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PHENOLOGICAL PATTERNS IN MEDITERRANEAN PASTURES AND SCRUBS OF CATALONIA

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A tribute to Professor Dr. Oriol de Bolòs, who through his outstanding contribution to the Floristics, Taxonomy and Phytocoenology of the Catalan Countries, has aroused in his students an interest in understanding plant functionalism.

ABSTRACT

On the basis of two parallel data sets refering to phenological events in open scrubs and pastures at two sites (Balaguer and Vic), the authors present a comprehensive report of the phenology of these Mediterranean communities. Four main phenophases (vegetative growth, flowering, fruiting and resting) were recorded monthly in 11 communities over 15 months. The results allow comparisons to be drawn between localities and communities, both at community and species levels, and to consider the effects of contemporary climatic data. This yielded useful information on general trends and on the particular responses of each community type to their corresponding constraints.

The phenological sequence in all the communities as a whole showed a strong correlation to seasonal climatic features. A marked phenological reaction was seen in autumn after the summer drought. This was mainly reported in vegetative growth and in emergence of annuals. The reaction was considerably more abrupt the stronger the summer stress had been. The first half of winter was generally a resting period, though scrubs maintained some activity. In contrast, a sudden production of photosynthetic structures characterised the late winter period, although still experiencing quite low temperatures. Blooming achieved maximum values in April for the most xerophilous communities and in May for the majority of the others; but flowering actually occured over an eight months period, at least in low percentages. A marked rise in the potential evapotranspiration during late spring and early summer reduced the flowering phase and led to fruiting and senescence or resting.

Each phenophase was longer and overlapped more with the others in scrubs than in pastures; the most xerophilous pastures showed the sharpest peaks in the percentage graphs. In this sense, the communities proved to be from more to

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less independent of climatic constraints. Between localities, in the milder Vic the communities developed longer phenological phases than in the drier Balaguer.

In general, the timing and intensity of the summer drought and the rainfall distribution in autumn and spring proved to be the chief constraints on the phenology of the Mediterranean communities studied, by conditioning the length of their productive periods. Interannual variation in these climatic features directly influenced phenological behaviour, mainly in the most xerophilous communities.

Key words: Phenology, Climate constraints, Water stress, Mediterranean communities, Scrubs, Pastures, Catalonia.

RESUM

Comportament fenològic de pastures i matollars mediterranis de la Noguera i la plana de Vic

A partir de dos seguiments fenològics fets a les zones de Balaguer i de Vic relatius a diversos tipus de brolles i de pastures, assagem una síntesi de la fenologia d'aquestes comunitats mediterrànies. Hem pres en consideració quatre fenofases principals: creixement vegetatiu, floració, fructificació i repòs, i n'hem calculat els percentatges per a cadascuna de les 11 comunitats estudiades durant 15 mesos; també hem comparat el cicle de 19 espècies comunes a totes dues localitats. Aquestes dades i els registres de temperatures i precipitacions del període d'estudi, ens permeten exposar el comportament fenològic general, i també les respostes particulars de cada tipus de comunitat o de cada zona, en relació amb els corresponents condicionants ecològics.

En conjunt, la seqüència fenològica va mostrar, a totes les comunitats, una forta correlació amb els trets climàtics estacionals. La tardor va comportar una notable reactivació després de l'eixut estival, reactivació que es va centrar principalment en el creixement vegetatiu de mates i herbes perennes i en la germinació de teròfits, i que va ser més sobtada com més dràstic havia estat l'estrés estival. La primera meitat de l'hivern va representar un període de repòs molt generalitzat, tot i que les brolles van mantenir una certa activitat, que comprengué fins i tot alguns episodis secundaris de floració. Entre els mesos de gener i febrer es va iniciar sobtadament l'activitat vegetativa, consistent en la formació i l'elongació de brots i de fulles, fet que havia de permetre aprofitar al màxim el període primaveral subsegüent. Com que les temperatures de la segona meitat d'hivern van ser similars o poc més baixes que les de la primera meitat de l'estació, cal concloure que no és un factor tèrmic el que desencadena el creixement hivernal.

Els pics de floració varen tenir lloc per l'abril a les comunitats més xèriques, i pel maig a quasi totes les altres. D'altra banda, entre març i octubre quasi totes les comunitats van mantenir algunes espècies en flor. Entre final de primavera i principi d'estiu, el fort increment de l'evapotranspiració potencial va significar el pas de floració a fructificació i, en percentatges elevats, a les fases de senescència i mort (teròfits) o de repòs (hemicriptòfits i camèfits). Aquesta transició va ser més precoç i ràpida a les comunitats més xeròfiles, i més a Balaguer en general que a Vic.

A les brolles cada fenofase va ser globalment més dilatada que a les pastures, de manera que les fenofases es van encavallar més entre elles. A les pastures més xeròfiles és on els pics de creixement, floració i fructificació van ser més sobtats. Per tant, cal considerar que davant les limitacions climàtiques les brolles manifesten un grau d'independència més gran que les pastures, i que dins d'aquestes les més xeròfiles són les més dependents. En l'aspecte geogràfic, les comunitats de Vic van poder desenvolupar fenofases més llargues que no pas les de Balaguer, localitat afectada per un estrés hídric força més dilatat i intens.

Com a fet general, les característiques de l'eixut estival (inici, durada i intensitat) i la distribució de pluges a la tardor i a la primavera esdevenen els principals condicionants de la fenologia de les comunitats mediterrànies estudiades, ja que en depèn la longitud dels períodes productius, tant vegetatius com reproductors. La variabilitat interannual d'aquests fenòmens climàtics fa que el comportament fenològic dels vegetals variï d'un any a l'altre, d'una manera més intensa com més xeròfila és cada comunitat.

1. Introduction

The timing of phenological events in plants, such as flowering, fruiting or vegetative growth, are determined by both abiotic and biotic environmental factors. At the community level, the coexistence of species reinforces individual patterns in such a way that they coordinate their activity, either with coincident rythms or by spreading their activity over the year (KEMP, 1983).

Few studies have taken a synphenological approach to Mediterranean communities, despite the evident interest of this topic. Although a number of papers describing the phenological behaviour of Mediterranean plants has been written (CARDONA, 1980; BONET, 1991; CABEZUDO *et al.*, 1993; HERRERA, 1986), the relationships between the plants' seasonal activity and climatic conditions are still by no means fully understood.

Several years ago, the authors analysed the phenology of several communities at two sites, Balaguer and Vic (GUÀRDIA & NINOT, 1991b; CASAS, unpubl. data). Although these studies were not designed in conjunction, both focused on the most common pastures and scrubs of each area. Moreover, the studies coincided during a 15 months period, and they were performed with quite similar methods.

The communities analysed may be considered representative of non-forest Mediterranean vegetation in the Catalan Ebro depression. They are open scrubs and diverse pastures, which differ from the typical sclerophyllous Mediterranean vegetation in that they are seasonally heteromorphic (*sensu* ORSHAN, 1989). One of the localities (Balaguer) represents the western extreme of the region, and is characterised by its low precipitation, while the other site (Vic) is an example of its mildest, northeastern edge. The thermal regime is similar, though in Vic temperatures are always slightly lower than in Balaguer, particularly minimum temperatures.

