



PARTITIONING OF SEASONAL ABOVE-GROUND BIOMASS OF FOUR VINEYARD-GROWN VARIETIES: DEVELOPMENT OF A MODELLING FRAMEWORK TO INFER TEMPERATURE-RATE RESPONSE FUNCTIONS

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Abstract

Aims: Forecasting the biomass allocation among source and sinks organs is crucial to better understand how grapevines control the distribution of acquired resources and has a great meaning in term of making decisions about agricultural practices in vineyards. Modelling plant growth and development is one of prediction approaches that play this role when it concerns growth rates in response to variation in environmental conditions. This study was aimed to model the dynamics of current year's above-ground biomass in grapevine. Furthermore, the development of a relatively simple growth modelling framework aimed at the derivation of cardinal air temperatures for growth in grapevine.

Methods and Results: Trials were carried out over three growing seasons in field conditions with four grapevine cultivars. To compare the differences of growth-allocation models among cultivars, the non-linear extra-sums-of-squares method was used. Using measurements of mean daily air temperature and dry mass increments a beta-function model was fitted to the data and used to estimate cardinal air temperatures. Shoot growth and biomass allocation differed significantly among cultivars. The application of the non-linear extra-sums-of-squares procedure demonstrated to be a feasible way of growth models statistical comparison among cultivars. The results of this study highlight parameters most involved in the phenotypic variability of shoot growth. Variations among cultivars result from environmental and genetic factors. The temperature response functions obtained, confirm the initial working hypothesis that because the varieties may have either different temperature optima or different thresholds that a unifying model cannot be achieved.

Conclusions: These results suggest that some caution should be taken when incorporating shoot development and biomass partitioning coefficients in a growth model. Use of common coefficients estimates for all cultivars for dynamic modelling approaches, in fact, may result in a poor representation of the data early or late during the course of the season.

Significance and Impact of the Study: The described approach can be used to account for complex variation in seasonal growth patterns and provides insight into how well a cultivar may be matched to a particular site.

Keywords: Above-ground grapevine biomass, growth model, biomass partitioning coefficients

Introduction

The analysis of biomass allocation rate among source and sink organs is crucial to better understand how grapevines control the partitioning of acquired resources in response to variation in environmental conditions. While the general vine growth patterns remain almost constant, the timing and duration of the developmental phases are subject to great variations due to the grape variety, local climate, and seasonal weather (Bates *et al.*, 2002; Tandonnet *et al.*, 2010). The seasonal growth and assimilate-partitioning patterns have been widely modelled during the last decades in grapevines (Vivin *et al.*, 2002; Lebon *et al.*, 2004; Greer *et al.*, 2010). However, less information exists on the temporal patterns of the vegetative and reproductive structures development during the growing season and on growth rates of individual leaves, shoot or grapes during their development (Wermelinger *et al.*, 1991; Palacio *et al.*, 2008; Tsialtas *et al.*, 2008; Pallas *et al.*, 2008, 2011). Thus, understanding shoot biomass partitioning among leaves, stems and clusters assumes great importance in viticulture as it greatly affects vine growth rates in response to the abiotic environment. Plant growth, as measured by dry matter increase, has been reported rising from around 10°C mean temperature or little less, reaching an optimum at means around 22–25°C, but beyond that, unlike phenological development, the rate declines progressively.

This paper describes an inferential modelling method for deriving threshold temperatures from growth models obtained from seasonal growth and partitioning measurements under field conditions. Three consecutive seasons were used for sampling collections and biometrical measurements, i.e. shoot elongation, leaves number, leaf area and dry matter partitioning. Non-linear regression analysis, using logistic model form, was applied to produce average patterns of shoot and cluster growth on a day of the year basis. Four vineyard-grown grapevine cultivars, with contrasting qualities of vigour and earliness, namely *V. vinifera* cv. 'Carmenère N.', *V. vinifera* cv 'Manzoni bianco B.', *V. vinifera* cv. 'Pinot gris G.' and *V. vinifera* cv. 'Verduzzo trevigiano B.', were studied with the aim of (i) identification and characterization of the phenotypic parameters involved in the expression of varietal differences in the build-up of vegetative and reproductive structures; (ii) empirically model the dynamics of current year's above-ground vegetative and reproductive biomass of grapevine varieties under field conditions; (iii) use these models to infer growth temperature-rate responses to be used for parameterizing more detailed process-based models.

