PHENOLOGICAL ORGANIZATION OF MEDITERRANEAN PASTURES IN DIFFERENT ENVIRONMENTS STUDIED THROUGH DIVERSITY PARAMETERS

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RESUMEN

Organización fenológica de pastizales mediterráneos en **diferentes** ambientes estudiada mediante parámetros de diversidad

Se ha estudiado la fenología de pastizales mediterráneos en relación a la altitud, geomorfología y consumo del ganado. Algunos parámetros de diversidad fueron utilizados para analizar el porcentaje de especies en **4** estados fenológicos (crecimiento vegetativo, floración, fructificación y decaimiento) durante un ciclo anual. La distribución temporal de **estados** fenológicos varía desde situaciones más heterogéneas propias de los pastizales de poca altitud - e n los cuales varios estados **fenológicos** predominaron en diferentes tiempos—, a las situaciones-más uniformes de las posiciones altitudinales **más** elevadas, en las que predominó el **estado** de crecimiento vegetativo. El aumento de altitud fue acompañado de un retraso y acortamiento de las **fenofases** reproductivas. Estas tendencias también aparecieron cuando se compararon zonas altas y bajas de ladera o parcelas pastoreadas y no pastoreadas. La organización fenológica parece estar relacionada con la proporción de especies perennes y anuales, asi como con la riqueza específica.

Palabras clave: Diversidad, Entropía, Fenología, Geomorfología, Gradiente altitudinal, Pastizales, Pastoreo, Teoría de la Información.

Abreviaturas: HS= Escalamiento Multidimensional Híbrido.

SUMMARY

The phenology of Mediterranean pastures was **studied** along an altitudinal gradient in relation to **geomorphology** and consumption of plants by large and medium-size herbivores. Diversity **parameters** were used to **analyze** the percentage of species in four phenological states (vegetative growth, flowering, **fruiting** and decay or dormancy) throughout an annual cycle. The distribution of phenological states in time varied from the most heterogeneous situations in low **altitude** pastures —in which different phenological states **predominated** at different **times**—, to more uniform situations at higher altitudes **with** a **predominance** of vegetative growth. The altitudinal rise was **also** accompanied by a shortening and **delay** in the reproductive phenophases. These trends **also** appeared when comparing upper and lower slope **zones** or unfenced and fenced plots. **Phenological** organization seemed to be related to the proportion of perennial and annual species as **well** as species richness.

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INTRODUCTION

Most plants in Mediterranean pastures germinate after the first persistent autumnal rains, grow slowly during Winter, and flower and mature their seeds in Spring. This temporal distribution of phenological states, with a growth peak prior to the summer drought, is characteristic of Mediterranean-type ecosystems (KUMMEROW, 1983; CHIARELLO, 1989). However, the phenological pattem varies spatially and temporally in accordance with biotic and abiotic variables which affect species phenology. Some abiotic variables such as temperature, photoperiod, soil moisture and rainfall have been studied in relation to the phenology of the vegetation in these ecosystems (WI-LLIAMS, 1961; EVANS, 1971; FRENCH & SAUER, 1974; MOONEY et al., 1974; KALIN et al., 1981; KUMMEROW, 1983). Biotic variables such as internal physiological rhythms (VOGTS, 1982) and effects of the behavior of animals acting as pollinators, dispersal agents and consumers of reproductive tissue (JANZEN, 1969; THOMPSON & WILLSON, 1979; RATCHKE, 1983; RATCHKE & LACEY, 1985; ROTENBERRY, 1990) have also been considered in different ecosvstems.

The study of community organization based on diversity parameters of species (MARGA-LEF, 1957, 1963, 1968; GODRON, 1966; PIELOU, 1975) has been developed and applied to spatial and temporal gradients in Mediterranean pastures in central Spain (PINEDA et al., 1981, DE PABLO et al., 1982, PECO et al., 1983, 1991, among others). It has been used much less often, however, with non-taxonomic variables in spite of their unquestionable value (WAYNE & BAZZAZ, 1991). The application of diversity parameters to the proportion of species in different phenological states and their variation in time or space can provide information on the phenological organization of the community. By determining community seasonality, patterns of theoretical interest can be detected, permitting speculation on evolutionary and

biogeographic pattems (PIERCE, 1984). For example, PINEDA et al. (1984), in a study in therophyte-dominated ploughed pastures, found that the phenological organization of the community changes dunng succession. In the early stages, most species have coincident phenophases during the growing season, while in the advanced stages there is less overlap in the phenology of the different species in the community.

