

## Flowering patterns in sub-Mediterranean grasslands: a functional approach

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**Background and aims** – Temporal phenological segregation among species within a plant community can be viewed as a niche differentiation that promotes species co-existence. Following this hypothesis the functional assessment of the flowering pattern was analysed in sub-Mediterranean mountain grassland.

**Methods** – The study was carried out in two sites at different elevations. Four fenced plots of 50 m<sup>2</sup> each were established in both sites. Phenological relevés were carried out in each plot every fifteen days and soil samples were collected in each plot. The functional traits sets of the flowering species were analysed at each considered time interval.

**Key results** – Each phenological phase tends to be linked to a group of functional traits (e.g. bulbs or tuber/rhizome, low height and spring green leaves for the early spring period; rhizome or tuber, hemicryptophyte caespitose, mid height, presence of stolons and persistent green leaves for the late spring period). Dominant species reach their maximum phenological forwardness in the middle of the vegetative season, while non-dominant species ‘exploit’ the beginning and end of the vegetative season. Two main sets of strategies allowing non-dominant species to co-exist with the dominant ones were highlighted. The first characterizes the tall graminoids-dominated patches, where a pattern of traits allows subordinate species to differentiate the flowering temporal niche compared to the dominant ones. The second set of strategies is related to some small-sized species, which can co-exist with dominant species by exploiting gaps due to livestock disturbance, or by forming patches given their clonal ability. This strategy allows them to share the optimal temporal niche with dominant species.

**Conclusions** – Flowering pattern promotes species co-existence and is driven by functional differentiation of species that in turn is filtered by environmental stress/disturbance type and intensity.

**Key words** – Species competition, co-existence, flowering patterns, Functional traits, mountain grasslands, phenology, temporal niche.

### INTRODUCTION

Phenological studies are important for understanding species interactions and community functions as well as the ones concerning the spatial aspects (Tilman 1982, Fenner 1998). The selection pressures, coming from environmental constraints, are the first determinant of timing and patterns of phenological events in a plant community (Primack 1985). These pressures arise from abiotic factors such as air temperature and soil moisture (Smith-Ramírez & Armesto 1994, White 1995, Diekmann 1996, Fitter et al. 1995, DeBussche et al. 2004), photoperiod (White 1995, Keller & Körner 2003), and biotic factors such as pollinators (Rathcke 1983, Totland 1993, Smith-Ramírez & Armesto 1994), or the timing and kind of grazing (Watkinson & Ormerod 2001). Community structure is by itself an important factor because it

regulates the type of interaction among individuals and species (Heinrich 1976).

Flowering phenology is known to be determined by many abiotic factors such as temperature, photoperiod and resource availability (e.g. nutrient and water; Rathcke & Lacey 1985). In turn, the resource uptake ability is function of the area, the activity, and the distribution in space and time of the plant surface through which resources are intercepted (Grime 2001). Afterwards, plant traits linked to competition for light and soil resources uptake and storage (e.g. plant height, life form, leaf persistence, storage organs) are expected to play an important role in the determination of the flowering pattern inside a plant community, due to a tradeoffs between competition and reproduction (Martinková et al. 2002, Golluscio et al. 2005, Sun & Frelich 2011).

**Table 1 – Pedo-climatic characteristics of site A and site B.**

AWC: available water capacity; WD: water deficit; GI: growing period index.

Site	Average annual temperature (*C)	Total annual precipitation (mm)	Summer precipitation (mm)	AWC (mm)	WD (no. of months)	GI (no. of days)	Beginning of growing season (t min > 6°C)	End of growing season
A	9.7	900-1000	180	19	4	150	early May	end October
B	6.4	1400-1500	240	37	0	120	early June	end September

In spite of that, there is a dearth of data on the relationship between flowering phenology, plant community characters and plant traits, especially for sub-Mediterranean mountain grasslands. Taking into consideration these issues, the research analyzed the flowering pattern of sub-Mediterranean mountain grassland. The following questions were addressed: (i) how is the flowering pattern related to the functional trait shift? (ii) how do observed functional patterns contribute to the coexistence of species? (iii) how does altitudinal gradient affect the flowering functional pattern?

MATERIALS AND METHODS

Study area

The study was carried out in two sites of the Umbria-Marches Apennines (central Italy). Site A (43°16'N 13°05'E) is between 1000 and 1200 m a.s.l., on lithic haploxeroll loamy-skeletal mesic soils, with OiACCR profile and a depth of 30–35 cm (Pieruccini 2007). Site B (42°57'N 13°15'E) is between 1700 and 1900 m a.s.l., on lithic ustorthent coarse-loamy frigid soil with OiACR profile and a depth of 40–45 cm (Pieruccini 2007). Slopes range from 5 to 15 degrees with north-facing aspect, and the bedrocks are limestones. The study area falls into the bioclimatic Temperate Region (Rivas-Martínez & Rivas-Saenz 1996–2009). Site A is drier and warmer than site B and has a longer growing period (table 1). The growing season (days with a daily average temperature higher than 6°C; Bonan 2008) begins in the first days of May in site A and in the first days of June in site B, while it concludes at the end of October and September respectively. Site B takes place at the border of the subalpine bioclimatic belt, namely near the potential upper timberline (Biondi & Baldoni 1995, Orsomando & Catorci 2000).

Site A is usually grazed by sheep and cattle from mid May to late October, while site B is grazed by sheep from mid June to the end of September.

