



Day length modulates precocity and productivity through its effect on developmental rate in *Origanum vulgare* ssp.



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ARTICLE INFO

Article history:

Received 2 September 2016

Received in revised form 9 February 2017

Accepted 12 February 2017

Available online 20 February 2017

Keywords:

Day-length

Photoperiod response

development rate

Node differentiation

Essential oil composition

ABSTRACT

In *Origanum* spp. knowledge about mechanisms controlling development and growth in response to environmental factors such as temperature and photoperiod, is critical to improve management practices and varietal selection for an efficient use of natural resources. The aim of this research was to assess the influence of photoperiod on development, biomass and essential oil productivity in two subspecies of *O. vulgare* (ssp. *vulgare* and *hirtum*). For this purpose, photoperiod during vegetative phenophases up to the flowering stage (R_6) was artificially extended in 6 hday^{-1} . Extended photoperiod accelerated development and floral initiation but a genotype*photoperiod effect was found (*hirtum* > *vulgare*). Shorter cycle duration to R_6 under extended photoperiod increased node differentiation, but decreased stem length and consequently stems biomass, being these effects more accentuated in *O. vulgare*. Essential oil productivity was always higher in *O. vulgare* subspecies and under the extended photoperiod treatments. Both subspecies showed a greater proportion of sabinene hydrate and thymol when day length was increased. In *Origanum*, thermal time to floral initiation and flowering was dependent on photoperiod with a direct consequence on cycle length, biomass accumulation and essential oil composition. This first approach to analyse the photoperiodic response of *Origanum* can contribute to a better understanding of the environmental and genetic regulation of growth and yield.

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1. Introduction

Oregano is an important multipurpose aromatic plant which belongs to *Lamiacea* family. Its essential oil is employed in the food (as a fresh or a dehydrated spice), cosmetic, aromatherapy and pharmaceutical industries (Economou et al., 2011; Farías et al., 2010). The cultivation of “oregano” comprises species belonging to the genus *Origanum*, within which *O. vulgare* is the most variable species, widespread throughout the world (Ietswaart, 1980; Kordali et al., 2008 Xifreda, 1983). Subspecies can differ in

height, growth habit, flowering time or precocity and cycle length (Davidenco, 2015; Torres et al., 2012), and hence in crop adaptability, biomass and oil productivity.

The quality of the harvested product in oregano, either dry herb or essential oil, depends directly on the amount of floral organs (ISO, 1999). In turn, the crop productivity is defined by the amount of accumulated biomass until harvest and the proportion of floral organs (Nurzynska-Wierdak and Dzida, 2009). The flowering stage is hence, the most important stage of the crop cycle for both biomass productivity and oil quality. Temperature and photoperiod determine crop productivity (i.e. crop biomass) through their effect on development and flowering timing, and duration of the growth cycle (Ritchie and NeSmith, 1991). Longer cycles (e.g. time to flowering) are associated with higher biomass production (Langbehn et al., 2001). It is known that in *Origanum*, initiation of the floral transition occurs under increasing day length (Circella et al., 1995; Dudai et al., 1989) but scarce studies demonstrated genotypic variation in this mechanism. In a previous study under natural conditions in Central Argentina, thermal time to full blooming was

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found to differ among *Origanum vulgare* subspecies (*vulgare* and *hirtum*) and this was associated with a different switch timing to reproductive development (V_3 stage: presence of apical floral buds on the principal stem, (Davidenco et al., 2015) which suggested intraspecific variability in photoperiodic sensitivity.

Time to flowering directly impacts on the crop cycle duration and hence on biomass production and final crop yield. Reduced length of vegetative phases can decrease the number of nodes, branches, leaves and reproductive sites as shown in several species (Clerget et al., 2008; Cookson et al., 2007; Nico et al., 2015; Slafer et al., 1994).

