**Effects of high temperatures on winegrape flowering phenology**

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**Abstract**

Climate change has challenged growers and researchers alike to better understand how warm temperatures may impact winegrape plant development, especially at critical stages, such as flowering. We studied the budburst and flowering phenology of 50 varieties of *Vitis vinifera* subsp. *vinifera* in the lab, then exposed 9 varieties to higher temperatures (20 **°**C to 34 **°**C mean temperatures in growth chambers) during flowering. We found high variability in flowering success across varieties in the lab (28 out 50 total varieties had no flowering). In chambers, temperatures did not have a significant effect on speed with which the plants progressed through the flowering stage to 10% flowering or 50% flowering (10%: F(1,20)=0.432, p=0.52; 50%: F(1,15)=0.50, p=0.49). However, plants in higher temperature chambers aborted a greater number of buds before they flowered (F(1,24)=7.43, p=0.01). These results suggest a potential decrease in winegrape yields in a warmer climate due to flower abortion. Variability in our results, however—both in the percent of plants flowering in the lab and in responses to higher temperatures—suggests differences between varieties could be high.

**Introduction**

As the climate changes, the viticulture industry needs to adapt to shifting terroir. Climate change is predicted to raise temperatures 1-3°C in winegrowing regions across the world, which is already driving major changes in the viticulture industry. The industry has shifted growing areas towards the poles and higher elevations to maintain ideal growing temperatures for winegrapes, and this is predicted to continue (Schultz and Jones 2010, Hannah, Roehrdanz et al. 2013), raising concerns that vineyards could move to land that is currently conserved for biodiversity and ecosystem services (Hannah, Roehrdanz et al. 2013).

Alternatively, vineyards could take advantage of the high geno- and phenotypic diversity that already exists by planting varieties better suited to the new climate (Ollat 2015, Ollat 2016, Wolkovich, Burge et al. 2017). *Vitis vinifera* subsp*. vinifera* (winegrape) has at least 6000 genetically distinct varieties grown for many purposes, but only ~1100 are grown currently by the viticulture industry, and an even smaller number dominate the global market (Lacombe 2012, Wolkovich 2017). However, for this adaptation to be effective, growers need better information on how different varieties fare in warmer climate regimes, with phenology being one important component (Ollat 2016).

Studying the phenology of different varieties of winegrapes would help viticulturists better adapt to climate change, because winegrape phenology is extremely sensitive to temperature (Jones 2013, Chuine and Régnière 2017). Timing for leafout and flowering of diverse plant species have advanced six to 20 days in the last 30-40 years of warming (Root, Price et al. 2003, Menzel, Sparks et al. 2006), equivalent to four to six days per °C. A similar advance is seen for winegrape harvest dates, which can change about 6 days per °C (Benjamin and Elizabeth 2016). In winegrapes, phenological timing varies across varieties, and it is this variation that could be used to better adapt to future climates. Generally, timing of phenology can vary from three to six weeks across varieties (Boursiuot 1995, Wolkovich, Burge et al. 2017). However, most varieties have very little phenological data from which to infer where they could best be grown, and how they respond to higher temperatures during critical phenological phases, such as flowering. Harvest dates are the only data available for over 90% of varieties, so for phenological data to be used for adaptation, more varieties need to be studied (Parker, De CortÁZar-Atauri et al. 2011, Parker, de Cortázar-Atauri et al. 2013).

Because successful flowers become berries, understanding how climate change will affect winegrape flowering is an important aspect of the overall effect on phenology and directly relates to harvest yields. Petrie and Clingeleffer (2004) found that Chardonnay buds exposed to elevated temperatures just before or just after budburst produced 24.2-32.6% fewer flowers per °C warming. Other research has found that Semillon winegrapes exposed to four days of elevated temperatures (40 °C during the day and 25 °C at night) during flowering aborted all flowers (Greer and Weston 2010). Studies of vegetative growth and photosynthesis in other perennial crops exposed to a range of temperatures exhibited that extreme temperatures tend to slow or inhibit certain processes in the plants (Zaka, Frak et al. 2016, Zaka, Ahmed et al. 2017), and thus we would expect that flowering development may similarly slow down at higher temperatures.