Materials and Methods

Study Site Description

Trials were carried out over three growing seasons from 2006 to 2008 in North-Eastern Italy on a commercial vineyard located in Negrizia di Ponte di Piave (Italy) (45°44'51" N, 12°26'48" E, 11 m a.s.l.) in D.O.C. Piave wine-producing region. In an extensive flatland vineyard, four grapevine cultivars: *Vitis vinifera* L. Carmenère (C), Manzoni bianco (M) (ex Incrocio Manzoni 16.0.13), Pinot gris (P), Verduzzo trevigiano (V) grafted on SO4 rootstock, were used for sampling. The vineyard was planted in 1992 and covers an area of about 18 hectares with north-south oriented rows (500 – 600 m long) spaced 2.50 m between rows and 1.30 m within the row. Cultivars were planted in contiguous rows within the vineyard resulting in adjacent quarter sections of the vineyard. Vines were trained to Moveable Spur-pruned Cordon system for vertical shaker harvesting, with a single trunk at about 1.7 m aboveground. Vines were winter pruned mechanically and canopy was hedged two times during the season (early June and middle July respectively). The vineyard was equipped with a sub-irrigation system thus avoiding summer drought spells to occur. The data used in the present manuscript were thus from a well-watered trial so it is supposed that the growth responses account only for seasonal differences in air temperature and specific varietal behaviors. Since 2005 a complete meteorological station has been deployed within the vineyard over turf for the measurement of basic meteorological parameters.

Vine Growth Measurements

During each growing season, starting from a week after bud break, 15 randomly selected shoots, from as many selected vines, were harvested weekly until veraison and biweekly afterwards from both eastern and western sides of the canopy. For each sample, all leaves were removed and the specific surface measured using imaging software (UTHSCSA ImageTool, version 3.00). Measurements included the following: total (T), primary (P) and lateral (L) shoots length (L_T , L_P , L_L), dry weight (DW_T , DW_P , DW_L), number of leaves per shoot (N_T , N_P , N_L), leaf area (A_T , A_P , A_L) were determined from one week after bud break to harvest for all cultivars. Dry weight of the following organs were determined separately (oven-dried at 65°C to a constant weight): primary stem without cluster ($DW_{P,stem}$), primary leaves (with petioles intact) ($DW_{P,leaf}$), inflorescence/cluster of the primary shoot

($DW_{T,cluster}$), sum of all lateral stems including tendrils ($DW_{L,stem}$) and the sum of all lateral leaves ($DW_{L,leaf}$). Biomass dry weight partitioning data among primary and lateral shoots were not available for 2006 season.

Growth Curves Modelling Analysis

We characterized the growth curves of each cultivar on a calendar time basis, using a three-parameter logistic model of the form:

$$Y = a/1 + \left(\frac{X}{X_0}\right)^b \quad (\text{Equation 1})$$

where: a represents the upper asymptote and, in this case, is the theoretical maximum mass or ratio, X_0 is associated with the inflection point and, in this case, is the number of days required to reach 50% of a , and b is a curvature parameter related to the slope of the curve.

The biometric growth curve model was fitted to the raw data as a function of calendar time by nonlinear regression (Sigmaplot version 12; Jandel Scientific Software, San Rafael, CA) minimizing the sum of the squares (SS) of the differences between the predicted and measured values and then calculating the set of parameters with the lowest residual SS. For each dataset, model agreement (i.e. deviation between estimates and observations) was assessed using the following statistics: the coefficient of determination (R^2) and the root mean square error (RMSE) (see Meggio and Pitacco, 2019).

