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Development in *Origanum* ssp.: A simple phenological scale to determine thermal time requirements to critical reproductive events

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ABSTRACT

Origanum spp. is commercially important as a main aromatic herb. However, little eco-physiological information is available regarding plant development and its control by genotype and environmental factors. Here, we aimed at developing (i) a simple phenological scale based on morphological features in common of the genus and (ii) a model that allows quantifying the thermal time requirements for critical events, such as vegetative to reproductive transition (V_3) and flowering (R_6). Plants of *O. vulgare* ssp. *vulgare* (O. Compacto) and *O. vulgare* ssp. *hirtum* (Ietsw.) (O. Criollo) were evaluated through sequential observations of bud development. Despite genotypic differences in morphology, a robust key was built to describe main vegetative and reproductive stages. The resulting scale comprises seven phenophases, from V_0 to V_3 (vegetative stages) and from R_4 to R_6 (reproductive stages). Phenological stages V_3 and R_6 showed to be critical, because they represent the time to transition from vegetative to reproductive phases, and full blooming, respectively. Phenology modelling based on thermal requirements was accurately described by logistic curves in both subspecies. Subspecies differed in the thermal time requirement to V_3 and R_6 (lower in O. Compacto). This key is a generic tool with potential use in crop eco-physiological studies because it can describe main developmental phases without taking into account morphology or cycle length.

1. Introduction

Oregano (*Origanum* spp. L.) is a highly valued spice in the food industry as its essential oil has antifungal, antimicrobial and antioxidant activity (Bakkali et al., 2008; Farías et al., 2010; Kulisic et al., 2004). In this perennial species, the agronomic cycle spans from cutting transplanting to flowering, the most appropriate moment for harvest (Berghold et al., 2008). *Origanum vulgare* includes subspecies that differ in height, growth habit, flowering time or precocity and cycle length, such as *vulgare* and *hirtum* (Chauhan et al., 2013; Torres et al., 2010). Both species are particularly valuable for production due to their oil quality and crop adaptability.

Despite the commercial importance of oregano, ecophysiological aspects such as phenology regulation and its interaction with environmental variables have been poorly studied. In this species, no specific phenological scale has been developed for an accurate identification of the different development stages, i.e., vegetative, reproductive and full maturity stages. Currently, the extended BBCH-scale (Lancashire et al., 1991) is a generic system for uniform coding of phenology that can be used in crops lacking phenological scales. Although this scale has been adapted for a great diversity of species, such as trees, shrubs and herbaceous plants (Jenni and Bourgeois, 2008; Ramírez et al., 2013; Salazar et al., 2006; Wei et al., 2013), it has been argued that BBCH would not be appropriate for determining growth stages of herbaceous perennial crops (Ciha and Wilhelm, 1997). An alternative approach is the development of a phenological classification system based on specific morphological characteristics of *Origanum*, which might also be used to explore genotypic variation in terms of development and to guide agronomic management.

Predicting the critical moments of a crop based on chronological time is not accurate because the length of phenophases is regulated by environmental factors, such as temperature and photoperiod (Ahmad Nazarudin et al., 2012). Therefore, determining phenology requires using models based on thermal time, i.e., accumulation of degree days (°Cd). A thermal-time-based model is a simple tool because it can be run with easily obtainable weather data (Baker and Reddy, 2001). In oregano, no predictive phenology

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models based on thermal time have been developed, nor has the requirement in thermal time to critical crop phenophases been quantified. Quantifying phenology through a mathematical model based on thermal time would allow a best description of genotypic or management-dependent differences in maturity progress. Additionally, models may help improve predictions of developmental stages in environments with variable temperature (Miller and Lanier, 2001; Stöckle et al., 2003).

The aims of this work were to (i) construct a specific scale for simple phenological description based on common morphological characters of the genus and (ii) build a model of phenological development based on thermal requirements until critical phenophases, i.e. full blooming, in two oregano subspecies of contrasting architecture.

2. Materials and methods

2.1. Study site

The study was conducted at the experimental farm of the National University of Córdoba in Capilla de los Remedios (31°26′S; 63°49′W, 360 m a.s.l.), Córdoba, Argentina, during the 2011 and 2012 growing seasons. Annual precipitation in the area is 794 mm. During this study mean monthly air temperature and daily incident solar radiation data were recorded in a weather station installed at about 200 m from the experimental site.

