

The challenge of adapting grapevine varieties to climate change

Eric Duchêne^{1,2,*}, Frédéric Huard³, Vincent Dumas^{1,2}, Christophe Schneider^{1,2},
Didier Merdinoglu^{1,2}

¹Institut National de la Recherche Agronomique (INRA), UMR1131, BP 20507, 68000 Colmar, France

²Université de Strasbourg, UMR1131, 67000 Strasbourg, France

³INRA, Agroclim, 84914 Avignon, France

ABSTRACT: Climate change is expected to advance grapevine phenological stages. After the calibration and the validation of a degree-days model, we were able to accurately simulate dates of bud-break, flowering and véraison for Riesling and Gewurztraminer, 2 winegrape varieties grown in Alsace, France. Projected daily temperatures were calculated for the local meteorological station with the ARPEGE-Climat general circulation model using 3 distinct greenhouse gas emissions scenarios. Compared with its timing in 1976–2008, véraison is predicted to advance by up to 23 d and mean temperatures during the 35 d following véraison are projected to increase by more than 7°C by the end of the 21st century for both varieties. Such changes will likely have a significant impact on grape and wine quality. Using the same framework, the genetic variability of phenological parameters was explored with 120 genotypes of progeny from a Riesling × Gewurztraminer cross, along with 14 European varieties. In addition, we created a virtual late ripening genotype, derived from a cross between Riesling and Gewurztraminer. This modelled genotype was projected to undergo véraison 2 to 3 d before Muscat of Alexandria, one of the latest ripening varieties studied. Even with this virtual genotype, or with Muscat of Alexandria, grapes would ripen by the middle of the 21st century under higher temperatures than in the present years. This study highlights the important changes that viticulture will likely face in a future warmer climate and emphasises the need to create very late ripening genotypes or genotypes able to produce high quality wines under elevated temperatures.

KEY WORDS: Grapevine · Climatic change · Phenology · Temperature · Genetic variability

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

The effects of global warming on the environmental conditions of natural ecosystems and on human activities, including agriculture, have been extensively described (IPCC 2007, EEA 2008). A change in grapevine phenology during the past decades has been reported for several grape-growing areas (Duchêne & Schneider 2005, Petrie & Sadras 2008, Ramos et al. 2008).

The increase in temperatures is likely to continue, allowing future wine production in areas that are presently too cold for vine cultivation, whereas the

present grape growing regions will have to adapt to these changes (White et al. 2006, Hall & Jones 2009). The impact of climate change on wine production will presumably vary according to the type of wine produced and the geographical location, with milder effects expected in coastal regions (Jones et al. 2005, Webb et al. 2007, Hall & Jones 2009).

If phenological stages advance, the maturation of berries is likely to take place under warmer conditions. Experiments have shown that the accumulation of anthocyanins, which are responsible for berry coloration, is lower when maturation occurs at higher temperatures (Mori et al. 2007) and, despite a lack of

*Email: duchene@colmar.inra.fr

direct experimental data, this is certainly true for terpenols, the molecules responsible for floral aromas (Bureau et al. 2000). The idea that increasing temperatures can lower the quality of grapes and wines is widely accepted (Jackson & Lombard 1993, Jones et al. 2005).

Possible responses towards the projected future warming in vineyards include (1) accepting changes in the typicity of wines and altering production accordingly, going as far as producing red wines or dessert wines instead of white wines; (2) adapting varieties in order to maintain a constant typicity; and (3) moving grapevine cultivation to areas that are presently cooler (e.g. higher elevations).

Alsace is a white-wine-producing region in north-eastern France, and the evolution of phenological stages during the past decades and the consequences for grapevine physiology have been described (Duchêne & Schneider 2005). The next logical steps in this line of study are to assess the future climatic conditions in this region, to evaluate their impact on the currently cultivated varieties and to determine which varieties could be adapted in the future.

Three main phenological stages can be used to describe the grapevine developmental cycle: budbreak, flowering and véraison. Budbreak is the onset of vegetative growth, flowering is the time when the fertilisation process leads to the formation of berries and véraison is the beginning of the ripening process, which ends at harvest when sugar content and acidity meet required levels. At véraison, berries undergo major changes, i.e. cell wall degradation, skin colouration, sugar accumulation and malic acid degradation. 'Maturity' is not a phenological stage due to the difficulty in establishing uniform criteria for different varieties. Sugar content cannot be treated as a standard maturity indicator because it varies according to training systems, crop load and cultural practices (Jackson & Lombard 1993), as well as climatic signals.

The objectives of this study were to model future changes in phenology and temperature during berry ripening and to explore the consequences of such changes for the adaptation of grapevine varieties.

In this paper, we describe a model for predicting the developmental stages of Riesling and Gewurztraminer. Using this model, we assess the genetic variability in other grapevine varieties grown in the same location and in the progeny of a cross between Riesling and Gewurztraminer. The models are then used to predict future developmental stages using 3 greenhouse gas emissions scenarios developed by the Intergovernmental Panel on Climate Change (IPCC 2000) and to evaluate the genotypes that would be better adapted to these projected conditions.

2. DATA AND METHODS

2.1. Developmental stage data sets

Budbreak, flowering and véraison dates were gathered in 3 data sets, all obtained from the Institut National de la Recherche Agronomique (INRA) experimental vineyard at Bergheim (Alsace, France, 48° 21' N, 7° 34' E). The vineyard is located on a vertic calcisol soil (FAO/WRB) at an elevation of 309 m. Vines were trained on a vertical trellis at a planting density of 4500 to 4850 plants per ha, depending on the experiment.

Thirty-three yr of records (1976–2008) for Riesling (RI) and Gewurztraminer (GW) from an experiment planted in 1973 were used for the first data set. For the second data set, observations were collected from the 'Viticultural Ecology' collection, consisting of 14 varieties planted in 1975. The third data set was provided by the characterisation of offspring. Between 1998 and 2000, 527 seeds were collected from 3 crosses between RI clone 49 and GW clone 643. After a year of growth in the greenhouse, grafts of the offspring were prepared in 2002 with the Couderc 161-49 rootstock using a green grafting technique (Walter et al. 1990). In 2003, 120 genotypes were planted in the vineyard according to a randomised 5-block design. Developmental stages were recorded for 3 of the 5 blocks.

Since 1976, the methods for evaluating phenological stages have been standardised. After successive observations, budbreak, flowering and véraison dates were determined as the dates when 50% of buds, flowers and berries, respectively, reached the required stage. For budbreak, this stage corresponded to stage C 'Green tip', as described by Baggiolini (1952). As observing colour change in white varieties is more difficult than in red varieties, véraison timing was based on berry softening.

2.2. Observed and simulated climatic data

Meteorological data were not available in Bergheim before 1987, instead we exclusively used records from the INRA Station in Colmar (48° 03' N, 7° 19' E, 193 m elevation, 15 km south of Bergheim), available since 1976. These data were provided by Météo-France and the INRA STEFCLI database. The coefficient of determination R^2 between the 2 meteorological stations has been higher than 0.98 for daily mean or maximum temperatures (T) since 1987. The bias is limited: $T_{\text{mean}}(\text{Bergheim}) = 1.02 T_{\text{mean}}(\text{Colmar}) - 0.2$ and $T_{\text{max}}(\text{Bergheim}) = 0.98 T_{\text{max}}(\text{Colmar}) - 0.6$.