In aromatic species, photoperiod can also influence essential oil quality (Burbott and Loomis, 1967; Circella et al., 1995; Fahlén et al., 1997). In oregano, sabinene hydrate, thymol, γ -terpinene and 4-terpineol are the major components (Dambolena et al., 2009). Sabinene hydrate along with thymol and carvacrol are responsible for the essential oil antioxidant activity (Quiroga et al., 2015). Previous studies (Circella et al., 1995) demonstrated that the sabinene hydrate component is positively associated with long photoperiod. However, no other studies analysed how the photoperiodic effect modulates oil quality in terms of other main components.

The aim of this research was to assess the influence of photoperiod on development, length of critical phenophases and productivity. Two subspecies of oregano, *O. vulgare* ssp. *vulgare* (“O. Compacto”) and *O. vulgare* ssp. *hirtum* letsw. (“O. Criollo”), differing in precocity and productivity were used as study cases.

2. Materials and methods

2.1. Study site and biological material

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 (S1) and 2012 (S2) growing seasons. Mean monthly air temperature during both crop cycles were 19.8°C and 20.2°C for S1 and S2 respectively. In general, both rainfall and temperature were representative of the historical weather variation of the region (794 mm and 19.6°C, respectively).

Subspecies *O. vulgare* ssp. *vulgare* (“O. Compacto”) and *O. vulgare* ssp. *hirtum* letsw. (“O. Criollo”) were selected owing to their frequent cultivation in the study area. Subspecies differ in time to flowering, architectural traits and productivity (Davidenco et al., 2015; Torres et al., 2012). Plants grown from cuttings of 1-year-old mother plants were transplanted in early September in both seasons, and planted in rows spaced at 0.70 m apart with a distance of 0.2 m between plants. The experiments were maintained under irrigated conditions, and cultural labors required for proper crop development (as weed control) were also carried out.

2.2. Experimental design

The experiment was arranged in a split-plot design with three replicates in a 2 × 2 factorial design. Photoperiodic regime was the main plot (Natural Photoperiod, NP and 6-h extended photoperiod, EP) and the subspecies was the subplot factor. Each subplot (experimental unit, EU) comprised three (S1) or five (S2) plants. Extended photoperiod (EP) had the purpose of simulating the long-day condition and was imposed from September 7th (S1) or 9th (S2), when the mean photoperiod was 11 h 47 min, until December 14th (S1) or 16th (S2) when the mean photoperiod was 14 h 1 min. Extension of photoperiod was achieved through two low-intensity fluorescent tube lights (radiation of 3.08 $\mu\text{mol m}^{-2} \text{s}^{-1}$) hung up on a portable acrylic frame placed 90 cm above the ground. The system was connected to a timer that automatically turned lights on and off. To

maintain a 6-h difference between NP and EP, the timer was set weekly.

2.3. Photoperiodic response of phenology development

Development was weekly monitored until full blooming using a phenological scale previously built for *Origanum* spp. (Davidenco et al., 2015). The stems of each plant were categorized into the proper phenological stage (V_0 – V_3 for the vegetative macrostage, and from R_4 to R_6 for the reproductive macrostage). Phenological stage per plant was determined based on the predominant phenophase of stems. At a crop level, phenological stage was determined as the phenophase exhibited by more than the 50% of plants within each EU. Thermal time (TT, in degree days °Cd) accumulated up to V_3 and R_6 was determined as the summation of the differences between mean daily temperature and crop base temperature (considered as 0°C; Kintzios, 2002; Thanos et al., 1995). V_3 is the phenological stage where the 50% of plants have apical floral buds on the principal stem and R_6 is the full blooming phenophase (Davidenco et al., 2015).

In each treatment, the proportion of plants reaching V_3 and R_6 stages was modeled as a binomial variable. Curves for the phenological progress of the plants proportion to the vegetative V_3 and reproductive R_6 stages were fitted through non-linear mixed models (logistic) including a random effect on the phenological evolution slope [eqn 1].

$$y = 1 / (1 + \beta \exp^{-(y+u) \times TT}) \quad (1)$$

where, y is the proportion of plants that reached the V_3 or R_6 ; β is the parameter related to thermal time (°Cd) accumulated until the beginning of the exponential maturity point; γ is the parameter related to the 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).