2.2. Biological material and experimental design

O. vulgare L. is a perennial *Lamiacea* whose agronomical management involves a sprouting-flowering-harvest scheme that is maintained for 3–5 years. Flowering is the optimal time for harvest because it is the moment of maximum essential oil production (Berghold et al., 2008; Kizil et al., 2008; Yaldiz et al., 2005). The species has a gradual and indeterminate flowering process (Porter, 1967), i.e. an open axis system in which the apical bud of the floral branch remains at vegetative stage (Davidenco et al., 2014). Flowers are arranged in compound inflorescences, epicastros forming groups of (2) 3, supported by a pedicel (Xifreda, 1983). The epicastros form terminal corymbose cymes, with each flower being protected by an oblong-elliptic bract (Rouquaud and Videla, 2000).

Plants of two oregano subspecies, “Compacto” (*O. vulgare* ssp. *vulgare*) and “Criollo” (*O. vulgare* ssp. *hirtum* Ietsw. (Torres et al., 2012) were studied. Plant samples of both subspecies were deposited at the ACOR herbarium (Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba; coded as AMP 3482 and AMP 3483, respectively). Seedlings obtained by vegetative propagation were transplanted on September 9, 2011 (experiment 1, Exp. 1), and on September 6, 2012 (experiment 2, Exp. 2) and distributed in rows spaced at 0.70 m apart with a distance of 0.2 m between plants. Plants were irrigated every 3 days to complement natural rainfall, avoiding water stress throughout the trials. The experimental design was a randomized complete block with three replications.

2.3. Phenological determination and thermal time recording

Observational units for phenological recording consisted of three plants per experimental unit (EU). In both seasons, duration of vegetative (V) and reproductive (R) macrostages in calendar days and thermal time was recorded with the specific aim of searching for differences between subspecies. In the Exp. 1, a more detailed assessment included determining the phenology status and number of stems per plant weekly until full blooming.

Phenophases of *O. vulgare* ssp. were determined by adapting a phenological classification system developed for alfalfa by Kalu and Fick (1981). We opted to adapt this scale because alfalfa and *Origanum* have similar features in terms of growth habit, agronomic cycle and crop management. This staging scale recognizes vegetative, flower bud, flowering and fruiting maturity stages. In this study, fruiting stage was not surveyed because agronomically, the oregano cycle ends with crop harvesting during flowering. An additional phenophase was included considering seed and emergence period (hereafter denominated the S-E stage), although *Origanum* is generally propagated as an agamic species.

The resulting key was based on the organs that were generated from stem buds (leaves, branches and flower structures). Phenology was determined at three levels, i.e. stems, plant and crop. Phenological stage of each stem was defined using a maturity state category (*MS*) that ranges from 0 to 3 (vegetative phenophases, V_0–V_3), and from 4 to 6 (reproductive phenophases, R_4–R_6). Detailed description of each phenological stage is included in Results Section 3. Phenological stage per plant (*MS*p) was determined based on the predominant *MS* of stems (median concept). At the crop level, phenological stage was determined as the *MSp*exhibited by more than the 50% of plants within each EU.

Due to the perennial nature of *Origanum*, regrowth occurring during most part of the cycle masks maturity progress. Hence, after 30 days from initial growth the *MSp*was calculated without considering sprouts that had $MS \leq 1$. Similarly, after 60 and 80 days from initial growth, sprouts having $MS \leq 2$ and $MS \leq 3$, respectively, were excluded to determine plant phenology.

From the start of the trial until full blooming, thermal time was determined for each *MS* as the summation of the differences between mean daily temperature and crop base temperature (TT, °Cd). Here, base temperature was considered to be 0 °C (Kintzios, 2002; Thanos et al., 1995).

2.4. Statistical analyses

Phenological evolution in terms of thermal time to vegetative or reproductive macrostages was studied separately. Firstly, curves of phenological progress were described through graphical analyses to quantify the observed proportion of plants that reached *MS* 3 and *MS* 6 as a function of accumulated thermal time, because *MS* 3 and *MS* 6 represent the end of V and R macrostages, respectively. Curve shape and moments for the beginning of *MS* 3 and *MS* 6 stages were observed.