Here, we reanalyse both data sets so as to present a comprehensive account of the phenology of these Mediterranean communities. We seek to identify the most general phenological trends and the differences between community types and localities. Comparisons of the phenological patterns of the same species in these two extremes of the gradient may provide useful information regarding plant responses to environmental factors.

2. The study areas

2.1. Balaguer

Within the Ebro basin, the area around Balaguer belongs to the Sicoric territory, and is formed by flat Tertiary rocks rich in lime (marls, gypsum and limestones, chiefly Oligocene) and mainly flat. A low, but long, system of hills crosses the area. This is the result of Alpine folding and includes gypsum outcrops. In these hills, sourrounded by sown fields, the alternation of gypsaceous and non-gypsaceous soils –all carbonated– and also the topography give rise to an interesting mosaic of light, dwarf scrubs and dry pastures dominated by xerophytic grasses. All of these are mainly secondary communities, originating from the depletion of the former holm oak woodland (*Quercetum rotundifoliae*), which at present only occurs in the form of very small, scattered, degradated patches.

All these communities are related to a sub-continental, dry, Mediterranean climate –according to BOLÒS & VIGO (1984), a low altitude, xerotheric climate. In Balaguer, the mean annual temperature is 14.4°C and total rainfall reaches only 434 mm. As shown in the corresponding diagram (Fig. 1), there is a severe summer drought, which constitutes a theoretical resting period of about 3 months. Moreover, it must be taken into account that most of the communities studied mainly inhabit rocky, south-facing or shallow soils, with harsher microclimates. Low temperatures in winter are also rather limiting, as mean temperatures remain under 7°C for 2.2 months.

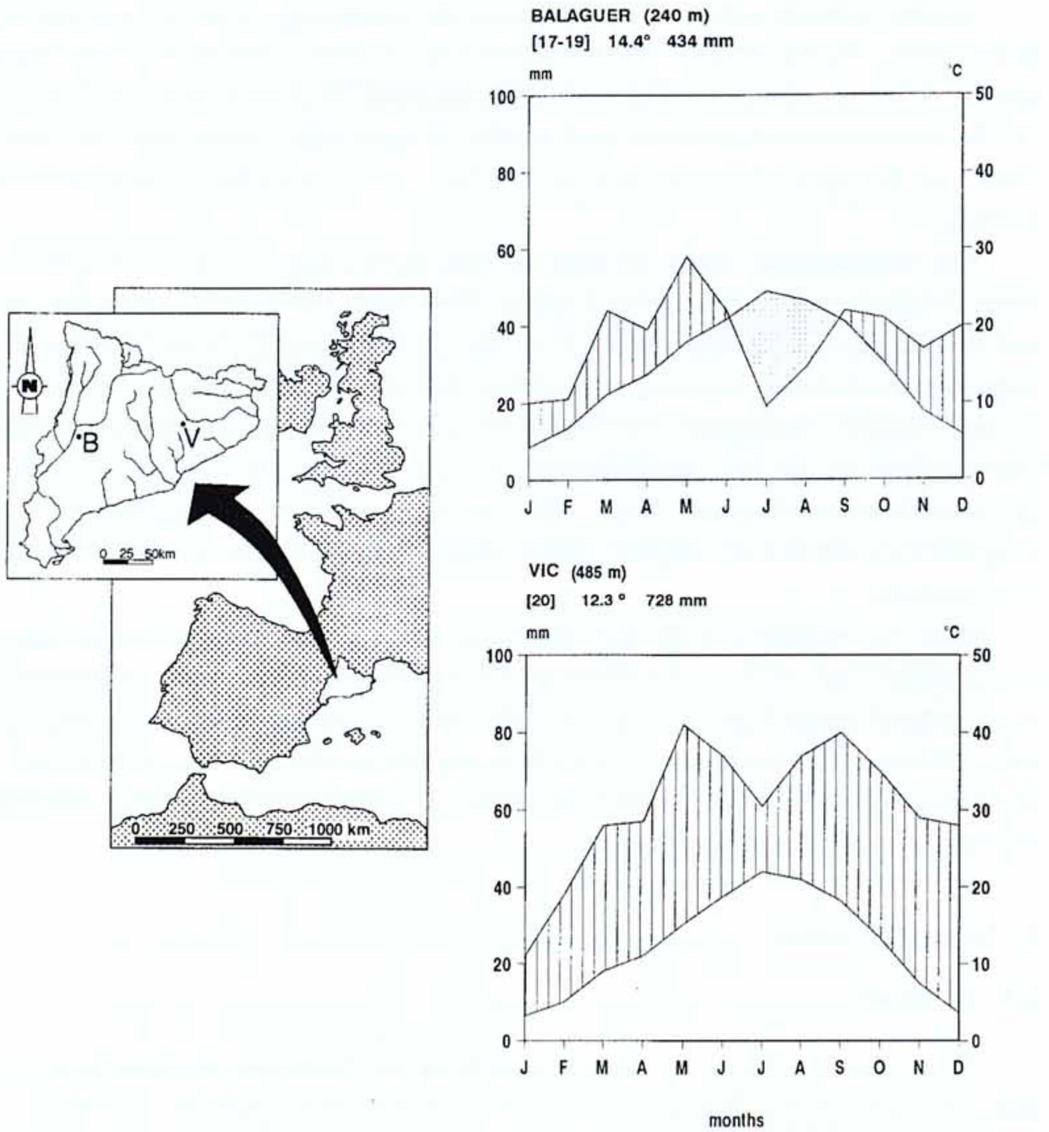

Figure 1. Location of the two areas studied (B, Balaguer and V, Vic) and climatic diagrams of these localities (data from the official observatories, diagram representation according to WALTER & LIETH system).

2.2. Vic

The Vic site lies at the bottom of a small depression, limited to the south and east by the Mediterranean, Catalanidic mountains, and to the north by the pre-Pyrenean ranges. It is also made of flat, lime rich, Tertiary rocks, mainly Eocene marls. The vertical alternation of soft marls and harder outcrops (conglomerates, limestones) gives rise to a very typical relief of thin steep levels and more extensive taluses tailing off into glacis. This is evident on the surrounding slopes of the plateau and even more so in a number of typical hills in the area, which arise from the flat, intensively farmed bottom of the basin.

According to BOLÒS & VIGO (1984), Vic is located in the western part of the Auso-segàrric territory, and its general climate is of the sub-Mediterranean axeromeric type. This is a transition climate between Mediterranean and Montane (Pyrenean). The mean annual temperature in Vic is 12.3°C and the annual rainfall is 728 mm (see the diagram in Fig. 1). A particular feature of the area is the frequency of thermal inversions, mainly in winter, which cause very low temperatures in the bottom of the basin, preventing a number of Mediterranean species from settling there. As no arid period occurs around Vic, the landscape is mainly mesoxerophilous in character, with xerophilous Mediterranean communities restricted to the dryest habitats. The climax vegetation of the area is a deciduous, meso-xerophilous oak forest (*Buxo sempervirentis-Quercetum pubescentis*), which at present can be observed on some mild aspects. Deforested slopes, with all exposures and a gradation from well preserved to highly eroded soils, bear a wide variety of pasture communities. The combination of these degradation processes enhances the extension of xerophilous, Mediterranean communities. As for cold limitations, the winter is only slightly longer than in Balaguer (3.4 months with mean temperatures under 7°C).