The present paper compares the phenological organization of Mediterranean pasture communities in different altitudinal, geomorphological and grazing usage environments, and relates this to macroscopic community parameters such as species richness and life forms.

The altitudinal gradient assumes mesoclimatic variability (temperature, magnitude and predictability of water deficit). An increase in the proportion of perennial species has been detected in association with this type of gradient, along with a fall in species richness and a change in communities as altitude increases (KEMP & DOWLING, 1991; MONTALVO et al., 1991). On the other hand, geomorphology defines a gradient which conditions parameters of water availability and temperature. On a local scale, geomorphology can produce a qualitatively similar type of variability as that represented by an altitudinal gradient, although it does not have the same magnitude. Geomorphological influence on the phenology of the communities can thus be expected to be related to the one obtained with the altitudinal gradient.

The cessation of grazing alters this type of ecosystem, whose structural and functional characteristics are largely the result of interaction between herbivores and pasture plants. This alteration is primarily manifested through a fall in floristic richness and the predominance of few species, generally perennials (WILLIAMS, 1961; HEADY, 1977; ELLIOT & WEHAUSEN, 1974; JACKSON & ROY, 1989; MONTALVO et al., 1993 and others).

Altitude, geomorphology and grazing seem to affect species richness and species life forms, The relations between these two macroscopic characteristics of the community and their phenological organization is yet to be clarified. As a working hypothesis, floristic richness ought to be related to a higher diversity of phenological niches as it favours coexistence (GRUBB, 1977). On the other hand, perennialization ought to act in the opposite direction as the persistence of the species that present this life form is relatively independent of sexual reproduction, and furthermore their longevity gives them more time to segregate their phenologies.

MATERIAL AND METHODS

The study area is located on the southern slope and piedmont of the Sierra de Guadarrama (central Spain) with a continental Mediterranean climate. The soils, on siliceous substrata, have a sandy loam texture. Five pasture communities were selected along an altitudinal gradient corresponding to different mesoclimatic environments: 642m, 891m, 1215m, 1449m and 1719m. This gradient is characterized by a mean annual temperature which falls as altitude rise from 13.2 to 6.5°C, and a mean annual rainfall which increases linearly from 560 to 1510 mm. All pastures are predominantly grazed by farm herbivores (mainly cattle).

A south-facing slope was selected in each locality. Two 8 x 10m plots were marked in the upper and lower part of the slope. In each zone, one of the two plots was fenced off in 1986 (two years prior to this study) in order to exclude medium and large herbivores.

The present study differentiates four phenological states in the plants: vegetative growth, flowering, fruiting and decay or dormancy. The vegetative state covers the period of plant development from emergence until the formation of the reproductive flower buds. The flowering state ranges from the end of the bud stage to the start of fruit formation. Seed production or fruiting state begins with fruit formation and extendes to the start of the period of individual senescence. Finally, the state of

decay or dormancy covers the time period in which the individuals die, although the species may remain in seed or rhizome form in the soil.

The phenological state of 155 pasture species (appendix I) was recorded 15 times at variable intervals of approximately 30 days. The data were registered between October 1988 and December 1989, in four 20x20 cm permanent quadrats placed at random within each plot. In each quadrat and each time, each species was assigned the most advanced phenological state of its tillers.

In order to characterize the phenological organization of the communities, each plot was assigned the mean percentage of species in each phenophase in all four quadrats. Each community's phenological organization was analyzeú via the parameters derived from the theorem of total entropy $H(P.T) = H(P) + H(T/P)$ (appendix II) which permits total entropy $H(P.T)$ to be broken down into two values of entropy (PIELOU, 1975; PINEDA et al., 1981). $H(P.T)$ represents the uncertainty of finding a phenological state, P, in a given time, T, where H is diversity or entropy measured by the Shannon index (SHANNON & WIENER, 1949). $H(P)$ represents the total diversity of the phenological states and is thus a measure of the predominance of a given state for the group of monthly records. In the four phenological states considered, their maximum value is 2 bits ($\log_2 n^o$ of states) and is reached when all four states are equiprobable. $H(T/P)$ is the weighted measure of the diversity of the times conditioned by the phenological states, and measures the distribution of states through time. This parameter acquires its maximum value, 3.9 bits ($\log_2 n^o$ of times), when all phenological states are distributed equiprobably in all times. This measure may also be applied independently to each phenological state — $H(T/P_i)$—, in this case reporting on the temporal distribution of state i.

