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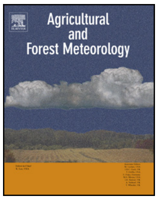

Classification of varieties for their timing of flowering and veraison using a modelling approach: A case study for the grapevine species *Vitis vinifera* L.

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Abbreviations: CI, confidence interval; DOY, day of the year; *EF*, model efficiency; GFV, Grapevine Flowering Veraison; RMSE, roots mean squared error; SW, spring warming.

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ABSTRACT

Understanding differences in phenology for varieties of a given species is important for making informed decisions on variety choice in the context of climate change and breeding new cultivars. Phenological models that incorporate temperature as a key environmental factor can be used to describe the differences in phenological timing between cultivars. This paper outlines a methodology, based on a phenological model, for classifying the timing of flowering and veraison for a substantial number of varieties of the grapevine (*Vitis vinifera* L.). 95 varieties were characterized for flowering and 104 varieties for veraison. Various statistical measures were used to assess the performance and predictions of the model at the varietal level: model efficiency, root mean squared error and confidence intervals. The methodology might be used to understand varietal differences for other species in future studies. Model outputs can be used in combination with predicted climate change scenarios to assess the suitability of varieties under climate conditions of the future.

1. Introduction

Temperature is considered a fundamental driver of plant development and phenological cycles. It can modify profoundly the timing of cycles and such changes have been documented in many studies for different plant species under increasing temperatures in the past. Several studies have indicated that increased temperatures have been associated with earlier phenological development of many wild and cultivated plants (Chmielewski et al., 2004; Cleland et al., 2007; Gordo and Sanz, 2009; Menzel et al., 2006; Schwartz et al., 2006), however, delays have also been documented for specific events, notably leaf colouring and leaf fall (Menzel et al., 2003; Estrella and Menzel, 2006; Gordo and Sanz, 2009). Phenology is modified by a complex interaction of (1) the sensitivity of the species phenology to climate drivers such as temperature but also photoperiod and water stress and (2) the phenological stage in question.

Different varieties within a species can have marked differences in phenology. In the context of climate change, a deeper understanding of varietal differences in phenology for agriculture is critical to select varieties that are adapted for production under future climate conditions. Phenological process-based models can be used to predict phenological development in response to temperature and can aid our understanding of plant development in this context (see Chuine et al., 2003 for model details). Many studies have characterized differences in the phenology of cultivated crops varieties with some studies having assessed these differences using phenological models; some recent examples are muskmelons (Baker and Reddy, 2001; Baker et al., 2001), olives (Garcia-Mozo et al., 2009), kiwifruit, cherries, pear and olives (Crepinsek et al., 2006) and for 14 grapevine cultivars (Duchene et al., 2010).

Previous research has used process-based phenological models to describe differences between grapevine varieties (Duchene et al., 2010; Moncur et al., 1989; Oliveira, 1998; Winkler, 1962) or advances in phenology (Chuine et al., 2004; Nendel, 2010; Duchene et al., 2010), or as a basis for pest management (Hoppmann and Berkelmann-Loehnertz, 2000) but these have often be limited to one location or few varieties. Up to now, no phenological model has been simultaneously applied to a large number of grapevine varieties. A new species model for flowering and veraison, the Grapevine Flowering Veraison model (GFV) that was recently developed using an extensive phenological database (Parker et al., 2011) has not been evaluated to this end. The database developed in this study also potentially represents the most extensive phenological resource for grapevines to characterize and evaluate phenological model predictions at a varietal level.

The objectives of this article are (1) to define a general methodology to classify phenology of different varieties of a cultivated species and (2) to use the methodology to classify different varieties for two important phenological stages, flowering and veraison (a stage during which berries soften and their colour changes from green to red for red varieties and green to translucent yellow for white varieties) for *Vitis vinifera* L. and (3) to assess the magnitude of error that is obtained by applying the phenological model to different varieties with respect to (i) the number of observations and (ii) the number of sites used to calibrate a phenological model and (4) the error and significance of parameterization of the model for the contribution of one variety at one site for different years and of one year with one variety at different sites. We illustrate this methodology for the case of the grapevine *V. vinifera* L., classifying 95 and 104 varieties for flowering and veraison respectively. The principle of the classification is that it is sufficiently simple to be used by the agricultural profession in order to diagnose when a variety may flower or undergo veraison or in future climate conditions. Moreover, the methodology presented in this study provides two key outputs beyond a simple classification. Firstly, it provides the degree of confidence in the model predictions for each individual variety and therefore within the classification. This information also indicates the minimal size of the dataset required to provide a robust classification. Secondly, it characterizes the intra-specific variability of important adaptive traits (in this case phenology), allowing to evaluate the capacity of adaptation of the species, and define possible breeding strategies.

2. Materials and methods

2.1. Phenological and temperature data

This study used the updated version of the grapevine phenological database established in Parker et al. (2011) combining all data from the original calibration and validation datasets plus any newly acquired observations for grapevine flowering and veraison observations. Details on the original phenological database and temperature data are provided in Parker et al. (2011).

2.2. Grapevine Flowering Veraison model (GFV)

The Grapevine Flowering Veraison model (GFV) was developed in Parker et al. (2011) with the objective of selecting the simplest model that gave best trade-off between model parsimony and efficiency for flowering and veraison for *V. vinifera* L. This model was calibrated and validated using a database corresponding to 81 varieties and 2278 flowering observations and 2088 veraison observations, spanning from 1960 to 2007 and from 123 different locations (predominantly in France). The same database was used herein to test the model at the variety level. The model selection process involved calibrating three different models, Spring Warming, Uniforc and Unichill (Chuine, 2000; Chuine et al., 2003) and selecting the best fitted model according to Akaike Information

Table 1

Classification and statistical assessment of 95 varieties for their timing of flowering using the GFV model. F^* is the critical degree-day sum (above 0 °C, starting on the 60th day of the year) fitted for each variety. *EF* is the efficiency of the model; RMSE is the root means squared error in days.

Variety	Number of sites	Number of observations	F^*	RMSE	*EF*
Meunier	1	4	1120	2.4	0.48
Poulsard	1	5	1122	0.8	0.93
Jacquère	1	3	1151	2.2	0.72
Savagnin	1	3	1155	1.6	0.69
Elbling	1	6	1155	3.1	0.74
Pinot gris	2	14	1171	3.9	0.91
Altesse	1	3	1172	2.9	0.38
Garanoir	1	9	1179	2.8	0.72
Trousseau	1	3	1179	1.3	0.74
Pinot noir Mariafield	1	9	1183	3.1	0.57
Tempranillo	1	5	1188	2.5	0.59
Gamaret	1	9	1189	2.8	0.68
Orbois	1	6	1192	3.0	−0.02
Aghiorgitiko	3	6	1193	4.2	0.63
Carmenère	1	2	1194	2.1	0.66
Enfariné noir	1	5	1195	4.4	0.48
Muscat à petits grains blancs	1	6	1200	3.5	0.53
Rivairenc	1	2	1201	0.3	0.70
Muscat de Hambourg	6	10	1207	3.5	0.34
Œillade noire	1	3	1209	2.6	−0.21
Nebbiolo	1	8	1211	2.0	0.70
Pinot noir Cortaillod	1	9	1213	3.3	0.43
Chardonnay	21	170	1217	4.9	0.76
Roussanne	1	4	1217	3.5	0.03
Mondeuse noire	1	6	1219	3.9	0.46
Gamay	11	109	1219	5.0	0.63
Pinot noir	12	151	1219	5.1	0.77
Piquepoul blanc	1	2	1222	1.6	−1.69
Aligoté	2	9	1227	3.1	0.92
Pinot blanc	1	9	1228	3.2	0.54
Gewürztraminer	4	26	1230	5.3	0.89
Viognier	2	7	1232	4.3	0.49
Tressot noir	1	5	1236	3.0	−0.09
Fer	1	2	1236	1.4	0.13
Diolinoir	1	9	1236	3.1	0.67
Charmont	1	9	1238	2.7	0.73
Petit Verdot	3	18	1243	4.6	0.34
Cabernet franc	20	102	1245	5.1	0.72
Mancin	1	2	1246	1.0	−2.59
Riesling	5	56	1249	5.9	0.77
Kerner	1	9	1251	3.1	0.61
Piquepoul noir	1	6	1255	3.7	0.55
Xynomavro	1	4	1255	3.7	0.53
Zweigelt blau	1	7	1256	5.9	0.46
Terret gris	1	6	1258	2.5	0.68
Sylvaner	1	9	1258	2.7	0.69
Colombard	4	22	1258	2.6	0.65
Grolleau	1	18	1260	4.3	0.66
Brun Fourca	1	3	1262	2.4	0.47
Terret blanc	1	7	1263	2.3	0.72
Cornalin	1	8	1263	2.0	0.71
Portugais bleu	1	8	1265	4.5	0.71
Cinsaut	3	13	1265	2.8	0.27
Bourboulenc	1	4	1266	3.9	0.57
Grenache blanc	1	2	1267	0.7	0.52
Portan	2	12	1268	3.7	0.77
Merlot	14	107	1269	5.6	0.79
Vermentino	1	2	1270	0.6	0.95
Clairette	1	9	1271	3.7	0.63
Calitor	1	2	1271	1.1	−3.41
Colombaud	1	4	1276	2.7	0.56
Chasselas	4	68	1276	6.2	0.81
Räuschling	1	9	1277	2.9	0.66
Grenache	35	127	1277	6.0	0.78
Humagne rouge	1	9	1278	2.3	0.77
Arvine	1	9	1278	3.3	0.63
Bondola	1	9	1278	2.4	0.73
Syrah	26	126	1279	4.8	0.84
Chenin	4	29	1280	4.8	0.73
Sauvignon	9	102	1282	5.1	0.82
Humagne blanc	1	9	1286	2.9	0.62
Sangiovese	4	49	1287	4.8	0.65
Carignan	6	44	1288	4.8	0.87
Doral	1	8	1296	2.7	0.44
Amigne	1	9	1297	2.8	0.65

