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Exploring grapevine phenology and high temperatures response under controlled conditions

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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 ten varieties to higher temperatures (20, 26, 30, 34, 37°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). Results of vines exposed to the different mean temperatures in the growth chambers suggested that higher temperatures did not have a significant effect on the rate at which vines progressed through the flowering stage (no variation with temperature in time to 10% or 50% flowering: 10%: $F(1,20)=0.432$, $p=0.52$; 50%: $F(1,15)=0.50$, $p=0.49$). However, vines exposed to higher temperatures resulted in a greater number of aborted flowers ($F(1,24)=7.43$, $p=0.01$). 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 vines 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. Terroir—the critical link between the flavor and style of a wine and the characteristics of the environment in which it is grown—is shaped strongly by climate, and the matching of climates to varieties (Van Leeuwen et al., 2019). Thus, as climate change continues to raise temperatures in winegrowing regions across the world, the viticulture industry will be continually challenged to adapt to new terroirs over future decades. Already, the industry has shifted growing areas towards the poles and higher elevations to maintain ideal growing temperatures for winegrapes. This trend is predicted to continue (Schultz and Jones, 2010; Hannah et al., 2013), raising concerns that vineyards could move to land that is currently conserved for biodiversity and ecosystem services (Hannah 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 et al., 2015, 2016; Wolkovich et al., 2017) or breeding new varieties (Myles, 2013; Duchêne, 2016). *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; Anderson, 2013). 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 et al., 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 (Parker et al., 2011, 2013; Jones, 2013; García de Cortázar-Atauri et al., 2017). Timing for leafout and flowering of diverse plant species has advanced six to 20 days in the last 30-40 years of warming (Root et al., 2003; Menzel 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 (Cook and Wolkovich, 2016; Labbé, 2019). The time between flowering and veraison also decreased by a little more than 1 day per °C. (Duchêne and Schneider, 2005). In winegrapes, phenological timing varies across varieties, and this variability could be used to better adapt to future climates. Generally, timing of phenology can vary from three to six weeks across varieties (Boursiquot et al., 1995; Wolkovich et al., 2017).

However, most varieties have still little phenological data and far fewer varieties have data from many different environments. In this context, it is difficult to describe where many varieties could best be grown and how they respond to higher temperatures during critical phenological phases, such as flowering. While recent efforts have greatly expanded our resources for understanding phenological responses to climate in the field across varieties—yielding information on approximately 100 varieties (Parker et al., 2011, 2013) this is still less than 10% of currently planted varieties. For growers to ideally select varieties for shifting terroir, they will need information on more varieties and across diverse temperature regimes.

A first step towards this goal is research on an increased number of varieties and an understanding of whether phenology in semi-artificial conditions (i.e., greenhouses, labs, and growth chambers), where temperatures can be controlled more easily, matches field-based phenology. To date, much research has focused on a limited number of varieties (Sepúlveda et al., 1986; Mullins, 1992), making it difficult to know how much results for one variety can be extrapolated to another. Yet, if a greater diversity of varieties can be grown in lab conditions, lab studies could quickly increase our understanding across varieties. Further, if lab phenology appears similar to field phenology, it would suggest such results could be relevant to field conditions. Beyond this first step then, researchers will want to examine how varying temperature regimes affect particular phenological stages.

Understanding how climate change will affect winegrape flowering may be a particularly important aspect of the overall effect on phenology and the impact of temperature on the flowering process will ultimately influence harvest yields. Petrie and Clingeleffer found that Chardonnay buds exposed to elevated temperatures just before or just after budburst produced 24.2-32.6% fewer flowers per °C warming (2005). 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 et al., 2016, 2017). In this context, we would expect that grapevine flowering development may similarly slow down at higher temperatures.

Here we report on a study with two major aims: (1) we tested whether phenology (budburst and leafout) in lab conditions correlated with field phenology for 50 varieties in the lab, and (2) we examined the effect of higher temperatures on flowering development, by following the flowering response of a small subset of these varieties across mean temperatures of 20 °C to 34 °C in growth chambers.