Data on frequency of species found in each plot at the end of the study period were used to detect floristic trends, which in turn were used as a basis for understanding the phenological organization of the communities. The affinity of the communities according to the species composition was quantified using the Kulczynski similanty index (HAJDU, 1981; FAITH et al., 1987). Three-dimensional Hybrid Multidimensional Scaling (HS) was used as the

ordination technique (BELBIN, 1987). The PATN statistical package (BELBIN, 1987) was used for all the multivariate analyses.

RESULTS

Environmental framework and communities

Figure 1 show climatic and meteorological diagrams from four stations near the study localities. The summer drought becomes less severe and more delayed as altitude increases. The period of temperatures below a monthly average of $7.5°C$ increases with altitude. This temperature is considered sufficient for growth to start in most Mediterranean species (MONTERO DE BURGOS & GONZÁLEZ REBOLLAR, 1974).

In Figure 2, the interannual climatic variability of the stations is analyzed via the variation coefficient of monthly rainfall and temperature over 30 years (1951-1980). Annual temperature distribution is quite similar from one year to the next, while there are extreme fluctuations in rainfall (high coefficient of variation) (Student t-test=19.36, $p < 0.001$). Periods of maximum temperature variability occur in winter, when there is no apparent trend related to the altitudinal gradient. Interannual rainfall variability, however, reaches a maximum in summer and the first months of autumn (July-October). These rainfall fluctuations also tend
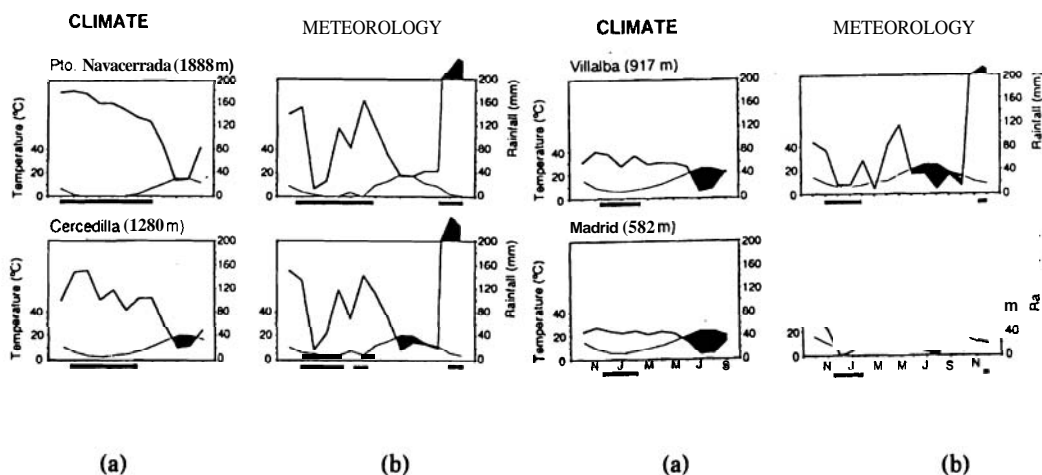

FIGURE 1. (a) Climatic diagrams of 30 years period (1951-80) for 4 localities near the study pastures (thick line: rainfall; thin line: temperature). Shaded part of the wet area indicates rainfall over 200 mm; beyond 200 mm, scale falls by a proportion of 1/10. Horizontal black bar indicates period during which mean monthly temperature was under $7.5°C$, and was thus inadecuate, in general, for vegetation growth (MONTERO DE BURGOS & GONZÁLEZ REBOLLAR, 1974). (b) Meteorologic diagrams (October 1988 to December 1989) for the same localities. Simbols as in (a).

