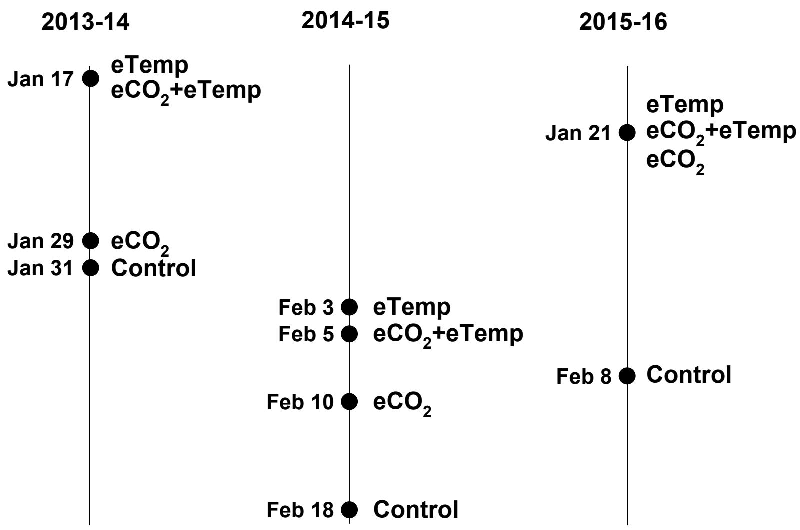

Figure 2 - Timeline of harvest dates for the four OTC treatments for three growing seasons. Harvest dates were based on a target TSS of 24 °Brix.

such as leaf gas exchange (data not shown), but these were not consistent. Consequently, we have presented the non-heated, ambient CO_2 OTC chambers as ‘controls’ in the following figures and discussion.

1. Phenology and harvest

As the experimental system was only begun a few days prior to budburst in 2013 it was not expected that any effect of the treatments would be observed on the timing of budburst in that season and this was indeed the case (Figure 1a). However, by anthesis in that same season (approximately 45 days later) the two heated treatments reached 50 % capfall earlier than the non-heated treatments (Figure 1b). This advancement of phenology continued and veraison was also advanced in the two warming treatments, with the 50 % coloured berries stage reached ahead of the non-heated treatments, approximately 110 days after budburst (Figure 1c). No significant effect of eCO_2 nor interaction between warming and eCO_2 treatments was observed on phenology during the 2013/14 growing season. The effect of warming in advancing phenology was maintained during the two subsequent seasons of treatment, with the addition that from spring 2014 budburst was also advanced (Figure 1). Again, no significant effect of eCO_2 was observed during the 2014/15 season, but anthesis and veraison were both advanced by the eCO_2 treatment, relative to controls, in the 2015/16 season (Figure 1), suggesting that the direct effects of eCO_2 on phenology may increase over time. However, phenology of vines exposed to the combined eCO_2+eTemp was not advanced relative to the eTemp treatment.

Harvest date was determined by attainment of 24°Brix and was advanced by at least two weeks in the eTemp treatments in all growing seasons (Figure 2). This represented a shorter maturation period, despite the advancement in veraison that was also observed in these treatments. The eTemp and eCO_2+eTemp treatments only separated in one season (2014/15) and only by two days. However, the eCO_2 treatment had an increasing effect with each season; two days advancement in the first season, eight days in the second and 18 days in the third. As with the phenology results, the effect of eCO_2 on the rate of TSS accumulation, represented by harvest date, indicated that the effect of increasing atmospheric CO_2 concentration was increasing with the duration of the eCO_2 treatment.

Fruit yield of control vines varied from 12.8 kg vine^{-1} in 2014 to 18 kg vine^{-1} in 2015. The lower figure may have been due, at least partly, to a heat wave prior to harvest that appeared to have the greatest impact on the eTemp treatment; resulting in a yield of only 9.7 kg vine^{-1}. There were no significant effects of warming on yield in either 2015 or 2016. There was also no significant effect of eCO_2 in 2014 or 2016, but both the eCO_2 and eCO2+eTemp treatments had a greater yield in 2015; 16.9 and 17.4 kg vine^{-1}, respectively. Bindi *et al.*, (2001) reported increased fruit dry mass per m^2 of ground area from grapevines grown under 550 ppm and 700 ppm of CO_2 in two consecutive seasons, albeit from vines with a very different management system than in use here.