Inflection points (V_3 -i, R_6 -i) and plateau points (full- V_3 , full- R_6) were set as the beginning and plenitude of the phenophases, respectively. They were calculated using the second derivative of the logistic functions (Passos et al., 2012) [eqn 2], and with equation 3, respectively.

$$V_3i \text{ or } R_6 - i = (\ln(1/\beta)) / (-(\gamma + u)) \quad (2)$$

$$\text{full} - V_3 \text{ or full} - R_6 = (\ln(1/(49 * \beta))) / (-(\gamma + u)) \quad (3)$$

We opted to estimate the beginning (V_3 -i, R_6 -i) and full (full- V_3 , full- R_6) critical phenophases through mathematical functions instead of using simple interpolation of the logistic curve (Paine et al., 2012).

2.4. Growth dynamics and productivity

In both seasons, the number of stems per plant and nodes in the main stem (NdN) were registered weekly until R_6 . In S1, stem length was measured weekly in two stems per plant and EU until R_6 . Stem elongation rate (ER, cm.d^{-1}) was calculated from non-linear regression models (Gompertz) fitted to the relationship between stem length and time in days. At the R_6 stage, plants were harvested and total plant biomass and mean stem biomass (SB) were measured after oven-drying and weighing.

At R_6 , three samples of 300 g of fresh biomass were taken in each treatment for essential oil (EO) extraction by hydro-distillation with a Clevenger-type equipment (Evans and Trease, 1995; Robbers et al., 1996). EO yield was calculated as the ratio between the extracted cold oil volume and plant biomass expressed on a dry weight basis.

2.5. Essential oil composition analysis

A gas chromatograph (Perkin-Elmer Clarus 600, Shelton, CT, USA) coupled with an ion trap mass detector equipped with a capillary column DB-5 (30 m long, 0.25 mm i.d. and 0.25 mm coating thickness) was used for the separation of the essential oil components. Ionisation was performed by electron impact at 70 eV. Mass spectral data were acquired in the scan mode in the m/z range of 35–450. The column temperature was programmed according to the following gradient: 60 °C during 5 min, increasing at 5 °C/min to 250 °C. The injector and detector were maintained at 260 °C and 280 °C, respectively. Main oil components were identified by comparing their retention time and mass spectra with published data (Adams, 2007) and NIST libraries. The quantitative composition was obtained by peak area normalization, and the response factor for each component was considered to equal 1.

2.6. Statistical analysis

Treatment effects on thermal time to V_3 and R_6 and on productivity variables were determined using variance analysis following a split-plot design. In order to analyse whether the response to photoperiod length was the same or different between subspecies, the interaction between both factors (S^*P) was included in the statistical analysis. LSD Fisher test ($p < 0.05$) was used to compare averages for EO yield, EO composition, stem biomass, and stem length. Goodness of fit-criteria for the phenological models was evaluated with the square root of mean square error (RMSE) and the coefficient of determination.

Principal component analysis (PCA) was applied to the correlation matrix of the standardized (normalized) data formed by the main chemical composition of the EO (Johnson and Wichern, 2007). The purpose of the PCA was to explore associations between the main chemical components and the combination of subspecies and light conditions. Data were analysed using the InfoStat software (Di Rienzo et al., 2014).

3. Results

3.1. Development towards vegetative-reproductive transition (V_3) and full blooming (R_6)

Logistics models adequately described phenological evolution towards the V_3 (Fig. 1) and R_6 (Fig. 2) stages as a function of accumulated thermal time from planting date. Determination coefficients and RMSE values indicated a better fit of the data in the reproductive than in the vegetative models (Figs. 1 and 2). Longer photoperiods in comparison to natural conditions reduced phenophases duration and, hence, cycle length in both subspecies.

Significant effects of the interaction factor *subspecies*photoperiod* ($p < 0.0001$; Fig. 3) were found for thermal time requirements to V_3 and R_6 .

Time to initiation time of the reproductive transition (Fig. 3.A) and the rate of the vegetative phenological progress (Table 1) did not differ among species under extended photoperiod. In contrast, reproductive development rate differed between subspecies (Table 2), and blooming initiation (R_6 -i) began approximately 220 °Cd earlier in *O. Criollo* than in *O. Compacto* (Table 2). At the end of the crop cycle, differences between subspecies increased to almost 500 °Cd (full- R_6 ; Table 2).