3. The communities studied

The communities selected for this study, which are very representative of Balaguer and Vic sites, include some light, dwarf scrubs and a variety of pastures, from rather ephemeral, therophytic communities to dense, mesic grasslands. Their main features are summarised in Table 1. The nomenclature of the taxa follows BOLÒS *et al.* (1993).

The gentle relief features near Balaguer are covered mainly with xerophitic scrubs, in which the most significant species are shrubs and sub-shrubs showing light canopies and narrow, drought-revolute leaves. Of these, two gypsicolous and one non-gypsicolous associations were distinguished, belonging to alliances *Gypsophilion* and *Rosmarino-Ericion* respectively. Representative of pastures, we selected two associations of *Thero-Brachypodietea*, one gypsicolous and one non-gypsicolous, each dominated by one species of patchy, xerophytic grass and containing many therophytes.

	Li-Fm (%)	Cov (%)	Main species	Exposition, Slope angle	Position; Location	sps/ rel.
Agropyro-Lygeetum A-L-B (*Agropyro-Lygeion*)	Ch 53 Th 41 Cr 4 Hc 2	93	*Lygeum spartum* ** *Brachypodium distachyon* *Polygala monspeliaca* *Linum strictum* *Helianthemum salicifolium*	S (SW) 5	Glacis or toeslopes, on gypsum; Balaguer	42
Ruto-Brachypodietum retusi R-B-B (*Thero-Brachypodion*)	Ch 66 Th 18 Hc 16	69	*Brachypodium retusum* ** *Crupina vulgaris* *Phlomis lychnitis* *Cerastium pumilum* *Avenula bromoides*	NE (E-NW) 20	Diverse slopes; Balaguer	35
Brachypodio-Stipetum typicum B-S-V (*Thero-Brachypodion*)	Hc 68 Ch 18 Th 14	87	*Stipa iberica* ** *Koeleria vallesiana* *Festuca* gr. *ovina* *Leontodon taraxacoides* *Convolvulus cantabrica*	S (all) 1	Flat summits, gentle slopes; Vic	40
Brachypodio-Aphyllanthetum brachypodietosum retusi B-A-B-V (*Aphyllanthion*)	Hc 50 Ch 47 Th 3	89	*Brachypodium retusum* ** *Koeleria vallesiana* *Teucrium polium* ssp. *polium* *Thymus vulgaris* *Aphyllanthes monspeliensis*	S (SW-SE) 17	Diverse, steep slopes; Vic	38
Brachypodio-Aphyllanthetum typicum B-A-V (*Aphyllanthion*)	Hc 61 Ch 35 Th 4	88	*Festuca* gr. *ovina* * *Potentilla neumanniana* * *Aphyllanthes monspeliensis* * *Koeleria vallesiana* * *Teucrium polium* ssp. *polium*	S (NE-NW) 9	Gentle slopes; Vic	40
Plantagini-Aphyllanthetum P-A-V (*Aphyllanthion*)	Hc 78 Ch 20 Cr 2	89	*Brachypodium phoenicoides* ** *Avenula pratensis* ssp. *iber.* *Aphyllanthes monspeliensis* *Carex caryophyllea* *Festuca* gr. *ovina*	N (all) 4	Gentle slopes, toeslopes; Vic	50
Euphrasio-Plantaginetum E-P-V (*Mesobromion*)	Hc 86 Ch 11 Th 3	100	*Brachypodium phoenicoides* * *Trifolium pratense* * *Lotus corniculatus* * *Avenula pratensis* ssp. *iber.* *Helianthemum nummularium*	N (NE) 1	Shaded toeslopes; Vic	43
Helianthemetum squamati H-B (*Gypsophilion*)	Ch 84 Hc 11 Th 4 Cr 1	45	*Rosmarinus officinalis* * *Herniaria fruticosa* * *Ononis tridentata* * *Koeleria vallesiana* * *Thymus vulgaris*	S (W-SE) 10	Eroded hill summits, on gypsum; Balaguer	21
Ononidetum tridentatae O-B (*Gypsophilion*)	Ch 89 Hc 6 Th 3 Cr 2	71	*Rosmarinus officinalis* * *Ononis tridentata* * *Helianthemum marifolium* *Reseda stricta* *Brachypodium retusum*	N (all) 7	Diverse slopes, on gypsum; Balaguer	22
Rosmarino-Linetum R-L-B (*Rosmarino-Ericion*)	Ch 74 Hc 24 Th 2	69	*Rosmarinus officinalis* ** *Linum suffruticosum* *Stipa offneri* *Brachypodium retusum* *Fumana ericoides*	N (all) 10	Diverse slopes; Balaguer	23
Rosmarino-Lithospermetum R-L-V (*Rosmarino-Ericion*)	Ch 63 Hc 36 Th 1	97	*Rosmarinus officinalis* ** *Brachypodium retusum* * *Thymus vulgaris* * *Koeleria vallesiana* *Helichrysum stoechas*	S 15	Diverse slopes; Vic	26

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Table 1. Main characteristics of the communities considered, followed by the corresponding abbreviations (and alliances): life-forms (calculated from mean coverage coefficients of species), general mean coverage, species with highest abundancy, exposure and mean slope angle, topographic position and location, average number of species per relevé (data from CASAS & NINOT, 1995, 1996; and GUÀRDIA & NINOT, 1991). Abbreviations and symbols mean: Hc, hemicryptophytes; Ch, chamaephytes; Th, therophytes; Cr, cryptophytes (= geophytes); *, dominance; **, codominance.

One of the most interesting phytogeographic aspects of the Vic site is the great variety of pastures which share the small relief features wich rise up from the intensively farmed flat surfaces. On the most shaded, mild slopes of these hills occurs a dense pasture belonging to medio-European *Mesobromion*, while on the driest, south-facing slopes, typical chamaephytic, open Mediterranean pastures are common. Between these two extreme communities, a variety of meso-xerophilous *Aphyllanthion* pastures occurs; and also some therophytic associations of *Thero-Brachypodion* related to flat, shallow soils, and a *Rosmarinus officinalis* scrub in especially dry, irregular spots.

For comparative purposes and to facilitate discussion, in this paper these communities are distributed into three groups, according to their main physiognomic and phytogeographic characteristics:

a) open, xerophytic pastures containig a variety of therophytes among perennial grasses and sub-shrubs, clearly Mediterranean;

b) dense, meso-xerophytic pastures with very few therophytes, sub-Mediterranean in character;

c) light, open, xerophytic scrubs, dominated by narrow-leaved, dwarf shrubs, poor in herbs and grasses, clearly Mediterranean.

Groups a) and c) include communities found in both Balaguer and Vic, while all the communities in group b) come from Vic.