Projected climate data were obtained through the regionalised general circulation model ARPEGE-

Climat of Météo-France (Déqué 2007). The grid resolution of this model over France is 50 km. Three greenhouse gas (GHG) emissions scenarios were used: A2 (high emissions), B2 (low emissions) and A1B (intermediate emissions) (IPCC 2000). These data were available with a daily resolution for a control period (1950–2000) and for the future (2070–2100) for the A2 and B2 scenarios. For the A1B scenario, the simulated data set was uninterrupted from 1950 to 2100.

To estimate the regional impacts of climate change, a method based on anomalies was used (Déqué 2007). The closest grid point to Colmar in the ARPEGE-Climat model was chosen, and the modified climate for the future was calculated as follows:

$$\begin{aligned} & \text{Modified daily temperatures} = \\ & \text{Observed daily temperatures} + \text{Monthly difference} \quad (1) \\ & \text{between future and control simulations} \end{aligned}$$

For the A2 and B2 scenarios, the control period used was 1960–1989. For the A1B scenario, the projected shifts were calculated on a 20 yr sliding period instead of a single 30 yr period. The control period was 1987–2006. A first 20 yr period (2007–2026) was simulated with monthly anomalies calculated for a 20 yr sliding window. For example:

$$\begin{aligned} \text{Modified climate of 2010} &= \text{Observed climate in 1990} \\ &+ \text{Difference [(2010:2029) - (1987:2006)]} \end{aligned}$$

$$\begin{aligned} \text{Modified climate of 2011} &= \text{Observed climate in 1991} \\ &+ \text{Difference [(2011:2030) - (1987:2006)]} \end{aligned}$$

For the second period (2027–2036) and the subsequent ones, calculations started back with the 1987–2006 control period. Five 20 yr cycles are then visible in the simulated data set for the A1B scenario.

2.3. Models for phenological stages

Plant development rates are often described by thermal time or heat sums, expressed in growing degree-days (GDD). GDD are calculated as the difference between an observed temperature and a lower threshold, or 'base temperature', under which development is not possible. For the grapevine, GDD are generally calculated from daily mean temperatures and a 10°C threshold (Williams et al. 1985). However, except for the leaf emergence rate (Lebon et al. 2004), the base temperature of 10°C has not been widely validated with experimental data. Some authors have proposed using different base temperatures for the leaf emergence rate, budbreak and flowering (Moncur et al. 1989, Oliveira 1998) for different grape growing regions (Besselat et al. 1995), or using a daily maximum temperature instead of a daily mean temperature

(Besselat et al. 1995). Models based on thermal time are not the only means to predict phenological stages (Riou & Pouget 1992, Chuine et al. 2004), but we chose to restrict our study to this type of model because (1) the same framework can be used for predicting budbreak, flowering and véraison, (2) to assess parameters for 120 genotypes with 3 yr of data, the number of parameters to be estimated had to be less than 4, and (3) we are also interested in the genetic determinism of the traits and we expect more in the future from physiological approaches, more closely related to genes, than from more complex mathematical models. The model used is based on the equation:

$$HS = \sum_{i=1}^n \text{Max}(T_i - T_b ; 0) \quad (2)$$

where T_b (base temperature) and HS (heat sum) are parameters to be estimated, T_i is the daily temperature (mean or maximum) for day i and n is the number of days of the phase.

This model considers the response of grapevine developmental stages to temperature as linear, which is certainly not the case, as shown for other species (Yin et al. 1995) or for grapevine photosynthesis (Schultz 2000). A threshold for maximum temperature is sometimes used, for maize for instance (Brisson et al. 1998), and a model where values of maximum temperatures were limited to a 33°C threshold (Schultz 2000) has also been tested.

We did not attempt to predict harvest dates as (1) sugar content depends on yield level and soil water balance as well as on temperatures and (2) we do not have any validated model to predict sugar content and/or acidity in our conditions. Therefore, we did not work on a predicted véraison-harvest period.

2.4. Statistical tests

Models for phenological stages were evaluated using 3 statistical criteria (Greenwood et al. 1985, Garcia de Cortazar Atauri 2006). The Mean Absolute Error (MAE) was calculated as:

$$MAE = \frac{1}{n} \sum_{i=1}^n |P_i - O_i| \quad (3)$$

where n is the number of years in the data set, P_i is the predicted date for year i , O_i is the observed date for year i .

The Root Mean Square Error (RMSE) was calculated as:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (P_i - O_i)^2} \quad (4)$$

This criterion gives a higher weight to important errors of prediction.

The efficiency of the model (EFF) provides an estimation of the variance of the observations explained by the model. If $EFF = 0$ or less, the model does not explain any variation.

$$EFF = 1 - \left(\frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2} \right) \quad (5)$$

where \bar{O} is the mean of the observations.

Regression and analysis of variance were performed with the R software version 2.8.1 (R Development Core Team 2008).

3. RESULTS

3.1. Determination of base temperatures

To determine base temperatures, the inverse of the duration of a period D ($1/D$) was plotted against the average temperature \bar{T} over the period D (Durand et al. 1982). With $1/D = a\bar{T} + b$, the base temperature T_b , where D would be infinite, can be calculated as $T_b = -b/a$. Consequently, $\sum_{i=1}^n (T_i - T_b)$, where T_i is the temperature of day i of the period, is a constant. The confidence ellipses for the estimated parameters a and b were calculated using the 'ellipse' library in the R packages and were used to verify whether a chosen base temperature T_b was compatible or not with a confidence ellipse. To obtain the best estimates for these base temperatures, all of the available data for RI and GW were used. Both daily mean and daily maximum temperatures were tested.

For budbreak, the date when the calculation of temperature accumulation should start is theoretically the day when the period of dormancy ends (Pouget 1972). For practical reasons, 1 January is often considered as the starting point (Riou & Pouget 1992, Oliveira 1998), but 20 February has also been used (Williams et al. 1985). Seven starting dates, every 15 d from 1 January to 1 April, were tested independently for RI and GW. The coefficients of correlation between $1/D$ and \bar{T} were the highest with 15 February as the starting date, for both varieties, using either the mean or the maximum temperature (data not shown). Using 10 February or 20 February did not yield better results. The calculated base temperatures were very similar for the 2 varieties tested (Table 1). A simple integer value, in the confidence ellipses for RI and GW, was chosen for each stage for the remainder of the study (' T_b used' in Table 1).

3.2. Cross-validation of models

The first objective of the study was to set up models able to predict budbreak, flowering and véraison dates for RI and GW. For each of the 3 phases, 15 February to budbreak (15FB), budbreak to flowering (BF) and flowering to véraison (FV), each data set was divided into 2 parts. The heat sum required to reach a particular stage was calculated independently for RI and GW using 17 randomly chosen years. The MAE, RMSE and EFF criteria were calculated with the dates predicted for the 16 remaining years. The model using a 10°C base temperature was also included as a control.