Table 1 (*Continued*)

Variety	Number of sites	Number of observations	F^*	RMSE	*EF*
Cabernet-Sauvignon	11	131	1299	5.2	0.77
Cot	4	31	1306	4.4	0.74
Ségalin	1	6	1308	3.6	0.60
Chenanson	1	7	1309	3.1	0.68
Terret noir	1	3	1316	1.1	0.80
Semillon	3	26	1317	4.1	0.85
Marselan	2	11	1338	3.3	0.79
Marsanne	2	12	1338	4.5	0.89
Muscat d'Alexandrie	2	15	1343	6.3	0.87
Mourvèdre	25	93	1354	4.3	0.63
Egiodola	1	7	1354	1.7	0.82
Tannat	2	8	1363	3.8	0.79
Kadarka	1	8	1368	5.0	0.65
Ugni blanc	6	95	1376	5.0	0.79
Arinarnoa	2	15	1377	7.1	0.28
Ekigaina	1	7	1378	2.9	0.67
Muscadelle	1	16	1379	4.6	0.45
Pinotage	1	4	1387	4.0	0.62
Caladoc	2	8	1390	3.8	0.72
Semebat	1	7	1411	2.9	0.68

Criterion (AIC, Burnham and Anderson, 2000), that was called the GFV model. A daily temperature cap was tested across the range of daily average temperature 15–25 °C. Capping higher temperature values did not improve the performance of the model (see Parker et al., 2011 for details).

The GFV model is a parameterized model based on the Spring Warming model (SW) as described by Hunter and Lechowicz (1992) also known as Thermal time model (Robertson, 1968) and Growing Degree-Days model (Wang, 1960). In this latter model a phenological stage occurs when a critical state of forcing S_f, defined as a sum of degree-days from a starting date t_0, reached a particular value F^* (Eq. (1)).

$$S_f(t_s) = \sum_{t_0}^{t_s} R_f(x_t) \geq F^* \tag{1}$$

The state of forcing is described as a daily sum of the rate of forcing, R_f, which starts at t_0 defined as the 60th day of year (DOY) for the GFV model; flowering and veraison are therefore simulated independently of prior developmental stages.

$$R_f(x_t) = GDD(x_t) = \begin{cases} 0 & \text{if } x \leq T_b \\ x_t - T_b & \text{if } x_t > T_b \end{cases} \tag{2}$$

where T_b corresponds to a base temperature set at 0 °C for GFV (Parker et al., 2011), above which the thermal summation is calculated, x_t is the daily arithmetic mean temperature (the sum daily minimum and maximum temperature divided by two).

2.3. Model parameterization and statistical assessment of the GFV model at the variety level

The parameter F^* was adjusted independently for each variety for both phenological stages of flowering and veraison, with parameters t_0 and T_b fixed to 60 days and 0 °C as determined in Parker et al. (2011) for the grapevine. For each variety the following statistical criteria were considered: (1) model efficiency which corresponds to the percentage of variance explained by the model (*EF*; Nash and Sutcliffe, 1970; Greenwood et al., 1985, Eq. (3)) where a negative value indicates that the model performs worse than the null model (mean date of flowering or veraison) for a variety, and a value above zero indicates that the model explains more variance than the null model, with a maximum value of one when the model explains all the variance of the data; (2) the root mean squared error (RMSE; Eq. (4)) which gives the mean error of the prediction in days,

$$EF = 1 - \left(\frac{\sum_{i=1}^{n} (S_i - O_i)^2}{\sum_{i=1}^{n} (O_i - \bar{O})^2} \right) \tag{3}$$

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n} (S_i - O_i)^2}{n}} \tag{4}$$

where O_i is the observed value, S_i is the simulated value, $\bar{O}$ is the mean observed value, and n is the number of observations; and (3) calculation of the 95% confidence interval (CI). The CI is obtained by making the optimization algorithm (Metropolis algorithm) used to fit the model parameters explore the parameter space around the global optimum found at the end of its search. The Fisher statistic is calculated for each parameter set to retain parameter sets that provide a $p < 0.05$ of the Fisher statistics and therefore fall within the 95% CI around the optimal parameter set.

2.4. Spatial and temporal evaluation of the GFV varietal models

The five most represented varieties (combined total of flowering and veraison observations) were selected to characterize the relative importance of site (spatial) versus year (temporal) variation on the varietal models. For the site selection using the five selected varieties as the data subset, the five most represented sites were subsequently chosen for flowering and veraison independently (largest total number of observations); not all varieties were represented at each site even though the sites had the greatest number of observations for the data subset. The five most represented years were selected for flowering and veraison independently (from the five variety data subset) for analysis of temporal effects. The F^* value of the model was adjusted independently for the pooled data for the five selected sites (referred to as 'Mean' model) and for each variety by site or variety by year combination. RMSE, *EF*, and Mean Bias Error (*MBE*) (Eq. (5)) were calculated for each variety by site and variety by year combination

$$MBE = \frac{\sum_{i=1}^{n} S_i - O_i}{n} \tag{5}$$

where O_i is the observed value, S_i is the simulated value and n is the number of observations.

For each variety, the significance of the site effect or year effect was evaluated by the Fisher test following the methodology of Chuine et al. (2000): the site/year effect was estimated and tested

Table 2

Classification and statistical assessment of 104 varieties for their timing of veraison using the GFV model. F^* is the critical degree-day sum (above 0 °C, starting on the 60th day of the year) fitted for each variety. *EF* is the efficiency of the model; RMSE is the root means squared error in days.