Data collection

Four fenced plots of 50 m<sup>2</sup> each were established in both sites (distance among plots was of 500 m). To determine soil texture and depth, in each of them a sample was taken in the field. Each sample was a mixture of soil collected in five locations inside a 2 m × 2 m plot (next to each fenced plot) at depths ranging from 10 to 30 cm. Soil samples were analysed by the Marches Region agrochemical analysis and research laboratories according to the methodological standards established by Italian ministerial decree 13/09/99. Mean

monthly temperatures and mean monthly precipitation data (recorded over a period of thirty years) were collected from the Montemonaco (as indicator of site A) and Monte Terminillo (as indicator of site B) meteorological stations placed not far and at the same altitude of the study areas.

In 2005, phenological relevés were carried out in each plot every fifteen days from March to August and every month from September to November (27 Mar., 10 and 25 Apr., 10 and 25 May, 16 and 31 Jun., 15 Jul., 1 and 17 Aug., 16 Sep., 17 Oct., 15 Nov. in site A; 28 Mar., 11 and 26 Apr., 11 and 26 May, 17 Jun., 01 and 16 Jul., 02 and 18 Aug., 17 Sep., 18 Oct., 14 Nov. in site B).

The following data were collected: (a) phenological status of each individual of each species according to the phenological classes listed in table 2; (b) canopy height of community along a random transect following the method of Donita et al. (2003).

In addition, for each phenological relevé, the above-ground phytomass was collected in contiguous fenced sub-plots, each of 1 m<sup>2</sup>, oven-dried and weighed to estimate plant community productivity (Whalley & Hardy 2000).

For each listed species, the following six groups of functional plant traits were considered.

- (1) Raunkiaer life forms: chamaephytes (succulent: Chsucc, suffruticose: Chsuffr and reptant: Chrept), hemicryptophytes (scapose: Hscap, caespitose: Hcaesp, reptant: Hrept, rosulate: Hros and biennial: Hbienn), bulbous geophytes (Gbulb) and therophytes (scapose: Tscap and caespitose: Tcaesp).
- (2) Species average height (cm): 1–10 cm (h1), 11–20 cm (h2), 21–30 cm (h3), 31–40 cm (h4) and > 40 cm (h5).
- (3) Runners: present or absent.
- (4) Underground storage organs: tap root, rhizome/tuber, bulb and no storage organs.
- (5) Leaf persistence: spring green, summer green, overwintering green, persistent green.
- (6) Pollination strategy: biotic pollination, anemophily and self-pollination.

The abovementioned traits were chosen because potentially linked to species competition for pollinators, light and soil resources or because can facilitate the understanding of the temporal and spatial niches occupation.

Data were gathered from Grime et al. (1988), the Bioflor database (Klotz et al. 2002), and, as concern species height, Pignatti (1982); field observations also supplemented the data set.

**Table 2 - Phenological phases.**

State	Event	Phase
vegetative	growth	leaves visible growth
generative	flowering	floral buds completely developed
		full flowering
vegetative	drying up of green elements	beginning of yellowing
		full drying up

### Data analysis

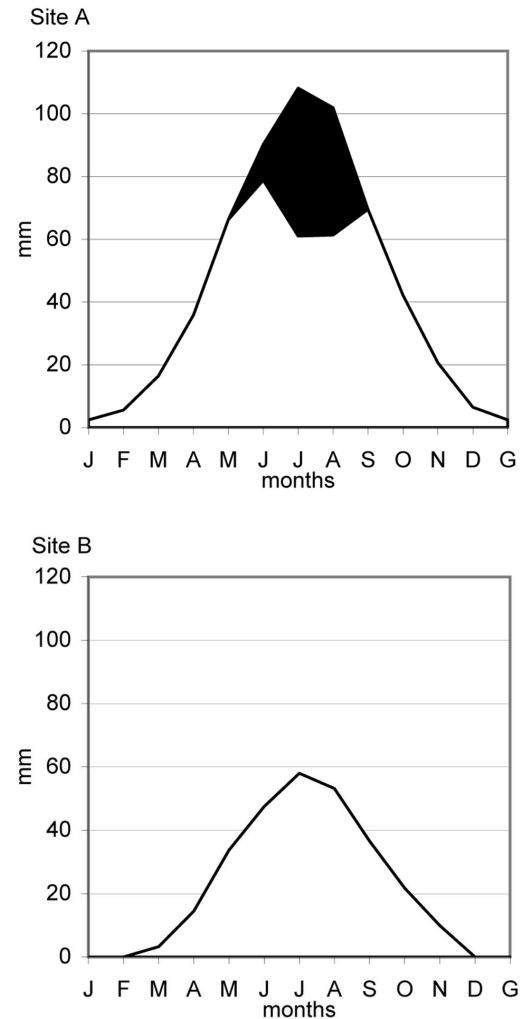
Climatic data (mean monthly temperatures and mean monthly precipitation), latitude, aspect and slope angle were averaged for each site and served to estimate potential evapotranspiration; soil texture and soil depth data were averaged for each site and used to calculate available water capacity and soil water reserve. All these data were processed using the calculation method developed in Microsoft Office Excel 2000 by Armiraglio et al. (2003), in order to evaluate soil water deficit (mm year<sup>-1</sup>), namely the difference between potential and actual evapotranspiration in a given site. Potential evapotranspiration is given by the not corrected evapotranspiration, calculated using Thornthwaite's formula, multiplied by two correction coefficients, *k* and *As*, depending, the former on latitude and month (day length), the latter on aspect and slope angle (amount of solar radiation hitting the topographic surface). Actual evapotranspiration is function of corrected evapotranspiration and soil water reserve. The last depends on available water capacity and cumulative water loss.