Comparison of Growth-Allocation Models Among Cultivars

To compare the differences of growth-allocation models among cultivars the non-linear extra-sums-of-squares method was used (Bates & Watts, 1988). In general, the extra sums-of-squares approach uses an F test to compare two treatments. For example, to test the hypothesis that a single growth curve best fits the data for both treatments, curves for the two datasets are first fit separately and represent the full model (F). Next, the data are combined, and one curve is fit to the combined data representing the reduced model I. Lastly, the sum of the sum of squares for the separate curves (SS_F) is compared with the sum of squares for the combined models (SS_R) using a calculated F ratio as follow:

$$F = \frac{(SS_R - SS_F)}{df_R - df_F} / \left(\frac{SS_F}{df_F}\right) \quad (\text{Equation 2})$$

where: df_R and df_F are the number of degrees of freedom for the reduced and the full model respectively. A corresponding significant p value indicates that the curves fit to the two datasets are different. The statistical decision rule at the specified $\alpha = 0.05$ or $\alpha = 0.01$ throughout this study was deemed significant by applying the Bonferroni correction each time a set of pairwise contrasts was used.

Temperature Rate-Response Functions Assessment

Using on-site measurements of mean daily air temperature and simulated DW_T growth increments, the assessment of temperature response functions was conducted following three steps. i) Computation of the first derivative of logistic DW_T growth functions, ii) mean air temperature analysis and sampling iii) temperature response functions fitting (Figure 1). The first step consists in the computation of the first derivative from the logistic functions, representing the growth rates per unit of time (DOY) (Figure 1a). The first derivative curve was further averaged on a 5-days basis. For the second step, air temperature data collected every minute on-site by a weather station placed within the vineyard, were averaged and daily means were calculated for the three growing seasons (2006-2008) (Figure 1b). In the third step, temperature responses functions were obtained using the non-linear beta function proposed by Wang and Engel (1998) to take into account temperatures with inhibiting action on development (Figure 1c).