3.2. Photoperiodic effects on growth parameters and essential oil productivity

Stem nodes number, stem elongation rate and EO content varied among genotypes and day length treatments (Table 3). Although

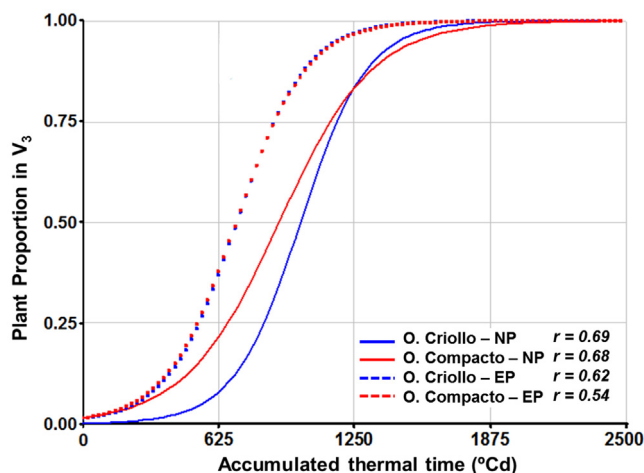


Fig. 1. Proportion of plants reaching the V_3 stage as a function of thermal time in two *Origanum* subspecies, *O. vulgare* ssp. *vulgare*: *O. Compacto* (red series); *O. vulgare* ssp. *hirtum* (letsw.): *O. Criollo* (blue series) grown under natural (NP) or extended photoperiod (EP). Solid lines, NP; Dotted lines: EP. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

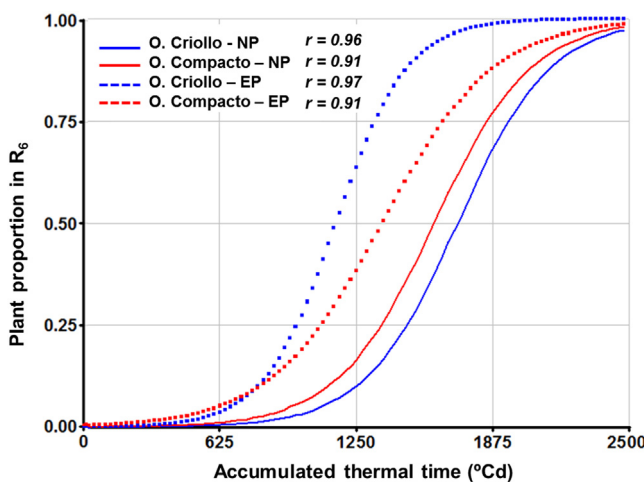


Fig. 2. Proportion of plants reaching the R_6 stage as a function of thermal time in two *Origanum* subspecies, *O. vulgare* ssp. *vulgare*: *O. Compacto* (red series); *O. vulgare* ssp. *hirtum* (letsw.): *O. Criollo* (blue series) grown under natural (NP) or extended photoperiod (EP). Solid lines, NP; Dotted lines: EP. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Parameters (\pm standard error, SE) of logistic models fitted to Vegetative macrostage evolution in two subspecies of *Origanum vulgare* (*O. Compacto* and *O. Criollo*) under extended photoperiodical conditions. Critical curve point V_3 -i indicates accumulated thermal time to beginning of vegetative to reproductive transition (phenophase V_3).

Parameters	Extended Photoperiod	
	<i>O. Compacto</i>	<i>O. Criollo</i>
β^1	79.98 \pm 47.4	93.20 \pm 49.5
γ^2	6.203 \pm 0.927 a	6.392 \pm 0.913 a
V_3 -i (°Cd)	707.6 \pm 6.5 a	714.1 \pm 9.7 a

Different letters indicate significant differences between subspecies according to T test ($P \leq 0.05$). ¹ β is the parameter for the thermal time requirement (°Cd) to begin the exponential phase towards maturity. ² γ is the parameter related to the phenological development rate.