For each phenological relevé, data concerning canopy height and aboveground productivity of plant community were averaged (in each site).

Aiming the comparison, among homogeneous groups of relevés and to identify the phenological patterns, hierarchical clustering (average algorithm, chord distance) was applied for each site on a matrix of flowering species × survey date. The elements of this matrix were the percentage of flowering individual of each species out of the total number of flowering individuals in a certain plot during the whole growing season. For each cluster obtained by the multivariate analysis, the days of relevés were assessed to define the time interval of the phenological pattern ( $t_n$ ).

Indicator Species Analysis (McCune & Grace 2002) was carried out (on two matrices relevés × functional traits and relevés × time period) to determine the indicator traits of each  $t_n$ . The statistical significance of results was tested using the Monte Carlo test. Indicator values (*Iv*) equal to or greater than 50 were considered of interest ( $p < 0.05$ ). Percentage of traits occurrence in each time interval (% of flowering individuals having a given trait out of the total number of flowering individuals) was calculated as well.

To test the importance of plant community structure and, indirectly, of environmental stress on phenological pattern, Canonical Redundancy Analysis (RDA) of each site matrix (frequency of functional traits), constrained by community canopy height, aboveground phytomass and leaf yellowing



**Figure 1** – Water balance of sites A and B. Black area represents the period of water scarcity. In site B this period is absent.

(we assumed this community features as indirect environmental stress indicator) were performed. To assess the contribution of each variable to the total variability of functional traits data sets, the total variance was partitioned into fractions explained by each of the predictor variables by partial RDA (Borcard et al. 1992, Borcard & Legendre 1994). Adjusted R-square values were calculated to produce unbiased estimates of the contributions of the independent variables to the explanation of the response variables (Peres-Neto et al. 2006). To test the significance of the adjusted R-squares (i.e. whether each independent fraction exhibits a significant influence on cover data), a permutation test with 1000 permutations was applied, in accordance with Legendre & Legendre (1998).

Numerical analyses were performed using SYN-TAX 2000 software (Podani 2001), PCOrd 5.0 software (McCune & Mefford 1999); RDAs were computed using *rda* function in R software, version 2.13.0 (R Development Core Team 2011), and the Vegan package, version 1.17-9 (Oksanen et al. 2011).

RESULTS

Long-term climatic data elaboration indicates that water deficit (drought stress) occurs only in Site A, between mid-June and the end of September (fig. 1).

Flowering in both sites has a bimodal summer pattern, shifted by about thirty days between site A and site B (fig. 2);

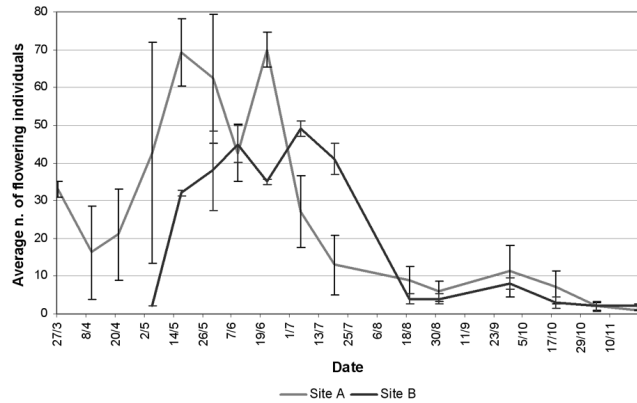


Figure 2 – Average number of flowering individuals and standard deviation.

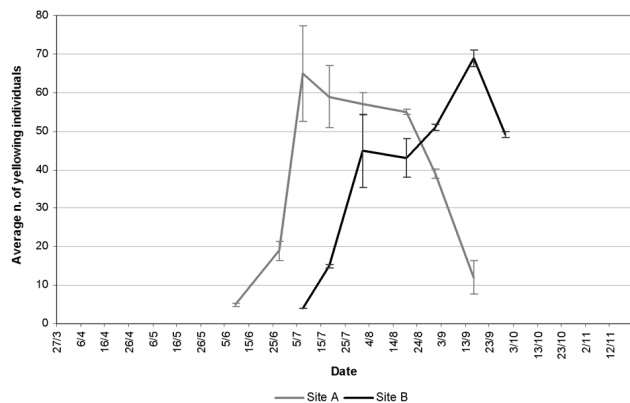


Figure 3 – Average number of yellowing individuals and standard deviation.

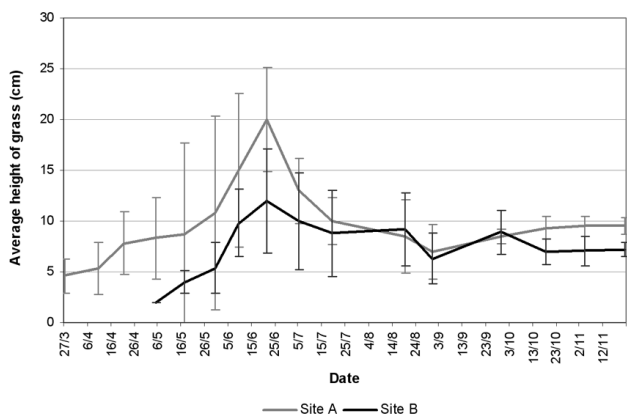


Figure 4 – Average height of grass and standard deviation.

in early autumn another flowering peak is evident but with a very low number of flowering individuals.

Leaf yellowing has a unimodal pattern (fig. 3) with the maximums shifted by almost three months (early July in site A, late September in site B).