Variety	Number of sites	Number of observations	F^*	RMSE	*EF*
Garanoir	1	9	2286	3.9	0.44
Verdelho	1	3	2337	3.3	0.69
Charmont	1	9	2363	4.6	0.21
Chasselas	4	72	2374	6.2	0.87
Meunier	1	11	2379	3.8	0.65
Gamaret	1	9	2406	3.6	0.32
Elbling	1	8	2420	4.4	0.73
Doral	1	8	2437	3.6	0.12
Poulsard	1	7	2441	3.2	0.27
Savagnin	1	6	2443	2.9	0.79
Pinot noir Mariafield	1	9	2450	4.9	0.07
Portugais bleu	1	7	2461	3.1	0.86
Pinot noir Cortaillod	1	9	2466	4.8	−0.06
Pinot gris	2	15	2472	4.7	0.89
Diolinoir	1	9	2476	4.3	−0.29
Tempranillo	1	11	2484	5.2	0.40
Orbois	1	11	2487	4.2	0.47
Sylvaner	1	9	2489	3.0	0.49
Gouais blanc	1	7	2493	3.9	0.71
Pinot blanc	2	12	2500	4.5	0.89
Aligoté	2	13	2502	4.2	0.85
Trousseau	1	10	2506	3.1	0.72
Gewurztraminer	4	28	2510	6.4	0.87
Pinot noir	7	80	2511	7.8	0.75
Muscat à petits grains blancs	2	15	2520	3.9	0.92
Kerner	1	9	2526	3.2	0.23
Sauvignon	9	73	2528	5.6	0.85
Gamay	8	75	2533	5.3	0.68
Portan	2	10	2537	5.7	0.79
Semillon	3	27	2537	4.1	0.87
Räuschling	1	8	2539	3.1	0.57
Chardonnay	17	105	2547	6.5	0.82
Muscadelle	1	15	2553	5.0	0.02
Bondola	1	9	2554	4.3	0.26
Zweigelt blau	1	6	2568	4.4	0.61
Jacquère	1	7	2569	4.6	0.57
Tressot noir	1	9	2584	4.1	0.67
Riesling	6	54	2590	6.8	0.78
Colombard	6	27	2591	3.5	0.75
Enfariné noir	1	7	2596	3.6	−0.02
Viognier	3	18	2600	5.9	0.51
Syrah	23	103	2601	5.6	0.89
Carmenère	1	4	2605	2.7	0.64
Altesse	1	9	2615	6.4	0.55
Grenache blanc	2	4	2626	1.3	0.94
Egiodola	2	10	2627	6.9	0.67
Humagne blanc	1	9	2627	3.8	0.48
Amigne	1	9	2629	3.7	0.56
Merlot	17	162	2636	6.6	0.73
Marselan	4	16	2641	5.2	0.79
Brun Fourca	1	4	2642	3.8	0.33
Œillade noire	1	4	2645	2.0	0.84
Grolleau	1	17	2650	4.3	0.71
Ruby Cabernet	3	10	2654	4.9	0.07
Cot	2	13	2658	6.0	0.60
Pardotte	1	4	2660	1.6	0.95
Gros Cabernet	1	3	2664	1.9	0.84
Ségalin	1	6	2670	2.4	0.84
Barbera	1	4	2675	3.0	−3.04
Marsanne	3	19	2676	4.0	0.93
Cinsaut	4	17	2680	5.4	0.09
Kardarka	1	7	2682	5.7	0.69
Muscat de Hambourg	3	7	2685	5.9	−1.89
Fer	1	6	2689	5.1	0.28
Cabernet-Sauvignon	15	178	2689	6.9	0.64
Arvine	1	9	2692	3.8	0.27
Bourboulenc	1	9	2692	9.4	0.00
Cabernet franc	20	87	2692	7.1	0.63
Rivairenc	1	4	2695	2.2	0.81
Mourvèdre	6	22	2706	4.9	0.88
Cornalin	1	8	2707	5.4	0.43
Chenin	1	6	2712	8.1	−1.56
Mondeuse noire	1	5	2713	4.0	0.36
Chenanson	1	6	2721	2.3	0.87
Sangiovese	6	72	2729	7.3	0.20

Table 2 (*Continued*)

Variety	Number of sites	Number of observations	*F**	RMSE	*EF*
Nebbiolo	2	11	2734	4.2	0.89
Xynomavro	1	7	2736	7.2	−2.34
Calitor	1	3	2738	6.7	−1.65
Vermentino	3	23	2739	6.7	−0.12
Piquepoul noir	1	7	2739	5.0	0.42
Piquepoul blanc	2	6	2739	4.6	0.62
Terret noir	1	4	2741	2.9	0.52
Aghiorgitiko	3	6	2741	10.0	−1.17
Muscat d'Alexandrie	3	23	2742	7.6	0.89
Carignan	9	44	2749	6.3	0.89
Humagne rouge	1	9	2758	4.4	0.14
Clairette	1	13	2759	5.2	0.60
Grenache noir	34	110	2761	6.4	0.87
Roussanne	3	12	2774	3.4	0.77
Primitivo	1	7	2776	5.2	0.01
Pinotage	1	4	2780	4.4	0.72
Colombaud	1	4	2785	4.4	0.61
Ugni blanc	6	89	2799	7.8	0.74
Mancin	1	4	2800	3.2	0.60
Terret gris	1	9	2802	6.1	−0.07
Gros Manseng	1	3	2804	3.2	0.69
Sciaccarello	1	9	2831	3.2	0.35
Terret blanc	1	7	2838	5.6	0.07
Tannat	2	12	2840	5.0	0.54
Petit Verdot	5	26	2849	6.6	0.36
Caladoc	2	7	2867	9.8	0.59
Arinarnoa	4	18	2879	8.7	0.39
Ekigaina	1	6	2934	6.2	0.55
Semebat	1	6	2941	7.1	0.53

by comparing the residual sum of squares of the model fitted with all sites/years ('Mean model') to the sum of the residual sums of square of the models fitted each with one site/one year.

3. Results

3.1. Flowering classification

*F** values were calculated for 95 varieties. The model predicted the time of appearance of flowering better than the null model (mean date) for 89 of these varieties (indicated by the positive *EF* values in Table 1). Negative *EF* values were obtained for varieties for which the sampling's spatial and temporal variability was low e.g. either data collected from one site or less than six years of records. However, despite negative *EF* values for six varieties, the corresponding RMSE values indicated that the quality of the model prediction was still accurate to within three days. The efficiency of the model was equal to or greater than 0.5 for 73 varieties and equal to or greater than 0.75 for 25 varieties. Overall the RMSE error was less than one week for all varieties except Arinarnoa (RMSE of 7.1). There was a 291 °C.d. difference between the earliest and latest variety, which for example, corresponds to 16 days, when taking into account an average temperature of 18 °C during the flowering period.

3.2. Veraison classification

*F** values corresponding to veraison were calculated for 104 varieties. The model predicted the veraison date better than the null model for 93 varieties (positive *EF* values in Table 2). Low spatial variability (only one site in the case of eight of these varieties) and temporal variability (nine observations or less with the exception of Vermentino) were again noted for the negative efficiency obtained for 11 varieties. The efficiency of the model was equal to or greater than 0.5 for 64 varieties and equal to or greater than 0.75 for 31 varieties. The RMSE values were less than one week in all cases except 12 varieties, with the largest RMSE value of 10 days for Aghiorgitiko. There was a 655 °C.d. difference between the earliest and latest variety which was almost two fold greater than the difference observed for flowering. This would for example correspond to 31 days calculated with an average temperature of 21 °C during the veraison period.

3.3. Order of classifications

In comparing the *F** values for flowering and those calculated for veraison, our results indicated that the order obtained for flowering was not the same for veraison and the length between these two stages as predicted by the model, differed by variety (Fig. 1a–c). For example, Cabernet franc which was the 31st position in the list for Flowering in Table 1 but at the 63rd position (equal with Arvine and Bourboulenc) for veraison in Table 2. Conversely, some varieties which flowered later had subsequently an early veraison (e.g. Semillon was 64th in the list for flowering but advanced to the position 29th equal with Portan for veraison).

3.4. Assessing the precision of *F** for each variety

The magnitude of the confidence interval was dependent on the number of observations and number of sites used to fit the model parameters for both phenological stages (Fig. 2a and b). In excess of approximately 20 observations and more than three sites for flowering and veraison, the precision of *F** did not improve substantially. Varieties with this combination of data all had CIs of 100 °C.d. or less except for Vermentino (145 °C.d.) and Petit Verdot (128 °C.d.) and Muscat d'Alexandrie (CI not possible to define) for veraison. It was still possible to estimate *F** values with a similar precision with less data, but in most of these cases the confidence interval increased drastically (Figs. 3 and 4). For flowering, eight varieties had only two observations (Table 1), and it was not possible to calculate a CI for these varieties. For veraison, all varieties had three or more observations but it was not possible to calculate CIs for nine varieties. However, for flowering (Fig. 2a and closed circles in Fig. 3a–c) 47 out of the 87 varieties for which it was possible to calculate CI values had a CI range of less than or equal to 100 °C.d., and 73 varieties had a CI range equal to or less than 200 °C.d. For veraison, 22