The plant proportion reaching *MSp*3 or *MSp*6 was modelled as a binomial variable as a function of accumulated thermal time. A non-linear mixed model (logistic) was fit including a random effect on the phenological evolution slope (Eq. (1)).

$$y = \frac{1}{\left(1 + \beta \exp^{(-(\gamma+u)\times \mathrm{TT})}\right)} \quad (1)$$

where, y is the plant proportion in *MSp*3 or *MSp*6; β is the parameter related to thermal time (°Cd) until the beginning of the exponential maturity advance point; γ is the parameter related to rate of phenological progress; u is the random effect associated with the slope; and TT is the accumulated thermal time. Modelling was performed using PROC NLMIXED procedure in SAS 9.1 (SAS, 2006).

Accumulated thermal time until the inflection point of the curve is the moment when the proportion of plants in a particular phenophase reaches 0.5. In the case of the Vegetative model, this inflection point was associated with the beginning of the transition between vegetative and reproductive period ($\mathbf{V_3} - \boldsymbol{i}$). The inflexion point in the reproductive model indicates beginning of full blooming ($\mathbf{R_6} - \boldsymbol{i}$). Both $\mathbf{V_3} - \boldsymbol{i}$ and $\mathbf{R_6} - \boldsymbol{i}$ were calculated using the second

Table 1
Historical and average weather data during two growing seasons of *Origanum* ssp. crops cultivated in Capilla de los Remedios, Argentina (31°26′S; 63°49′W). Mean Monthly Temperature (T°); Daily Mean Incident Radiation (IR), Mean monthly photoperiod (P); Season Average is the mean weather data of each season.

	SEP	OCT	NOV	DEC	Season average
T° (°C)					
Historical[a]	15.0	19.1	21.4	22.8	19.6
Experiment 1	16.1	17.7	22.0	23.3	19.8
Experiment 2	16.1	18.4	22.2	24.1	20.2
IR (Mj m^{-2})					
Historical[a]	18.8	22.0	25.5	26.0	23.1
Experiment 1	21.1	24.1	28.2	30.2	25.9
Experiment 2	19.9	22.1	26.9	31.0	25.0
P (h)					
Experiment 1	12.0	12.8	13.6	14.0	13.1
Experiment 2	12.0	12.9	13.7	14.0	13.1

[a] Mean of 2002-2012 period.

derivative of the logistic functions (Passos et al., 2012) (Eq. (2)) as follows,

$$\text{Phenophase beginning} = \frac{(\text{Ln}(1/\beta))}{(-(\gamma + u))}. \quad (2)$$

Logistic function hinders the prediction of accumulated thermal time to maximum plant proportion in a particular phenophase, i.e. plateau point, because the value of "x" when "$y = 1$" tends to infinity (Mischan et al., 2011). Therefore, to estimate thermal time to the maximum plant proportion, the "x" value (°Cd) was removed from the logistic function when the asymptotic value reached 0.95 instead of 1. In the Vegetative model, this moment was associated with the transition of most plants from vegetative to reproductive period (**full** – $\mathbf{V_3}$), whereas in the reproductive model, this moment was associated with the maximum proportion of plants at full blooming (**full** – $\mathbf{R_6}$). Both **full** – $\mathbf{V_3}$ and **full** – $\mathbf{R_6}$ were calculated using Eq. (3),

$$\text{Full phenophase} = \frac{(\ln(1/(49 \times \beta)))}{-(\gamma + u)}. \quad (3)$$

We opted to estimate the beginning and full critical phenophases through mathematical functions (Eqs. (2) and (3)) instead of using simple interpolation of the logistic curve (Paine et al., 2012).

The effect of the subspecies on the estimated parameters was evaluated using the Student's T test with 5% significance level (Di Rienzo et al., 2011). To evaluate goodness of fit-criteria for the vegetative and reproductive models, the square root of mean square error (*RMSE*) and the Pearson correlation coefficient were calculated to measure the strength of association between the observed and predicted proportions.

3. Results

3.1. Environmental conditions

In both seasons, average temperature and incident solar radiation were higher than values recorded for a previous 10-year period (Table 1). However, prevailing weather conditions were representative of the historical variation of the region.