The 10°C base temperature models were discarded as they created more variability than in the observed data, except for predicting flowering (Table 2). The use of daily mean temperatures or daily maximum temperatures provided satisfactory models with efficiencies greater than 62% (Table 2). The prediction of budbreak was better using a daily mean temperature above -2°C than using a maximum temperature above 2°C, whereas predictions of flowering and véraison were slightly better using maximum temperatures. As the models were validated by these cross tests, average heat sums were calculated with the complete data set and then used to compute simulated dates annually. Except for budbreak prediction with mean temperatures, RMSE were smaller than those obtained for the cross tests (Table 3). Efficiencies were always higher, or within a 1% range, for the complete data set. The use of maximum temperatures was slightly more

Table 1. Base temperatures ($T_b = -b/a$) calculated with the relationship $1/D = a\bar{T} + b$, where D is the duration of the period and \bar{T} is the average temperature during this period. 15FB: 15 February to budbreak; BF: Budbreak to flowering; FV: Flowering to véraison; GW: Gewurztraminer; RI: Riesling. ' T_b used' values are integer values within the confidence ellipses of the calculated T_b for both varieties

| Temperature | Period | Variety | R ² | T_b calculated (°C) | T_b used (°C) |
|-------------|--------|---------|----------------|-----------------------------|-----------------------|
| Mean | 15FB | GW | 0.65 | -1.8 | -2 |
| | | RI | 0.56 | -2.4 | |
| | BF | GW | 0.72 | 6.6 | 7 |
| | | RI | 0.77 | 7.3 | |
| | FV | GW | 0.55 | 2.6 | 3 |
| | | RI | 0.68 | 2.7 | |
| Maximum | 15FB | GW | 0.69 | 2.3 | 2 |
| | | RI | 0.64 | 1.9 | |
| | BF | GW | 0.81 | 10.4 | 10 |
| | | RI | 0.77 | 10.4 | |
| | FV | GW | 0.60 | 5.6 | 6 |
| | | RI | 0.70 | 5.2 | |

Table 2. Heat sums (HS, degree-days) calculated with 17 yr and criteria for goodness of fit calculated with 16 different yr. The base temperatures used are shown in Table 1. 1JB: 1 January to budbreak; 15FB: 15 February to budbreak; BF: budbreak to flowering; FV: Flowering to véraison; RI: Riesling; GW: Gewurztraminer; MAE: Mean Absolute Error; RMSE: Root Mean Square Error; EFF: Efficiency. A negative efficiency means that the model created more variability in the predicted data compared with the observed data

| Temperature | Period | HS for GW | HS for RI | MAE (d) | RMSE (d) | EFF (%) |
|------------------------------------|--------|-----------|-----------|---------|----------|---------|
| Mean with $T_b = 10^\circ\text{C}$ | 1JB | 32.1 | 47.0 | 7.5 | 10.4 | <0 |
| | BF | 299.2 | 295.5 | 3.0 | 3.8 | 87 |
| | FV | 598.0 | 633.0 | 10.6 | 21.9 | <0 |
| Mean with T_b from Table 1 | 15FB | 559.9 | 607.7 | 3.7 | 4.7 | 73 |
| | BF | 470.6 | 456.9 | 2.9 | 3.9 | 87 |
| | FV | 1048.5 | 1105.7 | 4.5 | 5.3 | 85 |
| Maximum with T_b from Table 1 | 15FB | 611.9 | 665.4 | 4.5 | 5.6 | 62 |
| | BF | 619.4 | 587.7 | 2.7 | 3.4 | 90 |
| | FV | 1244.5 | 1317.4 | 4.1 | 5.0 | 86 |

Table 3. Heat sums (HS, degree-days) and criteria for simulations with 33 yr of data. The base temperatures used are shown in Table 1. 15FB: 15 February to budbreak; BF: Budbreak to flowering; FV: Flowering to véraison; RI: Riesling; GW: Gewurztraminer; MAE: Mean Absolute Error; RMSE: Root Mean Square Error; EFF: Efficiency

| Temperature | Period | HS for GW | HS for RI | MAE (d) | RMSE (d) | EFF (%) |
|-------------|--------|-----------|-----------|---------|----------|---------|
| Mean | 15FB | 551.0 | 601.8 | 3.9 | 4.9 | 74 |
| | BF | 466.2 | 441.3 | 2.6 | 3.6 | 87 |
| | FV | 1038.3 | 1129.2 | 3.5 | 4.3 | 87 |
| Maximum | 15FB | 599.7 | 655.3 | 3.6 | 4.7 | 75 |
| | BF | 612.6 | 575.9 | 2.7 | 3.3 | 89 |
| | FV | 1229.5 | 1339.6 | 3.2 | 4.1 | 89 |

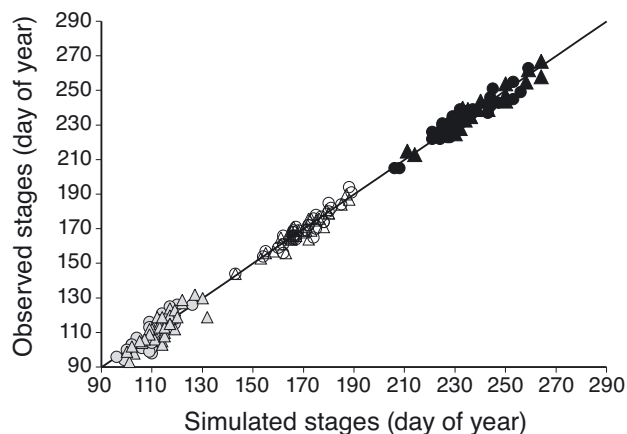


Fig. 1. Comparison between observed and simulated dates of budbreak, flowering and véraison over 33 yr for Riesling and Gewurztraminer in Bergheim. O: Gewurztraminer. Δ: Riesling. Grey: budbreak. White: flowering. Black: véraison

efficient than the use of daily mean temperatures. Using a 33°C threshold for maximum temperatures during the FV period did not improve the model (EFF = 89%, RMSE = 4.3 d).

Budbreak, flowering and véraison dates were also calculated one after the other. Overall, the simulations were very good (Fig. 1). The RMSE was 3.1 and 3.7 d for the flowering and véraison dates, respectively. This is less than the RMSE for budbreak (4.7 d) or for the duration of the FV period (4.1 d). The efficiency of the model in predicting flowering and véraison with only meteorological data was 91% for the 2 stages.

3.3. Genetic variability in the Viticultural Ecology collection

Heat sums for the 15FB, BF and FV periods were calculated as for RI and GW with maximum temperatures with T_b of 2, 10 and 6°C , respectively, for 14 varieties with 12 yr of data. The base temperatures used were the same as those employed for RI and GW (1) to make comparisons between varieties possible and (2) to be consistent with the calculations for the RI \times GW progeny, where base temperatures could not be reasonably evaluated individually for the 120 genotypes with only 3 yr of data. The overall efficiency of the simulation of the véraison dates with only

meteorological data was 81%, and the RMSE was 4.7 d. Mean errors of prediction were greater for late genotypes than for early genotypes. For example, the bias for Muscat of Alexandria, -2.9 d between simulated and observed dates, was due to 2 years, 1978 and 1987, with observed véraison dates after 10 October.