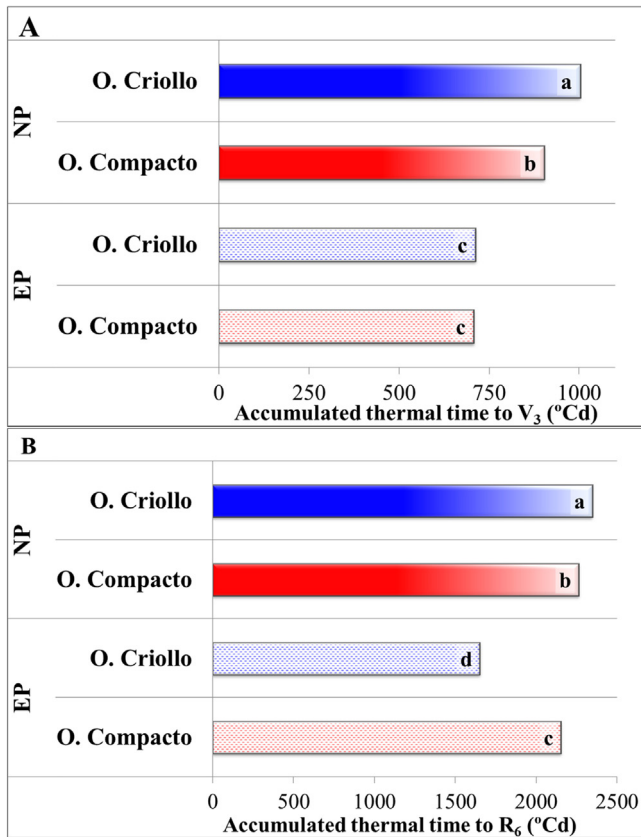


Fig. 3. Thermal time from planting date to the beginning of transitional stage $-V_{3i}$ (A) and full blooming stage $-full R_6$ (B) in two *Origanum* subspecies, *O. vulgare* ssp. *vulgare* (O. Compacto) and *O. vulgare* ssp. *Hirtum* (letsu), O. Criollo) grown under two photoperiodic conditions, natural photoperiod (NP) and extended photoperiod (EP). Different letters indicate significant differences between each photoperiod \times subspecies combination according to LSD Fisher Test, ($P \leq 0.05$).

longer days increased NdN, stem biomass was reduced in comparison to controls ($\cong 50\%$ reduction). A significant S*P interaction was found for stem biomass indicating that O Criollo was less sensitive (19% reduction in comparison to 70% reduction for O. Compacto). Final stem length was closely associated with stem biomass and was reduced by 26% in longer days.

O. Compacto exhibited higher EO yield than O. Criollo. Under longer days both subspecies increased EO in about 30% (Table 3). Qualitative analysis showed that more than 30 components were

Table 3

Nodes per stem (NdN), Stem elongation rate (ER; $cm \cdot d^{-1}$), stem biomass (SB; g), stem length (SL) and essential oil content (EO; % v/w, on a dry weight basis) in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo) grown under two photoperiodic conditions (natural, NP and extended photoperiod, EP) in Capilla de los Remedios, Argentina (31°26'S; 63°49'W).

Variance analysis	NdN	ER ($cm \cdot d^{-1}$)	SB (g)	SL (cm)	EO (%)
Subspecies * Photoperiod	ns	ns	<0.001	ns	ns
Photoperiod	0.006	<0.0001	<0.001	0.01	0.025
Subspecies	0.012	0.024	ns	ns	0.048
Factorial combination					
O. Compacto * NP	–	–	1.48 d	–	–
O. Criollo * NP	–	–	1.06 c	–	–
O. Compacto * EP	–	–	0.43 a	–	–
O. Criollo * EP	–	–	0.86 b	–	–
Photoperiod					
NP	22 a	0.015 a	1.27 b	38.3 b	2.04 a
EP	26 b	0.058 b	0.64 a	28.1 a	2.67 b
Subspecies					
O. Compacto	22 a	0.030 a	–	–	2.62 a
O. Criollo	26 b	0.044 b	–	–	2.09 b

Different letters indicate significant differences according to LSD Fisher Test ($P \leq 0.05$).

