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Low temperature exposure of root system and inflorescence affected flowering and fruit set in 'Chardonnay' grapevines (*Vitis vinifera*)

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Summary

The mechanisms by which low temperature affects flowering and fruit set of grapevines are poorly understood, as is the specific response of the grapevine root system and inflorescence to low temperature effects that reduce fruit set. This study aimed to determine the responses of the root system and inflorescence of the grapevine 'Chardonnay' to low temperature (10 °C) during flowering, and considered the possible mechanisms of low temperature effects on those parts. Temperature treatments of 10 °C or 20 °C were imposed to potted 'Chardonnay' grapevines in a glasshouse for up to two weeks during the early stages of flowering. When the root system alone was exposed to 10 °C (with the rest of the plant at 20 °C) during flowering, the number of attached berries and percentage fruit set were significantly reduced by 50 % than when the root system alone was exposed to 20 °C. Whereas, exposure of the inflorescence alone to 10 °C (with the rest of the plant at 20 °C) delayed flowering, allowed rachis to grow longer, and increased both the number of attached berries (from 22 to 62 per vine) and fruit set (from 8 % to 20 %), than when the inflorescence alone was exposed to 20 °C. This study will enhance our understanding of the possible mechanisms of low temperature effects on grapevine fruit set and productivity.

K e y w o r d s : berry, caps, ovaries, rachis, physiology.

Introduction

Grapevine yield is determined, in part, by the number of inflorescences, the number of berries in an inflorescence, and the number of berries that remain attached until maturity (Dunn and Martin 2000). Poor fruit set, where fewer than the usual 30 to 40 % of flowers develop into berries, occurs in some important cultivars, and can decrease yield (Coombe 1973). This is often attributed to cold weather (≤ 15 °C) at or around budburst and flowering, and is cultivar dependent. For example, the cultivars 'Chardonnay' and 'Merlot' are sensitive to a sudden drop in temperature at around flowering, whereas 'Shiraz' is less so (Ebadi *et al*. 1995a, Williams *et al*. 2004). Low temperature can directly impair the functioning of flowering, such as branching of the inflorescence, pollen tube growth, and development of pistil, pollen or ovary (Ebadi *et al*. 1995b). Indirectly, low temperature can also decrease the supply of carbohydrates, plant growth regulators (PGRs) or nutrients from the roots or leaves to the developing flowers (Friend and Trought 2007).

The formation of inflorescences, fertilization of the flowers and the period of berry development are critical phenological stages that determine the yield of the grapevine (Buttrose 1974, Sommer *et al*. 2000). Each of these stages is sensitive to the weather and hence, yield and berry quality can vary greatly between years. In most reports on the effects of low temperature on the development of flowers and berries, the entire grapevine has been subjected to the selected temperature regimes at the stages studied (Pouget 1981, Ezzili 1993, Ebadi *et al*. 1995a, b, Petrie and Clingeleffer 2005). It is unclear which specific grapevine part is affected by the low temperature, or the mechanisms involved. Unless the temperature effects on specific parts of the grapevines, and the associated mechanisms in the regulation of flowering and fruit set are understood, it will be difficult to develop reliable methods to control grapevine yield and berry quality. Therefore, we aimed to determine the effect of low temperature on the flowering and fruit set of 'Chardonnay' grapevines, when i) the root system (Experiment 1) or ii) the inflorescence (Experiment 2) is exposed to low temperature (10 °C).

Material and Methods

Cuttings of 'Chardonnay' grapevine (Clone 76), each 30 cm length and 8 mm diameter were stored at 4 °C for 3 weeks in cold storage to ensure subsequent bud break. After cold storage, the basal end of each cutting was then dipped in Rootex-L®, a liquid rooting hormone, and air-dried for 30 s. The cuttings were then planted in a plastic tub filled with perlite as the rooting medium. The plastic tub was placed in a water bath at 26 °C, which was inside a growth cabinet set at 4 °C. This ensured that a callus formed at the basal end of each cutting, and produced roots within 4 weeks; yet prevented budburst before the cuttings had produced sufficient roots to support new growth. The cuttings were sprayed with water as a mist to keep them moist, but not waterlogged.