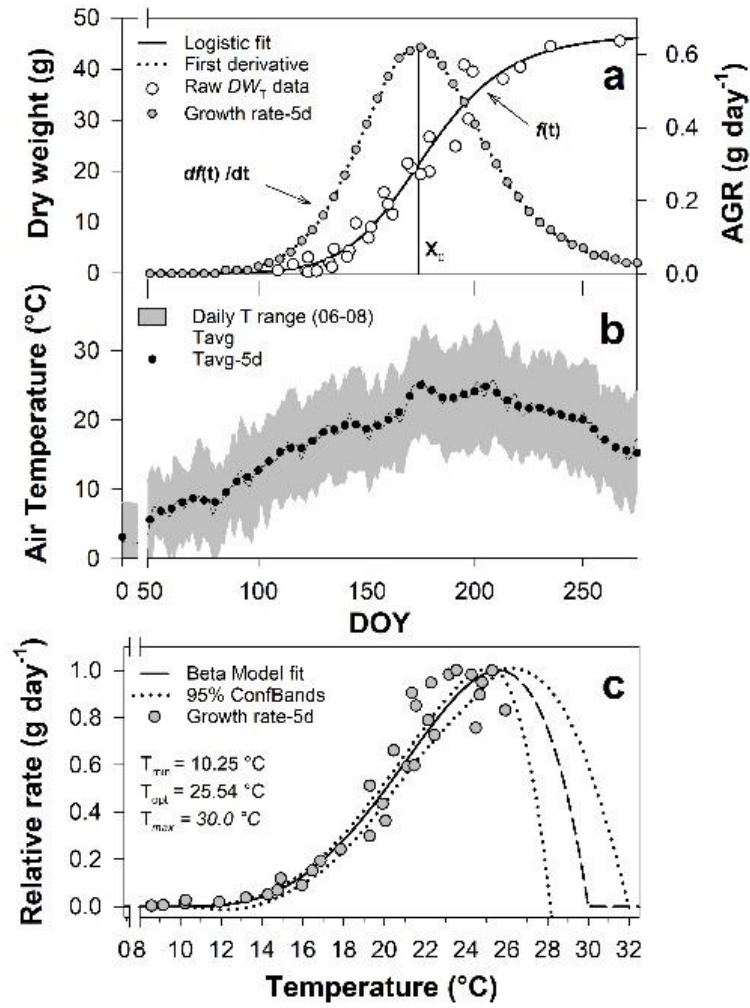


Figure 1: Three-step procedure proposed to infer temperature-rate response functions based on seasonal shoot dry weight growth models.

The beta-type model was fitted to absolute growth rates data, expressed as relative rates, on a mean air temperature basis. The advantage of the beta-type curve is that the cardinal temperatures T_{min} , T_{opt} and T_{max} have a physiological meaning, which allows model consistency to be checked against experimental data. The beta-type function developed by Wang & Engel (1998) is fully described by three cardinal temperatures as follow:

$$f(T_i) = \begin{cases} \frac{2(T - T_{min})^\alpha (T_{opt} - T_{min})^\alpha - (T - T_{min})^{2\alpha}}{2(T_{opt} - T_{min})^\alpha} & \text{for } T_{min} \leq T \leq T_{max} \\ 0 & \text{for } T < T_{min} \text{ or } T > T_{max} \end{cases} \quad (\text{Equation 3})$$

with the α parameter of equation (3), is the beta function shape factor given by:

$$\alpha = \ln 2 / \ln \left[(T_{max} - T_{min}) / (T_{opt} - T_{min}) \right] \quad (\text{Equation 4})$$

Where: $f(T_i)$ corresponds to the temperature function on grapevine growth by day; T is the mean daily temperature; T_{min} = the temperature below which the growth rate is zero (°C); T_{max} = the temperature above which the growth rate is zero (°C); T_{opt} = the temperature at which the growth rate is optimal (°C), at which the highest growth rate occurs.

Results and Discussion

Shoot Growth Modelling and Statistical Comparison

Fitted logistic curves on a calendar time basis, indicating significant differences found among cultivars across three years of study through extra-sum of squares method, are illustrated for biomass increments parameters in Figure 2. In particular, C showed the greatest total biomass accumulation in stem ($DW_{T,stem}$) for both primary ($DW_{P,stem}$) and lateral shoots ($DW_{L,stem}$), and thus the greatest DW_T overall development (Figure 2). Significant differences were found for total leaves dry weight allocation ($DW_{T,leaf}$). In the present study the extra-sums-of-squares procedure was used to evaluate model stability among cultivars across years by assessing significant differences among years and cultivars. The coefficients of fitting stability across cultivars and years was tested and the F values statistics results are reported in Table 2. Where significant differences were found between full (F) and reduced (R) for combined models, further multiple pair-wise comparisons were computed. Across cultivars, significant differences were found among years for most of growth parameters tested except for L_L , $DW_{T,cluster}$, DW_L , $DW_{L,stem}$, and $DW_{L,leaf}$ resulting not statistically different; thus meaning that a unique model for all three years resulted to be a better estimator across cultivars than three different model for each year. Across years significant differences resulted from F -test statistics among cultivars for N_p , L_T , L_L , A_T , DW_T , $DW_{T,cluster}$, $DW_{T,stem}$, $DW_{T,leaf}$, $DW_{P,stem}$, DW_L , $DW_{L,stem}$ and $DW_{L,leaf}$ meaning that four growth models, corresponding to four distinctively different cultivars, were needed.