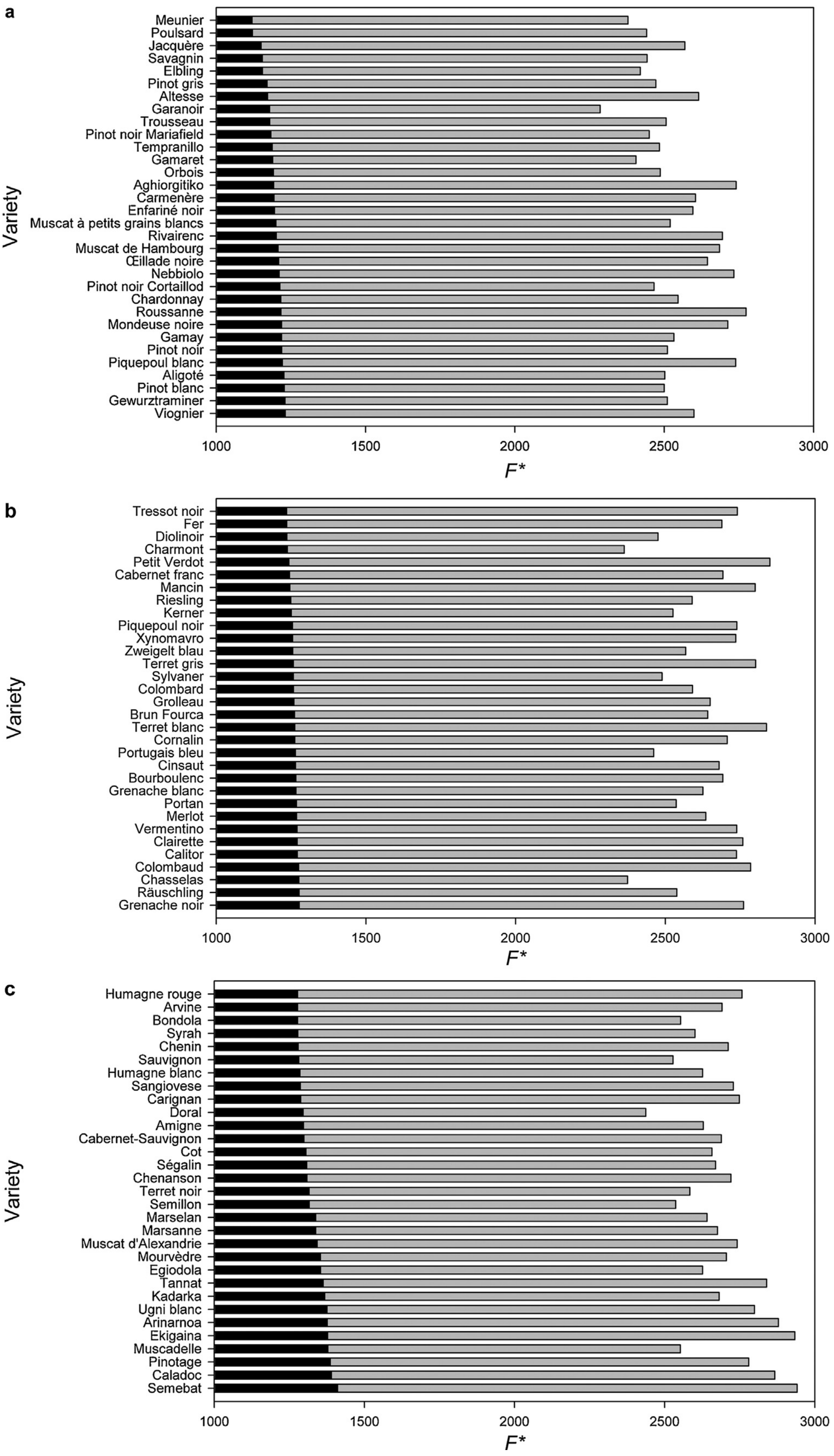

Fig. 1. Thermal time of flowering and veraison for 95 varieties for which there was both flowering and veraison data. Black columns represent the F^* value for flowering, grey columns represent the thermal time for flowering to veraison. Varieties are presented in order of appearance of flowering.

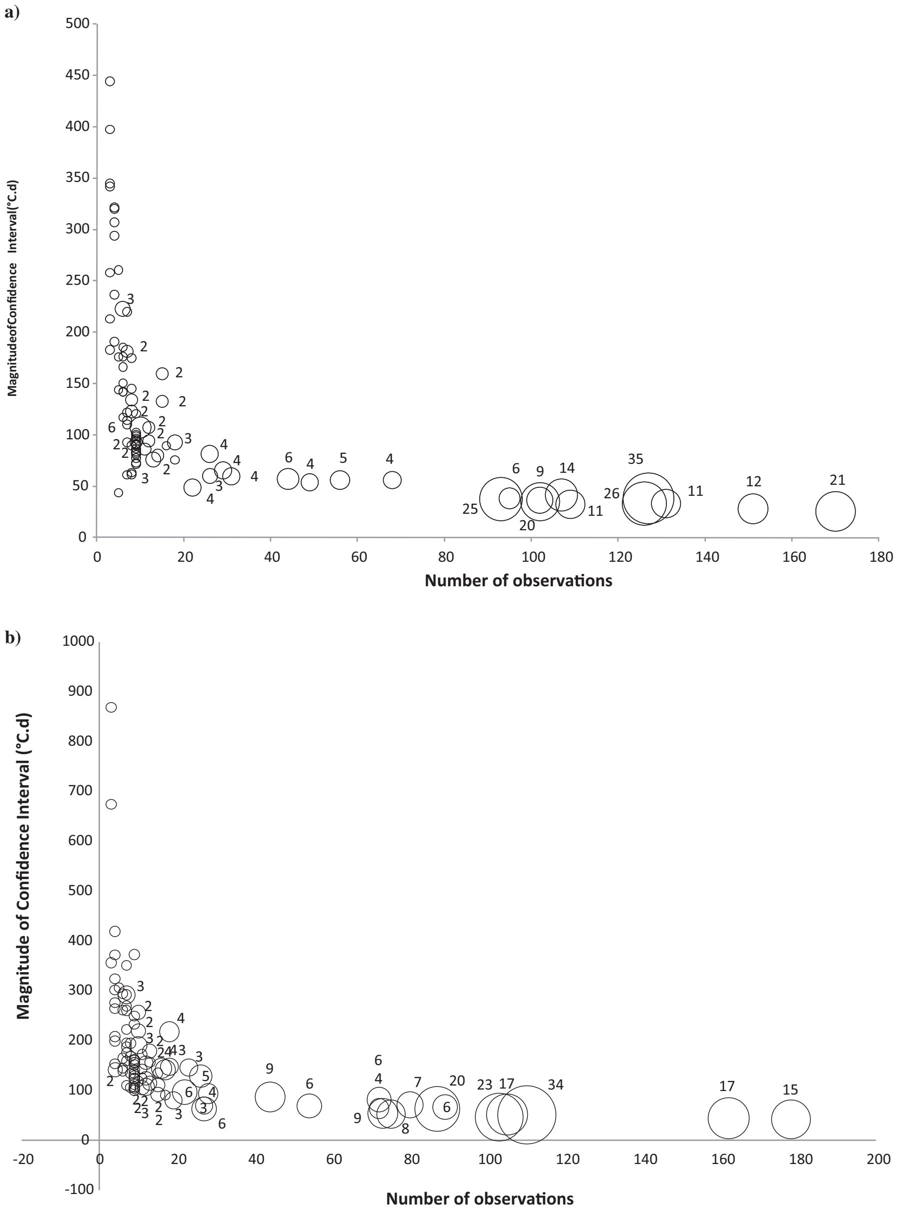

Fig. 2. Relationship between the magnitude of confidence interval for the thermal time (F^*), the number of observations and the number of sites used to calibrate this parameter for each variety. Data points were scaled to the number of sites used (numbers correspond to the number of sites and where no number is present, the number of sites = 1) (a) flowering and (b) veraison.

varieties had CI ranges less than 100 °C.d but a greater proportion of varieties ($n = 48$) had CIs within the range of 100–200 °C.d.

Given the overlaps of CIs and the number of varieties that were classified (Figs. 3 and 4), it was not possible to define distinct groups of varieties based solely on the F^* and CI values. Therefore the data was divided into approximately three equivalent sized groups: early, middle and late. For example although Gewurztraminer which is the last variety of the early group for flowering (Fig. 3a) with a CI less than 100 (CI = 81), its CI overlapped with that of all varieties of the middle group (Figure 3b) and the late group up to and including Amigne, after which there was still overlap with six of the remaining 20 varieties (Fig. 3c).

3.5. Spatial and temporal evaluation of variety F^* values

For all variety by site tests, the pooled varietal model (Mean model) described the majority of variance in the data (% variance greater than 75% in all cases) (Tables 3 and 4). For the four out of five varieties for flowering and the three out of five varieties that showed significant site effects when the GFV model was parameterized at the site level but the % variance accounted for by the site effect was less than 15% (and less than 5% in all cases for veraison). In considering the hierarchy of varieties by site, in most cases the order was consistent with the order obtained for the Mean model values (Tables 3 and 4). For flowering, this corresponded to Chardonnay < Cabernet-Sauvignon and Merlot < Syrah and Grenache and with a slightly different order for the site, Aude. For veraison the order of varieties from earliest to latest were Chardonnay < Syrah < Merlot < Cabernet Sauvignon < Grenache; Languedoc 2 had comparatively large F^* values a fewer number of observations than other sites for the same variety.