After 4 weeks, when roots had emerged, each rooted cutting was planted in a pot (10 cm wide at top, 8 cm wide at base, and 9.5 cm high) with wetted potting mix that con-

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sisted of perlite, vermiculite and peat in the ratio of 6:3:1, respectively. The pots with rooted cuttings were placed in a glasshouse at 15 °C day/night, with 14 h/10 h, light/dark (natural), and the temperature gradually increased to 20 °C over 5 d to avoid temperature shock to the rooted cuttings. Only one shoot with four leaves and an inflorescence was then retained per grapevine (as described in Mullins and Rajashekaran 1981).

Experiment 1 (Roots at 10 °C or 20 °C in insulated box): To control the temperature of the root system independently from other parts of the grapevines, an insulated box (15 L) without lid with temperature set at 10 °C (low temperature treatment) and 20 °C (control) was used. Potted grapevines each containing one inflorescence and four leaves per cutting were selected just before E-L (Eichhorn and Lorenz) stage 17 (when single flowers in the inflorescence separated). The 47 stages are described by Coombe (1995). The box was sealed at the basal portion of the stem with 3.5 cm thick foam to maintain the root system at 10 °C or 20 °C. The temperatures in the box were measured by inserting an alcohol-filled thermometer. The insulated box was then exposed to glasshouse temperature of 20 °C so that shoot received 20 °C. After two weeks, each pot was removed from the insulated box, and the whole grapevines were grown at 20 °C in the glasshouse until harvest of berries at E-L stage 38 (berries harvest-ripe). Every second day throughout the experiment, 35 mL of half strength Hoagland solution was added to each pot (Ebadi *et al*. 1995a, b) to maintain normal growth and development. There were nine single grapevine replicates for each of the two temperature treatments in a completely randomized design. One-way analysis of variance was performed with SPSS V.15 for Windows.

Experiment 2 (Inflorescences at 10 °C or 20 °C in Perspex box): To control the temperature of the inflorescence independently from other parts of the grapevines, a Perspex box with a lid and a water bath were used. Each of 3 sides of the Perspex box (Length × Width × Height = 30 cm × 30 cm × 60 cm), contained three holes (3 cm diameter) at 28 cm above the base, and about 4.5 cm apart. A layer of sand was placed in the Perspex box to a depth of 25 cm, to prevent the Perspex box from floating when in the water bath. The sand was covered with a 3-mm layer of white plastic beads to reflect light and ensure that there was no shading of inflorescences or leaves. The Perspex box was placed in a temperature controlled water bath so that the temperature around the inflorescence (30 mm above the white beads, and below the holes in the Perspex box) was maintained at 10.0 ± 0.4 °C and 20 ± 0.4 °C respectively.

Uniform grapevines were selected as described for Experiment 1. Each potted grapevine was placed outside the Perspex box, and opposite a hole in the Perspex box. The inflorescence of each grapevine was inserted almost horizontally into the Perspex box through the holes and kept for two weeks at 10 °C (low temperature treatment) or 20 °C (control), with rest of the plant parts exposed to glasshouse temperature at 20 °C. After two weeks, each inflorescence was removed from the Perspex box, and the grapevines were grown in the glasshouse (20 °C) until harvest of berries at E-L stage 36 (berries with intermediate sugar values) or 39 (berries over-ripe). Watering and nutrition were similar to Experiment 1. There were nine single grapevine replicates for each of the two temperature treatments in a completely randomized design. One-way analysis of variance was performed with SPSS V.15 for Windows.

Collection and measurement of plant parts (Experiments 1 and 2): After the temperature treatments were applied from day 7 at E-L stage 19 (beginning of flowering) to day 14 at E-L stage 25 (80 % flowering), i) a paper cone (width × height = 15 cm × 13 cm) was wrapped around each rachis below each inflorescence (Experiment 1) or ii) a paper box (length × width × height = 14.5 cm × 10.5 cm × 2 cm) was placed below each inflorescence inside the Perspex box (Experiment 2). The paper cone or paper box captured unopen dropped flowers, dropped caps, and dropped dead ovaries. The collected plant parts were stored in a vial at room temperature until counted. Dropped caps were weighed, and the number of caps was determined from a correlation based on the mass. Dead ovaries (attached to the peduncle) (May 2004) were individually removed with forceps at E-L stage 31 (berries pea size) from the grapevines in each treatment.