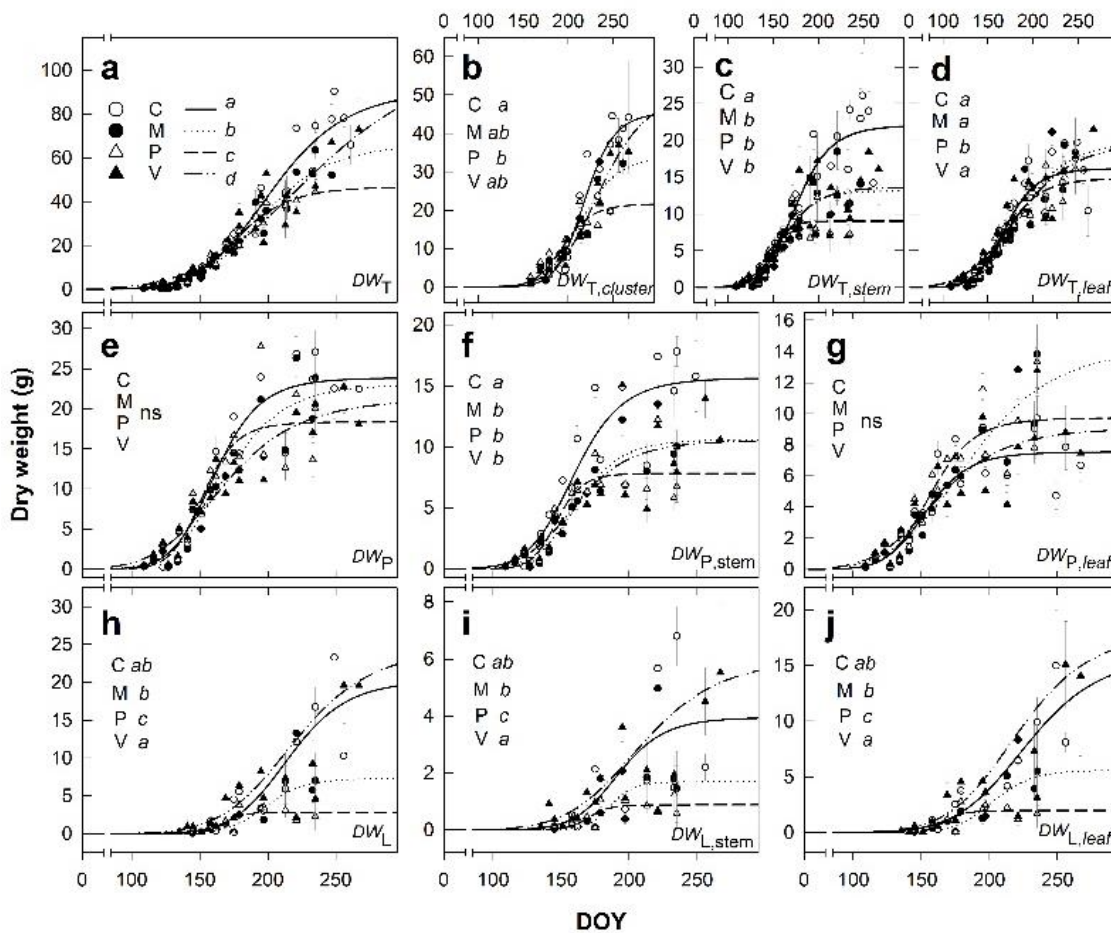


Figure 2: Logistic curve fitting for for total dry weight per shoot DW_T (a), $DW_{T,cluster}$ (b), $DW_{T,stem}$ (c), $DW_{T,leaf}$ (d); primary shoot dry weight DW_P (e), $DW_{P,stem}$ (f), $DW_{P,leaf}$ (g) and lateral shoots dry weight DW_L (h), $DW_{L,stem}$ (i), $DW_{L,leaf}$ (j) according to calendar time expressed on day of the year basis (DOY). Data are the mean \pm SE of 15 replicates shoots per cultivar. Dissimilar letters indicate significant differences among logistic curves through non-linear extra-sums-of-squares.