FIGURA 1. (a) Diagramas climáticos de un período de 30 años (1951-80) de 4 localidades cercanas a los pastizales estudiados (línea gruesa: precipitación; línea delgada: temperatura).La parte sombreada del área húmeda indica precipitaciones por encima de 200 mm; la escala desciende a una proporción de 1/10 pera valores superiores a 200 mm. Las barras horizontales negras indican períodos durante los cuales la temperatura media mensual fue menor de $7.5°C$ y por ello inadecuada,en general, para el crecimiento vegetativo (MONTERO DE BURGOS y GONZÁLEZ REBOLLAR, 1974). (b) Diagramas meteorológicos(octubre 1988 a diciembre 1989) de las mismas localidades. Símbolos como en (a).

to decrease as altitude increases (r=0.36, p<0.05), indicating that the unpredictability of the time of arrival of the summer drought decreases as altitude increases.

In response to the altitudinal mesoclimatic variation. the pasture plant communities have different characteristics in both floristic composition and life forms. The ordination of pasture communities on the basis of their floristic composition (Fig. 3) is thus clearly related to altitude in the direction of HS axis 1. Geomorphology and grazing are covered by axis 2, with the lower slope zones and the fenced plots tending to lie on the positive side of the axis with respect to their control plots. Moreover, species richness (Fig. 4a) falls (r=-0.60, p<0.001) as altitude increases, while the proportion of perennials as opposed to annuals (Fig. 4b) increases (r=0.77, p<0.01). Grazing and topography are lmked to both parameters. The percentage of perennial species tends to be greater in the lower than the upper slope

zones (paired t-test=4.28, p<0.01), and in the fenced than the unfenced plots (paired t-test=3.37, p<0.01). Species richness is also greater in the unfenced pastures (paired t-test=5.23, p<0.001).

Grassland phenological **organization**

The altitudinal gradient under consideration causes great changes in the phenological development of the pastures (Fig. 5). The phase of vegetative growth tends to be greater as altitude increases, to the detriment of the other three phenophases. This phenological state is significantly larger in lower as opposed to upper slope zones (paired t-test=2.28, p<0.05). Flowering and fruiting are significantly larger in unfenced than the fenced plots (paired t-test=3.32, p<0.01, and paired t-test=3.87, p<0.01, respectivily). Table 1 shows that the frequency of perennial species that do not arri-
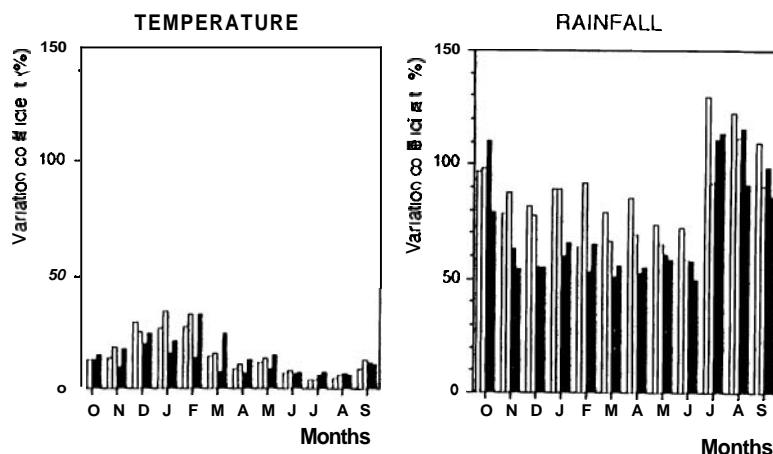

FIGURE 2. Interannual climatic variability measured by the monthly variation coefficient of a) rainfall and b) temperature, calculated for the series of 30 years (1951-1980) on the 4 sites in Fig. f. Rising altitude is indicated by increasing intensity of bar shades.