Canopy height has a single peak in both sites and the maximums are quite synchronous (fig. 4). After the peaks,

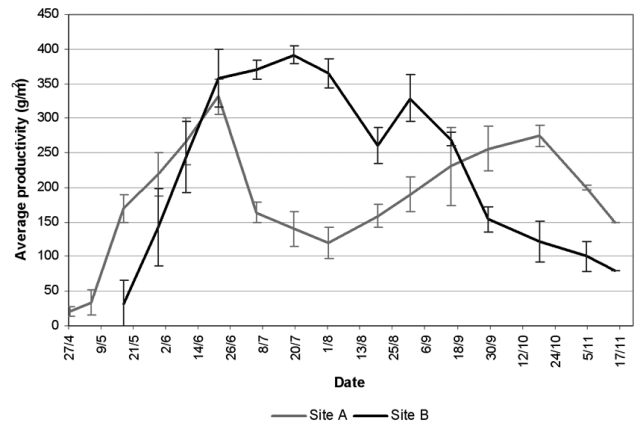
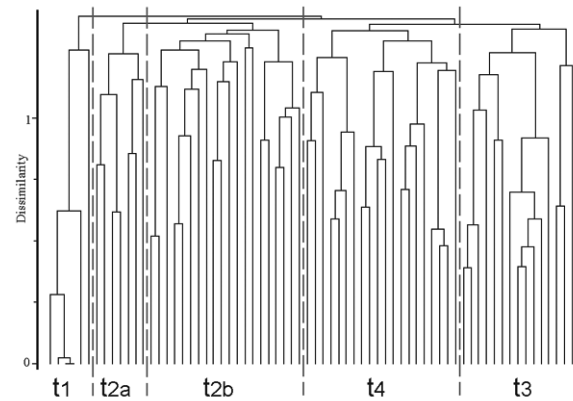


Figure 5 – Average productivity and standard deviation.

Site A



Site B

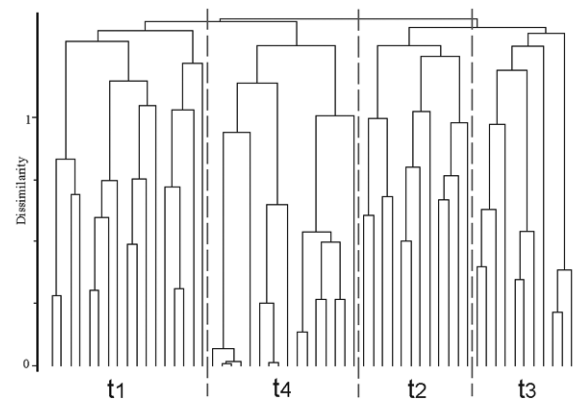


Figure 6 – Cluster analysis on survey dates (dendrogram clusters) according to the number of flowering individuals per species.

**Table 3 – General scheme of the environmental change, plant community structural features and differential traits during the growing season in the analyzed study areas.**  
Abbreviations are given in the caption of table 4.

	Site A					Site B				
	t <sub>1</sub>	t <sub>2a</sub>	t <sub>2b</sub>	t <sub>3</sub>	t <sub>4</sub>	t <sub>1</sub>	t <sub>2</sub>	t <sub>3</sub>	t <sub>4</sub>	
Soil water deficit	absence	absence	absence	presence	presence	Absence	Absence	Absence	Absence	
Lowest temperature > 6°C	no	no	yes	yes	yes	no	yes	yes	yes	
Aboveground phytomass (g/m <sup>2</sup> )	3.5 ± 3.8	31.5 ± 25.9	215.3 ± 113.1	120 ± 45.7	194.6 ± 49.6	104.5 ± 110.6	347.4 ± 157.7	335.7 ± 122.1	166.4 ± 107.3	
Leaf yellowing (mean number of individuals)	Absence	Absence	6.6 ± 13.7	26.1 ± 25.6	32.1 ± 42.0	Absence	20.1 ± 17.4	35.5 ± 10.9	59 ± 14.1	
Canopy height (cm)	5 ± 1.2	7.5 ± 1.6	15 ± 3.4	8.4 ± 2.1	8.7 ± 2.5	6.9 ± 4.4	9.9 ± 3.1	11 ± 2.7	7.3 ± 3.2	
Differential Traits	Gbulb, h1, runner absence, rhizome/tuber, bulb, biotic pollination strategy, spring green	Hscap, Hros, h2, runner presence, rhizome/tuber, selfing pollination strategy, spring and persistent green	Hcaesp, h3, no storage organs, anemophily pollination strategy, overwintering green	h4, tap root, summer green	h4	Gbulb, h2, rhizome/tuber, bulb, no storage organs, anemophily pollination strategy, spring green	Hcaesp, Chsuff, Chrept, h3, h4, runner presence, rhizome/tuber, anemophily pollination strategy, persistent green	Hcaesp, h3, h5, no storage organs, biotic pollination strategy, persistent green	Hbienn, Tscap, h1, tap root	

the average heights decrease in both sites, becoming equal and constant until autumn.

The pattern of aboveground productivity (g/m<sup>2</sup>) is opposite in site A and site B (fig. 5): in site A the central part of the summer is characterized by the lowest productivity, while in site B the situation is reversed, except for an isolated outlier in mid August.