4. Methods

Phenological records were collected monthly from April 1985 to July 1986 in both areas; this pattern was interrupted on occasions during August, when most plants were inactive. Sampling was undertaken using permanent plots, one (less frequently 2 or 3) plot for each community considered. Plot size was determined for each community according to its structural features. All plants within the plots were examined and their phenological state was recorded. For the purpose of this paper we considered the following main phenophases:

a) Vegetative growth: this includes seedling emergence (therophytes), stem elongation or leaf production (therophytes and perennial plants);

b) Resting: for the therophytes this means senescence of complete body plant or absence of above-ground biomass, and for perennials it includes dieback of foliage or no vegetative growth observed;

c) Flowering: from presence of flower buds to periant senescence;

d) Fruiting: from ripe fruit production to onset of seed dispersal.

Although most species showed individual variation, only the most general phenophase was recorded for each taxon. Thus, vegetative and reproductive phases are reciprocally exclusive. More details in the procedure are given in GUÀRDIA & NINOT (1991b).

For each community studied, the percentage of the species in each phenophase was calculated, in reference to the total number of the species recorded throughout the study period. Annuals and cryptophytes (= geophytes) were computed as resting plants when no above-ground structure could be observed.

The phenological patterns of 19 species common to the 2 areas were compared by means of their respective phenogrames. The species were categorised into three groups: therophytes, perennial herbs (including grasses) and shrubs (including dwarf-shrubs).

5. Results

5.1. Climatic conditions during the study period

Monthly rainfall and mean temperature recorded at the observatories of Vic and Balaguer during the years 1985 and 1986 are shown in Figure 2. Comparison of these data with the general climatic diagrams (Fig. 1) shows that interannual climatic variability is a noticeable feature at both sites, especially with regards to rainfall (Table 2).

1985 and 1986 were comparably dry years, especially 1985. In general, all months experienced less rainfall than was expected from interannual data; September-October 1985 and May 1986 were the driest. The difference in winter rainfall between the two sites was not very significant, with the exception of January of the second year. From mid spring to early summer rainfall totals at Balaguer became progressively lower than those at Vic. June was the first dry month in Balaguer in 1985, while in 1986 May was already experiencing water-stress. This dry spring was much more limiting in Balaguer than in Vic, as only 10.4 mm of rain fell in May and June in Balaguer, while Vic received 76.2 mm. The lower summer rainfall and the lower spring reserves resulted in a much severer summer drought at the former site. September and October, generally rainy months in both areas, were very dry in Balaguer in 1985.

Mean temperatures in 1985 and 1986 were roughly similar to interannual data. However, maximum values were a little higher than usual (about 0.5-1°C in monthly data); this was especially noticeable in spring, 1986 (in Balaguer, the mean temperature in May was actually 19.2 compared to 14.2°C), which coincided with low rainfall. In both areas the biggest temperature increase took place from April to June, and the biggest fall in November. Vic had lower values than Balaguer in all monthly data (maxima, minima and means) during the period studied. Inter-site differences between monthly maxima (1.4 +/-0.8°C on average) were lower than differences between monthly minima (2.2 +/-0.78°C). Spring and autumn, in general, showed the highest thermal differences; in 1985 these

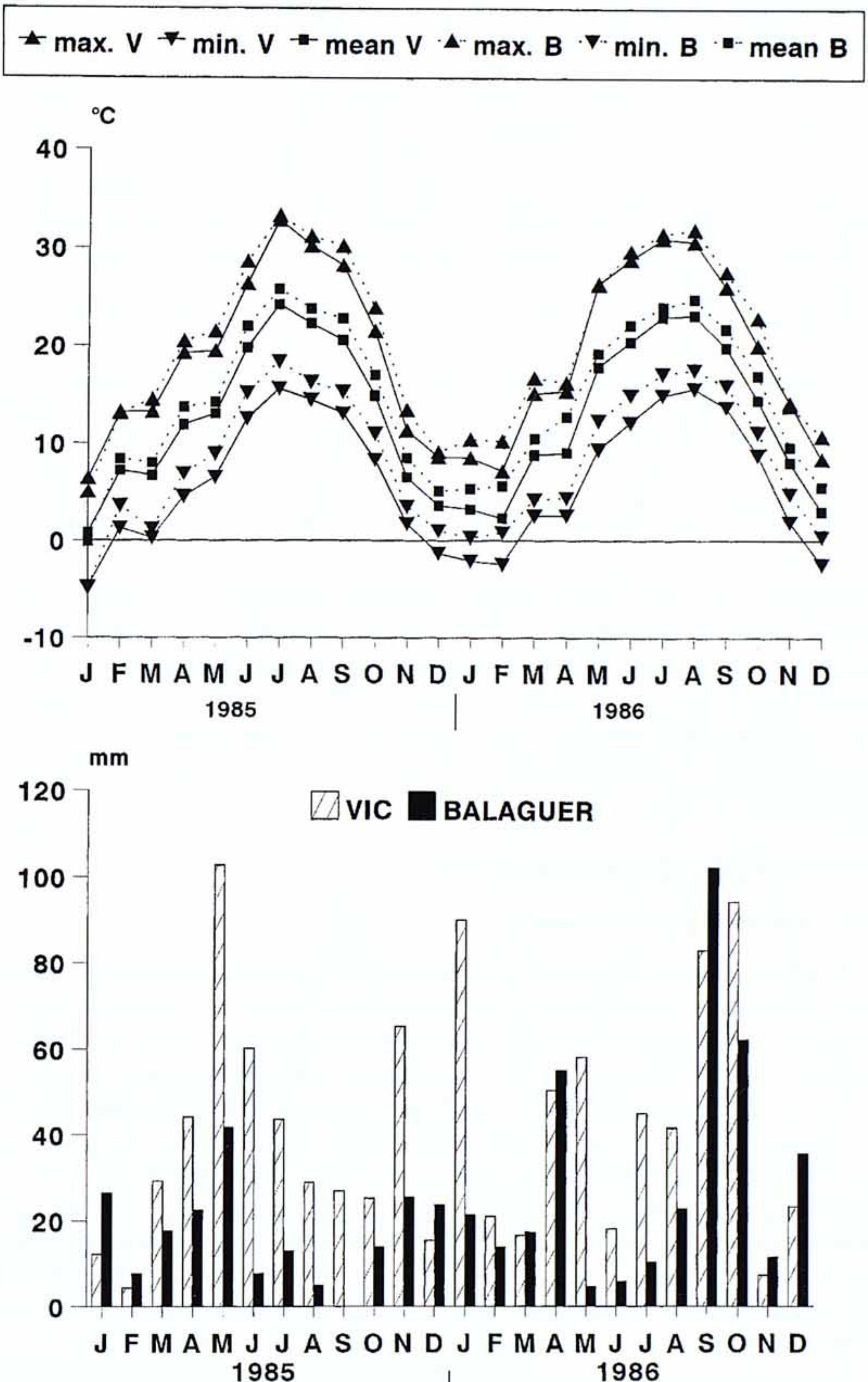


Figure 2. Monthly mean temperatures (top; average of maxima, average of minima and mean average, in °C) and rainfall (bottom, in mm) during 1985 and 1986 at the two study sites (B, Balaguer; V, Vic).

Table 2. Annual and seasonal rainfall (mm) at the two study sites. Seasons are taken as three-month periods (i.e., Winter: January, February and March; etc.). For each site, the three columns show inter-annual average, 1985 and 1986.