In Experiment 1, berries subjected to 20 °C were harvested at E-L stage 38 and berries exposed to 10 °C were harvested 1 week later than E-L stage 38 as they grew more slowly. In Experiment 2, berries subjected to 20 °C were harvested at E-L stage 39 (delayed when clear that berries at 10 °C would never ripen beyond E-L stage 36), and those at 10 °C were harvested at E-L stage 36. Harvested berries were sliced and seeds collected. Seeds were separated into sinkers (fertilized seeds, sank in water) and floaters (no endosperm, floated in water) and counted.

At the end of experiments 1 and 2, the root system was separated from the rest of the grapevines in each treatment and washed with tap water, followed by distilled water to remove any adhered potting mix. The root system was scanned with a flatbed scanner, and the images were saved as JPG files and analysed with the software package WinRHIZO.pro v2003b (Regent Instruments Inc.) to estimate total root length (cm), total root surface area (cm^2), mean root diameter (mm), and number of root tips.

Results

Experiment 1: The number of attached berries produced on vines with the root system at 20 °C was significantly higher than at 10 °C (Tab. 1) due in part to a significantly lower proportion of dead ovaries at 20 °C (Tab. 1). As the number of attached berries differed between treatments, the percentage fruit set at 20 °C (13 %) was significantly higher than that at 10 °C (6 %). There was no difference in the total number of flowers or number of open flowers between the two root temperature treatments (Tab. 1). The total number of seeds per berry at 20 °C was significantly higher than that at 10 °C (Tab. 1), however there were no differences between root temperature of 10 °C and 20 °C in the number of unopened dropped flowers, dead ovaries or

Table 1

Effect of temperature on the root system alone (rest of plant at 20 °C) for two weeks at around flowering on various physiological parameters of 'Chardonnay' grapevines measured at E-L stage 19[A] to E-L 38[B] (Experiment 1)

Temperature	Total flowers	Unopen dropped flowers	Total open flowers[C]	Dead ovaries	Dead ovaries as percentage of total open flowers	Attached berries	Percentage fruit set	Total seeds per berry	Sinkers per berry
20 °C	289	56	101	64	62	37	13	1.60	1.00
10 °C	328	61	91	73	81	18	6	1.20	0.80
F	ns	ns	ns	ns	**	**	**	*	ns

[A] Growth stage E-L 19 = Beginning of flowering. [B] Growth stage E-L 38 = Berries harvest-ripe. [C] Total open flowers = Dropped caps, F = Level of significance: ns = Not significant; * = $p \leq 0.05$, ** = $p \leq 0.01$.

sinkers per berry. Root system traits of 'Chardonnay' grapevines at the two root temperature regimes showed that the number of root tips was significantly higher at 20 °C than that at 10 °C, but the total root length, total surface area and diameter of roots were similar (Tab. 2).

Experiment 2: The total number of open flowers was higher on vines with inflorescence exposed to 10 °C than that at 20 °C (Tab. 3). Since the number and proportion of dead ovaries were lower at exposure of the inflorescence to 10 °C, the number of attached berries was also significantly higher at 10 °C than that at 20 °C (Tab. 3). The total number of flowers and number of unopen dropped flowers were similar between the two treatments.

As there was no difference between 10 °C and 20 °C treatments in the total number of flowers produced, the higher percentage fruit set at 10 °C was mostly due to the significantly higher number of attached berries per inflorescence (Tab. 3). The number of sinkers per berry in the 20 °C treatment was significantly higher than that at 10 °C (Tab. 3). There was no difference in the total number of seeds per berry between the two temperature treatments (Tab. 3).

Root system traits of the 'Chardonnay' grapevines at the two temperature regimes showed that the total root length and surface area of roots was significantly lower when the inflorescence was exposed to 10 °C compared to 20 °C (Tab. 4). The total number of tips at 10 °C was significantly higher than that at 20 °C, with no significant difference in the root diameter produced by grapevines at the two inflorescence temperatures.