In both sites, dendrograms indicated the presence of four clusters clearly divided at the higher level of dissimilarity (fig. 6). The check of the date showed that each cluster grouped the relevés carried out in two or more consecutive dates. Thus we assumed that each cluster represent a time interval (t<sub>n</sub>) of the flowering pattern. In site A the second cluster was divided into two sub-clusters while the third one included two seasonal phases (early summer and autumn) another cluster grouped the phenological relevés carried out in mid summer (August). The outgoing temporal intervals of each cluster were: t<sub>1</sub> from end March to beginning April, t<sub>2a</sub> from beginning April to beginning May, t<sub>2b</sub> from beginning May to end June, t<sub>3</sub> from beginning to end August, t<sub>4</sub> from beginning to end July and from beginning September to beginning November. In site B, four intervals were identified: t<sub>1</sub> from beginning of May to mid-June, t<sub>2</sub> from end June to end July, t<sub>3</sub> from beginning to end August, t<sub>4</sub> from beginning September to beginning November.

The list of flowering species for each t<sub>n</sub> is shown in electronic appendix 1.

Summarizing the results (table 3), in both sites the first flowering period (t<sub>1</sub>) was characterized by very low canopy height, low aboveground productivity, and absence of leaf yellowing. As indicated by the long-term climatic assessment, this time interval is generally characterized by low temperature and by absence of soil water deficit.

In both sites the second period (t<sub>2</sub>) was characterized by mid/high sward height, and by the aboveground productivity increase, besides the absence of leaf yellowing. The pedoclimatic analysis showed that usually during this period there is no water deficit in both sites.

In Site A the summer period (t<sub>4</sub>) was divided into two seasonal phases placed around the driest period (t<sub>3</sub>). The aboveground productivity was lower than that of previous phase (t<sub>2</sub>) while leaf yellowing had a high value. As the long term climatic elaboration highlighted, this time intervals are characterized by the lowering of rainfall and by drought stress (more severe in t<sub>3</sub>).

In Site B, during the third period (t<sub>3</sub>) the aboveground phytomass decreased but the leaf yellowing had a low value. This time interval is generally characterized by the lowering of rainfall but without drought stress. During the fourth flowering period (t<sub>4</sub>) the aboveground phytomass increased again, but the leaf yellowing was the highest of the whole growing season.

Indicator Species Analysis pointed out the indicator traits set linked with each t<sub>n</sub> (table 4).

Some traits showed a peak of frequency in different time intervals. In Site A: Gbulb, h1, bulbs, rhizomes, absence of runners and spring green leaves had their peak in early spring (t<sub>1</sub>); Hscap, Hros, Hcaesp, Tscap, h3, presence of run-

**Table 4 - Trait list identified by ISA.**

Abbreviations are: Raunkiaer life forms: chamaephytes (succulent - Chsucc, sufruticose - Chsuffr and reptant - Chrept), hemicytrophytes (scapose Hscap, caespitose Hcaesp, reptant Hrept, rosulate Hros and biennial Hbienn), bulbous geophytes (Gbulb) and therophytes (scapose Tscap and caespitose Tcaesp). Species average height (cm): 1–10 cm (h1), 11–20 cm (h2), 21–30 cm (h3), 31–40 cm (h4) and > 40 cm (h5). Runners: present or absent. Underground storage organs: tap root, rhizome/tuber, bulb and no storage organs. Leaf persistence: spring green, summer green, overwintering green, persistent green. Pollination strategy: biotic pollination, anemophily and self-pollination. Symbol (\*) highlight the indicator trait in each time interval (tn) in each site ( $P < 0.05$  and  $Iv > 50$ ).

Traits	t <sub>n</sub>	Site A				Site B				
		t <sub>1</sub>	t <sub>2a</sub>	t <sub>2b</sub>	t <sub>3</sub>	t <sub>4</sub>	t <sub>1</sub>	t <sub>2</sub>	t <sub>3</sub>	t <sub>4</sub>
Raunkiaer life forms	Hscap		*							
	Hcaesp			*				*	*	
	Hrept									
	Hros		*							
	Hbienn									*
	Tscap									*
	Tcaesp									
	Chsucc									
	Chsuff							*		
	Chrept							*		
species average height	Gbulb	*					*			
	h1	*								*
	h2		*				*			
	h3			*				*	*	
	h4				*	*		*		
runners	h5								*	
	present		*					*		
underground storage organs	absent	*								
	tap root				*					*
	rhizome/tuber	*	*				*	*		
	bulb	*					*			
pollination strategy	no storage organs			*			*		*	
	biotic	*							*	
	anemophily			*			*	*		
	selfing		*							
leaf persistence	spring green	*	*				*			
	summer green				*					
	overwintering green			*						
	green									
	persistent green		*					*	*	

ners, overwintering/persistent green leaves and absence of storage organs had their peak in late spring and early summer (t<sub>2a</sub>, t<sub>2b</sub>); Hscap, h4, tap root and summer green leaves had their peak in summer and early autumn (t<sub>3</sub>, t<sub>4</sub>). In Site B: Gbulb, h1, h2, bulbs and spring green leaves had their peak in early spring (t<sub>1</sub>); Chrept, Hcaesp, h3, h4, h5, and persistent green leaves had their peak in late spring and early summer (t<sub>2</sub>, t<sub>3</sub>); Hbienn, Tscap, h1, tap root and summer green leaves had their peak in autumn (table 4).