	Balaguer			Vic		
	avg.	1985	1986	avg.	1985	1986
Year	434	204.4	361.8	728	458.6	548.3
Winter	85	51.6	52.4	116	45.9	127.6
Spring	141	71.8	65.3	213	207.1	126.5
Summer	92	22	135	215	81.2	169.5
Autumn	116	63	109.1	184	105.9	124.7

ranged from 2 to 2.9°C. If we consider minimum temperatures during these two seasons, temperatures increased (spring) slightly delayed in Vic and decreased (autumn) a little earlier. As for extreme data, the maximum temperatures in the warmest month were similar at the two sites (32.85°C in Vic, 33.3°C in Balaguer), while minimum temperatures in the coldest months were clearly lower in Vic than in Balaguer. Temperatures below 0°C were much more frequent in Vic from December to February.

5.2. Phenology at the community level

5.2.1. Vegetative growth phase

In all the communities this phase started in early autumn, after a short period (about 1-2 months) of minimum values (always 0%; see Fig. 3). Autumn and early winter involved moderate growth, which increased markedly from the January sampling to that of February. All the communities displayed maximum vegetative activity in late winter and spring, reaching percentage values between 80-90% in most of the pastures and slightly lower values in the scrubs. In April and May, with most of the species still building new vegetative structures, the increase in blooming is shown in the graphs as a sharper decrease in growth than was actually experienced, because the species that began to bloom during vegetative growth were recorded as flowering. This effect is more evident in the xerophilous pastures and scrubs, which bloomed earlier and more synchronically than did dense pastures.

Among the open pastures, *Agropyro-Lygeetum* in the gypsum soils of Balaguer were remarkable for several aspects. Mainly, it started growing and peaked one month earlier than the others, and showed lower summer and higher autumn values. Dense pastures, all of them in Vic, produced a similar pattern to open pastures in

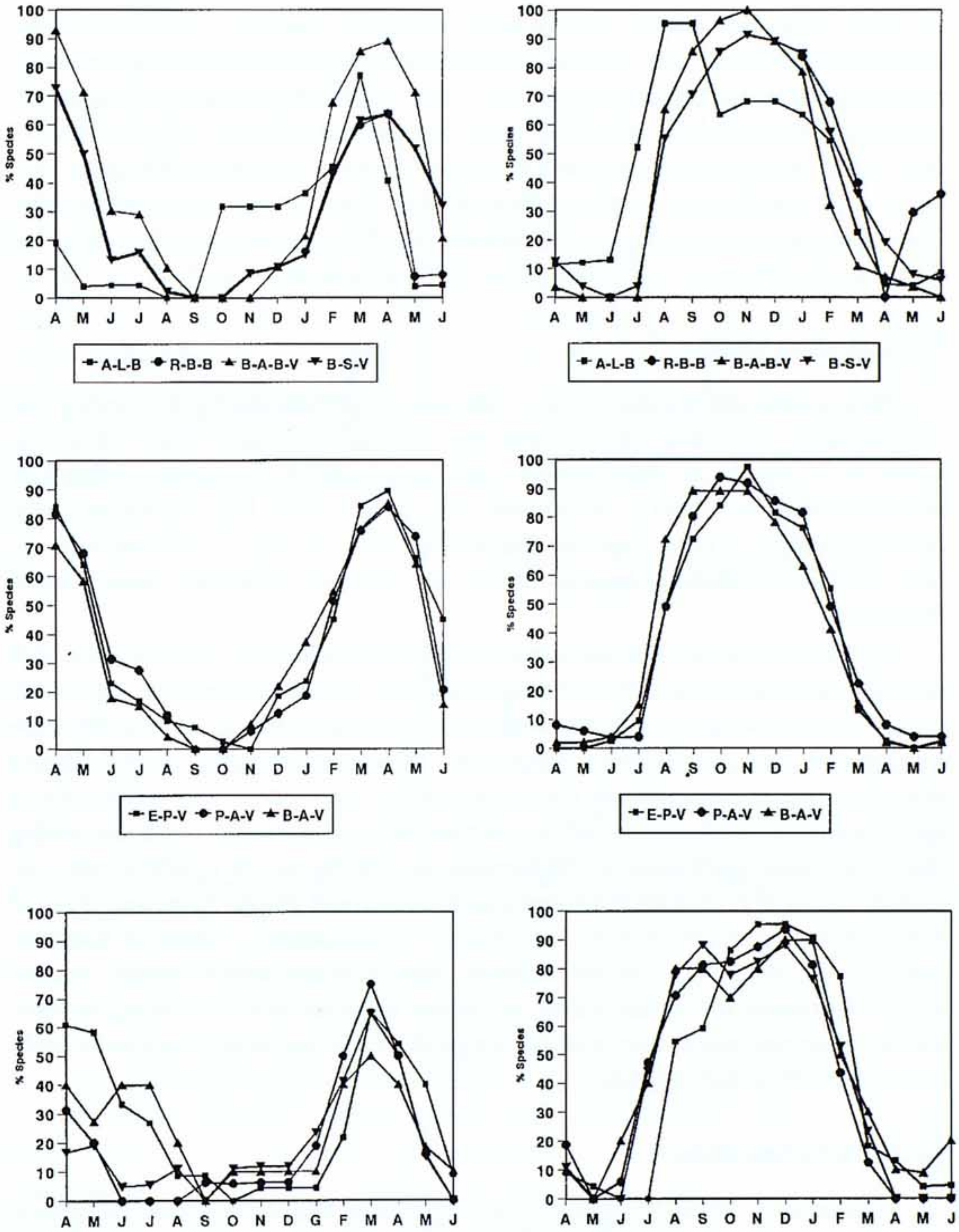


Figure 3. Percentages of species in growing (left) and resting (right) phase for the communities studied from spring 1985 to summer 1986. These are grouped within each column and abbreviated as follows:

a) open pastures: A-L-B, *Agropyro-Lygeetum*; R-B-B, *Ruto-Brachypodietum*; B-BR-V, *Brachypodio-Aphyllanthetum brachypodietosum retusi*; B-S-V, *Brachypodio-Stipetum*

b) dense pastures: E-P-V, *Euphrasio-Plantaginetum*; P-A-V, *Plantagini-Aphyllanthetum*; B-A-V, *Brachypodio-Aphyllanthetum typicum*

c) scrubs: R-L-V, *Rosmarino-Lithospermetum*; O-B, *Ononidetum tridentatae*; R-L-B, *Rosmarino-Linetum*; H-B, *Helianthemetum squamati*.

The last letter in the abbreviations, B or V, means Balaguer or Vic.

the same area, but showed slightly more activity in summer. The mesophilous *Euphrasio-Plantaginetum* maintained some activity even into the early autumn, and did not fall to 0% until November. The scrubs dominated by *Rosmarinus officinalis* behaved in a similar way to the xerophilous pastures. A delay of about one month was observed in that of Vic with respect to that of Balaguer; this became clear in the only sample with no activity (October instead of September). The gypsicolous communities (*Ononidetum* and *Helianthemetum*) showed a very long period with low or no activity, from late spring to late winter.

5.2.2. Resting phase

Most of the species dried out or showed no growth during late spring and early summer, after their fruits became ripe and had been shed. They fell into an enforced resting phase, which in most cases lasted until the late winter. Therefore, all the communities spent a considerably long period, from July to February, with high percentages of resting species (higher than 50%; see Fig. 3) and reached very high values (85-100%) at least in one of the samples –generally, November or December.