Materials and Methods

Observations of field-grown winegrapes in the UC Davis Robert Mondavi Institute (RMI) 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 (data and full methods available at: https://knb.ecoinformatics.org/view/doi:10.5063/F18G8J29). 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 (9.6L) pots in January 2016 (9.6L). 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. About every two days, the plants' soil was checked for moisture, and they were watered as needed to keep soils moist. Starting 1 October, plants were also fertilized once a week with a 50% dilution.

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 $m^{-2}s^{-1}$ 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, CO_2 levels were set at 400 ppm during the day and 600 ppm at night, because plants respire at night, increasing CO_2 levels. Each inflorescence was contained in a paper bag to collect the flower caps as they fell. Every 10 days, the plants and their assigned temperatures were rotated to a new chamber to minimize individual chamber effects on the experiment.

Observations of the percent of flower buds that flowered on each inflorescence (% 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 abscised, each plant had spent a minimum 14 days in the chamber, it was returned to the greenhouse. No further observations were made once no more plants were developing inflorescences and all plants in the chambers had finished flowering.

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, 2013).

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 reached this stage (EL 12) later, with substantial variation in terms of the number of plants of each variety that flowered at all (Table 1). Most varieties (28/50 total) did not form inflorescences, while for a few varieties nearly half of the plants underwent flowering (e.g., Sauvignon blanc, Tempranillo, Verdelho). Due to this high variation in inflorescence appearance, only 26 of the flowering plants were used in the experiment corresponding to 10 varieties (Table 1).

Given the low number of plants that formed inflorescence, most varieties could be placed in only one or two temperature treatments (with very low or no replication per variety: chamber 1 (20°C) had one plant each of Cabernet Sauvignon, Durif, Sauvignon Blanc, and Verdelho. Chamber 2 (26°C) had one plant each of Durif, Pinot Gris, Sauvignon Blanc, and Verdelho. Chamber 3 (30°C) had three Durif plants, then one plant each of Gewürztraminer, Tempranillo, and Verdelho. Chamber 4 (34°C) had two Tempranillo plants, then one each of Dolcetto, Pinot Gris, Sauvignon Blanc, Syrah, and Verdelho. Chamber 5 (mean of 37°C) had two Tempranillo plants, and one each of Sauvignon Blanc, Verdelho, and Vinhão). 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: $F(1,24)=0.05$, $p= 0.83$).

Chamber temperatures did not affect the time 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 after forcing it took plants to reach 10% flowering ranged from 34 to 51 days (mean = 42.6 ± 0.9).

The number of flower 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 flower buds lost during the time in the chamber, with the greatest average number of flower buds aborted seen in 37 °C treatment (mean number of flower 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 (García de Cortázar-Atauri et al., 2010; Cuccia et al., 2014) and previous growth chamber studies (Buttrose and Hale, 1973), we found that flowering phenology was not significantly delayed in either the coldest or warmest chambers. However, plants in the hotter treatments aborted a higher number of flowers than those in the cooler treatments. This abortion, because it translated to fewer observations of higher percentages of flowering (i.e., 50%), may have limited detection of slowed phenology at higher temperatures. Furthermore, our plants were only exposed to the higher temperatures during flowering, not before, which could have diminished potential differences in timing of phenology during that developmental phase.

While we did not observe impacts on phenological timing, 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 traded-off reproduction for the growing season to ensure they were able to survive the elevated temperatures. This response to elevated temperature has been seen in previous studies. 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, therefore not reaching fruit set (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 were much less vulnerable and suffered few ill-effects when compared with those treated at flowering, veraison, and mid-ripening. When heat-treated at fruit set, berry growth was unimpeded and sugar content increased normally. This could mean that winegrapes are more vulnerable to high temperatures during certain periods of development, i.e. flowering. If winegrapes are especially susceptible to heat during flowering, viticulturists will have to take extra precautions during this period to ensure the survival of the flowers through to fruit set.