EF values indicated that only for veraison were four site by variety models better described by mean data (negative values corresponding to the null model performing better) than using thermal

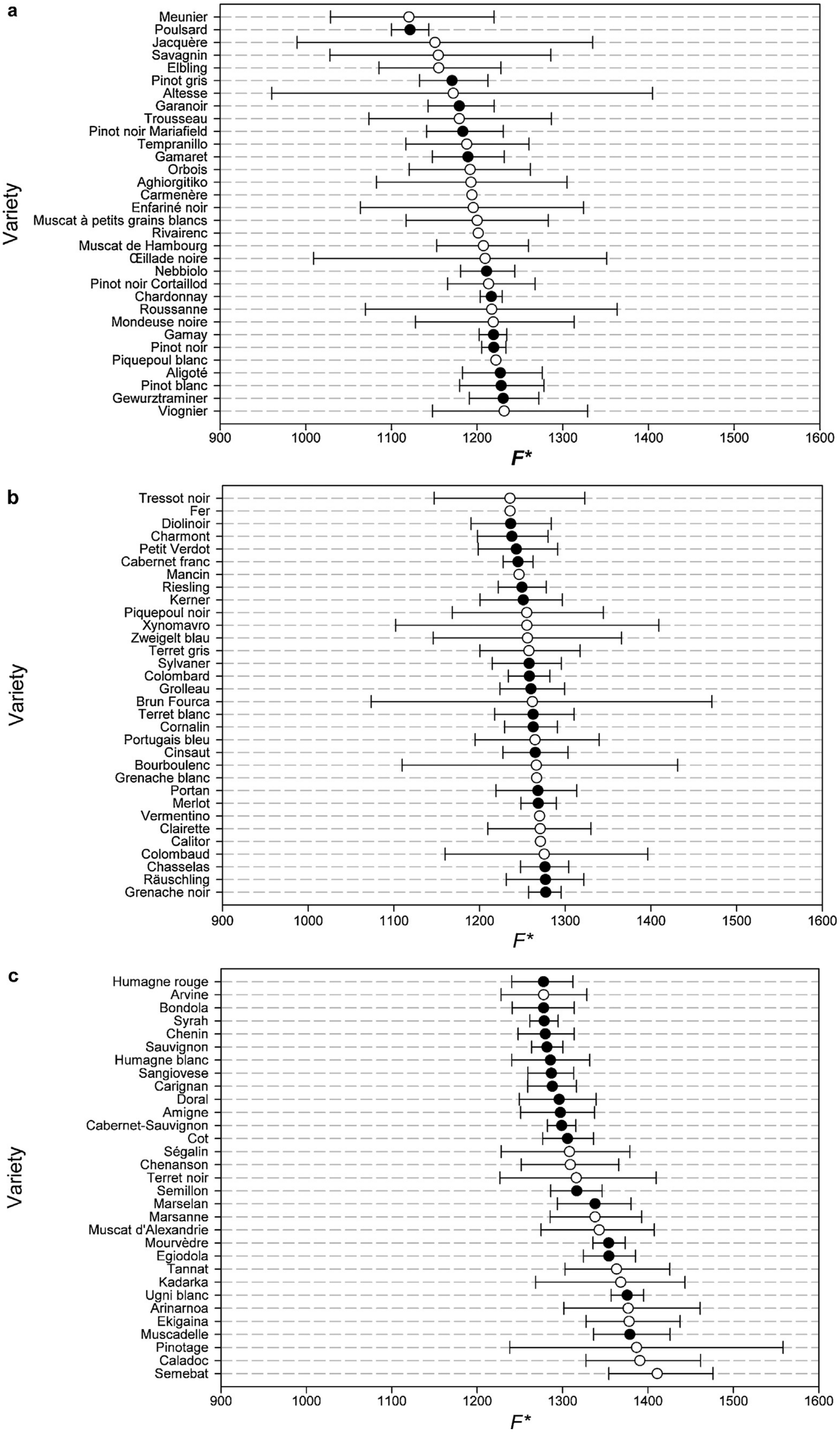

Fig. 3. Time of flowering for early (a), middle (b) and late varieties (c) based of the F^* parameter estimates. Closed circles (●) represent F^* values where the total Confidence Interval (CI) size was less than 100 °C.d; open circles (○) represent CIs greater than 100 °C.d or no CI; where no CI is present, it was not possible to calculate a CI due to small sample size or data that was too greatly dispersed.

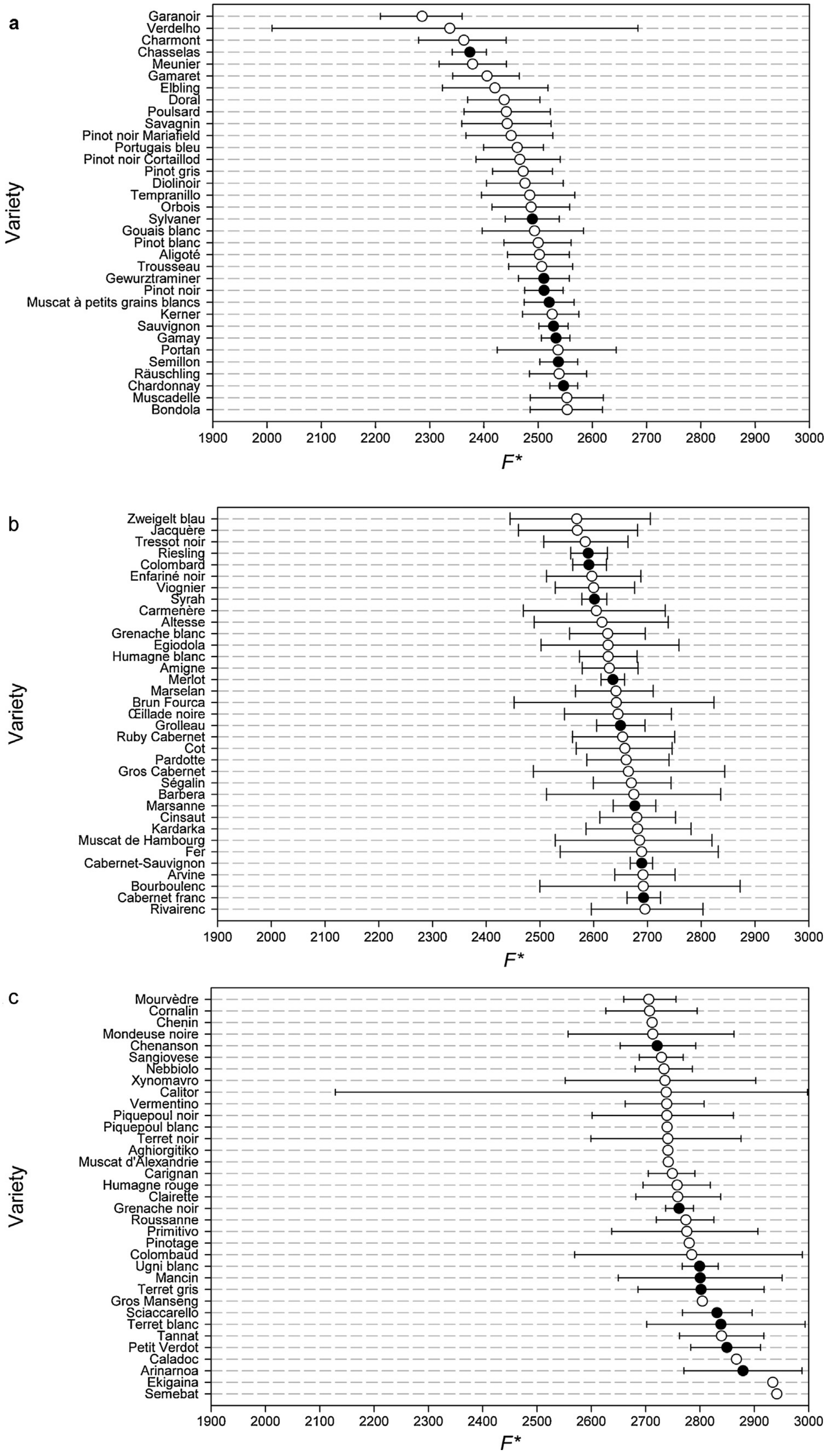

Fig. 4. Timing of veraison for early (a), middle (b) and late varieties (c) based on the F^* parameter estimate. Closed circles (●) represent F^* values where the total confidence interval (CI) size was less than 100 °C.d; open circles (○) represent CIs greater than 100 °C.d or no CI; where no CI is present, it was not possible to calculate a CI due to small sample size or data that was too greatly dispersed.