Here we studied the phenology of 50 varieties in the field and lab and examined the flowering response of a small subset of varieties across mean temperatures of 20 **°**C to 34 **°**C in growth chambers. We were particularly interested in the effect of higher temperatures on flowering development.

**Methods**

Observations of field-grown winegrapes in the UC Davis Robert Mondavi Institute Vineyard (Davis, California, USA) using the modified Eichorn-Lorenz (EL) scale (Coombe 1995) began 6 March 2015 and continued generally every 3-4 days until 2 April 2015, when almost all plants had reached EL stage 11 or higher. Dormant winegrape cuttings were then taken in December of 2015.

Following collection, cuttings were chilled for 21 days (4° C) at the Arnold Arboretum (Boston, Massachusetts, USA), then forced in greenhouses in 26 cm diameter pots in January 2016. After several months of growth, on 27 May they were placed in growth chambers with day/night temperatures of 6/4 °C and an 8-hour photoperiod to induce dormancy, though the plants did not appear visibly dormant until 20 June 2016.

On 15 August 2016, the 351 potted cuttings were moved out of the chambers and into a greenhouse where the initial day temperature was 18.5 ± 1.5 °C and night temperature was 16.75 ± 1.25 °C. After the first week, the temperatures were slowly raised to 25.5 ± 2.5 °C during the day and lowered to 10 °C at night. The cuttings were pruned the day they were removed from the chambers so that each cutting had two spurs and each spur had two nodes. Then, the diameter of each spur and node and the distance between the two nodes on each spur were measured with calipers.

Twice a week, beginning 22 August, each plant’s development was recorded using the modified Eichorn-Lorenz scale (Coombe 1995) and soil moisture was measured with a probe in three locations in each pot. Each spur was kept at two shoots, but only the dominant shoot on each spur had observations recorded. Each shoot was trained up a stake for support. When an inflorescence had developed (EL stage 12), the plant was randomly assigned to one of five growth chambers if it was a part of the heat tolerance experiment*.* Otherwise, observations on each plant continued in the greenhouse. Varieties were chosen for inclusion in the experiment to include a diversity of phenology from those varieties for which there were five or more replicates growing.

The five chambers all had a 12-hour photoperiod with 800 m-2s-1 of fluorescent light, but varied in their temperature: Chamber 1 was set at 17/23 °C Chamber 2 was set at 23/29 °C, Chamber 3 was set at 27/33 °C, Chamber 4 was set at 31/37 °C, and Chamber 5 was set at 34/40 °C (all temperatures given as night/day). Initially, CO2 levels were set at 400 ppm during the day and 600 ppm at night, because plants respire at night, increasing CO2 levels. Each inflorescence was contained in a paper bag to collect the flower caps as they fell.

Observations on the percent of buds flowering, leaf number, stem length, and number of fallen flower caps were made three times a week, along with soil moisture. On 19 September, it was noted that some inflorescence bags also contained aborted buds that had yet to flower, and thereafter observations of aborted buds were also recorded. Once a plant had reached 100% flowering, or, in the case of plants where the entire inflorescence had died and fallen off, the plant had spent a minimum 14 days in the chamber, it was returned to the greenhouse.

To determine if there was any correlation between the chamber temperatures and the other variables, we used ANOVA. Linear regression was used to compare the development of the plants in the greenhouse with the data collected in the RMI Vineyard growing season. All analyses were performed in R version 3.3.3 (R Core Team).

**Results**

The plants underwent budbreak (EL 4) between 17 August and 6 September (mean = 29 August) and leafout (EL 7) between 22 August and 22 September (mean = 4 September). Budbreak and leafout timing among the varieties were similar in the lab and field (Figure 1, budburst: F(1,47)=14.55, p<0.001; leafout: F(1,47)=18.51, p<0.001). The first inflorescence formed on 5 September, and 51 plants eventually reached this stage (EL 12), with substantial variation in flowering across varieties (Table 1). Most varieties (28/50 total) did not flower, while for a few varieties flowering was at 40% or higher (e.g., Sauvignon blanc, Tempranillo, Verdelho). Unfortunately, because varieties were pre-selected for the experiment, before the high variation in flowering was noted, only 26 of the flowering plants were used in the experiment (Table 1). Plants that had thicker spurs were more likely to develop inflorescence (Z(340)=2.21, p=0.03), and more likely to reach 50% flowering (Figure 2, Z(340)=2.85, p=0.004).