3.2. Morphological description of subspecies

The subspecies differed in the length of internodes in secondary branches (Fig. 1), being 2–3 mm in O. Compacto and 5–10 mm or higher in O. Criollo. O. Compacto exhibited shorter epicastros with a lower number of flowers than O. Criollo. This internode elongation pattern along with epicastro length generated typical contracted and compact floral cymes in O. Compacto and lax ones in O. Criollo (Figs. 1 and 3). The typical branching pattern of each subspecies generates a creeping growth habit in O. Compacto and an erect one in O. Criollo. At advanced development stages, i.e., when formation of floral branches occurred, we observed that these characteristics

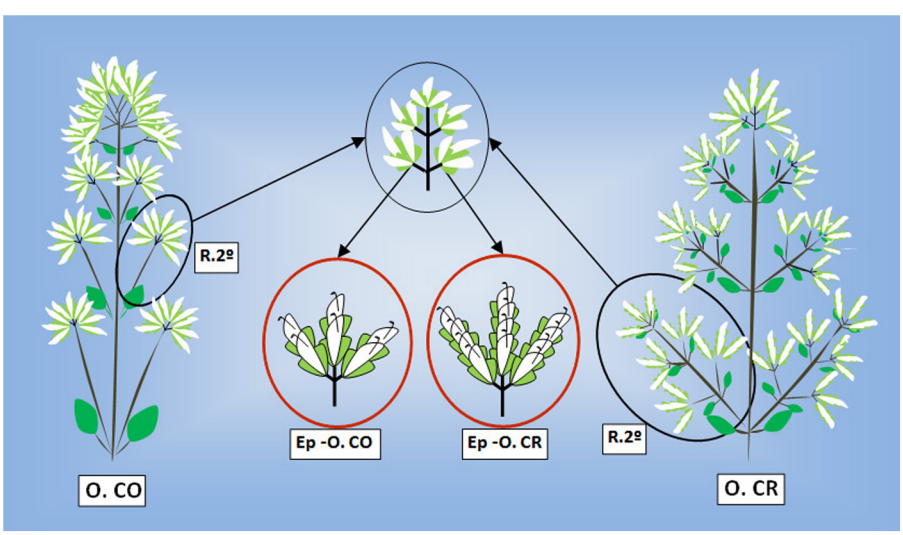

Fig. 1. Scheme of the architecture of the floral branch and arrangement of epicastros (Ep) and secondary branches (R.2°) in two subspecies of *O. vulgare*: O. Compacto (O.CO) and O. Criollo (O.CR).