2. Leaf physiology

Whilst the warming treatment had the potential to directly impact any enzymatic processes, the major

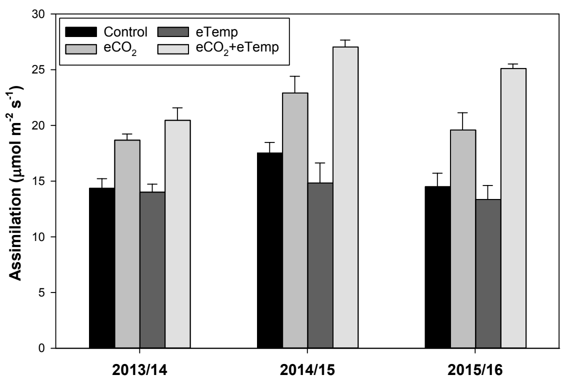

Figure 3 - Assimilation under saturating light of leaves from vines grown under control conditions (black bars), 2 °C of warming (dark grey and pale grey bars) and elevated CO_2 (grey and pale grey bars).

Data are means of field reps ±SE (n=4), averaged across three (2014/15) or four (2013/14 & 2015/16) timepoints.

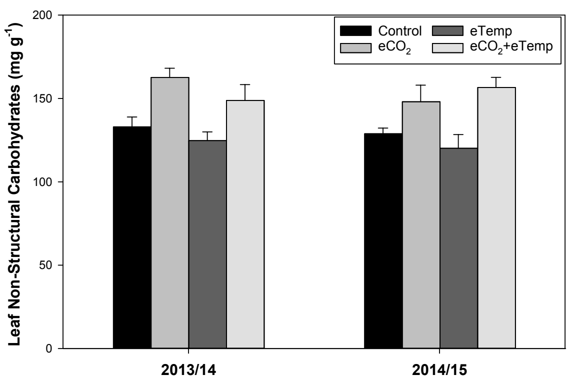

Figure 4 - Non-structural carbohydrate concentration of leaves from vines grown under control conditions (black bars), 2 °C of warming (dark grey and pale grey bars) and elevated CO_2 (grey and pale grey bars).

Data are means of field reps ±SE (n=4), averaged across four timepoints effect of elevated CO_2 on C_3 plants is to increase photosynthetic rates (Campbell *et al.*, 1990), affecting carbohydrate availability and thus other processes limited or regulated by that availability. Measurements of photosynthesis (as A_{sat}), made throughout the three seasons demonstrated this; A_{sat} was 30-40% higher in the eCO_2 treatments than the treatments with ambient air CO_2 concentrations (Figure 3), approximately 390 ppm of CO_2.

There was no reduction in the CO_2 effect during the season (data not shown) or between seasons. In all three seasons, the eTemp treatment had A_{sat} rates that were not different to controls, but the eCO_2+eTemp treatment had significantly higher photosynthetic rates than eCO_2 alone (Figure 3).

This interaction between eCO_2 and warming on maximum photosynthetic rates has the potential for a significant impact in the long-term, due to its potential effect on carbohydrate availability, and demonstrates the ongoing need for experimental work that examines the interaction between these two climate variables in the field.

The influence of the treatments on carbohydrate availability was examined by analyzing the NSC in leaves, specifically the same leaves on which photosynthetic rates were measured. The 2015/16 season data was not available at the time of writing, but the data from the two previous seasons demonstrated a significant effect of the eCO_2 treatments, with a 15- 20% increase in NSC, relative to ambient CO_2 treatments (Figure 4). There was no clear effect of the warming treatments, even the thougheCO$_2$+eTemp treatment that had higher photosynthetic rates. However, respiration rates, which could be expected to have been influenced by warming as leaf temperatures were higher (data not shown), and NSC export were not measured and differences in these processes could explain differences between treatment effects on A_{sat} and on NSC.

Stomatal conductance of C_3 plants grown under eCO_2 is commonly lower than plants grown under current atmospheric CO_2 concentrations (Ainsworth and Rogers 2007). This was observed in all three seasons for the eCO_2 treatment, relative to control (Figure 5). In contrast, the eTemp treatment did not significantly alter stomatal conductance, corroborating the observations in our previous work (Sommer *et al.*, 2012). The eCO_2+eTemp treatment also did not significantly affect conductance, relative to controls. The intercellular CO_2 concentration of the eCO_2+eTemp treatment was not different to the eCO_2 treatment, suggesting that the higher photosynthetic rates of this treatment, compared with eCO_2 alone, may be driving a higher stomatal conductance due to the impact of those rates on intercellular CO_2 concentrations (Mott 1988).