FIGURA 2. Variabilidad climática interanual medida por coeficiente de variación de a) precipitación y b) temperatura, calculado para le serie de 30 años (1951-1980) de las 4 localidades de la Fig. 1. El aumento altitudinal está indicado por el incremento de intensidad de la sombra de las barras.
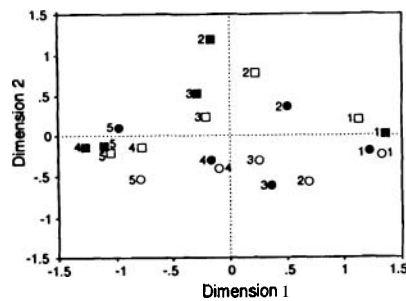
FIGURE 3.   **Projection** of study pasture communities onto the plane defined by the **first** two axes of the HS ordination analysis. Empty and **full symbols indicate** upper and lower slope **zones** respectively; **circles** are unfenced **plots;** squares are fenced. **Numerical** index of pasture **altitude** is: 1= **642m; 2**= 891**m; 3**= 1215m; **4**= 1449m; **5**= 1719m.

FIGURA 3.   **Proyección** de las comunidades **de** pastizal estudiadas **sobre** el plano defmido por los dos **primeros** ejes del análisis de ordenación HS. **Los** símbolos **vacíos** y **llenos** indican urnas alta y baja de la ladera. respectivamente; los **círculos son parcelas** no **cercadas** y los cuadrados son las **cercadas.** El indicador **numérico** de la altitud de los **pastizales** es: **1**= **642m; 2**= 891m; **3**= 1215m; **4**= 1449m; **5**= 1719m.
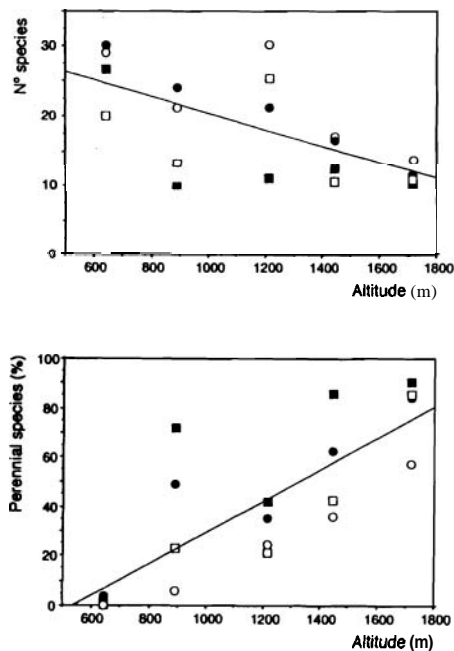

FIGURE 4.   Altitudinal variation of a) species nchness and b) proportion of perennial species vs. annuals in sampled pasture communities. Vanance analysis of regression lines is: a) **F=44.87 p<0.001** and **b) F=116.70 p<0.001 Symbols** are as in Fig. 3.

FIGURA 4.   Variación **altitudinal** de **a)** riqueza **de** especies y **b)** proporción **de** especies **perennes** vs. anuales en las **comunidades** de pastizal **muestreadas.** El análisis de la **varianza** de las **líneas** de regresión es: a) **F=44,87 p<0.001** y **b) F=116,70 p<0.001.** Símbolos **como** en la Fig.3.

ve at the flowering stage is **greater** in enclosed than grazed pastures (paired **t-test=2.68 p<0.05).** There is no difference in **decay** in relation to **geomorphology** and grazing.

Figure 6 shows the altitudinal variation of the begining and duration of the **reproducti-ve** period (flowering and fruiting). There is a clear **delay** and a shortening of this period for the whole'community as **altitude** increases. Flowering and **fruiting** tend to be shorter in the lo-