There were significant differences between varieties for the 3 phases (Table 4). Heat requirements were independent between phases: the BF period for Chasselas blanc was one of the longest, but the FV period was the shortest. Conversely, flowering for RI took place quite quickly after budbreak, but reaching véraison required more degree-days than for Syrah. Cabernet Sauvignon was a late-ripening variety, but this was mainly due to late budbreak. A véraison index was calculated for each variety as the sum of the 3 heat sums to allow for quick comparisons between varieties. This approach enables an accurate characterisation of genetic variations in developmental stages.

Table 4. Heat sums (HS, degree-days) with maximum temperatures and standard errors for genotypes grown in Bergheim. Twelve yr of data were available for the Viticultural Ecology collection. Only extreme values (3 yr of data) are presented for the RI × GW progeny. 15FB: 15 February to budbreak; BF: Budbreak to flowering; FV: Flowering to véraison. Bold: extreme values

| Genotype | HS 15FB | HS BF | HS FV | Véraison index |
|--|--------------|--------------|---------------|-------------------|
| Viticultural Ecology collection | | | | |
| Cabernet Sauvignon | 774.3 | 619.8 | 1189.8 | 2583.9 |
| Carignan | 756.6 | 649.9 | 1380.8 | 2794.8 |
| Chasselas blanc | 653.8 | 656.0 | 1042.5 | 2352.4 |
| Gewurztraminer | 628.1 | 635.5 | 1193.5 | 2457.1 |
| Grenache | 735.1 | 664.8 | 1366.2 | 2767.9 |
| Kadarka | 696.1 | 672.2 | 1275.8 | 2644.0 |
| Limberger | 597.1 | 649.1 | 1205.1 | 2451.2 |
| Muscat of Alexandria | 711.3 | 675.6 | 1387.9 | 2792.5 |
| Pinot noir | 691.4 | 587.2 | 1190.1 | 2468.7 |
| Portugais bleu | 653.4 | 604.4 | 1107.3 | 2365.1 |
| Riesling | 685.0 | 589.2 | 1291.3 | 2565.6 |
| Sauvignon | 666.6 | 641.9 | 1167.8 | 2476.3 |
| Syrah | 669.3 | 641.3 | 1242.3 | 2552.9 |
| Ugni blanc | 798.9 | 641.6 | 1327.0 | 2771.3 |
| Standard error | 12.8 | 10.5 | 15.3 | 19.1 |
| RI × GW progeny | | | | |
| 9E | 591.5 | – | – | – |
| 47E | 702.5 | – | – | 2635.9 |
| 26E | – | 597.6 | – | – |
| 13D | – | 666.1 | – | – |
| 4E | – | – | 1059.4 | – |
| 237E | – | – | 1345.5 | – |
| 58E | – | – | – | 2345.4 |
| Virtual 9E:26E:4E | 591.5 | 597.6 | 1059.4 | 2248.5 |
| Virtual 47E:13D:237E | 702.5 | 666.1 | 1345.5 | 2714.1 |
| Standard error | 27.4 | 10.0 | 23.3 | 31.6 |

3.4. Genetic variability in the RI × GW progeny

As for RI and GW, heat sums were assessed for 3 yr of observation for 120 genotypes among the progeny of a RI × GW cross. Calculations were carried out using meteorological data from Colmar in order to be consistent with the other data sets. The heat sum values observed in this progeny cover approximately 55% (budbreak), 77% (flowering) and 83% (véraison) of the ranges observed in the Viticultural Ecology collection (Table 4). The latest genotypes in the RI × GW progeny have a véraison index lower than Kadarka, Carignan, Grenache and Muscat of Alexandria but a higher index than Cabernet Sauvignon or Syrah.

To explore the potential extent of the variation of the phenology response, we created a 'virtual' genotype by adding the largest values observed for each period in the RI × GW progeny results. This 'virtual' genotype has a véraison index of 2714 (Table 4) and would theoretically reach véraison a few days before Grenache.

3.5. Projected temperatures

The temperatures simulated with the ARPEGE-Climat model on the closest grid-point to Colmar were compared with the actual data from Colmar for the control period 1986–2007. The month-to-month average temperature does not differ by more than 0.36°C (T_{\max} in May). The average differences over the grapevine growing period of April to September were 0.10 and 0.07°C for T_{\min} and T_{\max} , respectively. Consequently, we considered the model as acceptable. To further validate the projected climatic data, comparisons were made with IPCC data. Under scenario B2, the mean annual temperature in Colmar is projected to increase by 2.1°C at the end of the century compared with the period 1973–1999 (Table 5). The increases are 1.0 and 1.3°C higher under scenarios A1B and A2, respectively. These increases in temperatures are in the range of the changes expected for the global average surface temperature with the same scenarios (IPCC 2007). The A1B projected changes are, however, closer to A2 projected changes in our region than at the global level. The increase is predicted to be +0.3 to 0.4°C higher for maximum temperatures than for minimum temperatures.

3.6. Projected stages

Simulated daily temperatures were available for Colmar for scenario A1B from 2010 to 2100 and for scenarios A2 and B2 from 2073 to 2099. For each year and scenario, budbreak, flowering and véraison dates were calculated for RI and GW according to the models previously developed with maximum temperatures (Table 3). To summarise the results, dates of phenological stages were averaged over periods of 27 to 32 yr. By the end of the century, véraison could advance for both varieties by 16 (B2) to 24 (A2) d when compared with the period 1976–2008 (Fig. 2). As expected, the effects of climatic conditions in scenario B2 are of lower magnitude than in scenario A2. In scenario A1B,

Table 5. Increase of predicted average annual temperatures (°C) in 2073–2099 compared with the observed values (1973–1999) for Colmar according to 3 IPCC emissions scenarios using the ARPEGE-Climat model

| Dataset | Minimum temp. | Maximum temp. | Mean temp. |
|-----------------|------------------|------------------|---------------|
| Observed values | 5.7 | 15.0 | 10.3 |
| B2 | +2.0 | +2.3 | +2.1 |
| A1B | +3.0 | +3.3 | +3.1 |
| A2 | +3.2 | +3.6 | +3.4 |