Table 2

Effect of temperature on the root system alone (rest of plant at 20 °C) for two weeks at around flowering on root traits of 'Chardonnay' grapevines measured at E-L stage 38[A] (Experiment 1)

Temperature	Length (mm)	Surface area (cm^2)	Diameter (mm)	Number of tips
20 °C	1725	432	0.79	2085
10 °C	1752	466	0.79	1875
F	ns	ns	ns	*

[A] Growth stage E-L 38 = berries harvest-ripe.
F = level of significance: ns = not significant; * = $p \leq 0.05$.

Discussion

Fruit set of 'Chardonnay' grapevine was affected by exposure of the root system to the low temperature (10 °C) at flowering. Low temperature caused a higher percentage of total open flowers lost as dead ovaries, which in turn reduced the number of attached berries (Tab. 1). As a result, the percentage fruit set was also reduced (Tab. 1). A similar decrease in grapevine fruit set has been reported when the root systems of 'Sultana' grapevines were grown in Hoagland solution at 11 °C in the glasshouse from budburst until 10 % flowering (Woodham and Alexander 1966). Lower fruit set in grapevines may be due to slow growth of pol-

Table 3

Effect of temperature on the inflorescence alone (rest of plant at 20 °C) for two weeks at around flowering on various physiological parameters of 'Chardonnay' grapevines measured at E-L stage 19[A], E-L 36[B] or E-L 39[C] (Experiment 2)

Temperature	Total flowers	Unopen dropped flowers	Total open flowers[D]	Dead ovaries	Dead ovaries as percentage of total open flowers	Attached berries	Percentage Fruit set	Total seeds per berry	Sinkers per berry
20 °C	292	64	77	55	71	22	8	1.80	1.00
10 °C	305	55	91	29	31	62	20	1.70	0.70
F	ns	ns	*	**	**	**	**	ns	*

[A] Growth stage E-L 19 = beginning of flowering. [B] Growth stage E-L 36 = berries with intermediate sugar values.
[C] Growth stage E-L 39 = Berries over-ripe. [D] Total open flowers = Dropped caps.
F = Level of significance: ns = Not significant; * = $p \leq 0.05$; ** = $p \leq 0.01$.

Table 4

Effect of temperature on the inflorescence alone (rest of plant at 20 °C) for two weeks at around flowering on root traits of 'Chardonnay' grapevines measured at E-L stage 36[A] or 39[B] (Experiment 2)

Temperature	Length (mm)	Surface area (cm^2)	Diameter (mm)	Number of tips
20°C	1662	463	0.80	2109
10°C	1335	346	0.82	1517
F	**	*	ns	**

[A] Growth stage E-L 36 = Berries with intermediate sugar values (10 °C).
[B] Growth stage E-L 39 = Berries over-ripe (20 °C).
F = Level of significance: ns = Not significant; * = $p \leq 0.05$; ** = $p \leq 0.01$.

len tubes, or formation of abnormal ovules (Ebadi *et al*. 1995b). No research reported in the literature has subjected individual plant parts to low temperature, as done in our experiments. Nevertheless we found that temperature had similar effects on flowering, fruit set, and seed physiology as reported in the literature for entire grapevines. For example, fewer seeds per berry have been observed in large Sylvaner grapevines grown at 15 °C/10 °C day/night from about a week before flowering until veraison, than that at 25 °C/20 °C (Ewart and Kliewer 1977).

Exposure of roots to low temperature may have little influence on grapevine root traits, except perhaps the number of root tips. The similar root length and root surface area of grapevines subjected to two root temperature regimes, but differences in fruit set, between 10 °C and 20 °C suggest that these root traits had limited influence on flowering and fruit set under the studied conditions. However, the lower number of root tips (*i.e.* less branching of roots) in the root temperature treatment at 10 °C than that at 20 °C (Tab. 2) may have decreased uptake of nutrients from the soil. High numbers of root tips have been related to increased nutrient uptake by both grafted and ungrafted grapevines (Kodur *et al*. 2010).