wer as opposed to **the** upper slope zones **(paired t-test=2.28, p<0.05).**

Figure 7 shows the phenological diversity parameters —H(P) and H(T/P)— of the **sampled** plots, taking **the possible** maximum and minimum values for these data as the **reference** scale. For the set of plots, the diversity of **phe**-nological states H(P) (Fig. 7a) **decrease** at higher elevations along the gradient, indicating that, for the **entire** period of study there is a
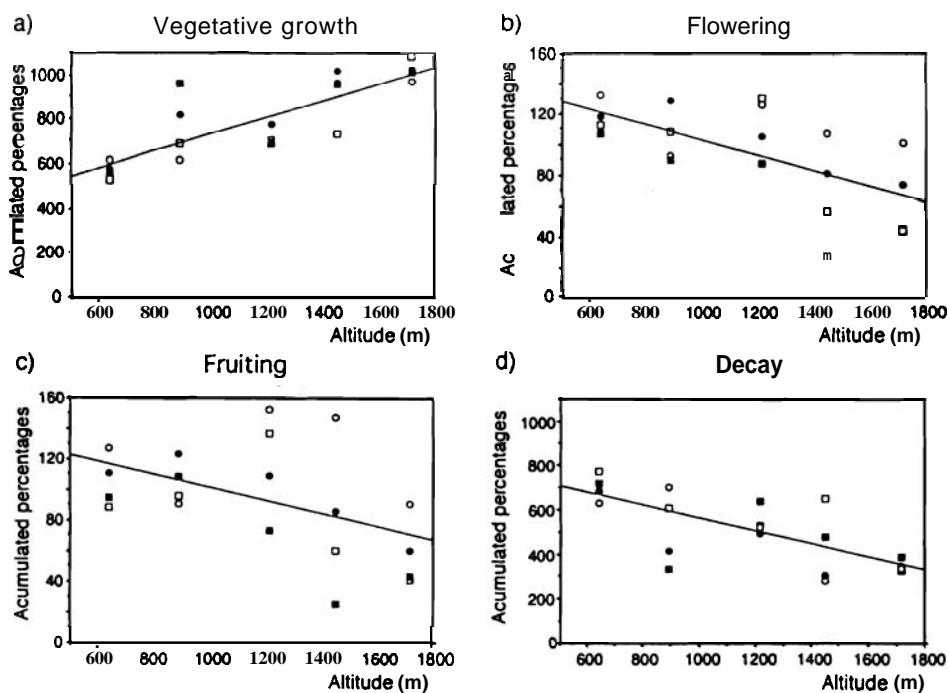

FIGURE 5. **Altitudinal variation of percentages accumulated in the study period of species in each phenological state: a) Vegetative growth; b) Flowenng; c) Fruiting; d) Decay. Vanance analysis of regression lines is: a) F=37.88 p<0.001, b) F=13.13 p<0.01, c) F=5.24 p<0.05 and d) F=18.47 p<0.001. Symbols are as in Fig. 3.**

FIGURA 5. Variaciónaltitudinal de los porcentajes acumulados en el período de estudio de especies m cada estado fenológico: a) Crecimiento vegetativo; b) Floración; c) Fructificación; d) Decaimiento. El análisis de la varianza de las líneas de regresión es: a) F=37,88 p<0.001, b) F=13,13 p<0.01, c) F=5,24 p<0.05 y d) F=18,47 p<0.001. Símbolos como en la Fig. 3.

range of variation from situations with **relati-**vely equiprobable phenological states (at lower altitudes) to situations in which one phenological state is predominant. In general, H(P) is significantly greater in upper zones than in lower zones (paired **t-test=2.44, p<0.05**) and in unfenced than fenced plots (paired **t-test=3.43, p<0.01**). The temporal distribution of the phenological states —H(T/P), a measure of the mean breadth of phenophases in the study period— tends to increase with **altitude (Fig. 7b)**. Situations in which the phenological states are segregated into different months (typical of lower localities of the altitudinal gradient) are replaced by ones in which **some** states remain uniform throughout time. H(T/P) is greater in lower than upper zones (paired **t-test=2.86, p<0.05**) and in fenced as opposed to unfenced plots (paired **t-test=2.78, p<0.05**).

The variation of the temporal distribution of each phenological state —H(T/Pi)— is shown in Figure 8. Focussing on the diversity values, one can distinguish two general types of behaviour in the phenophases. Vegetative growth and decay (vegetative stages) is characterized by its broad uniformity throughout the annual cycle (high values of diversity), while flowering and fruiting (reproductive stages) tend to be **only** represented at specific times of the year (low diversity values). **Altitude** changes these broad patterns, accentuating the temporal uniformity of the vegetative stage

(r=0.82, p<0.001) and relegating **both** flowering and fruiting to shorter periods (**r=-0.44, p<0.05** and **r=-0.66, p<0.01**). The decay stage, however, tends to be more constant through altitudinal variation (**r=-0.07, ns**). Geomorpho**logy** further shortens the flowering period in the lower slope zones in comparison with the upper ones (paired **t-test=3.34, p<0.001**) and the decay phase in the upper as opposed to lower slope zones (paired **t-test=2.80, p<0.05**). The cessation of grazing **also** accentuates the uniformity of the vegetative growth stage (paired **t-test=4.99, p <0.001**).