Although we did not measure fruit-set, future studies may want to investigate how it could be affected by elevated temperatures during the flowering period. There could be a delay in response between the period of warming and the effects of high temperatures that was not seen in our experiment because the plants were heated during the developmental phase in which we were interested. Continuing observations through fruit set could be an important next step to help understand more exactly how harvest yields might be impacted in a warming climate.

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 ten 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 et al., 2018).

Further, we found high variation in flowering success—plants with larger spurs were more likely to form inflorescence and flower and some varieties were far more successful in flowering than others. This suggests plants with greater carbohydrate reserves were more likely to develop inflorescence and flower, similar to the results of Eltom's study of the effects of girdling and leaf removal on inflorescence development (2013), but with additional variation across varieties, as other studies have found (Lebon et al., 2005). Thus, future experiments may want to (at least initially) focus lab efforts on these more successful varieties and tease out high and low temperature limits to help guide future studies.

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 responses to climate change. Our finding that plants with larger spurs were more likely to flower, however, suggests that our results regarding flower development in the greenhouse and flowering (and flower abortion) in the growth chambers should be interpreted cautiously. Our potted vines were in only their second growing season, and we expect flowering success across varieties would be greater for older, larger potted vines.

Conclusions

Helping growers adapt to shifting terroirs requires research on a greater diversity of *Vitis vinifera* varieties across diverse temperature regimes. Here we showed that budburst and leafout phenology of 50 varieties grown in the field correlated with field-based phenology and that higher temperatures can negatively impact flowering. While heat treatments during flowering did not affect the phenology of the grapes we studied, we found a significant impact from the elevated temperatures on flower abortions, which could lead to substantial negative impacts on yield. Our findings underscore the importance of modeling more than the plants' phenology to fully understand the impacts climate change will have on the viticulture industry. As data across more diverse varieties and temperature regimes increases, it can help support mapping when and where different varieties may perform best as warming continues.

Acknowledgements

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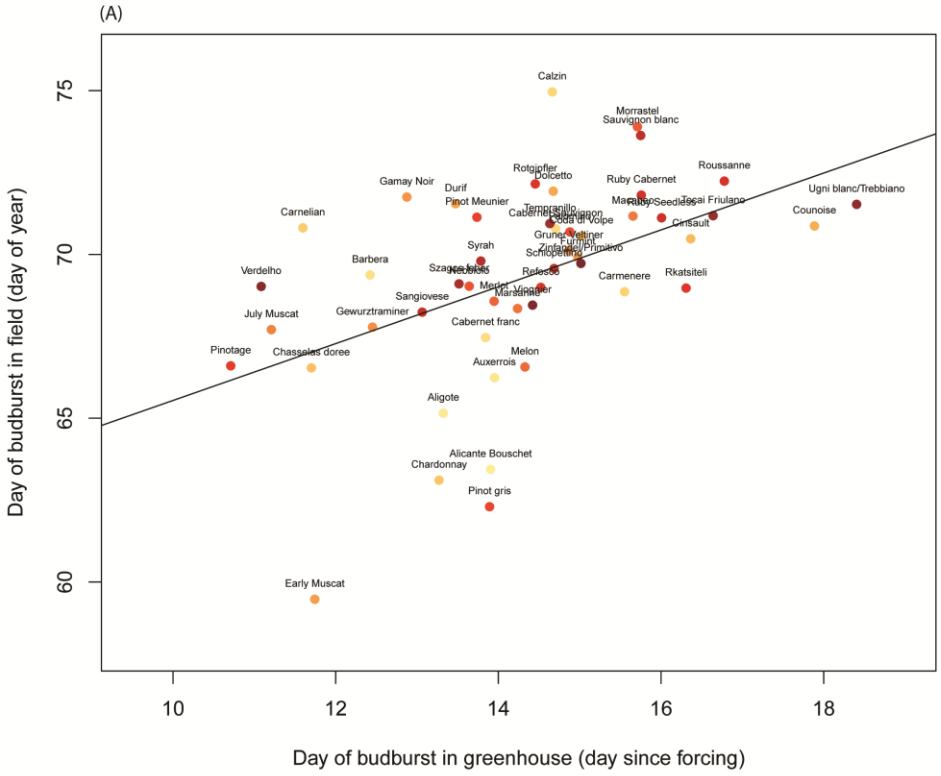
Figures (below)