Table 2

Parameters (\pm standard error) of logistic models fitted for reproductive development in two subspecies of *Origanum vulgare* (O. Compacto and O. Criollo) grown under extended photoperiodic conditions. Critical curve points R_{6-i} and full- R_6 indicate thermal time to the initiation and full blooming stages, respectively.

Parameters	Extended Photoperiod	
	O. Compacto	O. Criollo
β	214.2 \pm 84.6	1203.8 \pm 567.7
γ	3.916 \pm 0.351 a	6.124 \pm 0.462 b
R_{6-i} ($^{\circ}Cd$)	1387.0 \pm 18.63 b	1165.3 \pm 11.74 a
Full- R_6 ($^{\circ}Cd$)	2147.9 \pm 28.84 b	1649.0 \pm 16.62 a

Different letters indicate significant differences between subspecies according to T test ($P \leq 0.05$). ¹ β is the parameter for the thermal time requirement ($^{\circ}Cd$) to begin the exponential phase towards maturity ² γ is the parameter related to the rate of phenological progress/development rate.

present in the extraction of essential oil. Only components that constituted at least the 3% of the total EO are shown in Fig. 4. Sabinene hydrate and thymol were the most abundant components ($>10\%$) and their relative proportion was increased under longer photoperiods. 4-terpineol showed an opposite effect while no significant effects were detected in the rest of oil components (Fig. 4). For the rest of main components shown in Fig. 4, subspecies evidenced dissimilar responses according to the photoperiodic condition.

In order to explore correlations between essential oil components, subspecies and day-length, a multivariate PCA analysis was performed (Fig. 5). Although the biplot obtained from the first two principal components explained 85% of the variability of the data, no clear photoperiodic effects were conspicuous. The first axis (PC1) explained 48.5% of essential oil variation and was mainly associated with the proportion of gamma terpinene or alpha terpineol. These components appeared as negatively correlated as they formed a plain angle between them. Variability between subspecies was reflected on the second axis (PC2), as they projected separately along this axis. The oil component sabinene hydrate was negatively associated with thymol and carvacrol and it was more abundant in O. Compacto.

4. Discussion

4.1. Photoperiod effects on development and growth varied between subspecies

Origanum spp. is known as a long day species (Circella et al., 1995; Dudai et al., 1989). In agreement, increasing day length fastened development towards floral transition (V_3) and full blooming

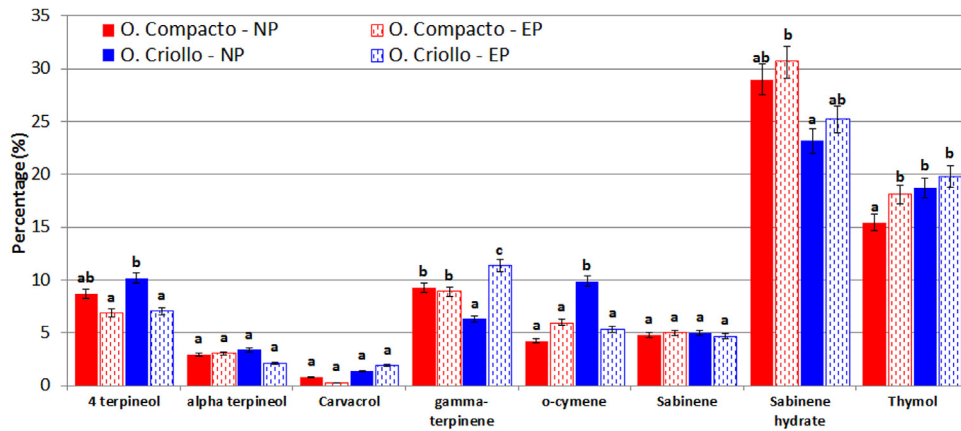


Fig. 4. Main essential oil components proportion (in%) at the full blooming stage (R_6) in flowers of two subspecies of *Origanum vulgare* (*O. Compacto* and *O. Criollo*) cultivated in Capilla de los Remedios, Argentina ($31^{\circ}26'S$; $63^{\circ}49'W$) under two photoperiodic conditions (natural photoperiod –NP– and extended photoperiod –EP–). Different letters indicate significant differences between each *photoperiod* \times *subspecies* combination according to LSD Fisher Test, ($P \leq 0.05$).