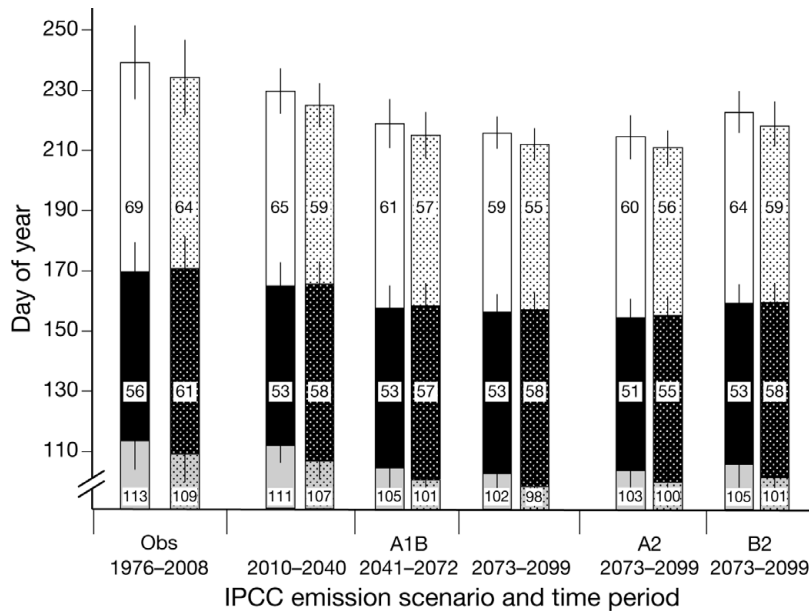


Fig. 2. Observed and projected dates of budbreak (grey), flowering (black) and véraison (white) for Riesling (left, plain) and Gewurztraminer (right, dotted) according to 3 IPCC scenarios. Figures in the bars represent the durations of the different phases, and whiskers indicate standard deviations

the difference between the beginning of the century (2010–2040) and mid-century (2041–2073) will be greater than from mid-century to the end of the century (2073–2099). If these simulations are correct, a large number of climate change effects will be apparent by the first half of the century.

The model with a 33°C threshold for maximum temperature was also used to predict the véraison dates. Delays in véraison dates are predicted when using the threshold model instead of the model without a threshold, but the largest effect on average values is limited to +1 d, as evident for RI in scenario A2 from 2071–2099. Using a 30°C threshold, the delay for the same data set would be +2.4 d.

The model used for budbreak assumes that chilling requirements are satisfied for all years, which had to be verified. Chilling requirements necessary to release bud dormancy are not clearly defined. Pouget (1972) suggested that a period of 7 consecutive days with a mean temperature below 10°C was required for Merlot. More recently, Garcia de Cortazar Atauri (2006) proposed a model that included an accumulation of daily chilling units (Cc) to predict the end of dormancy. For RI, the estimated value for Cc was 108.2. Under scenario A1B, both criteria were satisfied every year before 15 February. According to the current knowledge on budbreak and to the meteorological data used, a delay in budbreak due to insufficiently low winter temperatures is unlikely for Colmar in the future.

3.7. Consequences on climatic conditions during ripening

The requested natural alcohol level in the 'Alsace Grand Cru' top level wines is currently 11% v/v for RI and 12.5% v/v for GW (Association des Viticulteurs d'Alsace, May 2009), which corresponds to 185 and 210 g l⁻¹ of sugar in the berries, respectively. Projected climatic conditions were therefore compared to the years when these levels of sugar content were actually reached in samples taken all over the region (Duchêne & Schneider 2005). Twelve and 19 years, called 'favourable years' in the following text, were selected for RI and GW, respectively (Table 6). Average minimum and maximum temperatures were calculated for the 35 d following véraison (Duchêne & Schneider 2005) for each year of observed data and of the A1B scenario. This period was chosen to compare the climatic conditions during the ripening phase and does not correspond

to an actual, or projected, véraison–harvest period. Our purpose was to compare present and future conditions rather than to predict grapevine quality at harvest. Surprisingly, the years favourable to high sugar content, although different, have the same temperature profile for RI and for GW despite differences in véraison dates (Table 6). When compared with the observed favourable years, an increase of approximately 1°C for RI and 1.5°C for GW is predicted for 2010–2040 (Table 7). For 2041–2072, the increase will clearly be greater for maximum temperatures than for minimum temperatures, reaching 5.3°C for RI and 5.9°C for GW (3.9°C and 4.5°C for minimum temperatures, respectively). As observed for developmental stages, a slowing down of the rate of increase is projected for the last years of the century. The average maximum temperature during ripening for GW could, however, reach 31°C at this time, compared with 23.7°C in the observed favourable years and 22.4°C for 1976–2008 (Table 7).

Table 6. Average véraison dates and average temperatures (°C) during the 35 d following véraison for years favourable for sugar accumulation within the 1976–2008 period (185 g l⁻¹ for Riesling, 210 g l⁻¹ for Gewurztraminer)

| Genotype | Véraison date | Minimum temp. | Maximum temp. | Mean temp. |
|----------------|---------------|---------------|---------------|------------|
| Riesling | 18 August | 11.7 | 23.7 | 17.7 |
| Gewurztraminer | 15 August | 11.6 | 23.7 | 17.7 |

Table 7. Differences in véraison dates (d) and in average temperatures (°C): observed and projected data (scenario A1B) are compared to the years favourable for sugar accumulation (Table 6)

| Genotype | Data set | Period | Véraison date | Minimum temp. | Maximum temp. | Mean temp. |
|-----------------|-----------------|-----------|---------------|---------------|---------------|------------|
| Riesling | Observed | 1976–2008 | +8 | –1.6 | –2.1 | –1.8 |
| | | 2003 | –15 | +2.4 | +6.5 | +4.4 |
| | Projected (A1B) | 2010–2040 | –1 | +0.9 | +1.1 | +1.0 |
| | | 2041–2072 | –11 | +3.9 | +5.3 | +4.6 |
| Gewurztraminer | Observed | 1976–2008 | +6 | –1.0 | –1.3 | –1.2 |
| | | 2003 | –22 | +3.6 | +8.0 | +5.8 |
| | Projected (A1B) | 2010–2040 | –2 | +1.4 | +1.7 | +1.5 |
| | | 2041–2072 | –12 | +4.5 | +5.9 | +5.1 |
| Projected (A1B) | 2073–2099 | –15 | +6.0 | +7.3 | +6.6 | |

Year 2003 was included as a reference for an exceptionally hot summer (Schär et al. 2004). Maximum temperatures during ripening in 2003 are comparable to the projected temperatures for the end of the century, but mean temperatures similar to those seen in 2003 could be common as soon as the middle of the century (Table 7).

3.8. Adaptation of genotypes to projected conditions

Temperatures over the growing season, integrated in indexes such as the Huglin Index, determine the suitability of varieties to a given environment (Huglin 1978). Temperatures are of major importance for wine quality (Jones et al. 2005), but there are no scientific data on the range of temperatures during the ripening period suitable for producing wines with specific characteristics, i.e. 'typical' wines, in our conditions. A working hypothesis is to assume that temperatures during ripening in the future should remain in the