(A)
Day of budburst in field (day of year)
Day of budburst in greenhouse (day since forcing)
Calzin
Morrastel
Sauvignon blanc
Roussanne
Rotgipfler
Dolcetto
Gamay Noir
Durif
Ruby Cabernet
Ugni blanc/Trebbiano
Pinot Meunier
Tocai Friulano
Carnelian
Counoise
Cinsault
Syrah
Barbera
Verdelho
Carmenere
Rkatsiteli
Sangiovese
July Muscat
Gewurztraminer
Cabernet franc
Pinotage
Chasselas doree
Melon
Auxerrois
Aligote
Alicante Bouschet
Chardonnay
Pinot gris
Early Muscat

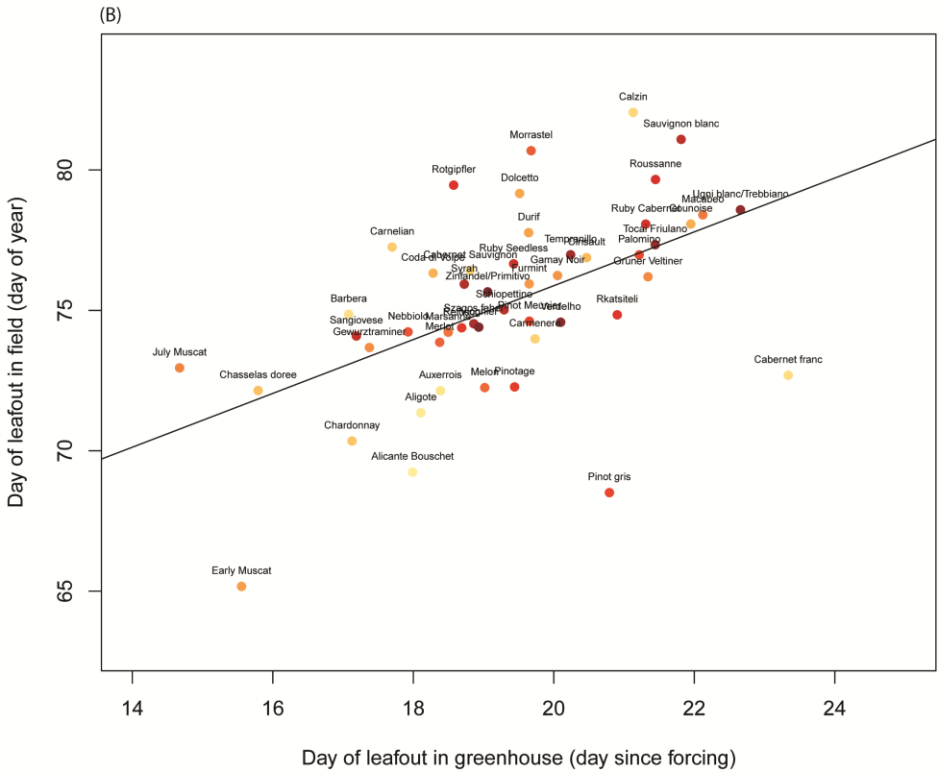

(B)
Day of leafout in field (day of year)
Day of leafout in greenhouse (day since forcing)
Calzin
Sauvignon blanc
Morrastel
Roussanne
Rotgipfler
Dolcetto
Ugni blanc/Trebbiano
Ruby Cabernet
Counoise
Durif
Carnelian
Tocai Friulano
Cinsault
Ruby Seedless
Gamay Noir
Gruner Veltiner
Syrah
Barbera
Rkatsiteli
Verdelho
Sangiovese
Gewurztraminer
July Muscat
Cabernet franc
Chasselas doree
Auxerrois
Pinotage
Aligote
Chardonnay
Alicante Bouschet
Pinot gris
Early Muscat