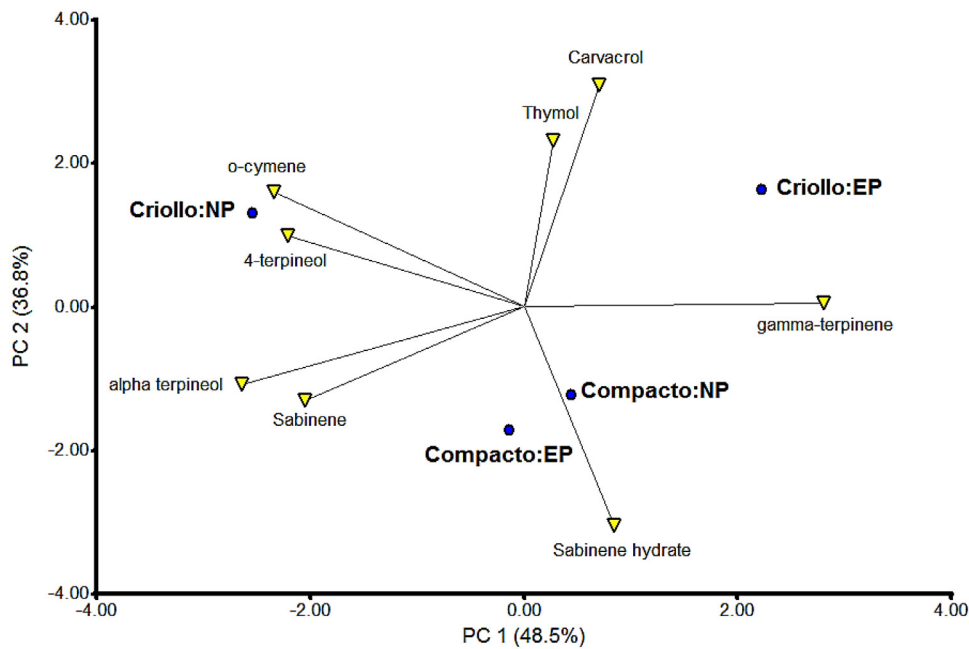


Fig. 5. Principal components analysis (PCA) biplot obtained from the first and second principal components (PC) of essential oil (EO) composition of two subspecies of *Origanum vulgare* (*O. Compacto* and *O. Criollo*) cultivated in Capilla de los Remedios, Argentina ($31^{\circ}26'S$; $63^{\circ}49'W$), under two photoperiodic conditions, natural photoperiod (NP) and extended photoperiod (EP). Eight main EO components (yellow triangles) are shown under the effect of four treatments combinations (blue circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 3) in this study. Although selected genotypes were different in terms of architectural traits (e.g. creeping growth habit in *O. Compacto* and an erect growth habit in *O. Criollo*), both followed a similar development pattern with slight blooming time differences ($<100^{\circ}Cd$) under natural conditions (Davidenco et al., 2015). Under EP treatments, both genotypes followed a similar trend towards V_3 (Fig. 3A). Due to the perennial nature of *Origanum*, regrowth occurring during most part of the cycle could lead to overestimation of the thermal time to V_3 for the complete plant population (full V_3). A lower goodness of fit for the vegetative macrostage evolution reinforces this. It was possible, however, to conclude that genotypes differed in the magnitude of their response to increases in day length, and greater cycle shortenings were observed in *O. Criollo* (e.g. 24% reduction). These results demonstrate a differential day length sensitivity, which can be related with an earlier induction or a lower photoperiod threshold in *O. Criollo*. Differences among genotypes were more conspicuous after V_3 and towards

full blooming. Increases in day length increased the rate of flowers production mainly in *O. Criollo* (e.g. slope = 6.1 in Fig. 2) and the time elapsed between R_6 -i and full blooming was 36% ($484^{\circ}Cd$ vs $761^{\circ}Cd$) shorter in this genotype in comparison to *O. Compacto*.