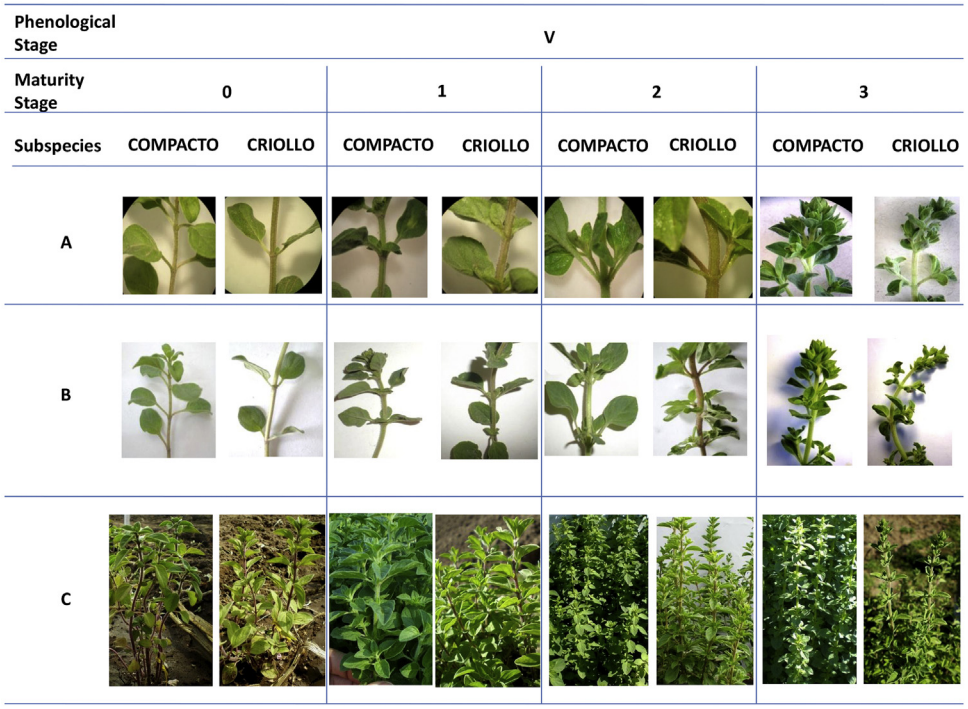

Fig. 2. Vegetative phases for two oregano subspecies. *O. vulgare* subsp. *vulgare*: O. Compacto; *O. vulgare* subsp. *hirtum* (Ietsw.): O. Criollo. V_0: Early Vegetative; V_1: Mean Vegetative; V_2: Late Vegetative; V_3: Transitional. A, 10x view; B, individual view; C, Crop view.

Table 2
Phenological scale of *Origanum* ssp. describing Vegetative (V) and Reproductive (R) macrostages. The phenological stage is determined according stem maturity state (*MS*, from 0 to 6). *MS* is based on the organs that are being generated from stem buds (leaves, branches and flower structures) at the moment of phenological observation.

Phenogical Stage	Denomination	Morphological Description
S-E	Seed-emergence	Dry seed or shoot emergence through the soil surface
V_0	Early vegetative	Axillary buds are not visible along the principal stem
V_1	Mean vegetative	At least two nodes with visible axillary buds (first pair of leaves in secondary branches) along the principal stem
V_2	Late vegetative	At least two nodes with secondary branches developed (detached from the principal axis) along the principal stem
V_3	Transitional	Presence of apical floral buds on the principal stem
R_4	Pre-flowering	Presence of floral buds in at least three secondary branches of the principal stem
R_5	Initial flowering	Up to three secondary branches of the principal axis with an open flower per epicastro
R_6	Full blooming	More than three secondary branches of the main axis with more than one open flower per epicastros

were attenuated due to the typical erect habit of flower branches (Fig. 3C).

3.3. Phenological scale description

Based on the prevailing development stage, the plant cycle was separated into two main macrostages: Vegetative (V) and Reproductive (R) phenophases. Phenological progress was evaluated by calculating *MSp* weekly, which in turn was divided into seven categories (from 0 to 6; Figs. 2 and 3), depending on the development degree of the axillary buds of the principal stem. Vegetative phases included *MS* 0 to 3, whereas R phases included *MS* 4 to 6 (Table 2). In this study, the seed-emergence stage (S-E) was not experimentally determined since crops were established from stems cuttings, the typical propagation management in this perennial species.

3.4. Modelling of phenological development

In both experiments, the cycle duration both in thermal time and calendar time was higher in O. Criollo than in O. Compacto, and transition between macrostages was observed earlier in the former subspecies (Table 3).

Phenology evolution of each macrostage (V and R) was represented by logistic models (Eq. (1)) in both subspecies. Subspecies differed in thermal requirements to inflection (Vegetative and Reproductive models) and plateau points (Reproductive models), being significantly lower in O. Compacto than in O. Criollo ($P \leq 0.05$, Tables 4 and 5; Fig. 4).

O. Compacto required a lower thermal time (approximately 100 °Cd) than O. Criollo to reach the beginning of V_3 phenophase (Table 5). Concerning reproductive development, $\mathbf{R_6} - \boldsymbol{i}$ in O. Compacto occurred about 6 days (considering an average temperature ≈ 19 °C) or 111 °Cd earlier than in O. Criollo. Moreover, O. Compacto required an accumulation of 84 °Cd less than O. Criollo to reach full maturity, represented as **full** – $\mathbf{R_6}$. Finally, the end of

Table 3
Duration of the critical phenophases $\mathbf{V_3}$ (transition from vegetative to reproductive development) and $\mathbf{R_6}$ (full blooming) in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo). Duration is expressed in accumulated thermal time (degree days from the beginning of the experiment) and calendar days (in parenthesis). Experiments conducted in Capilla de los Remedios, Argentina (31°26′S; 63°49′W).

Subspecies	Experiment 1		Experiment 2	
	V_3	R_6	V_3	R_6
O. Compacto	960.6 a (53)	2052.6 a(104)	1147.6 a(64)	2029.4 a(102)
O. Criollo	1024.8 a(57)	2194.0 a(108)	1395.5 b(76)	2253.3 b(112)

Different letters indicate statistically significant differences between subspecies according to LSD test ($P \leq 0.05$).