Soil moisture in the chambers varied by chamber temperature (F(1,24)=8.05, p=0.01), ranging from 69% to 76% over time. There was no directional relationship between the moisture levels and the chamber temperature (i.e., the warmest chambers were not the driest) and means were similar across treatments, ranging from 71% to 74%.

There was also no directional relationship between chamber temperature and either change in stem length or change in leaf number (stem length: F(1,24)=0.53, p=0.47; leaf number: F(1,24)=0.05, p= 0.83). Plants at 30 °C had the greatest change in stem length during their time in the chamber. Similarly, plants at 26 °C had the greatest change in leaf number during the experiment.

Contrary to expectations, chamber temperature did not affect the days it took for the plants to reach 10% and 50% flowering and there was no trend in the duration of flowering (Figure 3, 10%: F(1,20)=0.43, p=0.52; 50%: F(1,15)=0.50, p=0.49). Within treatments, the number of days it took plants to reach 10% flowering ranged from 34 to 51 days (mean = 42.6 ± 0.9).

The number of buds aborted per plant was significantly affected by the chamber temperature (Figure 3, F(1,24)=7.43, p=0.01). The two warmest chambers saw the greatest number of buds lost during the time in the chamber, with the greatest average number of buds aborted seen in at 37 °C (mean number of buds aborted at 20 °C: 4.5, 26 °C: 2.8, 30 °C: 5.8, 34 °C: 27.6, 37 °C: 57.3).

**Discussion**

*Effects of high temperatures on winegrape flowering*

Overall, we studied the effects of temperatures between a minimum of 17°C and maximum of 37 °C (means of 20 **°**C to 34 **°**C) on flowering for 26 winegrape plants. We found no directional relationship between temperature and soil moisture, stem length, leaf number, or the number of days it took to reach 10% or 50% flowering. Contrary to expectations of most phenological models (Garcia de Cortazar-Atauri, Chuine et al. 2010, C. Cuccia 2014) we found that phenology was not significantly delayed in either the coldest or warmest chambers. However, plants in the hotter treatments aborted a higher number of flower buds than those in the cooler treatments.

While phenological timing was not affected, the plants in the two warmest chambers showed signs of stress: plants in those chambers aborted a significantly higher number of flower buds. Thus, it appeared that the plants may have sacrificed their reproduction for the growing season to ensure they were able to survive the elevated temperatures. Semillon grapes subjected to day/night temperatures of 40/25 °C for four days at flowering saw similar effects: inflorescences grew much less—gaining only 22 mm in length compared to the 85 – 90 mm of growth seen in plants treated with heat after flowering—and subsequently aborted all flowers (Greer and Weston 2010).

The majority of literature on winegrape heat tolerance focuses on the effects of heat on berry ripening. In their aforementioned 2010 study of Semillon winegrapes, Greer and Weston noted that plants treated with elevated temperatures at fruit set and veraison were much less vulnerable and suffered few ill-effects when compared with those treated at flowering and mid-ripening (Greer and Weston 2010). This could mean that winegrapes are more vulnerable to high temperatures during flowering than they are later in development. If winegrapes are especially susceptible to heat during flowering, viticulturists could take extra precautions during this period to ensure the survival of the flowers through to fruit set.

*Utility of lab-grown winegrape plants for future research*

Because the majority of the plants’ development did not progress to the flowering stage (EL stage 11), sample sizes for our heat experiment were smaller than planned (each chamber had four to six plants). This meant there were not enough plants of each variety in each chamber to test for a difference in varietal response to the heat treatments. In fact, most varieties were only represented in a single treatment. Still, it is important to note that we studied nine different varieties in the chambers, which greatly increased the genetic diversity of the experiment. It has been shown that controlled ecological experiments in labs that include greater genetic diversity are more easily replicated (Milcu, Puga-Freitas et al. 2018). Further, we found high variation in flowering success—plants with larger spurs were more likely to flower and some varieties were far more successful in flowering than others. Thus, future experiments may want to (at least initially) focus lab efforts on these varieties.