The effect of low temperature on grapevine physiology is also related to PGRs. For example, cytokinins at higher amounts may have been produced and/or translocated from the root tips at 20 °C (Davis and Lingle 1961, Skene and Kerridge 1967, Cutting *et al.* 1991) and redirected carbohydrates to the flowers and young developing berries. Cytokinins have been found at higher concentration at budburst in the xylem sap of 'Shiraz' grapevines when roots were held at 23 °C compared with those at 13 °C (Field *et al*. 2009). In contrast, decreased cytokinin production and its translocation during bud burst were observed with apple *(Malus domestica)* at low root temperature (Young 1989). However, further research is needed to determine the extent of involvement of PGRs and genes that regulate the activity of PGRs in flowering and fruit set under low temperature in various cultivars of *Vitis*. In contrast to the exposure of 'Chardonnay' root system to low temperature (10 °C), exposure of the inflorescence to 10 °C delayed growth and development of flower parts and increased fruit set (Tab. 3). When the inflorescence was exposed to 10 °C at flowering, fewer flowers were lost as dead ovaries. As a result, more berries were retained, leading to higher percentage fruit set (Tab. 3). The similar total number of seeds, but fewer sinker seeds, when the inflorescence was exposed to 10 °C, agrees with results obtained using whole grapevines of the cultivar 'Chardonnay' exposed to low temperature of 12 °C/9 °C at around flowering (Ebadi *et al*. 1995a).

Increased fruit set in 'Chardonnay' at lower temperature may be due to delayed flowering and fruit set. Lower temperature led to slower but continued growth of the rachis over a longer period than at 20 °C. The low temperature may have delayed expression of genes responsible for formation of terminal flowers (Boss *et al*. 2003), so that the rachis continued to grow and produce more visible branches and a higher proportion of fertile flowers and berries (Tab. 3). When the rachis of wheat (*Triticum aestivum*) elongated under shorter photoperiod between spikelet initiation and flowering, more fertile flowers were formed which, in turn, led to a higher yield (González *et al*. 2003).

The slower growth of the 'Chardonnay' grapevine inflorescence at 10 °C may also have decreased competition between flowers and ovaries. This in turn may have led to the higher percentage fruit set at 10 °C. The fewer sinkers per berry with the inflorescence at 10 °C were associated with fewer dead ovaries (Tab. 3). This suggests that at 10 °C, there was more competition between attached berries, so that each seed that did form had fewer carbohydrates to enable it to form healthy seeds. With the inflorescence at 10 °C, the developing flower may have had more carbohydrates and the fertilised seeds fewer carbohydrates, than that at 20 °C (Friend *et al*. 2009).

The root traits may have little or no direct influence on flowering and fruit set when inflorescence was at 10 °C, as fruit set was higher at 10 °C. However, poor root growth at low temperature may have delayed flowering and fruit set. For example, rooted cuttings of Sultana placed in Hoagland solution produced new roots within four days at 20 °C and 30 °C, but only after 6 weeks at 11 °C (Woodham and Alexander (1966). Conversely, higher flowering and fruit set at low temperature may be due to slower growth and development (including roots), which in turn may lead to the exploitation of more resources. For example, rate of nutrient uptake may be lower but the net uptake of nutrients may be higher due to delayed flowering and fruit set at low temperature. The interpretation of our results on the effect of temperature and root traits on flowering and fruit set was restricted by the difference in the time of harvest for the two temperature treatments. Interpretation of results therefore should consider this difference. Further research is needed to confirm and clarify the effect of i) delayed growth and development on flowering and fruit set, and ii) low temperature exposure of grapevine parts on flowering and fruit set under field conditions.

Conclusions

Exposure of the 'Chardonnay' grapevine root system to low temperature (10 °C) affected flowering and fruit set by causing a higher percentage of total open flowers to be lost as dead ovaries. By contrast, low temperature of the inflorescence delayed flowering and fruit set and reduced the number of dead ovaries. This in turn increased the number of attached berries and led to a higher percentage fruit set. Low temperature of the inflorescence reduced total root length and surface area but flowering and fruit set were unaffected. However, delayed grapevine growth and development (including roots) under low temperature may have increased net nutrient uptake. These results will enhance our understanding of the possible mechanisms of low temperature effects on grapevine growth and productivity and in turn help to tackle negative effects of low temperature on grapevine physiology.

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