The application of the non-linear extra-sums-of-squares procedure demonstrated to be a feasible way of growth models comparison to statistically assess significant differences among grapevine cultivars. Statistical analyses allowed identifying the growth parameters that better demonstrate differences among cultivars. Lateral shoot

length (L_L) and clusters dry weight ($DW_{T,cluster}$) resulted to be less affected by intra- and inter-annual variability. These growth parameters may be accounted to be genetically characteristic of the cultivar and to better represent proxies of shoot vigour and thus assume great importance to enable reliable genetic difference assessment among cultivars. On the contrary, the non-significance of the cultivar differences obtained across years revealed a lack of genetic differences among cultivars for their response to different years. This is the case for N_T , N_L , L_P , A_P , $DW_{T,leaf}$ and $DW_{P,leaf}$ where differences resulted to be driven more by seasonal and cultural practices than by varietal differences. Parameters that resulted non different across years and cultivars were N_P , $DW_{L,stem}$ and $DW_{L,leaf}$, which resulted affected by management practices for principally.

Table 1: F-test statistics run for each growth variable among years across cultivars (A) and among cultivars across years (B).

Variable	Stability among year across cultivars (A)									Stability among cultivar across years (B)									
	Full model			Reduced model			Year			Full model			Reduced model			Cultivar			
	df _F	SS _F	df _R	SS _R	n	F-value	06	07	08	df _F	SS _F	df _R	SS _R	n	F-value	C	M	P	V
N_T	69	1030	72	1350	75	7.06 **	a	b	c	49	1470	52	1520	55	0.518 ns				
N_P	111	624	117	713	120	2.64 ns				108	714	117	714	120	0.00963 ns				
N_L	70	1190	76	3330	79	20.8 **	a	b	c	67	2650	76	1870	79	2.21 ns				
L_T	107	190	113	231	116	3.84 **	a	b	b	104	154	113	231	116	5.76 **	a	b	b	a
L_P	117	85.9	123	100	126	3.22 *	a	b	a	114	91.8	123	100	126	1.15 ns				
L_L	61	130	67	155	70	1.93 ns				58	93.7	67	155	70	4.2 **	ab	bc	c	a
A_T	94	823	100	1120	103	5.65 **	a	b	b	91	489	100	1120	103	13.1 **	a	b	b	c
A_P	100	169	106	225	109	5.46 **	a	b	b	97	181	106	225	109	2.63 ns				
A_L	68	479	74	767	77	6.8 **	a	b	b	65	430	74	620	77	3.2 *	ab	a	a	b
$A_{P,leaf}$	106	3.11	112	4.84	115	9.85 **	a	b	a	103	2.97	112	4.84	115	7.22 **	a	a	a	b
DW_T	119	3890	125	5420	128	7.76 **	a	b	a	116	4120	125	5420	128	4.07 **	a	b	b	ab
$DW_{T,cluster}$	53	1120	59	1300	62	1.45 ns				50	777	59	1300	62	3.76 **	a	ab	b	a
$DW_{T,stem}$	106	725	112	1270	115	13.2 **	a	b	a	103	614	112	1270	115	12.2 **	a	bc	c	b
$DW_{T,leaf}$	107	312	113	577	116	15.2 **	a	b	a	104	486	113	577	116	2.16 ns				
DW_P	73	1520	76	1980	79	7.35 **	n/a	a	b	67	840	76	1980	79	10.1 **	a	b	b	b
$DW_{P,stem}$	70	218	73	389	76	18.3 **	n/a	a	b	64	181	73	389	76	8.19 **	a	ab	c	b
$DW_{P,leaf}$	68	54.3	71	88.1	74	14.1 **	n/a	a	b	62	72.2	71	88.1	74	1.52 ns				
DW_L	39	377	42	457	45	2.77 ns				33	215	42	457	45	4.12 **	abc	a	b	c
$DW_{L,stem}$	38	45.5	41	52.9	44	2.07 ns				31	34.8	40	52.2	43	1.73 ns				
$DW_{L,leaf}$	38	45.5	41	52.9	44	2.07 ns				31	34.8	40	52.2	43	1.73 ns				