The rate of development seen in the plants grown in the greenhouse was significantly correlated with that seen in the winegrapes grown in the Robert Mondavi Institute Vineyard, from which the cuttings in this experiment were taken (Figure 1). This suggests that the overall progression and timing of phenological development was not dramatically altered by the lab setting and supports the use of potted plants in the lab used alongside field data to better understand and predict winegrape response to climate change.

*Conclusions*

While heat treatments during flowering did not affect the phenology of the grapes we studied, we still saw a significant impact from the elevated temperatures that could become a harsh reality for viticulturists around the world. Fewer flowers means reduced yields for wine grape producers. These findings also underscore the importance of modeling more than the plants’ phenology to fully understand the impact climate change will have on the viticulture industry. Future research should strive to include a greater diversity of *Vitis vinifera* varieties so that the results can be used by a larger number of researchers and wine growers to plan for future climates around the world.

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**Figures (below)**



Figure 1

This figure compares the day of budburst and leafout in the Robert Mondavi Institute Vineyard 2015 growing season to the day of budburst and leafout in the greenhouse during the experiment. Each data point represents a different variety that was grown both in the vineyard and in the greenhouse.



Figure 2

This figure shows the relationship between the spur diameter (measured when plants were removed from dormancy) and the probability that a plant would reach 50% flowering.

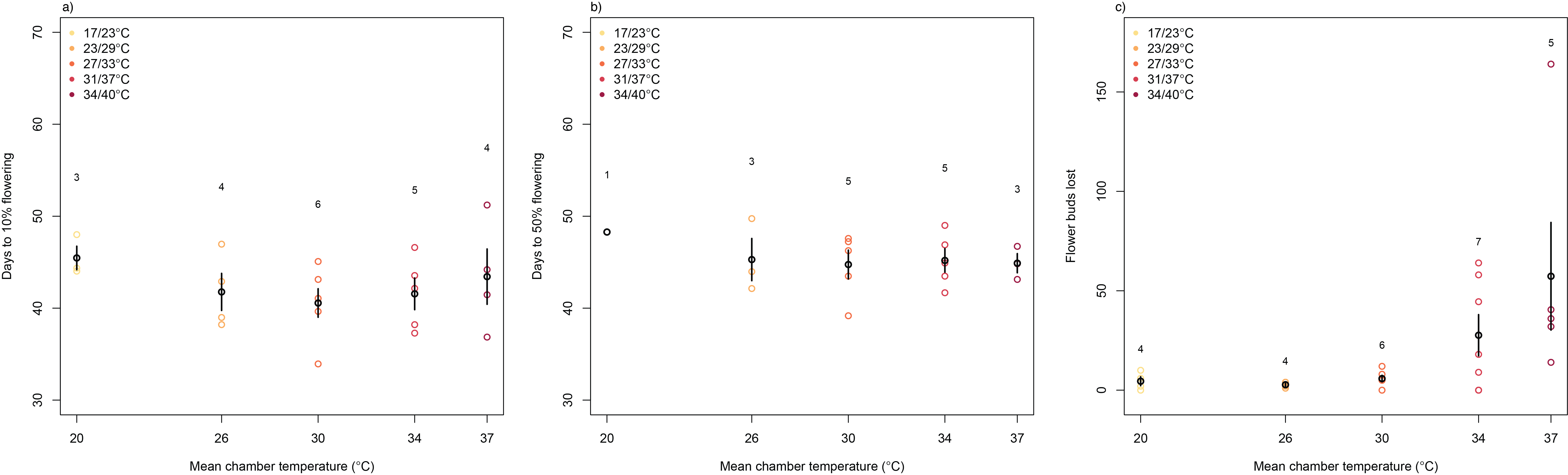


Figure 3

These figures illustrate the relationship between mean chamber temperature and a) the days it took the plants to reach 10% flowering, b) the days it took the plants to reach 50% flowering, or c) the number of flower buds lost while in the chamber. The black points and bars show the average and error in each chamber. The number above each chamber’s data is the sample size. The colored points represent individual plants. The legend in the top left corner gives the night/day temperature for each chamber.