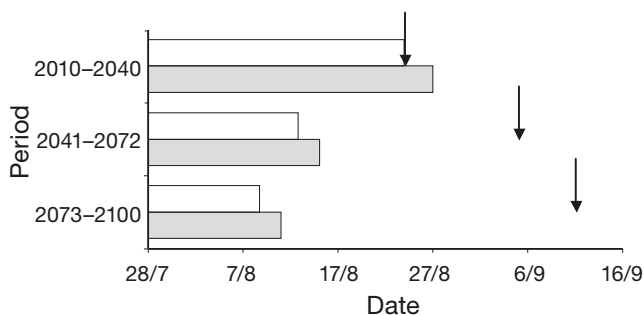


Fig. 3. Véraison dates under scenario A1B. White: virtual genotype from a Riesling \times Gewurztraminer progeny. Grey: Muscat of Alexandria. Arrows indicate the date when the mean temperature of the following 35 d is projected to be 17.7°C, on average

same range as currently observed to maintain a constant typicity. We therefore determined the date when ripening should start so that the mean temperature during the following 35 d would be the same as the mean temperature observed in the favourable years as previously defined. Average daily mean temperatures were calculated for 3 periods for the A1B scenario. An average mean temperature of 17.7°C (Table 6) during ripening would be observed if ripening started on 24 August, 5 September and 11 September during 2010–2040, 2041–2072 and 2073–2100, respectively (Fig. 3). In parallel, véraison dates were calculated for Muscat of Alexandria and for the virtual genotype from the RI \times GW progeny that would have the latest véraison. Muscat of Alexandria was chosen because it was one of the latest ripening genotypes studied. For 2010–2040, it appears possible to find genotypes whose ripening could take place in temperature conditions similar to the favourable years actually observed (Fig. 3). For 2041–2072, there is a 20 d gap between the véraison of Muscat of Alexandria (15 August) and the start of the period when the mean temperature would be 17.7°C (5 September). The virtual RI \times GW genotype would undergo véraison before Muscat of Alexandria. Therefore, the feasibility of creating a new variety, a progeny of RI and GW, that could ripen in the same range of temperatures as currently observed, does not seem possible.

In the last years of the century, it is unlikely that any *Vitis vinifera* variety could start ripening on 11 September, knowing that Muscat of Alexandria, one of the latest ripening varieties in Europe, would undergo véraison on 9 August, on average. These results illustrate the effects of global warming on both the advance in phenological stages and the increase of temperatures in summer.

4. DISCUSSION

4.1. A model for phenological stages

Here, we provide a model for predicting budbreak, flowering and véraison for RI and GW. This model, based on growing degree-days, is able to simulate accurately the observed stages from the past 30 yr.

Base temperatures were obtained by a regression model, and it can be shown mathematically that base temperatures obtained by minimizing the standard deviation of the heat sums are very close (Durand et al. 1982). Moncur et al. (1989) reached the same conclusion empirically. Base temperatures vary widely in the literature, depending on the varieties studied (Moncur et al. 1989) or on grape-growing regions (Besselat et al. 1995). The values of base temperatures calculated for the FV period, 3 and 6°C for T_{mean} and T_{max} , respectively, are surprisingly low. They result from statistical adjustments and are far from the range of average temperatures observed during this period (22.8 to 29.2°C for T_{max}). If the response of the phenology is not linear, these calculated base temperatures are not indicators of actual physiological thresholds. An indirect validation of our calculated base temperatures is the fairly good predictions of the models. For budbreak, a RMSE of 4.7 d and an efficiency of 75% (Table 3) are satisfactory when compared with similar studies (Mandelli et al. 2003, Garcia de Cortazar Atauri 2006). Improving budbreak prediction is difficult, as this stage also depends on soil temperature (Kliewer 1975) and on pruning dates (Martin & Dunn 2000). As already shown (Moncur et al. 1989), a 10°C base temperature is not appropriate for budbreak prediction.

Previous studies also obtained good relationships between flowering dates and heat sums expressed in degree-days (Williams et al. 1985, Besselat et al. 1995, Garcia de Cortazar Atauri 2006). Our final model (maximum temperatures, 10°C base temperature) is the same as the model retained by Besselat et al. (1995) for Pinot Noir in Burgundy and has a similar accuracy, with a MAE between 2.5 and 3 d in each case. With our data, using mean temperatures with the classical 10°C base did not significantly change the goodness of fit for this stage (Table 2).

We are not aware of a published heat sum model for véraison. Chuine et al. (2004) proposed a model using daily mean temperatures that could explain approximately 90% of the variance of véraison dates for Pinot Noir. This model, however, requires 5 parameters and was not appropriate for the simple comparison of grapevine genotypes. The goodness of fit of our model is high, with a final RMSE of 3.7 d and an efficiency of approximately 90%.

4.2. Genetic variability

Costantini et al. (2008) have shown that flowering and véraison time segregated in an Italia × Big Perlon progeny. Quantitative Trait Loci (QTL) and molecular markers associated with these traits could be identified for these genotypes. A similar work is in progress for our RI × GW progeny. Our results show that heat sums can be used to characterise the genetic variability, and this should lead to a better analysis of the genetic determinism of the phenological traits. The genetic variability for the véraison dates was 39 d within 279 genotypes in the INRA collection at Vassal (Galet 1990). The range in the véraison dates in our study was 6 d between RI and GW, 16 d in the RI × GW progeny and 28 d in the collection of 14 varieties. The range of stages created in our progeny is quite large when we consider that the parents are adapted to the same growing conditions. Among the progeny of Italia × Big Perlon, 2 genitors with a 20 d difference in time of véraison, the observed range of véraison dates was 45 d (Costantini et al. 2008). Breeding new late ripening varieties is a way to increase the existing genetic variability and to adapt the grapevine phenology to climate change.

4.3. Phenological stages in the future

The impacts of future climate change on Cabernet Sauvignon and Chardonnay phenology have been assessed in Australia (Webb et al. 2007). Except for one of the regions of the study, budbreak should be earlier by 2 to 9 d in 2030 and 3 to 18 d in 2050. Our simulations are compatible with these estimations (Fig. 2). Figures for the advance of harvest in Australia (approx. 20 d in 2050 without the Margaret River region) are also similar to our results for the véraison dates. The predicted advance of phenological stages is, however, smaller in our study than in a previous work conducted in France (Garcia de Cortazar Atauri 2006). By extrapolating the observed tendencies (Duchêne & Schneider 2005), véraison dates could be 40 d earlier in 2050 compared with those in 1976–2008. Limited canopy development due to more frequent water shortages in the future could also increase grape exposure and berry temperature during ripening (dos Santos et al. 2007). The uncertainty in véraison advance in climate modelling is also in part due to our incomplete understanding of the relationship between high temperatures and grapevine phenology. The arbitrary use of a threshold for maximum temperatures did not significantly modify the projected véraison dates (approximately 2 d) when compared with the uncertainty between scenarios (more than 7 d between scenarios A2 and B2). This

limited effect can be explained by the shift of the FV period earlier in the season in the future. This partially counteracts the higher frequency of warm days during summer: for RI under scenario A2 in 2073–2099, the average maximum temperature during the FV period falls outside the range of observed years in only 5 years. Nevertheless, the models could certainly be improved by the use of a non-linear response of phenology to temperatures.