Agropyro-Lygeetum also showed a differentiated behaviour in this phase within open pastures, as it started its resting phase one month earlier than the others, peaked even earlier and decreased to medium values in October. Among the dense pastures, the less xerophilous a community is, the less abruptly the percentages tended to rise in summer and the higher values were achieved. Especially in the xerophilous *Brachypodio-Aphyllanthetum brachypodietosum retusi*, the resting phase increased more abruptly in summer than it decreased in late winter. In contrast, most of the scrubs produced a more symetrical graph. Also, they showed a more irregular transition from late summer to late autumn. Those of Balaguer reached a secondary peak in late summer, then decreased and eventually peaked at their maximum in autumn-winter, while the Vic scrub started a strong increase and decrease one month later and did not produce any secondary maximum, only a discontinuity in late summer.

5.2.3. Flowering phase

Flowering occurred during a long period, as from March to October there were some blooming species in almost all the pastures and scrubs. In most communities, entering the flowering phase was an abrupt event. They showed no blooming or just very low percentages in winter through to March and reached maxima of about 50-60% of the species in the flowering phase a mere few weeks later (Fig. 4). A rapid decrease also occurred in a short period (within late spring or early summer) and percentages remained low during summer and autumn.

As for the open pastures, an interesting difference between the two areas was the faster sequence in those of Balaguer, which went from very low percentages to maxima in just one month. Although the starting points coincided (it was one month later in the Vic *Brachypodium retusum* community), the peaks in Vic were

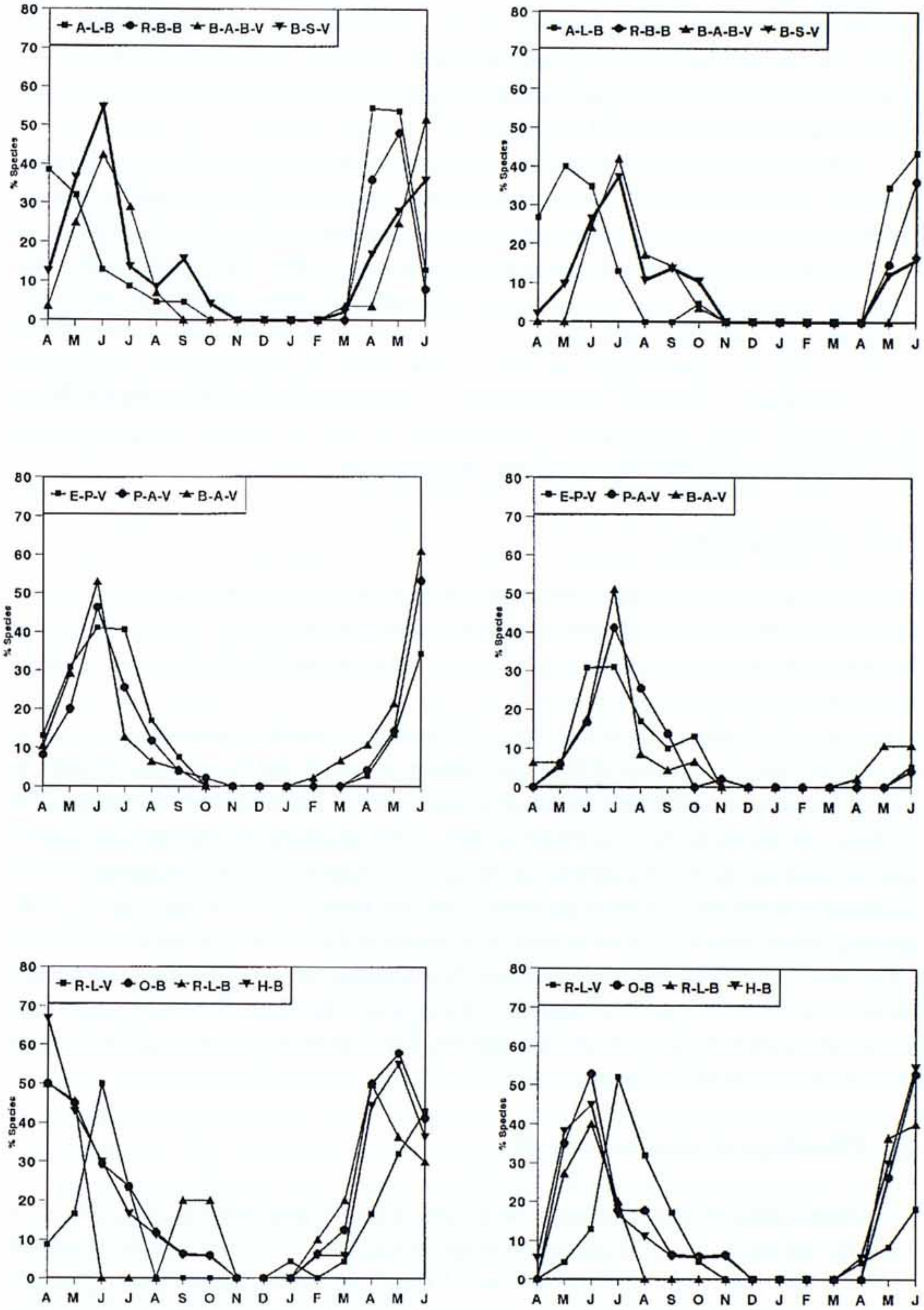


Figure 4. Percentages of species in flowering (left) and fruiting (right) phase for the communities studied. These are abbreviated as in Figure 3.

reached one to two months later (June for April-March), because the increase in blooming was more moderate there. The dense pastures displayed a similar behaviour to that of the open pastures of Vic. Among them, the more mesic they were, the less abrupt the rising and the lower value the peak reached; moreover, *Euphrasio-Plantaginetum* maintained a high level of blooming in July and decreased quite gradually until October.

In the scrubs, the flowering rythms displayed were quite different. Although maxima were achieved in early spring (mainly April or May) through a fast increase, in a similar way as in open pastures, medium and low levels were maintained or newly achieved during summer, autumn and even winter. The gypsicolous communities in Balaguer decreased more or less regularly from spring maxima to 0% in November, while the calcicolous *Rosmarinus* scrub from the same site had fallen to 0% in June and produced a secondary peak (20%) in autumn. The Vic *Rosmarinus* community showed a marked delay in relation to the former, especially in its maximum value (two months); flowering fell to 0% in August, and a secondary peak was also produced, but it did not take place until January.

5.2.4. Fruiting phase

The fruiting phase graphs for each community are very similar to those of the flowering phase, though delayed about one month; as a whole, fruiting took place from May to November and displayed maximum values (30-56.3%; see Fig. 4) in June-July.

Agropyro-Lygeetum was the first community to reach its maximum, as early as May or June. In general, fruiting dynamics occurred one to two months later in the open pastures of Vic than in those of Balaguer, as occured with blooming. The fruiting pattern in all the Vic pastures was quite uniform, be they open or dense, and parallel to their own flowering dynamics. *Euphrasio-Plantaginetum* again displayed an extreme behaviour, producing the lowest and the least sharp peak. Among the scrubs, after a coincident maximum in June, the gypsicolous communities stood out from the others in that they maintained low fruiting percentages until November, as expected from their flowering dynamics. The two *Rosmarinus* communities behaved similarly, though the Vic community was slightly delayed in relation to that of Balaguer.