The total explained variances for functional traits data sets, constrained by canopy height of community, leaf yellowing and aboveground productivity, were 19.2% and 20.5% (adj.-R<sup>2</sup>) for site A and site B, respectively. The independent explained variance extracted from the functional traits data set showed that for site A aboveground productivity had the greatest effect (adj.-R<sup>2</sup> = 0.0696, P = 0.001), followed by canopy height (adj.-R<sup>2</sup> = 0.0296, P = 0.019), and yellowing (adj.-R<sup>2</sup> = 0.0296, P = 0.024). For site B yellowing showed the greatest effect (adj.-R<sup>2</sup> = 0.1626, P = 0.001);

**Table 5 – Percentage of trait occurrence in each  $t_n$  for every site.**

Traits	$t_n$	Site A					Site B			
		$t_1$	$t_{2a}$	$t_{2b}$	$t_3$	$t_4$	$t_1$	$t_2$	$t_3$	$t_4$
Raunkiaer life forms	Hscap	0.0	48.7	25.7	51.2	54.4	62.6	60.3	65.0	18.6
	Hcaesp	10.9	13.3	31.2	0.8	7.0	12.1	15.1	27.1	2.1
	Hrept	0.0	0.0	0.4	4.0	0.0	0.0	0.0	0.0	0.0
	Hros	0.0	21.3	3.6	1.6	7.0	9.9	5.4	3.5	0.0
	Hbienn	0.0	0.0	0.3	0.8	0.4	1.2	3.1	2.6	29.0
	Tscap	0.0	10.0	14.1	0.8	1.7	0.4	0.0	2.6	49.5
	Tcaesp	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0
	Chsucc	0.0	0.0	0.0	3.2	0.4	0.0	0.0	0.0	0.0
	Chsuff	0.0	4.7	7.3	8.8	3.1	1.4	2.5	0.0	0.0
	Chrept	0.0	0.0	5.4	0.0	5.3	2.0	13.0	3.5	0.0
	Gbulb	89.1	2.0	10.5	28.8	9.6	10.3	0.6	0.9	0.0
Species average height	h1	62.4	24.7	11.3	1.6	17.9	46.9	17.2	8.8	86.6
	h2	37.6	50.0	47.7	61.6	21.8	41.6	16.2	20.2	11.3
	h3	0.0	25.3	27.0	2.4	19.7	11.5	20.6	34.9	0.0
	h4	0.0	0.0	10.1	34.4	38.0	0.0	35.9	3.5	0.0
	h5	0.0	0.0	4.3	0.0	2.6	0.0	10.1	38.0	2.1
runners	present	0.0	29.1	24.7	12.6	18.0	32.3	28.3	21.8	3.1
	absent	100.0	70.9	75.3	87.4	82.0	67.7	71.1	78.2	96.9
underground storage organs	tap root	8.4	32.7	32.9	58.5	61.5	10.1	38.9	41.3	92.8
	rhizome/tuber	48.1	58.8	38.0	6.9	25.3	45.3	36.8	24.8	0.0
	bulb	43.5	8.5	15.0	27.7	6.1	3.8	0.0	0.0	0.0
	no storage organs	0.0	0.0	14.1	6.9	7.1	40.8	24.3	33.9	7.2
pollination strategy	zoochora	72.7	47.4	41.6	62.1	67.6	43.0	63.0	68.0	59.5
	wind	0.0	16.2	20.2	2.1	3.3	16.6	10.1	12.2	0.0
	selfing	27.3	36.5	38.1	35.9	29.1	40.5	26.8	24.8	40.5
leaf persistence	spring green	89.1	22.0	9.3	0.0	0.0	43.8	3.2	0.0	2.1
	summer green	0.0	14.7	22.7	80.8	63.2	28.5	47.8	54.1	79.4
	overwintering green	0.0	8.0	19.1	0.0	7.9	0.0	1.5	0.0	0.0
	persistent green	10.9	55.3	48.9	19.2	28.9	27.7	47.4	51.7	18.6

aboveground productivity (adj.- $R^2 = 0.0125$ ) and canopy height (adj.- $R^2 = 0.0047$ ), were not significant ( $P > 0.05$ ).

In site A, Gbulb, h2 and h3, persistent green leaves and runners absence were negatively related to canopy height and aboveground phytomass, while summer green leaves, Hscap and tap root were positively related to leaf yellowing (indirect indicator of drought stress). In site B Spring green leaves, h2, were negatively related to canopy height and aboveground productivity, while Hscap and persistent green leaves were positively related to them. Summer green leaves were positively related to leaf yellowing (table 5).