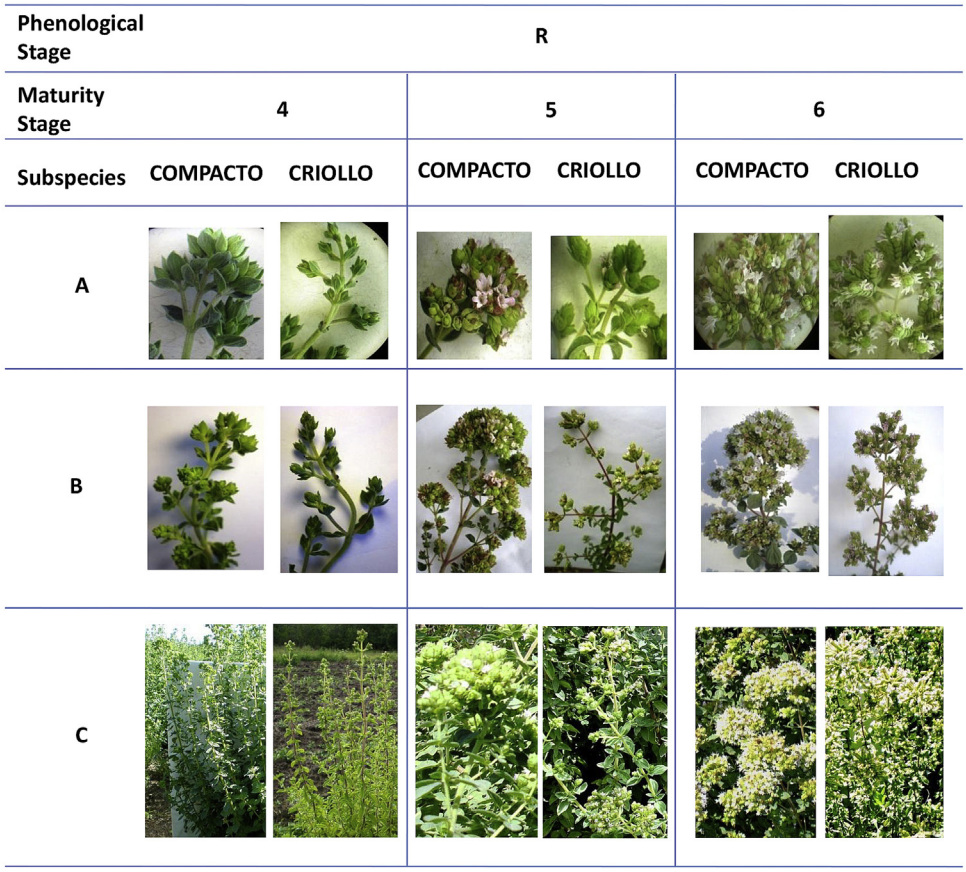

Fig. 3. Reproductive phenophases in two oregano subspecies. *O. vulgare* subsp. *vulgare*: O. Compacto; *O. vulgare* subsp. *hirtum* (Ietsw.): O. Criollo. R_4: Pre-Flowering; R_5: Initial Flowering; R_6: Full Blooming. A, 10x view; B, individual view; C, Crop view.

Table 4
Parameters (± standard error, SE) of logistic models fitted to Reproductive macrostage evolution in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo). Critical curve points $\mathbf{R_6} - \boldsymbol{i}$ and $\mathbf{R_6} - \boldsymbol{f}$ indicate accumulated thermal time to beginning of full blooming and to full blooming, respectively.

Parameters	Reproductive model	
	O. Compacto	O. Criollo
β[a]	1400.0 ± 860.0	3180.7 ± 1914.5
γ[b]	4.506 ± 0.382	4.700 ± 0.369
$\mathbf{R_6} - \boldsymbol{i}$ (°Cd)	$1607.98 \pm 2.8 \times 10^{-7}$ b	1718.17 ± 7.26 a
$\mathbf{R_6} - \boldsymbol{f}$ (°Cd)	$2261.53 \pm 3.9 \times 10^{-7}$ b	2345.47 ± 9.91 a

Different letters indicate statistically significant differences between subspecies according to *T* test ($P \leq 0.05$).
[a] β is the parameter related to thermal time (°Cd) until the beginning of the exponential maturity advance point.
[b] γ is the parameter related to rate of phenological progress.