df_F = degrees of freedom of the full model, df_R = degrees of freedom of the reduced model, SS_F = residual sum of squares for the full model, SS_R = residual sum of squares for the reduced model, n = number of samples. Dissimilar letters indicate significant differences by the F-test at p-value < 0.05 (*) and p-value < 0.01 (**) corrected according to sequential Bonferroni adjustment; n/a, data no available.

Temperature Rate Responses of Shoot Dry Weight Increments

The use of a calendar time basis to model shoot growth and biomass partitioning enabled daily rates of responses to be determined. Following the procedure proposed, the temperature-rate response of total shoot dry weight increment (DW_T) were modelled using a beta-type function (Wang and Engel, 1998) (Equation 3). The observed data, as they were normalized with respect to their maximum, all fell into a similar pattern of response to temperature, suggesting a general type of temperature response for different cultivars. At around 10 to 20 °C the rate of growth increases exponentially; at 20 to 25 °C, it levels off reaching its maximum at T_{opt} in the range of 24 - 26°C and then above the maximum a decrease when temperature departs from T_{opt} is observed. Temperatures that lie outside those ranges, both at high and low temperatures, decrease the production of dry matter and, at extremes, can cause growth rate to cease.

Table 2: Fit parameters for the beta-function growth models and goodness of fit metrics (Equation 3).

Cv	Beta model parameters (Wang & Engel, 1998)						Goodness of fit	
	T_{min}		T_{opt}		T_{max}		R^2	RRMSE
	$^{\circ}\text{C} \pm \text{SE}$	95% CI	$^{\circ}\text{C} \pm \text{SE}$	95% CI	$^{\circ}\text{C} \pm \text{SE}$	95% CI		
C	11.89 \pm 1.03	9.89-13.93	25.59 \pm 0.40	24.80-26.38	30.00 \pm 0.99	28.11-31.89	0.73	6.4%
M	9.31 \pm 0.97	7.39-11.23	25.82 \pm 0.66	24.16-27.12	30.00 \pm 1.23	27.56-32.44	0.83	3.6%
P	8.24 \pm 1.44	6.42-10.05	25.31 \pm 0.34	24.64-25.98	30.00 \pm 0.95	28.12-31.88	0.85	4.8%
V	9.15 \pm 1.34	6.51-11.79	25.17 \pm 0.42	24.35-26.00	30.00 \pm 1.01	27.92-32.08	0.81	7.7%
TOT	10.69 \pm 0.64	9.44-11.95	25.49 \pm 0.21	25.08-25.92	30.00 \pm 0.51	28.00-32.01	0.82	4.2%

T_{min} = base temperature, T_{opt} = optimum temperature, T_{max} = maximum temperature ($^{\circ}\text{C} \pm \text{SE}$); R^2 = coefficient of determination; RRMSE = relative root mean square error.