Figure 1
Day of budburst (A) and leafout (B) in the Robert Mondavi Institute Vineyard (Davis, California, USA) from the 2015 growing season correlates to the day of budburst ($F(1,47)=14.55$, $p<0.001$) and leafout ($F(1,47)=18.51$, $p<0.001$) in greenhouse conditions across 50 varieties (each point represents a different variety that was grown both in the vineyard and in the greenhouse).

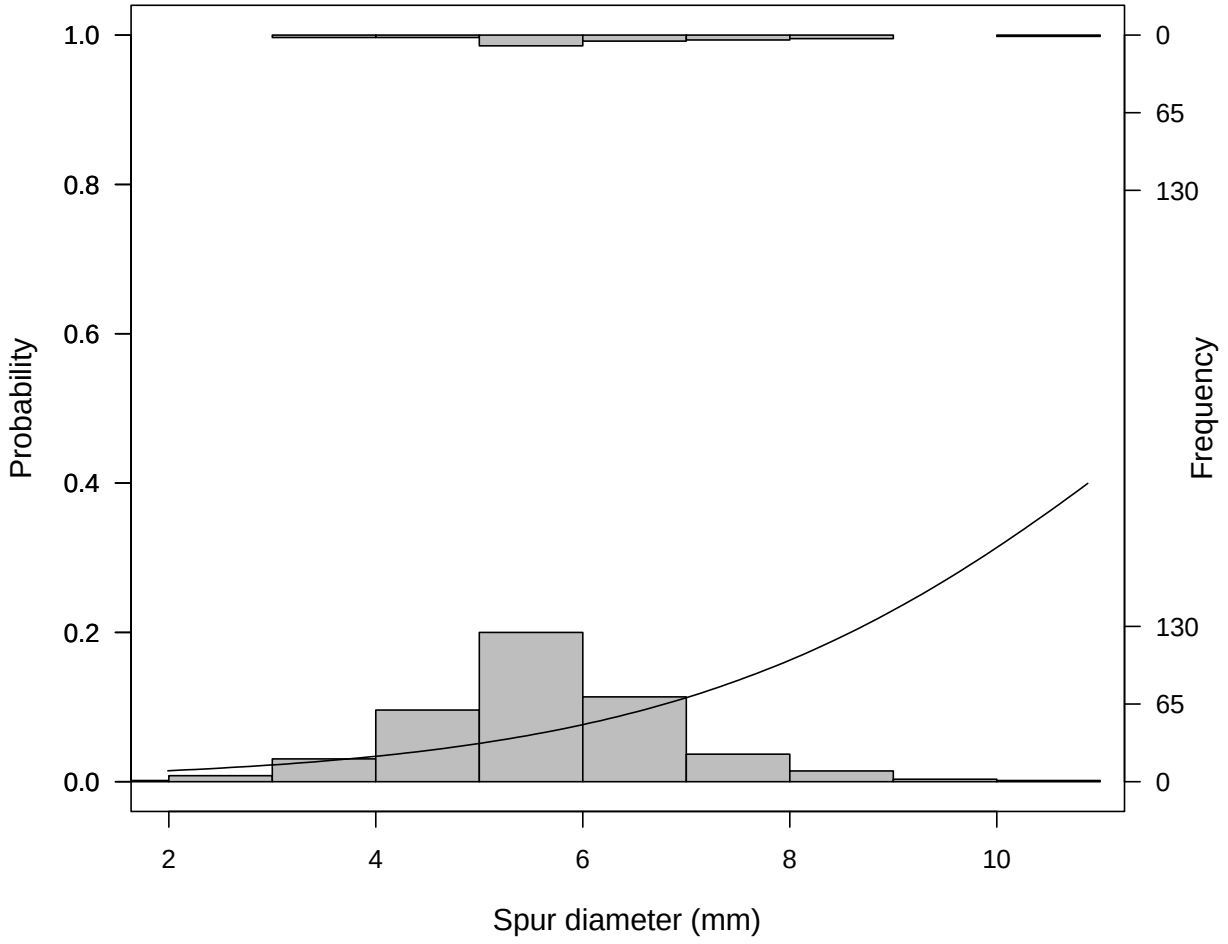
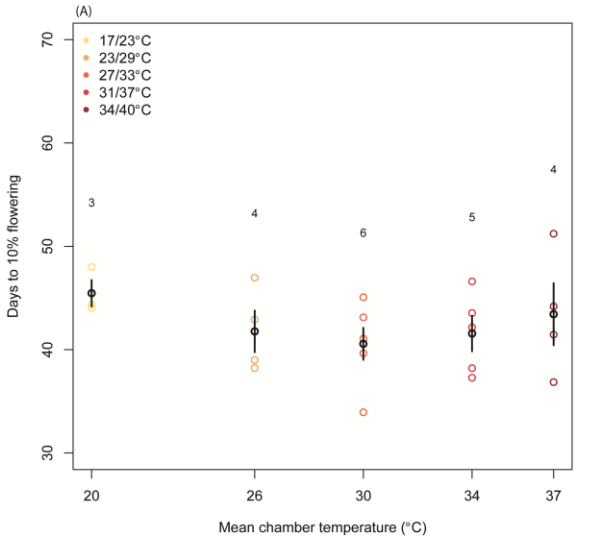
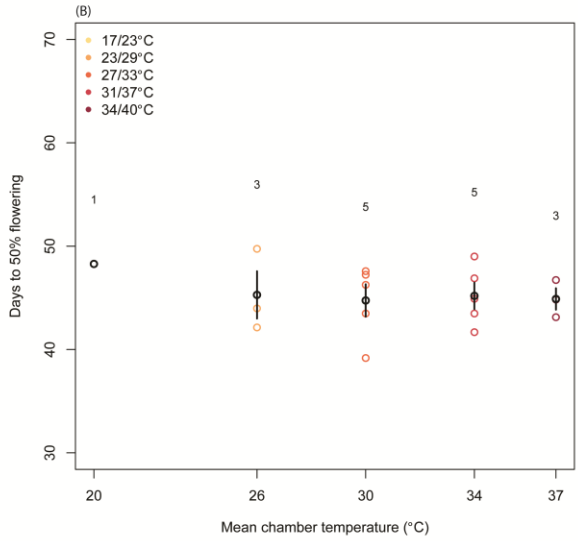