5.3. Phenology at the species level

Phenograms of the same species in both areas are presented in Figure 5. As a general feature, a delay in the reproductive phenological phases can be observed in Vic with respect to the Balaguer area for almost all the therophytes. Usually flowering started first in Balaguer and consequently seed dispersal occurred earlier in this area. However, the seedling emergence of these plants usually took place first in Vic, from October to February. Hence, the life cycle of therophytes in Balaguer was shorter than it was in Vic –two or three months at least, except for *Bombycilaena erecta*. A similar pattern can be observed in perennial herbs:

flowering and fruiting occured earlier in Balaguer, but the reinitiation of growth after the summer drought did not take place until early spring in almost all the taxa. *Brachypodium retusum* and *Koeleria vallesiana* showed a similar pattern of vegetative growth at the two sites, but in Balaguer they started flowering earlier than in Vic. No common phenological behaviour may be described for the shrubs. Some of them presented the typical flowering advance in Balaguer, such as *Coris monspeliensis* and *Thymus vulgaris*, but this was only true for spring 1985. The resting phase had a variable extension among species and localities.

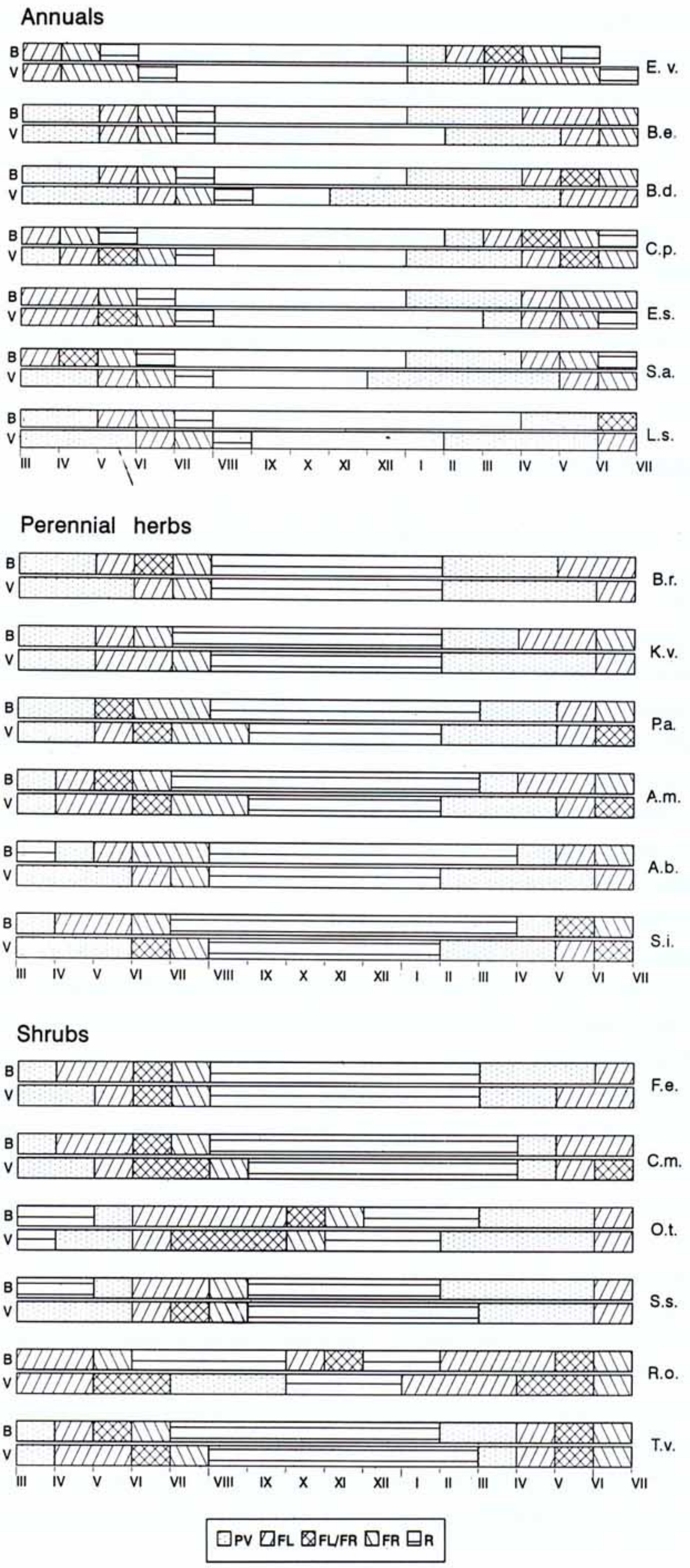
In general, plants in Balaguer were kept inactive mainly for a longer period than were the plants in Vic. This mind they could produce vegetative and reproductive structures for longer periods in the latter site.

6. Discussion and conclusions

The life cycle in the communities studied shows coincident or similar patterns than a wide scope of open Mediterranean communities (BONET, 1991; CARDONA, 1980; NAVARRO *et al.*, 1993; SANS & MASALLES, 1988). Their phenological sequence is strongly related to seasonal climatic features, involving vegetative growth mainly in late winter and early spring, a peak in blooming in spring and subsequent fruiting and death or resting in summer; late summer and autumn activity were variable depending on each community type. As reported elsewhere (HERRERA, 1984; MITRAKOS, 1980; ORSHAN, 1989), Mediterranean-type climate conditions impose a moderate to light cold stress in winter and a moderate to heavy drought stress in summer on plants. This means most Mediterranean communities thrive mainly within two separate seasons, spring and autumn, in which they tend to concentrate their most active phenological periods.

Autumn is a highly significant season in communities such as those studied here, as it is then when a good water supply and fairly favourable temperatures coincide. Here this led to a noticeable reaction after the summer resting period, which became abrupter the stronger the summer drought had been; a transition in this sense was seen from the mesophilous pasture of Vic to the most xerophilous communities of Balaguer. Nevertheless, the seasonal sequence to shorter days and lower temperatures prevented most of the species from being quite active. This inhibition was more evident in Vic than in Balaguer, owing to its temperatures which were about 2-3°C lower in autumn. Also, the activity decreased more suddenly in the pastures than in the scrubs, as these fruticose communities even showed some autumnal blooming. Autumn activity consisted mainly in the emergence and establishment of annuals and in the production of new leaves and shoots in chamaephytes and hemicryptophytes.

Rain distribution and quantities in autumn greatly affect the Mediterranean communities constrained by summer drought. This acts both through germination control, as seen in several annual pastures (PECO & ESPIGARES, 1994; VEENENDAL *et al.*, 1996) and by regulating the production of photosynthetic and


Annuals
B
V
E. v.
B.e.
B.d.
C.p.
E.s.
S.a.
L.s.
III IV V VI VII VIII IX X XI XII I II III IV V VI VII
Perennial herbs
B.r.
K.v.
P.a.
A.m.
A.b.
S.i.
III IV V VI VII VIII IX X XI XII I II III IV V VI VII
Shrubs
F.e.
C.m.
O.t.
S.s.
R.o.
T.v.
III IV V VI VII VIII IX X XI XII I II III IV V VI VII
PV FL FL/FR FR R

⟵

Figure 5. Phenogram over the study period of selected species common to the two study sites, ordered according to their biotypes. For each one, the two bars mean Balaguer (B) and Vic (V).