Table 5
Parameters (± standard error, SE) of logistic models fitted to Vegetative macrostage evolution in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo). Critical curve point $\mathbf{V_3} - \boldsymbol{i}$ indicates accumulated thermal time to beginning of transitional phenophase V_3.

Parameters	Vegetative model	
	O. Compacto	O. Criollo
β[a]	67.056 ± 35.0	699.8 ± 583.4
γ[b]	4.660 ± 0.640	6.543 ± 0.898
$\mathbf{V_3} - \boldsymbol{i}$ **(°Cd)**	$902.5 \pm 8.1 \times 10^{-7}$ b	$1001.6 \pm 1.4 \times 10^{-6}$ a

Different letters indicate statistically significant differences between subspecies according to *T* test ($P \leq 0.05$).
[a] β is the parameter related to thermal time (°Cd) until the beginning of the exponential maturity advance point.
[b] γ is the parameter related to rate of phenological progress.

the growth cycle in O. Compacto occurred about 4 days earlier than O. Criollo (considering a mean temperature of ≈ 23 °C during flowering in the study area).

The reproductive model showed a better fit than the vegetative one, as indicated by a relatively higher correlation coefficient and lower *RMSE*. Regression of estimated vs. observed plant proportion to R_6 indicated a slightly better fit in O. Criollo than in O. Compacto (Table 6).

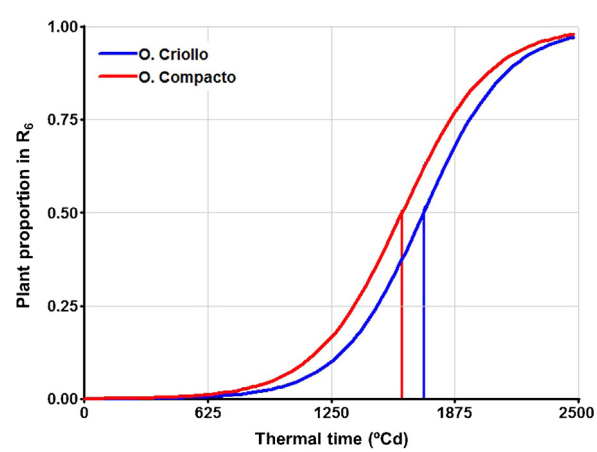

Fig. 4. Phenological evolution model in terms of plant proportion reaching the R_6 stage in two *Origanum* subspecies, *O. vulgare* ssp. *vulgare*: O. Compacto; *O. vulgare* ssp. *hirtum* (Ietsw.): O. Criollo. Vertical lines indicate $\mathbf{R_6} - \boldsymbol{i}$ the moment when the crop reaches to the beginning of flowering (accumulated thermal time to the inflection point of the curve).

Table 6
Goodness of fit Criteria of logistic models fitted to crop phenology evolution in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo).

Fit Criteria	Reproductive model		Vegetative model	
	O. Compacto	O. Criollo	O. Compacto	O. Criollo
r[a,b]	0.91	0.96	0.69	0.68
RMSE[b]	0.1151	0.1086	0.1460	0.1515

[a] Coefficient of determination.
[b] RMSE = square root of mean square error.

4. Discussion

4.1. Development of a phenological scale in Origanum

A non-destructive system to characterize developmental stages using qualitative and quantitative parameters is critically needed in *Origanum* spp. Such a system would be useful for establishing the basis for future ecophysiological studies, for incorporating new environments for crop production or adapting crop management practices. It would also allow quantifying differences among ecotypes by discriminating genotype-dependent traits (genotype effect) or genotype-environmental effects. In this study, we proposed a phenological system particularly suitable for perennial crops of agamic propagation which are annually harvested near full blooming.

We adapted a staging system used in alfalfa (Kalu and Fick, 1981). As a crop, alfalfa has many similarities with *Origanum*, like growth habit, the perennial trait, and key phenological events that define the crop value and harvest timing (flowering). Although the BBCH code (Lancashire *et* al., 1991) is a generic alternative and has been adapted for several species, two aspects explain the advantages of using the alfalfa scale to meet our objectives. Firstly, the BBCH code lacks the necessary precision for herbaceous perennial crops, including species that develop both in warm and cool seasons and additionally, it is ineffective to provide quantitative linking with photo and thermal timing, a very weak aspect if phenology needs to be predicted to understand environmental and management effects. Secondly, it has been suggested that already adjusted scaling methods that proved to be effective are preferable over the BBCH code (Ciha and Wilhelm, 1997).