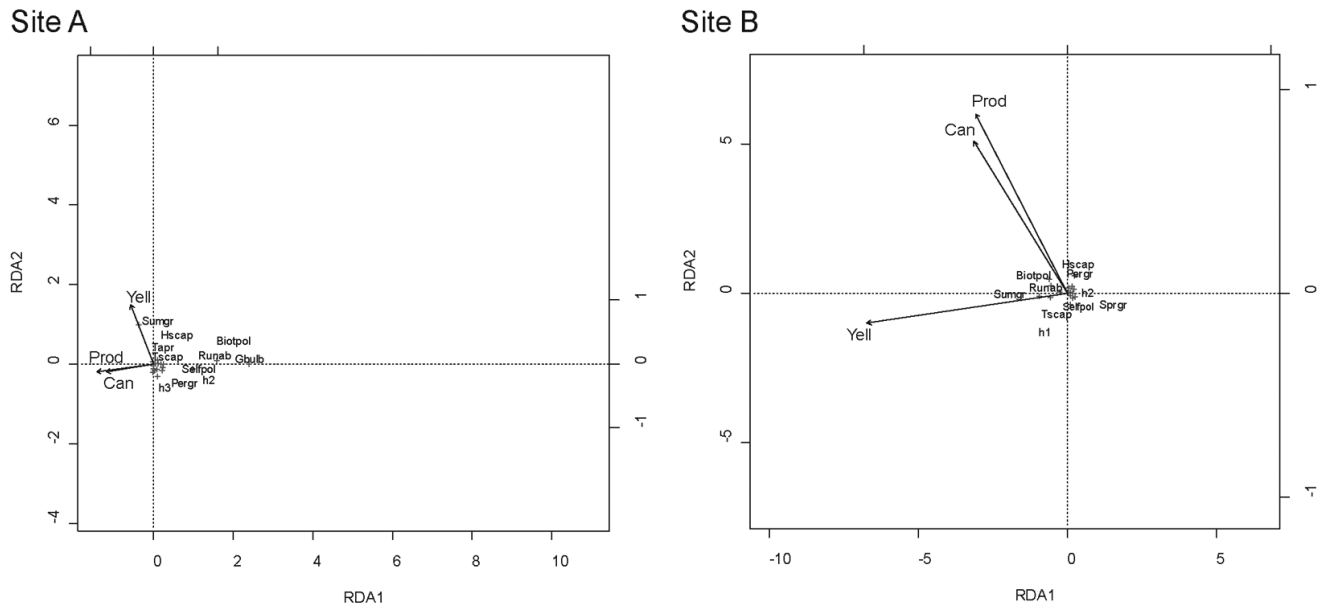
## DISCUSSION

### Temporal functional pattern

In the analysed plant communities, species flowering follows a temporal sequence, as observed in several studies

(e.g. Stiles 1977, Poole & Rathcke 1979, Cole 1981, Gleeson 1981, Kochmer & Handel 1986, Sala et al. 1989, Losvik 1991, Gordon & Rice 1992, Mortimer 1992, Montaña et al. 1995, Dalaka & Sgardelis 2006).

The characteristics of the highlighted temporal sequences differ between the sites. In fact, in site A the period with more severe drought stress ( $t_3$ ) change the flowering sequence and it was interposed between the early summer and autumn phenological phases ( $t_4$ ). In site B, it should be noted that the phenological phases are compacted (for instance the  $t_2$  period is not divided in sub-periods) because of its reduced vegetative season due to higher altitude (Komárková 1993, Stanton et al. 1994) and, in turn, to the higher and longer winter cold stress (Orsomando & Catorci 2000). As indicated by Cesaretti et al. (2009), in sub-Mediterranean climate, seasonal variation in cold and drought stress intensity are related to changes of canopy height and aboveground productivity, that



**Figure 7** – Redundancy analysis ordination graph for life strategies data set constrained by environmental variables (Can: canopy height; Prod: aboveground productivity; Yell: leaf yellowing). Raunkiaer life forms: hemicryptophytes (scapose Hscap); bulbous geophytes (Gbulb); therophytes (scapose Tscap). Species average height (cm): 1–10 cm (h1); 11–20 cm (h2); 21–30 cm (h3). Runners absent (Runab). Underground storage organs: tap root (Tapr). Leaf persistence: spring green (Sprgr); summer green (Sumgr); persistent green (Pergr). Pollination strategy: biotic pollination (Biotpol); self-pollination (Selfpol).

affect in turn light and the soil resources availability (Catorci et al. 2011a).

Therefore, it is plausible to state that some factors affect the flowering phenological pattern in the studied plant community, and act as driving forces filtering the functional composition of the flowering species during each phenological phase. These factors are community structure, stress intensity and type, besides the seasonal period in which they are acting on the system. Indeed, it is possible to state that in both sites, in the first flowering period ( $t_1$ ), the affirmation of low statured flowering species with storage organs (bulbs and tuber) and spring green leaves is led by the absence of competition for light (Abrams 1995; Catorci et al. 2011b) and soil resources with tall grasses and forbs. Grime (2001) argued that the early flowering geophytes are adapted to grow in the moist and cool period of the vegetative season and survive during the dry period and in the following winter season, in the form of underground storage organ. In this way they can exploit a very early temporal niche when other species cannot grow. Indeed,  $t_1$  time interval happens when the daily minimum temperature is generally above 6°C, a temperature often considered a threshold for tissue formation in plants (see Bonan 2008, Monteiro et al. 2011); in fact the sword canopy height was the lowest of the whole growing season.

In site A, during the first sub-period of the second time interval ( $t_{2a}$ ), flowering species have storage organs (rhizome and tuber) and spring or persistent green leaves. The presence of storage organs affords a competitive advantage arising from rapid foliage expansion and then leaf canopy pre-emption (Grime 2001), by using energy reserves accumulated during the previous growing season (Bradbury & Hofstra 1976). Probably persistent green leaves have

the same function and allow this group of species to anticipate the full growth of leaves and the flowering peak of tall grasses and forbs. The flowering peak of species with runners could be interpreted as a strategy finalized to maximize the species competitive ability when soil resources exploitation is higher, allowing individuals to explore the neighbour area to find unexploited soil niches (Maillette 1982, Tissue & Nobel 1988, Friedman & Alpert 1991). Scapose and rosulate hemicryptophyte life forms were also highlighted as indicator life form; this means that they are in bloom (as well as bulbous geophyte life forms, which flower in the previous phase) before the caespitose life forms, which in the studied plant community is the dominant group (Catorci et al. 2007).

In the  $t_{2b}$  sub-period (Site A), aboveground phytomass and canopy height increase and reach the maximum values, and the flowering species belong to the intermediate and higher height classes. During this period caespitose life forms (dominant group) reach the flowering peak. The other indicator traits are: absence of storage organs, wind pollination and overwintering green leaves. These plant community features besides the indicator traits set suggest that the dominant species tend to bloom when no stress is acting in the system, during the period with the most favourable climatic conditions, resulting in species monopolization of space during the whole growing period. This traits set probably reduces the competition with subordinate species for resource interception, and the necessity to store reserve. Instead, the flowering peak of Tscap is probably due to their ability to colonize the sward gaps (where there is no competition for soil resources and light with the surrounding dominant species) opened by livestock disturbance (Van Braeckel & Bokdam 2002, Kohler et al. 2006) as well as to the optimal period for seedlings before the summer drought. Instead, reptant

chamaephyte life forms flowering peak could be linked with patches formation.