Table 3
Measure of spatial variation between populations for the five most represented sites for flowering of the five most represented varieties. *n*: number of observations; RMSE: root mean squared error; *EF*: model efficiency; MBE: Mean Bias Error; *F**: the critical degree-day sum using the Grapevine Flowering Model; SS: sum of squares; MS: minimum square (sum of square/degree of freedom); *F*: Fisher statistic; *p*: probability. Varieties are presented in alphabetical order, sites are presented in order of *F** values. *F* and *p* values reported for site effect; bold values indicate significant variance between sites ($p < 0.05$).

	n	RMSE	*EF*	MBE	*F**		df	SS	MS	*F*	*p*	% variance
Cabernet-Sauvignon												
Mean[a]	67	5.2	0.83	0.24	1296	Model[b]	1	8638.16	8638.16			82.89
Languedoc 1	20	3.6	0.45	0.09	1201	Site	4	807.46	201.87	**12.62**	**0.000**	**7.75**
Switzerland	9	3.2	0.55	−0.06	1293	Residual	61	975.48	15.99			
Loire	18	3.3	0.71	−0.03	1316	Total	66	10,421.10				
Alsace	13	5.2	0.60	−0.02	1327							
Aude	7	3.5	0.47	−0.06	1396							
Chardonnay												
Mean	40	6.7	0.80	0.37	1211	Model	1	7033.07	7033.07			79.51
Languedoc 1	17	7.6	0.24	0.08	1151	Site	2	312.57	156.29	3.75	0.033	3.53
Switzerland	9	3.6	0.63	−0.02	1211	Residual	36	1499.34	41.65			
Alsace	14	5.3	0.49	0.17	1266	Total	39	8844.98				
Grenache												
Mean	55	7.5	0.77	0.16	1313	Model	1	10,093.24	10,093.24			76.74
Languedoc 1	20	3.4	0.53	0.10	1202	Site	4	1505.66	376.42	**11.87**	**0.000**	**11.45**
Switzerland	6	2.6	0.47	0.13	1314	Residual	49	1554.45	31.72			
Loire	10	11.3	0.39	−0.26	1329	Total	54	13,153.35				
Aude	7	2.2	0.74	−0.01	1395							
Alsace	12	4.3	0.71	0.22	1408							
Merlot												
Mean	39	5.1	0.86	0.42	1297	Model	1	6446.21	6446.21			86.27
Languedoc 1	10	2.7	0.32	0.05	1187	Site	3	845.31	281.77	**53.11**	**0.000**	**11.31**
Switzerland	8	3.2	0.61	−0.31	1270	Residual	34	180.38	5.31			
Alsace	14	4.9	0.66	0.14	1341	Total	38	7471.9				
Aude	7	2.2	0.71	0.06	1344							
Syrah												
Mean	67	5.3	0.84	0.33	1298	Model	1	9886.38	9886.38			84.22
Languedoc 1	25	3.4	0.44	0.04	1214	Site	4	1192.48	298.12	**27.57**	**0.000**	**10.16**
Alsace	14	4.5	0.65	0.14	1321	Residual	61	659.59	10.81			
Switzerland	9	3.2	0.52	0.04	1335	Total	66	11,738.45				
Aude	7	2.5	0.70	−0.04	1340							
Loire	12	6.1	0.51	0.44	1354							

[a] Mean corresponds to varietal model calculated from the combined data across the sites (all spatial and temporal variation).

[b] Model refers to the varietal model parameterized across the five sites combined.

summations. There was no systematic bias across the different varieties: that is the *MBE* values were neither all positive nor all negative for a given site across all the varieties. The site by variety RMSE values were greater in three site by varietal models for flowering and six for veraison.

The magnitude of difference between mean varietal *F** values (for example the difference *F** between Syrah and Chardonnay) was greater than the average difference between the site by varietal models (i.e. sum of each site by variety difference to the mean/number of sites) compared to the Mean model varietal value.

For the year by variety tests, only Cabernet-Sauvignon had a significant year effect for both phenological stages accounting for 14 and 8% of the variance; the site effect was significant for veraison of Syrah accounting for 13.96% of the total variance (Tables 5 and 6). The hierarchy of varieties was more variable across the years than for the spatial analysis for flowering and veraison; however for both flowering and veraison, the Mean model *F** values were closer than for the dataset used for spatial analysis of the classification. For veraison, in general the order of varieties was maintained with interchange between the relative positions for Cabernet-Sauvignon for the different years. The differences between early and late varieties for the mean values were maintained in most cases for the variety by year models for both phenological stages. Adjusting the model by year, did not improve the *EF* in most cases and did not give a consistent directional error across varieties for each year assessed by *MBE*; three and five varieties for flowering and veraison had higher RMSE respectively compared to the Mean varietal models.

4. Discussion

4.1. Phenophases and characterization of flowering and veraison for varieties of V. vinifera L.

Using the GFV model and the accompanying extensive grapevine phenological database, we were able to provide an extensive and precise characterization for the timing of flowering and veraison for a wide range of varieties.

Each variety had a different number of observations and sites contributing to the estimated *F** values (Tables 1 and 2). Tables 1 and 2 indicate that there is no tendency for red varieties to have lower RMSE and higher *EF*s than white varieties although the assessment of colour change is more readily observed in the field than assessing the change from opaque to translucent for white varieties. Duchene et al. (2010) also obtained slightly different phenophases for several grapevine varieties in Colmar, so the results presented here are consistent with this idea. Given that most RMSEs obtained were less than one week, the model predicted well these two phenological stages even using a heterogeneous database. Thus, the precision obtained in this study and in the preceding work (Parker et al., 2011) is comparable or better than that obtained in previous studies on grapevine phenology (Bindi et al., 1997; Duchene et al., 2010; Garcia de Cortazar Atauri, 2006; Moncur et al., 1989; Oliveira, 1998; Williams et al., 1985) where authors worked with few varieties and usually one or two observation sites.

Veraison showed a larger amplitude in thermal summation than flowering between the earliest and latest variety. This was also demonstrated by Duchene et al. (2010) suggesting that this larger

Table 4

Measure of spatial variation between populations for the five most represented sites for veraison of the five most represented varieties. n: number of observations; RMSE: root mean squared error; *EF*: model efficiency; MBE: Mean Bias Error; F^*: the critical degree-day sum using the Grapevine Flowering Model; SS: sum of squares; MS: minimum square (sum of square/degree of freedom); F: Fisher statistic; p: probability. Varieties are presented in alphabetical order, sites are presented in order of F^* values. F and p values reported for site effect; bold values indicate significant variance between sites ($p < 0.05$).

	n	RMSE	*EF*	MBE	F^*		df	SS	MS	F	p	% variance
Cabernet-Sauvignon												
Mean[a]	50	5.4	0.89	−0.31	2646	Model[b]	1	11,775.86	11,775.86			88.93
Alsace	13	6.2	0.57	−0.09	2610	Site	4	391.21	97.80	**4.00**	**0.007**	2.95
Languedoc 3	8	3.7	0.46	−0.09	2635	Residual	44	1075.35	24.44			
Languedoc 1	17	4.1	0.35	0.04	2654	Total	49	13,242.42				
Switzerland	9	4.4	0.52	−0.36	2654							
Languedoc 2	3	1.4	0.89	−0.03	2890							
Chardonnay												
Mean	41	5.8	0.90	0.08	2494	Model	1	12,271.69	12,271.69			89.84
Languedoc 3	4	3.7	−0.91	0.20	2415	Site	4	123.50	30.87	0.85	0.501	0.90
Languedoc 1	10	5.1	0.19	0.10	2461	Residual	35	1264.86	36.14			
Switzerland	9	2.5	0.63	−0.13	2464	Total	40	13,660.05				
Languedoc 2	4	5.1	−2.94	−0.50	2536							
Alsace	14	7.5	0.51	0.41	2537							
Grenache												
Mean	40	5.6	0.92	0.21	2757	Model	1	15,089.24	15,089.24			92.42
Languedoc 1	19	4.2	0.19	1.40	2707	Site	3	134.63	44.88	1.42	0.252	0.82
Switzerland	6	6.4	0.20	−1.02	2757	Residual	35	1102.91	31.51			
Alsace	12	6.3	0.73	−0.03	2776	Total	39	16,326.78				
Languedoc 2	3	3.8	0.68	0.07	2828							
Merlot												
Mean	53	5.8	0.89	0.04	2603	Model	1	14,279.81	14,279.81			88.87
Languedoc 3	9	4.2	0.09	0.11	2533	Site	4	395.97	98.99	**3.34**	**0.017**	**2.46**
Languedoc 1	18	4.6	0.71	−0.08	2579	Residual	47	1391.69	29.61			
Alsace	14	6.6	0.62	0.01	2607	Total	52	16,067.47				
Switzerland	9	5.1	0.28	0.03	2619							
Languedoc 2	3	0.4	1.00	0.00	2834							
Syrah												
Mean	53	5.7	0.91	0.32	2591	Model	1	17,195.24	17,195.24			90.99
Languedoc 3	8	3.9	−0.24	0.18	2458	Site	4	619.11	154.78	**6.71**	**0.000**	**3.28**
Languedoc 1	19	3.3	0.37	−0.03	2547	Residual	47	1083.46	23.05			
Alsace	14	6.5	0.67	−0.25	2587	Total	52	18,897.81				
Switzerland	9	3.9	0.65	−0.22	2673							
Languedoc 2	3	3.8	−0.75	−0.07	2721							