Our phenological approach includes the determination of simple aspects, such as presence/absence of axillary or flower buds, which makes this scale very versatile for use in different ecotypes. The marked morphological differences between subspecies (Torres et al., 2012), mainly evident in internode and epicastro length (Figs. 1 and 3), did not prevent the use of the scale since it takes into account the progress of development of axillary buds (Table 2). In addition, the morphological description of the phenophases, especially V_3 and R_6, provides a practical tool to identify these critical events of the crop cycle (Figs. 2 and 3).

4.2. Origanum critical phenophases and thermal time requirements

Using this phenological scale, we could quantitatively assess differences between subspecies regarding thermal requirements to the critical stages V_3 and R_6.

Phenological progress was suitably represented by a logistic model based on accumulated thermal time. Although more years of observation are necessary to validate these preliminary results, differences in developmental rate between genotypes revealed a shorter cycle and lower thermal time requirement to full blooming (R_6) in O. Compacto than O. Criollo. This fact was explained by the earliest onset of $\mathbf{R_6} - \boldsymbol{i}$ and $\mathbf{R_6} - \boldsymbol{f}$ ($P \leq -0.05$; Table 4) in O. Compacto (Fig. 4).

We were particularly interested in determining the transitional V_3 stage as a specific phenophase, since it represents the end of the vegetative growth period of the crop and the moment at which the maturation rate starts to decelerate, probably because floral organs start to form. The earlier switch to reproductive development of O. Compacto ($P \leq 0.05$; Table 5), in correspondence with a lower thermal time requirement to blooming, reinforces the greatest precocity of this subspecies (Fig. 4).

According to the shapes of the curves in the reproductive model, subspecies started to differentiate one from each other early in the crop cycle, approximately at 900 °Cd in O. Compacto and 1100 °C in O. Criollo, similarly to the estimated values for $\mathbf{V_3} - \boldsymbol{i}$. Therefore, the transitional stage V_3 could also be visualized in the reproductive model.

Although the vegetative model was accurate in statistical terms, the parameter describing the plateau point was difficult to assess, probably because of the perennial nature of the species; i.e. new few sprouts continue to appear until blooming is well advanced. The short period of active vegetative growth and the large overlap between vegetative and reproductive growth made it difficult to establish a reliable indicator for $\mathbf{V_3} - \boldsymbol{f}$. However, this fact did not hinder adequate description of this macrostage, and the differences in the timing of the onset of V_3 stage (i.e., $\mathbf{V_3} - \boldsymbol{i}$) between subspecies could be clearly demonstrated.

In this study, the development of two *Origanum* subspecies was investigated under the natural conditions of the region during two growing seasons, from late autumn to early summer, with an average 13h-photoperiod (Table 1). Some studies, however, support the notion that the genus is responsive to photoperiod (long-day response, Circella et al., 1995). Accordingly, we hypothesize that differences among subspecies regarding their thermal requirements to critical events could be also controlled by photoperiodic effects. More studies are needed to investigate how photoperiod influences thermal time requirements in *Origanum* ssp. Our approach offers a tool to quantitatively characterize these aspects.

5. Conclusions

A simple phenological scale was built in crops of two *O. vulgare* subspecies, despite their differences in morphology and cycle length. The key divides the crop cycle in two macrostages according to predominant developmental stage of buds (V and R). Phenological development was accurately assessed through sigmoid-type models in which critical phenophases (V_3 and R_6) were parameterized. Thermal time to full blooming (R_6) was lower in O. Compacto (2260 °Cd) than in O. Criollo (2345 °Cd). Precocity of O. Compacto was associated with an earlier switch to reproductive development. Although the models were sufficiently accurate for predicting thermal time requirements throughout the crop cycle, further testing is needed to explore if differences between ecotypes could be related to genotype-dependent photoperiodic response.

This first approach to creating a specific *Origanum* phenological scale and quantitatively modelling development can contribute to diverse eco-physiological studies aimed at improving understanding of environmental and genetic regulation of growth and yield in *Origanum* genus.

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