Cardinal temperatures (T_{min} , T_{opt} , T_{max}) resulting from non-linear regression fitting procedures as well as goodness-of-fit metrics, coefficient of determination (R^2) and relative root mean squared error (RMSE) are reported in Table 1. While the use of a beta-type function well fitted the minimum (T_{min}) and optimum (T_{opt}) cardinal growth thresholds, the lack of mean air temperatures measured in the field above 28 $^{\circ}\text{C}$ did not allow realistic maximum temperature threshold to be estimated, thus resulting in T_{max} of 30 $^{\circ}\text{C}$ for all cultivars and with large 95% confidence limits above the T_{opt} threshold. Minimum temperatures below the threshold generally adopted for grapevine of 10 $^{\circ}\text{C}$ were obtained for M, P and V cultivars with values of 9.31, 8.24 and 9.15 $^{\circ}\text{C}$, respectively. Only C cultivar, which showed the highest maximum growth rates ($AGR_{max} = 0.93$ g/day) at 25.6 $^{\circ}\text{C}$, showed a minimum temperature greater than the base temperature of 10 $^{\circ}\text{C}$ with T_{min} of 11.89 $^{\circ}\text{C}$, in agreement with the latest bud break experienced among cultivars. No significant differences were observed among cultivars for T_{opt} , even if this could be related to the weak T_{max} estimation as explained above. When the beta-function was fitted on all the combining dataset (TOT) the generally adopted base temperature of 10 $^{\circ}\text{C}$ was obtained ($T_{min} = 10.69$ $^{\circ}\text{C}$) (Figure 3).

The effect of temperature on development rate has been often described by using the thermal time concept to predict the development of a species as a function of temperature assuming a linear and unlimited relationship between temperature and the development rate. Although many authors used the classical thermal time concept calculated by daily integration, starting from January the 1st, of mean air temperature minus a base temperature of 10 $^{\circ}\text{C}$, and assumed common to all the cultivars, this concept does not make it necessarily valid (Bonhomme, 2000). The concept of thermal time assumes that growth a priori must be linear functions of temperature for the thermal time relationships to be valid. However, since the amount of energy available to a plant increases with photosynthesis and decreases with respiration, the rates of photosynthesis and respiration both increase with temperature, but the rate of photosynthesis levels off at a lower temperature compared to respiration. As a result, the net energy available to plant development has a temperature optimal threshold beyond which the forcing effect of the temperature will not further increase or will even tend to decrease, resulting in a non-linear response of development rate of plants to temperature (Bonhomme, 2000; Wang and Engel, 1998; Yan and Hunt, 1999). Non-linear functions have also been used to simulate plant development and define grapevine response to temperature (Chuine *et al.*, 2013) and models with smoother curves, such as the Beta functions represent a wide range of distributions and require fewer parameters: the cardinal temperatures T_{min} , T_{opt} , and T_{max} , which have physiological significance (Yin *et al.*, 1995; Wang and Engel, 1998; Yan and Hunt, 1999).

The modelling framework presented in this study describes quantitatively the development of grapevine shoot in relation to temperature, enabling temperature rate responses to be inferred from shoot growth models on a calendar time basis starting from seasonal growth data. Accurate estimates of T_{min} and T_{opt} were obtained enabling differences among cultivars to be obtained in agreement to specific cultivar characteristics of vigour, earliness/lateness and growth data dynamics observed. The present investigations confirmed the suitability of non-linear beta-functions models for temperature-rate responses of shoot growth modelling. Interestingly, only 'Carmenere' showed T_{min} higher than the 10 $^{\circ}\text{C}$ threshold. The remaining cultivars both demonstrated to initial growth rates at air temperatures below the 10 $^{\circ}\text{C}$ threshold.

Conclusions

The results of this study highlight key patterns and parameters involved in the phenotypic variability of shoot growth in four grapevine cultivars. Shoot growth development and biomass partitioning were variable both within and among cultivar parameters. The distinction between 'within' and 'among' is important. Variation within a cultivar results from random and experimental error, and micro-environmental heterogeneity. Differences among cultivars, instead, result from environmental and genetic variations, and from differences in cultural practices among years. These results suggest that some caution should be taken when incorporating shoot development and biomass partitioning coefficients in a growth model. We have shown that the described approach can be used as a modelling framework to infer temperature rate responses of shoot dry mass growth in grapevine to account for complex variation in seasonal growth patterns and to provide insight into how well a species may be matched to a particular site. The temperature response functions obtained, confirm the initial working hypothesis that because the varieties may have either different temperature optima or different thresholds that a unifying model cannot be achieved.

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