[a] Mean corresponds to varietal model calculated from the combined data across the sites (all spatial and temporal variation).

[b] Model refers to the varietal model parameterized across the five sites combined.

difference for the veraison phase is not an effect of our database. Two simple explanations for the greater difference for veraison are (1) larger degree day differences for veraison due to heat summations actually having larger absolute values and (2) other processes like crop management, water status or clonal variability could potentially have a greater impact on veraison than on flowering.

4.2. Robustness of the classification

Where the magnitude for the confidence interval was less than 100 °C.d., it was difficult to improve the prediction by increasing the number of sites or observations. Below this threshold, other factors influencing phenology (notably crop management, water status, or clonal variability) likely contributed to the remaining variability. This result has two implications: (1) our methodology indicates that the predictability represented by CI due to other factors than temperature for the most part is small and consequently it does not hinder our ability to provide accurate predictions for flowering and veraison with the GFV model for many varieties and (2) this methodology indicated a minimum sample data required (number of data and sites) to minimize our confidence interval in describing the temperature effect on phenology. This corresponded to a conservative estimate around the inflexion of the curvilinear relationships in Fig. 2a and b, whereby a data quantity necessary for prediction would correspond to approximately 30 points and a minimum of 3 sites. It may not always be possible to obtain this level of data so the process presented here of statistical assessment by CIs, *EF* and RMSE values becomes even more important in this context. When defining new observation networks for other species the statistical assessment outlined here may aid decisions regarding the quantity of data required to characterize these kinds of processes (phenology or others).

We included in our classification varieties for which we could not calculate a CI due to a lack of data, because the F^* value obtained can still be used to indicate if the variety is early or late relatively to the varieties we have classified. However, the robustness of the F^* value must be treated with caution for some varieties and interpreted in the light of Fig. 2 results. The F^* value could change (and therefore the position of the variety in the classification) if more data becomes available in future studies notably for those varieties with less than 20 observations in less than 3 sites. Further data collection is warranted for the varieties for which a CI value could not be ascertained or for those which had confidence interval ranges in excess of 200 °C.d. Varieties that would still show a large CI even when largely enough data was available to parameterize the model, may either show a certain level of genetic variability for phenological traits or the data available for these varieties may be biased.

The assessment of site by variety and year by variety effects involved testing a subset of data; the variety, year and site selection corresponded to the most represented combinations in the data base. Even with a subset of data, the model accounted for most of the spatial and temporal variation. Given that the hierarchy of varieties was consistently maintained for the site by variety combinations, this indicates that our varietal parameterization were robust at predicting correctly the hierarchy of varieties and further

Table 5
Measure of temporal variation between populations for the five most representedyears for flowering of the five most represented varieties. *n*: number of observations; RMSE: root mean squared error; *EF*: model efficiency; MBE: Mean Bias Error; F^* the critical degree-day sum using the Grapevine Flowering Model; SS: sum of squares; MS: minimum square (sum of square/degree of freedom); *F*: Fisher statistic; *p*: probability. Varieties are presented in alphabetical order, years are presented in order of F^* values. *F* and *p* values reported for year effect; bold values indicate significant variance between years ($p < 0.05$).

	N	RMSE	*EF*	MBE	F^*		df	SS	MS	*F*	*p*	% variance
Cabernet-Sauvignon												
Mean[a]	23	4.2	0.72	0.26	1267	Model[b]	1	1039.65	1039.65			71.95
2003	5	4.1	0.03	0.40	1216	Year	4	201.67	50.42	**4.46**	**0.011**	**13.96**
1999	8	5.1	0.67	0.43	1266	Residual	18	203.64	11.31			
2004	3	1.7	0.87	−0.10	1275	Total	22	1444.96				
2002	5	2.8	0.84	−0.22	1292							
2005	2	2.6	0.85	0.25	1292							
Chardonnay												
Mean	57	3.3	0.81	0.22	1203	Model	1	2661.93	2661.93			80.73
2003	11	3.6	0.69	−0.04	1154	Year	4	77.63	19.41	1.81	0.141	2.35
2004	11	3.2	0.69	0.03	1188	Residual	52	557.95	10.73			
2005	14	2.6	0.80	0.03	1204	Total	56	3297.51				
2002	10	3.5	0.80	0.24	1212							
1999	11	2.3	0.89	0.11	1232							
Grenache												
Mean	23	5.8	0.45	−0.34	1230	Model	1	640.35	640.35			45.24
1999	5	10.5	0.43	−0.30	1186	Year	4	76.75	19.19	0.49	0.740	5.42
2005	5	4.5	0.08	−0.52	1221	Residual	18	698.38	38.80			
2002	4	2.0	0.78	−0.08	1239	Total	22	1415.48				
2003	5	2.2	0.24	0.06	1251							
2004	4	1.6	−0.15	0.05	1284							
Merlot												
Mean	25	3.2	0.71	0.07	1197	Model	1	611.27	611.27			71.19
2005	4	1.9	−0.77	−0.02	1174	Year	4	12.17	3.04	0.26	0.901	1.42
2003	6	2.8	−3.31	0.37	1189	Residual	20	235.20	11.76			
2002	6	1.5	0.89	−0.12	1191	Total	24	858.64				
2004	4	2.2	−0.75	0.05	1214							
1999	5	5.3	0.70	−0.12	1215							
Syrah												
Mean	29	3.4	0.77	0.09	1267	Model	1	1092.33	1092.33			77.07
2003	7	3.0	0.12	−0.19	1232	Year	4	92.55	23.14	2.39	0.079	6.53
2005	6	3.8	−2.21	−0.47	1239	Residual	24	232.36	9.68			
2002	5	1.8	0.84	0.04	1251	Total	28	1417.24				
2004	7	1.6	0.49	−0.06	1284							
1999	4	3.5	0.92	0.65	1339							

[a] Mean corresponds to varietal model calculated from the combined data across the years (all spatial and temporal variation).
[b] Model refers to the varietal model parameterized across the five years combined.

site parameterization did not necessarily improve the model output. Where there were differences in hierarchy, there were also few number of observations.

Only a few prior studies have classified grapevine varieties for their timing of flowering or veraison by days or were based on heat summations, and fewer varieties have been considered in these studies (Duchene et al., 2010; McIntyre et al., 1982; van Leeuwen et al., 2008; Villaseca et al., 1986). The established database did not include data from regions outside of Europe some of which may correspond to warmer growing regions or high diurnal temperatures; further tests are warranted to consider the current model and varietal results under these conditions. However in comparison to some other previous studies, for flowering the order is consistent to that found for the varieties studied in McIntyre et al. (1982) on one site from 1968 to 1974, with the exceptions of Muscat à petits grains blancs, Muscat de Hambourg and Trousseau being predicted earlier in this study. These varieties have large CIs (range of 166, 107, and 213 °C.d.), 10 or less observations but the *EF* and RMSEs values were satisfactory. The flowering classification presented here was different to that obtained for 14 varieties in Duchene et al. (2010), but not for veraison for which the two classifications are relatively consistent.