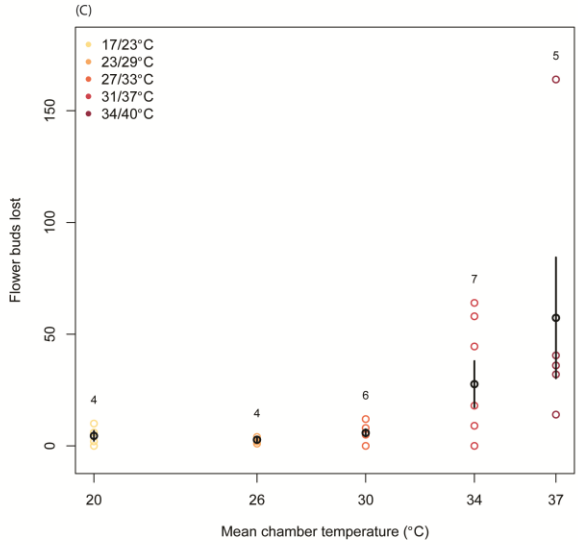


Figure 2
Spur diameter in greenhouse-grown vines (measured when plants were removed from dormancy) related to the probability that a plant would reach 50% flowering ($Z(340)=2.85$, $p=0.004$), with larger spur vines more often reaching 50% flowering. Histograms show the vines that did not reach 50% flowering (recorded in this analysis as 0 values, bottom) and those that did reach 50% flowering (recorded in this analysis as 1 values, top).