In fact, in their studies on competition between neighbouring individuals, Schmidt (1986) and Bazzaz (1991) demonstrated that species growing in competition with graminoid grass develop a successful strategy, which is to grow in strongly integrated patches by producing short genets.

During the  $t_3$  flowering period, characteristic traits were tap root, tall size (h4) and summer green leaves. It is possible to state that this traits set is probably filtered by the typical environmental constraints of Mediterranean summertime. In fact this functional traits set allows plants to reach the deepest and wettest soil layer, to use stored resources and to intercept light thanks to the summer green leaves. Furthermore, Roggero et al. (2002) indicated that these species (e.g. *Cyanus triumfetti* (All.) Dostál ex Á. & D.Löve, *Leucanthe-mum adustum* (W.D.J.Koch) Grelli, *Eryngium amethystinum* L., *Centaurea ambigua* Guss., *Bupleurum falcatum* L. subsp. *cernuum* (Ten.) Arcang.) have a very low palatability. Thus plants can flower and produce seeds during the driest seasonal period when other species have ended their reproductive cycle and under herbivorous disturbance.

The  $t_4$  period was differentiated only by tall plants (h4). Indeed, the main environmental constraint for species blooming in late summer is the sward canopy heights and then the competition for light.

In site B, both the  $t_1$  and  $t_2$  flowering time intervals are characterized by a trait pattern similar to that of site A. The main difference was represented by the leaf persistence trait; in fact, indicator trait of  $t_2$  and  $t_3$  time interval in site B was persistent green leaves. Grime (2001) argued that this kind of leaf persistence in subalpine and alpine climate is related to the fact that it is unlikely that there will be a surplus of photosynthate sufficient to sustain the annual turnover of dry matter. Moreover, Hadley & Bliss (1964) suggest that the older leaves may act as winter food storage organs since lipids and proteins are mobilised and translocated from the old to new leaves during the growing season.

The lack of a clear peak of caespitose hemicryptophyte life forms and of a strongly dominant life form group (Catorci et al. 2008) besides the low height of the sward canopy, partially mask the temporal division among the different life forms and probably this reflects in a less clear functional temporal pattern. Thus, in Site B the late spring and summer flowering periods are less differentiated than those of Site A.

During the  $t_4$  period the flowering species are characterized by tap root, biennial hemicryptophyte and scapose therophyte life forms. These guilds probably allow the exploitation of a very short temporal niche before the onset of winter. Indeed the stored resources in tap rooted species and in the biennial hemicryptophytes ones allow a fast stem growing, as well as the ones of scapose therophyte species. Furthermore flowering species had low height (h1). Stored reserves may also be useful to complete the seed maturation.

### General model

In accordance with Ansquer et al. (2009), our research showed that for each combination of environmental fac-

tors, species with similar traits tend to occur together, and that each phenological phase tends to be linked to a group of functional traits.

Furthermore, species with life forms different from caespitose hemicryptophyte life forms (the dominant species group) tend to avoid the flowering co-occurrence with that of caespitose hemicryptophyte life forms. This result is consistent with that of Ansquer et al. (2009), who demonstrated that the dominant species reach their maximum phenological forwardness in the middle of the vegetative season (in fact they do not show any particular strategy, except for the high space occupation), while non-dominant species show a tendency to bloom during periods at the edge of the vegetative season. However, as a consequence of the lack of a clear dominant species group, in site B this trend is not very clear. Nevertheless, this scheme is probably incomplete; in fact, in the studied plant communities, the phenological patterns seem to follow two main strategies. The first one, consistent with Ansquer's model, characterizes the tall graminoids dominated patches, where competition for light seems to be the main driving force throughout the growing season. Our findings revealed a pattern of increased species height and the presence of guilds (leaf persistence, storage organs, tap root or biennial hemicryptophyte life forms) that allow non-dominant species to have a flowering temporal niche different from the one of dominant species. The second set of strategies is related to some kind of short species, which persist inside the plant community by exploiting gaps due to livestock disturbance (scapose therophyte life forms), or by forming their own patches, given their clonal ability, whereas dominant graminoids lack this ability (reptant and suffruticose chamaephyte life forms). This kind of species can share the same optimal temporal niche used by the dominant ones.

### CONCLUSION

Our findings showed that phenological patterns contribute to co-existence mechanisms in the sub-Mediterranean mountain grassland thanks to the functional traits differentiation of each flowering phase. The comparison between the analysed plants communities confirmed that the presence of dominant species strengthens this tendency.

The flowering pattern of a plant community is driven by functional differentiation of species that in turn is filtered by environmental stress/disturbance type and intensity. Indeed, the comparison between the two studied sites seems to highlight that altitudinal gradient related in turn to the intensity and length of winter cold stress and summer drought stress modulate the functional composition of the flowering pattern. The plant community structure is in itself an important driver. Indeed, canopy height and aboveground productivity had a greater effect in site A (where they have a higher value) than in site B (in which their importance on traits variation were not statistically significant).

### SUPPLEMENTARY DATA

Supplementary data are available in pdf format at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/boitel/plecevo/supp-data>), and

consist of a list of the flowering species for each  $t_n$  in every site (pdf format).

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