**Table**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Variety** | **Number Plants** | **Number Flowered** | **Percent Flowered** | **In Experiment?** | **Mean Budburst Date** |
|
| Alicante Bouschet | 7 | 0 | 0.0 | N | 13.9 |
| Aligote | 6 | 0 | 0.0 | N | 13.3 |
| Auxerrois | 5 | 1 | 20.0 | N | 14.0 |
| Barbera | 9 | 1 | 11.1 | N | 12.4 |
| Cabernet franc | 7 | 0 | 0.0 | N | 13.8 |
| Cabernet Sauvignon | 9 | 1 | 11.1 | Y | 14.7 |
| Calzin | 5 | 3 | 60.0 | N | 14.7 |
| Carmenere | 8 | 0 | 0.0 | Y | 15.6 |
| Carnelian | 9 | 3 | 33.3 | N | 11.6 |
| Chardonnay | 7 | 0 | 0.0 | Y | 13.3 |
| Chasselas doree | 7 | 0 | 0.0 | Y | 11.7 |
| Cinsault | 7 | 0 | 0.0 | Y | 16.4 |
| Coda di Volpe | 5 | 0 | 0.0 | N | 15.0 |
| Counoise | 9 | 0 | 0.0 | N | 17.9 |
| Dolcetto | 7 | 1 | 14.3 | Y | 14.7 |
| Durif | 7 | 5 | 71.4 | Y | 11.1 |
| Early Muscat | 6 | 0 | 0.0 | N | 11.7 |
| Furmint | 8 | 0 | 0.0 | Y | 15.0 |
| Gamay Noir | 8 | 4 | 50.0 | N | 12.9 |
| Gewurztraminer | 9 | 1 | 11.1 | Y | 12.5 |
| Gruner Veltiner | 7 | 0 | 0.0 | N | 14.9 |
| July Muscat | 5 | 0 | 0.0 | N | 11.2 |
| Macabeo | 6 | 0 | 0.0 | Y | 15.7 |
| Marsanne | 9 | 2 | 22.2 | N | 14.2 |
| Melon | 5 | 0 | 0.0 | N | 14.3 |
| Merlot | 6 | 0 | 0.0 | Y | 13.9 |
| Morrastel | 6 | 0 | 0.0 | N | 15.7 |
| Nebbiolo | 6 | 0 | 0.0 | Y | 13.6 |
| Palomino | 4 | 0 | 0.0 | Y | 14.9 |
| Pinot gris | 8 | 1 | 12.5 | N | 13.9 |
| Pinot Meunier | 6 | 3 | 50.0 | N | 13.7 |
| Pinotage | 5 | 3 | 60.0 | N | 10.7 |
| Refosco | 6 | 0 | 0.0 | N | 14.5 |
| Rkatsiteli | 5 | 0 | 0.0 | Y | 16.3 |
| Rotgipfler | 7 | 1 | 14.3 | N | 14.5 |
| Roussanne | 6 | 0 | 0.0 | N | 16.8 |
| Ruby Cabernet | 8 | 4 | 50.0 | N | 15.8 |
| Ruby Seedless | 6 | 0 | 0.0 | N | 16.0 |
| Sangiovese | 7 | 0 | 0.0 | Y | 13.1 |
| Sauvignon blanc | 7 | 3 | 42.9 | Y | 15.8 |
| Schiopettino | 8 | 0 | 0.0 | N | 14.7 |
| Syrah | 8 | 1 | 12.5 | Y | 13.8 |
| Szagos feher | 7 | 1 | 14.3 | N | 13.5 |
| Tempranillo | 12 | 5 | 41.7 | Y | 14.6 |
| Tocai Friulano | 5 | 1 | 20.0 | N | 16.6 |
| Ugni blanc/Trebbiano | 5 | 0 | 0.0 | Y | 18.4 |
| Verdelho | 6 | 5 | 83.3 | N | 11.1 |
| Vinhao | 8 | 1 | 12.5 | Y | 15.6 |
| Viognier | 8 | 0 | 0.0 | Y | 14.4 |
| Zinfandel/Primitivo | 6 | 0 | 0.0 | Y | 15.0 |

Table 1

Data on the 50 varieties grown in the lab (greenhouse), including % plants of that variety that flowered, mean budburst date (days after 15 August, when the plants were moved out of dormancy). We selected a subset of varieties for the experiment after budburst, which is indicated in the ‘In experiment?’ column.

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