4.3. Application of the classification in the context of climate change

The F^* values obtained for each variety have 2 main potential uses: (1) to choose new varieties for planting in developing viticulture regions based on the understanding of which (if any) varieties will flower and undergo veraison at the optimum period for these phenological stages considered and (2) to use the F^* values in climate change scenarios for selecting alternate varieties suited to new temperature regimes.

Regarding the first possible application, the use of a process-based model, although it may be simple, differs from agro-climatic indices (Tonietto and Carbonneau, 2004) which although useful in characterizing climate conditions are not specifically calibrated to phenological stages as in this study. The GFV model could be used to calculate a fairly precise date of veraison for various varieties, and by a subsequent analysis of agro-meteorological conditions of the study area, one could determine the climatic conditions during the maturity period, and determine whether they would be optimal or not.

In terms of vine production, one way of adapting to the new climatic conditions relies on using varieties for which the phenological cycle and most importantly the timing of harvest would be similar to that achieved by present varieties. It has been indeed suggested that this could maintain a typicity of wine production which is the end product from this crop (Duchene et al., 2010; van Leeuwen and Seguin, 2006). However, forecasted increased temperatures as a result of climate change will certainly affect berry parameters independent of the effects on phenology. Acidity, aroma and flavour compounds may be considerably different in the context of increased temperatures (Jones et al., 2005). Furthermore, recent research by Sadras and Moran (2012) observed

Table 6

Measure of temporal variation between populations for the five most represented years for veraison of the five most represented varieties. *n*: number of observations; RMSE: root mean squared error; *EF*: model efficiency; MBE: Mean Bias Error; F^* the critical degree-day sum using the Grapevine Flowering Model; SS: sum of squares; MS: minimum square (sum of square/degree of freedom); *F*: Fisher statistic; *p*: probability. Varieties are presented in alphabetical order, years are presented in order of F^* values. *F* and *p* values reported for year effect; bold values indicate significant variance between years ($p < 0.05$).

	n	RMSE	*EF*	MBE	F^*		df	SS	MS	*F*	*p*	% variance
Cabernet-Sauvignon												
Mean[a]	41	4.6	0.70	−0.09	2664	Model[b]	1	2030.12	2030.12			70.33
2002	6	2.0	0.88	−0.03	2606	Year	4	220.46	55.12	**3.12**	**0.027**	**7.64**
2003	8	3.5	−0.26	0.10	2631	Residual	36	635.81	17.66			
2001	8	3.5	0.72	0.14	2651	Total	40	2886.39				
1999	10	5.0	0.62	−0.19	2658							
1998	9	4.3	0.74	0.07	2765							
Chardonnay												
Mean	30	5.5	0.87	0.18	2570	Model	1	6331.12	6331.12			87.32
1998	5	3.2	0.92	−1.06	2527	Year	4	57.86	14.47	0.42	0.793	0.80
2003	7	3.8	0.77	−0.01	2527	Residual	25	861.32	34.45			
2001	6	9.7	0.75	−0.35	2587	Total	29	7250.30				
1999	7	4.5	0.88	0.66	2592							
2002	5	1.2	0.99	0.06	2593							
Grenache												
Mean	28	5.6	0.79	0.12	2776	Model	1	3262.96	3262.96			78.97
2001	5	6.7	0.01	−0.14	2699	Year	4	181.23	45.31	1.51	0.231	4.39
2002	5	3.0	0.58	−0.10	2711	Residual	23	687.92	29.91			
1999	6	3.9	0.94	0.45	2785	Total	27	4132.11				
1998	6	3.5	0.93	0.17	2795							
2003	6	6.5	−0.10	0.05	2871							
Merlot												
Mean	41	4.2	0.78	0.01	2620	Model	1	2606.75	2606.75			78.28
2002	9	3.4	0.78	0.08	2565	Year	4	133.88	33.47	2.04	0.109	4.02
2003	9	2.6	0.17	0.07	2617	Residual	36	589.27	16.37			
1998	8	5.7	0.68	−0.15	2619	Total	40	3329.90				
1999	6	3.0	0.92	0.07	2638							
2001	9	3.5	0.78	0.28	2674							
Syrah												
Mean	29	4.2	0.87	0.08	2623	Model	1	3407.38	3407.38			86.72
2001	5	3.1	0.68	−0.02	2539	Year	4	192.71	48.18	**3.51**	**0.022**	**4.90**
2002	7	3.8	0.49	0.07	2570	Residual	24	329.08	13.71			
2003	7	2.7	0.63	0.07	2631	Total	28	3929.17				
1999	5	3.9	0.94	0.40	2678							
1998	5	3.4	0.92	−0.40	2692							

[a] Mean corresponds to varietal model calculated from the combined data across the years (all spatial and temporal variation).

[b] Model refers to the varietal model parameterized across the five years combined.

that the timing of onset of accumulation of anthocyanins was decoupled to the time of onset of soluble solids accumulation in Shiraz and Cabernet franc in relation to elevated temperatures; this indicates that different components will need to be considered independently for modelling in response to increased temperatures. Therefore, selecting a variety based on its phenological stage is an appropriate starting point, but further work would be required to understand its expression of maturation parameters under new climate change scenarios, as it was shown in Duchene et al. (2010) for Gewurztraminer and Riesling. Duchene et al. (2010) also indicated that adapting 'late' varieties like Muscat d'Alexandrie still may not entirely negate the effects of projected climate change scenarios by the end of the century. In this context, the intraspecific genetic variability of *V. vinifera* L. is important to determine if the genetics resources currently exist to achieve this adaptation.

The potential effects of climate change are not only increased temperatures (i.e. increased CO_2, water deficit changes, etc.). CO_2 is predicted to increase and the effect on the grapevine is an increasing vigour and therefore potential carbohydrate source size (Schultz, 2000). If water deficits increase as a result of warmer conditions, more carbohydrates are available for grape ripening in moderate water deficit conditions (Pellegrino et al., 2006); sugar accumulation may be increased (van Leeuwen et al., 2009) via reduced partitioning to alternative vegetative sinks (Roby et al., 2004).

4.4. Understanding intraspecific variability combining process-based models and breeding

Duchene et al. (2010) showed that it is possible to apply a phenological model for two varieties, Riesling and Gewurztraminer, and to assess variability in Riesling × Gewurztraminer crosses. By combining breeding and phenological modelling they successfully described an increase in genetic variability that could aid selection of new later developing varieties in the context of climate change. The classifications of flowering and veraison that have been presented here provide a characterization of the varietal response (F^* value) for these two stages. This currently provides an extensive understanding of the intra-specific variability for the timing of each stage for over 100 varieties, which is the first step in assessing the genetic suitability and adaptability of a variety. In future, these values can be considered and compared within breeding studies to generate new later developing varieties and to assess the limits of adapting a new cross versus changing a cultivar due to climate change. For example, Duchene et al. (2010) indicated that the virtual genotype of the Riesling × Gewurztraminer cross may not delay veraison sufficiently to compensate under projected climate change scenarios in the region of study. This further raises the question whether new varieties could be developed to escape extreme unfavourable climatic conditions during maturity. In this sense, breeding programmes may need to go beyond considering only phenology.

4.5. A methodology for characterizing phenology in future studies

The methodology outlined for modelling intraspecific differences in phenology involved the following steps: model choice and parameterization (Parker et al., 2011), followed by individual parameterization of the model for each variety, and statistical assessment notably determining the confidence interval for the model prediction at the varietal level. In this study the model used (GFV model) only takes into account temperature to characterize phenological events. However, other factors as water supply (Crimmins et al., 2008; Misson et al., 2011), or photoperiod (Korner and Basler, 2010; Chuine et al., 2010) could also impact phenological events. Therefore the first step for selecting an appropriate model depends on the species of interest, and the chosen model may need to be more complex to incorporate other environmental factors like photoperiod or water balance. The methodology presented could also be complementary to the one developed by Wilczek et al. (2009), where genetics and modelling are linked in order to test various hypotheses of plant responses to climate. When possible, this type of approach will provide a better understanding of the real capacity of adaptation of a species to new climatic conditions.

5. Conclusion

This study provides the most extensive classification to date for the timing of flowering and veraison for grapevine varieties using a phenological model. To the best of our knowledge, this is the first study that encompasses such temporal and spatial variability to characterize the timing of these stages for so many different varieties of one species. This paper outlines an approach to allow specific phenological stages, or other simple processes, to be characterized for a wide range of varieties, and in this sense to evaluate the intraspecific variability of the species. This kind of approach could help to better understand plant processes such as phenology, particularly in terms of climate change. A greater understanding of different varieties for any agricultural crop would allow adaptation and continuation of crop production in suitable regions.

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