4.4. Projected conditions during ripening

Projected temperatures and phenological stages show that ripening could occur under higher temperatures in the future because of both earlier véraison dates and a general increase in temperatures. By 2030 (2010–2040), the projected increase in temperatures is limited to 1–1.5°C, but by 2050 (2041–2072) temperatures could be 5 to 6°C higher than the average value for the past favourable years. High temperatures accelerate the degradation of organic acids (Kliewer 1971) and impair the accumulation of anthocyanins (Mori et al. 2007). As sugar content is likely to increase with accelerated ripening (Jackson & Lombard 1993, Duchêne & Schneider 2005), climate change will lead to wines with a modified sugar/acid ratio unless acid is added back to the must. Despite scarce direct experimental data, the negative effects of high temperatures on the aroma content of grapes and wines are widely accepted. Monoterpenols are the molecules responsible for the floral aromas found in GW grapes and wines (Duchêne et al. 2009b), and RI also contains more monoterpenols than 'neutral' grape varieties do (Razungles et al. 1993). A 30% loss of terpenols has been observed between naturally and artificially shaded bunches of Muscat of Frontignan, with the main difference being a temperature that was 7°C higher in the bags used for shading (Bureau et al. 2000).

In addition, 1,1,6-trimethyl-1,2-dihydronaphthalene (TDN) is a compound found in RI wines (Simpson & Miller 1983). TDN concentrations increase during ripening and under warmer conditions (Marais et al. 1992). High TDN content can be detrimental to wine quality in some hot summer growing areas, and this could occur in Alsace in the future.

The direct effects of [CO₂] should also be considered. When analysing wines made from grapes of Touriga Franca vines grown under ambient or elevated (500 ppm) [CO₂], Goncalves et al. (2009) showed a small but significant increase in the linalool concentration in wines made from grapes grown under elevated [CO₂]. Although the results of this experiment suggest that [CO₂] may affect wine quality, it does not provide a conceptual framework for how future CO₂ atmospheric concentra-

tions could increase monoterpenol content in aromatic varieties. In the same experiment, total anthocyanins and polyphenol concentrations were inhibited under elevated [CO₂].

Through a different alcohol/acidity balance and a different aroma profile, the typicality of wines could be modified by the middle of the century. From another point of view, these new ripening conditions will offer expanded opportunities to grow late ripening genotypes. Combined with a high diversity of geological substrates, new and original types of wines might be produced in Alsace.

4.5. Adapting varieties

We have no clear indication of the threshold of temperatures during ripening that can significantly modify the characteristics of RI and GW wines. We may be able to manage the predicted increase for the coming 30 yr (1 to 1.5°C), but this value is an average, and hotter summer temperatures or extreme temperature events are expected to become more and more frequent (Schär et al. 2004). To avoid hot ripening conditions, one strategy is to move the cultivation area to higher elevations or higher latitudes. Another strategy is to delay véraison. With the current varieties, the only technical means of accomplishing this is to delay bud-break by late pruning. This strategy is not realistic at a regional scale as, logistically, it is not possible to prune all vineyard plots late, and even if late pruning was practised, the effect would be limited to a few days (Martin & Dunn 2000) when weeks of delay would be necessary (Fig. 3).

The original purpose of this research was based on the hypothesis that creating new varieties would meet the challenge of climate change. Our results can be analysed from 2 points of view. On the one hand, we demonstrated that crossing RI and GW can generate a large genetic variability. Genotypes ripening almost as late as Grenache can be expected from such progenies, and we can potentially breed a new variety that reproduces the wine characters of the parents using molecular markers (Duchêne et al. 2009a). On the other hand, this variability does not seem sufficient to compensate for the effect of climate change after 2050. At this time, even a late ripening variety like Muscat of Alexandria would experience warmer ripening conditions than RI or GW do today. Whether such a variety originating from warmer Mediterranean countries is able to produce high quality wines in such conditions should be further investigated. Other alternatives are to explore in depth the existing genetic variability or to breed varieties from crosses with late ripening genotypes, for example, RI and Muscat of Alexandria.

5. CONCLUSIONS

Our work combined ecophysiological modelling, projected climate changes and exploration of genetic variability. The use of a degree-days model showed that compared to 1976–2008, véraison could advance by 23 d, and mean temperatures during the following 35 d could increase by more than 7°C by the end of the 21st century for RI and GW grown in Alsace. Using the same framework, the genetic variability of phenological parameters was explored with 120 genotypes resulting from a RI × GW cross and with 14 European varieties. We created a virtual late ripening genotype, derived from a cross between RI and GW, which would undergo véraison 2 to 3 d before Muscat of Alexandria. Even with this virtual genotype, as well as with Muscat of Alexandria, grapes should ripen under higher temperatures by the middle of the 21st century than in the present years.

Many uncertainties complicate the prediction of grapevine physiology in the future: GHG emissions scenarios and climatic models; the quantitative impact of temperatures on sugars, acids and aroma compounds; and the direct effects of CO₂ atmospheric concentration. Whatever these uncertainties, our work highlights the important changes that viticulture might have to face and the limits of our capacities to find adapted varieties. As such, our work emphasises the importance of research programs that target climate change and the new strategies needed to adapt to such projected changes.

Acknowledgements. This work was partially financed by the ERA-NET Plant Genomics Program (GRASP GRAPE WINE 074B).