Hastened development due to larger day length affected node production. On the contrary to what is generally observed in other long-day species (i.e. barley and wheat), larger photoperiods increased the rate of node production. In this study, the absolute node number per stem was 15% larger than in natural conditions. Stem biomass, however, was lowest under photoperiod extension (average reduction of 50%). These results are in agreement with the general positive association between phase duration, solar radiation capture and biomass accumulation. Therefore, in this study the low biomass was a direct consequence of a short cycle under extended photoperiod.

In general, and also in *Origanum*, productivity is associated with the growth period length (Ritchie and NeSmith, 1991), biomass

production (stems and branches) and dry matter partitioning to inflorescences. Since node number was increased but cycle length was decreased, it is reasonable to state that the rate of node appearance was increased when daylight hours were extended. Changes in the phyllochron, hence, could not be disregarded (Clerget et al., 2008).

O. Criollo had more nodes but lower stem biomass than O. Compacto, as also found in previous studies (Torres et al., 2012) but exhibited a lower stem biomass decrease with extended photoperiod. Although in this study, the number of flowers was not measured it is reasonable to say that the relative proportion of flowers (flower biomass per unit of plant or stem biomass) was increased under EP. This could explain the positive effect of larger photoperiods in oil concentration (Table 3) which increased up to 30%. In other aromatics species as peppermint, larger photoperiods were associated with enhanced EO production although the mechanism for this still remains unclear (Fahlén et al., 1997). O. Compacto always showed higher EO contents (2.6%) than Criollo (2.1%) and no significant interactions were found for subspecies*photoperiod (Table 3).

4.2. Essential oil quality is influenced by photoperiod

Among 30 EO components, sabinene hydrate and thymol were the most clearly affected by changes in photoperiod. Larger quantities of these components were found in plants of both subspecies grown under extended light conditions (Circella et al. (1995). Gamma-terpinene, an aromatic monoterpene and a thymol precursor, was more affected by long days (increased) in O. Criollo than in O. Compacto. Tibaldi et al. (2011) showed similar responses of this subspecies when comparing oregano grown at full light conditions or at 50% shade. Although carvacrol proportion was lower than 3% in agreement with other studies in the region (Asensio, 2013), its consideration in the chemical analysis was due to its relevance in the organoleptic quality of the essential oil (Juliani et al., 2008). Carvacrol along with thymol are jointly quantified as total phenolic compounds (Adam et al., 1998). Both are closely associated with the aroma of the essence, as they provide strong spicy notes, related to the resinous smell (Juliani et al., 2008). In this study, O. Criollo exhibited an improved phenolic content (Carvacrol + Thymol) with increasing daylength in a larger extent than O. Compacto. In brief, both the organoleptic quality in terms of sensory attributes and the antioxidant capacity (due to Sabinene hydrate, thymol and carvacrol (Quiroga et al., 2015) was sensitive to the luminous environment, in different extent between subspecies.

5. Conclusions

In oregano, photoperiod generates changes in cycle length with a variable effect in different subspecies. The two subspecies used in this study exhibited the typical behaviour of long-day plants as the thermal time requirement to full blooming was reduced when daylight was increased. O. Criollo, however, seemed to have a greater photoperiodic sensitivity since cycle shortenings reached 25%. Shorter cycle length under longer photoperiod significantly diminished oregano productivity in terms of biomass (O. Compacto < O. Criollo) but increased the rate of node differentiation and essential oil yield. Greater proportions of essential oil components sabinene hydrate and thymol were found under longer days. This first analysis of the photoperiodic response of *Origanum* in terms of development and productivity can contribute to diverse studies aimed at improving crop management and knowledge of the environmental and genetic regulation of growth and yield.

Acknowledgements

We thank the Argentinian National Research Council (CONICET) for funding this research with a Ph.D. grant to Vanina Davidenco. We also acknowledge Dra. Claudia Asensio from the Biological Chemistry Laboratory, National University of Córdoba, School of Agricultural Sciences and IMBIV (CONICET) for the essential oils quality determinations.

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