E.v., *Erophila verna*; B.e., *Bombycilaena erecta*; B.d., *Brachypodium distachyon*; C.p., *Cerastium pumilum*; E.s., *Euphorbia sulcata*; S.a., *Sherardia arvensis*; L.s., *Linum strictum*; B.r., *Brachypodium retusum*; K.v., *Koeleria vallesiana*; P.a., *Plantago albicans*; A.m., *Aphyllanthes monspeliensis*; A.b., *Avenula bromoides*; S.i., *Stipa iberica*; F.e., *Fumana ericoides*; C.m., *Coris monspeliensis*; O.t., *Ononis tridentata*; S.s., *Sedum sediforme*; R.o., *Rosmarinus officinalis*; T.v., *Thymus vulgaris*.

PV, vegetative growing; FL, flowering; FR, fruiting; R, resting (perennials) or senescence (annuals).

reproductive structures for subsequent seasons (STEYN *et al.*, 1996). In Balaguer we had already recorded noticeable differences in the behaviour of therophytes from one year to another, which result into interannual variability in the specific composition of pastures (GUÀRDIA & NINOT, 1991b). The years 1985 and 1986 showed great differences in amounts and distribution of rainfall from late summer to late autumn, particularly in Balaguer. Moreover, such variation seems to have had more influence on phenological behaviour in this site than in Vic, as drought stress is clearly stronger there.

Early winter represented a highly generalised resting period in the localities studied. The same finding has been reported in various Mediterranean plants and localities (SANS & MASALLES, 1988; ORSHAN, 1989). However, it must be taken into account that climatic features force Mediterranean species to perform some winter activity. This was found in all the communities studied, in which at least some species maintained and also partially produced new vegetative structures in early winter. In the more arid Tunisian zone, CHAIEB *et al.* (1992) point out that the C3 arido-passive plants are in the main active in winter.

The second half of winter was marked by a generalised increase in growth activity, though still under low temperatures. For Mediterranean plants, this meant entering spring with new leaves and shoots which are already productive. In most of the communities, the fastest rising took place between the samplings of January and February, or slightly later in some of the Vic communities. But no general delay in this onset could be clearly observed in Vic with respect to Balaguer, in spite of its lower temperatures. Although it seemed so in some communities, the comparison of common species yields no evidence in this sense; in the selected perennial herbs the evidence was sometimes to the contrary. Therefore, this late winter activity seems to be more closely related to longer daylight hours than to a rise in temperature.

Flowering is typically a spring event, with highest values in April for the most xerophilous communities and in May for most of the others. This general timing and also this tendency is a very general feature of Mediterranean habitats (HIDALGO & CABEZUDO, 1994; ISH-SHALOM-GORDON, 1993; ORSHAN, 1989). As experienced in several Mediterranean open scrubs, such as phryganas (PETANIDOU *et al.*, 1995), low scrubs of arid badlands (NAVARRO *et al.*, 1993) and heath-like communities (DOMÍNGUEZ *et al.*, 1995), the onset of blooming is correlated with rising temperatures. For the annuals, flowering generally means a vegetative growth decrease; the size and potential of seed production depends therefore on autumn rains and winter activity.

During late spring and early summer, the decrease or the small increase of rainfall together with the strong rise in potential evapotranspiration, led to the end of flowering and the transition to fruiting and senescence (annuals) or resting (perennials). Clearly, this sequence occured earlier and developed faster in Balaguer than in Vic, according to both community and species data in relation to climatic records; soils and plant communities must have dried out earlier there in 1985, and much earlier in 1986. Other studies have pointed out the importance of water stress in shortening the flowering phase, by the enhancement of fruiting and senescence (ARONSON *et al.*, 1992; DESCLAUX & ROUMET, 1996). This would suggest an interesting phenological plasticity in plants under Mediterranean climate, which is characterised by great interannual variation. However, diverse phenological behaviour within the same species may be partially due to genotipic diversity, as shown in some cases (JACKSON & ROY, 1986; RICE *et al.*, 1992) by cultivation under the same conditions of annual and perennial grasses sampled in different dry habitats.

Flowering and fruiting were more closely synchronised in the pastures than in the scrubs; i.e., these events peaked more suddenly and overlapped for less time in each pasture community. And within the pastures, this was more evident in the most xerophilous. In contrast, in the scrubs these two reproductive phases became longer and more overlapped, and they were even maintained at low levels during the summer stress. This seems to indicate a higher independence level from climate constraints in the shrubs, which have deeper and more difuse rooting systems, than annuals and most non-woody perennials. Moreover, in the community structure aspect, CARDONA (1980) showed in several Mediterranean communities that the more complex the community, the less marked are the phenological changes. In the xerophilous pastures most of the species are annuals, which are highly dependent on climate constraints. Perennial herbaceous species, more dominant in the less xerophilous pastures, generally show longer flowering and fruiting events than annuals do (GUÀRDIA & NINOT, 1991b).

When comparing the two localities, in Vic the same species were allowed to develop longer phenological phases than in Balaguer, both vegetative and reproductive. In some cases, this may lead to higher productions in Vic; this would agree with the larger sizes observed there in general for some common species, and with higher densities in comparable communities, such as the *Brachypodium retusum* dry grasslands or the *Rosmarinus officinalis* scrubs.

In the xerophilous communities, summer drought stress causes senescence and death through drying out of annuals, and a drastic reduction in the activity of perennials. However, a very typical feature is the occurence of a group of xerophytic shrubs and herbs which maintain some activity during such unfavourable conditions, some even flowering and fruiting. They correspond to the "arido-active drought tolerant plants" of CHAIEB *et al.* (1992), which remain active until very high soil water potentials, although productivity is low. *Limonium catalaunicum, Gypsophila hispanica, Coris monspeliensis, Dichanthium ischaemum* and *Sedum sediforme* are good exemples of such plants, being most of them characteristic of gypsicolous communities. This is in agreement with HERRERA (1985), in the sense that the phases of a phenological cycle are not independent events, but linked phenomena which result in a consecutive sequence.

In the less xerophilous Vic communities, summer is still a favourable season; the *Mesobromion* pasture even extended its flowering maximum until August. Probably, the possibility of maintaining the spring growth activity for longer leads these communities to delay their reproductive events.

As a general aspect, summer drought features (timing and intensity) and also rainfall distribution in the preceding and following seasons seem to be the chief constraints in the phenology of Mediterranean communities, as they directly conditioned the length of productive periods. Summer stress was clearly more limiting in Balaguer than in Vic; it directly conditioned the phenological events in the most xerophilous communities, such as the open pastures of Balaguer, while its effects were almost irrelevant in the most mesophilous pasture of Vic. Also, interannual climatic variation in these features causes a noticeable phenological behaviour variation from one year to another in the communities such as those studied here, being most apparent in the most xerophilous.

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