(A)
17/23°C
23/29°C
27/33°C
31/37°C
34/40°C
Days to 10% flowering
Mean chamber temperature (°C)


(B)
17/23°C
23/29°C
27/33°C
31/37°C
34/40°C
Days to 50% flowering
Mean chamber temperature (°C)


(C)
17/23°C
23/29°C
27/33°C
31/37°C
34/40°C
Flower buds lost
Mean chamber temperature (°C)

327

Figure 3

These figures illustrate the relationship between mean chamber temperature and (A) the days it took the plants to reach 10% flowering ($F(1,20)=0.43$, $p=0.52$), (B) the days it took the plants to reach 50% flowering (50%: $F(1,15)=0.50$, $p=0.49$), or (C) the number of flower buds lost while in the chamber ($F(1,24)=7.43$, $p=0.01$). 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.

340 **Table**
341

Variety	Number Plants	Number Flowered	Percent Flowered	Selected for Experiment
Alicante Bouschet	7	0	0.0	N
Aligote	6	0	0.0	N
Auxerrois	5	1	20.0	N
Barbera	9	1	11.1	N
Cabernet franc	7	0	0.0	N
Cabernet Sauvignon	9	1	11.1	Y
Calzin	5	3	60.0	N
Carmenere	8	0	0.0	Y
Carnelian	9	3	33.3	N
Chardonnay	7	0	0.0	Y
Chasselas doree	7	0	0.0	Y
Cinsault	7	0	0.0	Y
Coda di Volpe	5	0	0.0	N
Counoise	9	0	0.0	N
Dolcetto	7	1	14.3	Y
Durif	7	5	71.4	Y
Early Muscat	6	0	0.0	N
Furmint	8	0	0.0	Y
Gamay Noir	8	4	50.0	N
Gewurztraminer	9	1	11.1	Y
Gruner Veltiner	7	0	0.0	N
July Muscat	5	0	0.0	N
Macabeo	6	0	0.0	Y
Marsanne	9	2	22.2	N
Melon	5	0	0.0	N
Merlot	6	0	0.0	Y
Morrastel	6	0	0.0	N
Nebbiolo	6	0	0.0	Y
Palomino	4	0	0.0	Y
Pinot gris	8	1	12.5	Y
Pinot Meunier	6	3	50.0	N

Pinotage	5	3	60.0	N
Refosco	6	0	0.0	N
Rkatsiteli	5	0	0.0	Y
Rotgipfler	7	1	14.3	N
Roussanne	6	0	0.0	N
Ruby Cabernet	8	4	50.0	N
Ruby Seedless	6	0	0.0	N
Sangiovese	7	0	0.0	Y
Sauvignon blanc	7	3	42.9	Y
Schiopettino	8	0	0.0	N
Syrah	8	1	12.5	Y
Szagos feher	7	1	14.3	N
Tempranillo	12	5	41.7	Y
Tocai Friulano	5	1	20.0	N
Ugni blanc/Trebbiano	5	0	0.0	Y
Verdelho	6	5	83.3	Y
Vinhao	8	1	12.5	Y
Viognier	8	0	0.0	Y
Zinfandel/Primitivo	6	0	0.0	Y

Table 1

Data on the 50 varieties grown in the lab (greenhouse), including % plants of that variety that flowered and varieties that were pre-selected for the flowering experiment after budburst.

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