Transpiration rates, reflecting stomatal conductance, were lower for vines in the eCO_2 treatment compared to the controls (Figure 6). In contrast, vines in the eCO_2 +eTemp treatment had higher rates, but only in 2015/16, which also happened to be the season with the highest absolute rates, probably due to the warmer weather conditions in that season. Whole season water use, measured by sapflow, exhibited similar treatment effects to the leaf level transpiration rate in the control, eCO_2 and eCO_2 +eTemp treatments (Figure 7), but was highest in the eTemp treatment despite the lack of an effect on leaf level transpiration rates. This may have been due to the retention of leaves on vines longer compared to the controls (visual observation only, no formal assessment made), higher rates of transpiration outside the midday period where leaf level measurements were made, e.g. early/late in the day or at night, or a less obvious factor.

Conclusions

Warming had an impact on vine phenology from shortly after the treatment was applied onwards, advancing phenology significantly at all major stages. In contrast, eCO_2 only started to affect phenology in the third season after treatments began. To date, there has been no evidence of an additive effect of the two treatments, with phenology of the eCO_2 +eTemp matching that of the eTemp treatment. Although warming alone had little effect on leaf physiology, there was a strong interaction between

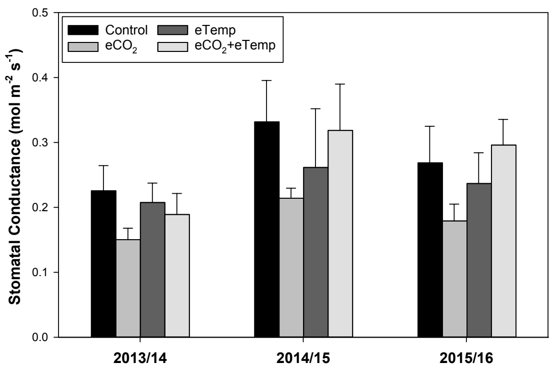

Figure 5. Stomatal conductance of leaves from vines grown under control conditions (black bars), 2°C of warming (dark grey and pale grey bars) and elevated CO2 (grey and pale grey bars).
Data are means of field reps ±SE(n=4), averaged across three (2014/15) or four (2013/14 & 2015/16) timepoints.

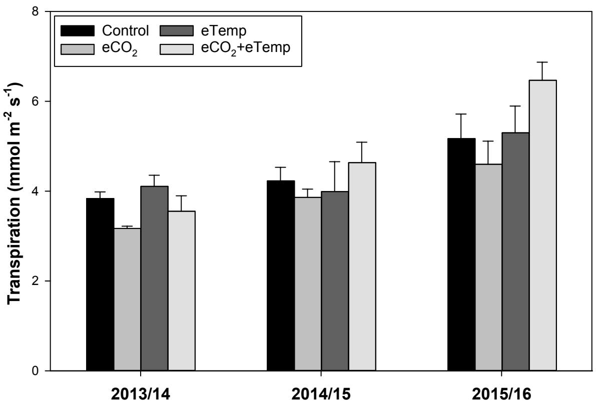

Figure 6. Transpiration of leaves from vines grown under control condi-tions (black bars), 2°C of warming (dark grey and pale grey bars) and elevated CO_2 (grey and pale grey bars).
Data are means of field reps ±SE (n=4), averaged across three (2014/15) or four (2013/14 & 2015/16)

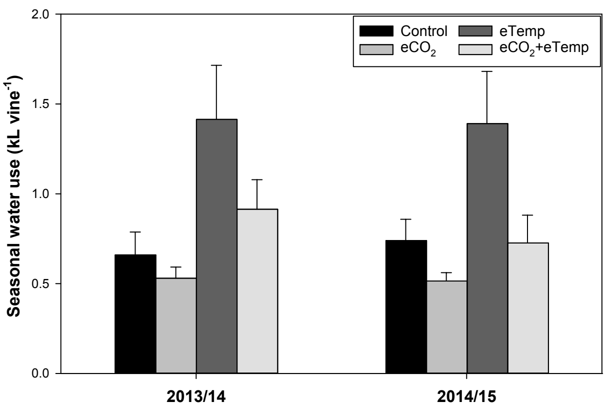

Figure 7. Whole of season water transpired of vines grown under control conditions (black bars), 2°C of warming (dark grey and pale grey bars) and elevated CO2 (grey and pale grey bars).
Data are means ± SE (n=4).

elevated CO_2 and warming, with higher rates of photosynthesis when the two were combined than for eCO_2 alone. This suggest that field experiments using only eCO_2 , without a concomitant warming treatment, may underestimate the effects of climate change on viticulture.

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