LITERATURE CITED

- Baggiolini M (1952) Les stades repères dans le développement annuel de la vigne et leur utilisation pratique. *Rev Rom Agric Vitic* 8:4–6
- Besselat B, Drouet G, Palagos B (1995) Méthodologie pour déterminer le besoin thermique nécessaire au départ de la floraison de la vigne. *J Int Sci Vigne Vin* 29:171–182
- Brisson N, Mary B, Ripoche D, Jeuffroy MH and others (1998) STICS: a generic model for the simulation of crops and their water and nitrogen balances. I. Theory and parameterization applied to wheat and corn. *Agronomie* 18:311–346
- Bureau SM, Razungles AJ, Baumes RL (2000) The aroma of Muscat of Frontignan grapes: effect of the light environment of vine or bunch on volatiles and glycoconjugates. *J Sci Food Agric* 80:2012–2020
- Chuine I, Yiou P, Viovy N, Seguin B, Daux V, Le Roy Ladurie E (2004) Grape ripening as a past climate indicator. *Nature* 432:289–290
- Costantini L, Battilana J, Lamaj F, Fanizza G, Grando MS (2008) Berry and phenology-related traits in grapevine (*Vitis vinifera* L.): from Quantitative Trait Loci to underlying genes. *BMC Plant Biol* 8:38
- Déqué M (2007) Frequency of precipitation and temperature extremes over France in an anthropogenic scenario: model results and statistical correction according to observed values. *Global Planet Change* 57:16–26
- dos Santos TP, Lopes CM, Rodrigues ML, de Souza CR and others (2007) Effects of deficit irrigation strategies on cluster microclimate for improving fruit composition of Moscatel field-grown grapevines. *Sci Hortic (Amsterdam)* 112:321–330
- Duchêne E, Schneider C (2005) Grapevine and climatic changes: a glance at the situation in Alsace. *Agron Sustain Dev* 25:93–99
- Duchêne E, Butterlin G, Claudel P, Dumas V, Jaegli N, Merdinoglu D (2009a) A grapevine (*Vitis vinifera* L.) deoxy-d-xylose synthase gene colocalizes with a major QTL for terpenol content. *Theor Appl Genet* 118:541–552
- Duchêne E, Legras JL, Karst F, Merdinoglu D, Claudel P, Jaegli N, Pelsy F (2009b) Variation of linalool and geraniol content within two pairs of aromatic and non aromatic grapevine clones. *Aust J Grape Wine Res* 15:120–130
- Durand R, Bonhomme R, Derieux M (1982) Seuil optimal des sommes de températures. Application au maïs (*Zea mays* L.). *Agronomie* 2:589–597
- EEA (2008) Impacts of Europe's changing climate—2008 indicator-based assessment. European Environment Agency, Copenhagen K, Denmark. www.eea.europa.eu/publications/eea_report_2008_4
- Galet P (1990) Cépages et vignobles de France. Tome II. L'Ampélographie Française. Montpellier
- García de Cortazar Atauri I (2006) Adaptation du modèle STICS à la vigne (*Vitis vinifera* L.). Utilisation dans le cadre d'une étude d'impact du changement climatique à l'échelle de la France. PhD thesis, Ecole Nationale Supérieure Agronomique de Montpellier, France
- Goncalves B, Falco V, Moutinho-Pereira J, Bacelar E, Peixoto F, Correia C (2009) Effects of elevated CO₂ on grapevine (*Vitis vinifera* L.): volatile composition, phenolic content, and *in vitro* antioxidant activity of red wine. *J Agric Food Chem* 57:265–273
- Greenwood DJ, Neeteson JJ, Draycott A (1985) Response of potatoes to N fertilizer: dynamic model. *Plant Soil* 85:185–203
- Hall A, Jones GV (2009) Effect of potential atmospheric warming on temperature-based indices describing Australian winegrape growing conditions. *Aust J Grape Wine Res* 15:97–119
- Huglin P (1978) Nouveau mode d'évaluation des possibilités héliothermiques d'un milieu viticole. *Compte-rendus de l'Académie d'Agriculture*:1117–1126
- IPCC (2000) IPCC special report on emissions scenarios. Summary for policy makers, WMO-UNEP, Geneva, Switzerland. www.ipcc.ch/pdf/special-reports/spm/sres-en.pdf
- IPCC (2007) Climate change 2007: synthesis report. In: Pachauri RK, Reisinger A (eds) Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Core Writing Team. WMO-UNEP, Geneva. www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf
- Jackson DI, Lombard PB (1993) Environmental and management practices affecting grape composition and wine quality—a review. *Am J Enol Vitic* 44:409–430
- Jones GV, White MA, Cooper OR, Storchmann K (2005) Climate change and global wine quality. *Clim Change* 73:319–343
- Kliewer WM (1971) Effect of day temperature and light intensity on concentration of malic and tartaric acids in *V. vinifera* grapes. *J Am Soc Hortic Sci* 96:372–377

- Kliewer WM (1975) Effect of root temperature on budbreak, shoot growth, and fruit-set of Cabernet Sauvignon grapevines. *Am J Enol Vitic* 26:82–89
- Lebon E, Pellegrino A, Tardieu F, Lecoeur J (2004) Shoot development in grapevine (*Vitis vinifera*) is affected by the modular branching pattern of the stem and intra- and inter-shoot trophic competition. *Ann Bot (Lond)* 93: 263–274
- Mandelli F, Berlato MA, Tonietto J, Bergamaschi H (2003) Predicting the date of budbreak of grapevine grown in the 'Serra Gaucha' region. *J Int Sci Vigne Vin* 37:229–235
- Marais J, van Wyk CJ, Rapp A (1992) Effect of sunlight and shade on norisoprenoid levels in maturing Weisser Riesling and Chenin blanc grapes and Weisser Riesling Wines. *S Afr J Enol Vitic* 13:23–32
- Martin SR, Dunn GM (2000) Effect of pruning time and hydrogen cyanamide on budburst and subsequent phenology of *Vitis vinifera* L. variety Cabernet Sauvignon in central Victoria. *Aust J Grape Wine Res* 6:31–39
- Moncur MW, Rattigan K, Mackenzie DH, McIntyre GN (1989) Base temperatures for budbreak and leaf appearance of grapevines. *Am J Enol Vitic* 40:21–27
- Mori K, Goto-Yamamoto N, Kitayama M, Hashizume K (2007) Loss of anthocyanins in red-wine grape under high temperature. *J Exp Bot* 58:1935–1945
- Oliveira M (1998) Calculation of budbreak and flowering base temperatures for *Vitis vinifera* cv. Touriga Francesa in the Douro region of Portugal. *Am J Enol Vitic* 49:74–78
- Petrie PR, Sadras VO (2008) Advancement of grapevine maturity in Australia between 1993 and 2006: putative causes, magnitude of trends and viticultural consequences. *Aust J Grape Wine Res* 14:33–45
- Pouget R (1972) Considérations générales sur le rythme végétatif et la dormance des bourgeons de la vigne. *Vitis* 11: 198–217
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Ramos MC, Jones GV, Martinez-Casasnovas JA (2008) Structure and trends in climate parameters affecting winegrape production in northeast Spain. *Clim Res* 38:1–15
- Razungles A, Günata Z, Pinatel S, Baumes R, Bayonove C (1993) Etude quantitative de composés terpéniques, norisoprénoides et de leurs précurseurs dans diverses variétés de raisins. *Sci Aliments* 13:59–72
- Riou C, Pouget R (1992) Nouvelles propositions pour évaluer la vitesse de débourrement des bourgeons de la vigne et modélisation de la date de débourrement. *J Int Sci Vigne Vin* 26:63–74
- Schär C, Vidale PL, Lüthi D, Frei C, Häberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature* 427: 332–336
- Schultz HR (2000) Climate change and viticulture: a European perspective on climatology, carbon dioxide and UV-B effects. *Aust J Grape Wine Res* 6:2–12
- Simpson RF, Miller GC (1983) Aroma composition of aged Riesling wine. *Vitis* 22:51–63
- Walter B, Bass P, Legin R, Martin C, Vernoy R, Collas A, Vesselle G (1990) The use of a green-grafting technique for the detection of virus-like diseases of the grapevine. *J Phytopathol* 128:137–145
- Webb LB, Whetton PH, Barlow EWR (2007) Modelled impact of future climate change on the phenology of winegrapes in Australia. *Aust J Grape Wine Res* 13:165–175
- White MA, Diffenbaugh NS, Jones GV, Pal JS, Giorgi F (2006) Extreme heat reduces and shifts United States premium wine production in the 21st century. *Proc Natl Acad Sci USA* 103:11217–11222
- Williams DW, Andris HL, Beede RH, Luvisi DA, Norton MVK, Williams LE (1985) Validation of a model for the growth and development of the Thompson Seedless grapevine. II. Phenology. *Am J Enol Vitic* 36:283–289
- Yin X, Kropff MJ, McLaren G, Visperas RM (1995) A nonlinear model for crop development as a function of temperature. *Agric For Meteorol* 77:1–16

Editorial responsibility: Nils Chr. Stenseth, Oslo, Norway

Submitted: September 21, 2009; Accepted: February 3, 2010
Proofs received from author(s): April 13, 2010