DISCUSSION

On the mesoclimatic gradient, the vegetative growth stage increases in **importance** with **altitude** to the detriment of the sexual reproductive stage (flowering and fruiting). The begining of the latter is **also** markedly delayed in higher localities. All of this leads to the annual **dominance** of the vegetative stage, in comparison with the more equiprobable distribution of **all** phenophases at lower **altitudes**. Differences related to **altitude** can **also** be found in the temporal distribution of these phases. At the upper end of the gradient, phenological diversity —H(P)— is low, and the mean width of the phenophases —H(T/P)— is **large because** of the long duration of the
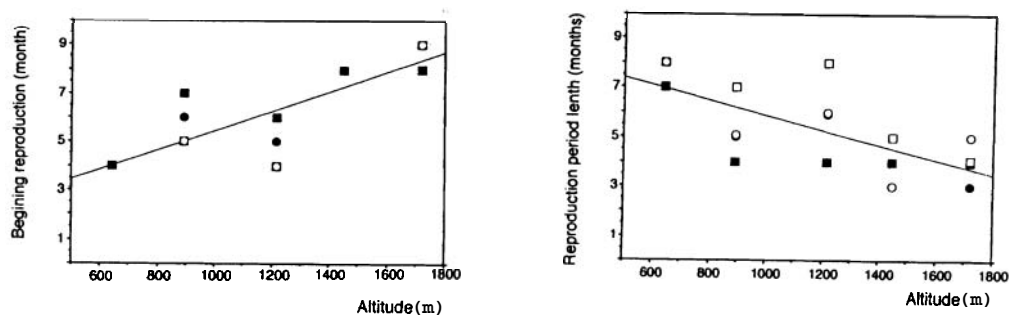

FIGURE 6. Altitudinal variation of a) begining and b) duration of reproductive period (flowering + fruiting). Variance analysis of **regression** lines is: a) **F=27.62 p and b) F=17.86 p. Symbols** are as in **Fig.** 3.

FIGURA 6. Variación altitudinal de a) comienzo y b) duración del período reproductivo (floración + fructificación). El análisis de la varianza de la línea de regresión es: a) F=27,62 p.001 y b) F=17,86 p,001. Símbolos como en la Fig. 3.
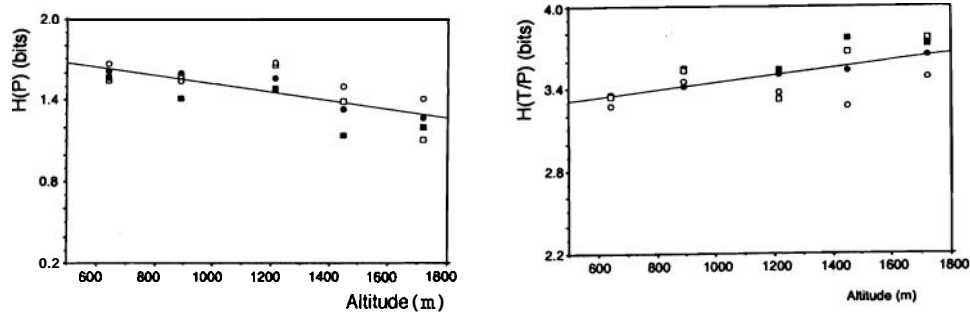
FIGURE 7.   Altitudinal vanation of a) phenological states —H(P)— and b) temporal distribution of phenological states —H(T/P)—. Vanance analysis of regression lines is: a) **F=21.29 p<0.001** and b) **F=13.17 p<0.01.** Symbols are as in Fig. 3.

FIGURA 7.   Variación **altitudinal** de **a) estados fenológicos** —H(P)— y **b)** distribución **temporal** de los estados **fenológicos** —H(T/P)—. El análisis de la **varianza** de la **línea** de **regresión** es: a) **F=21,29 p<0.001** y **b) F=13,17 p<0.01. Símbolos como** en la **Fig.** 3.
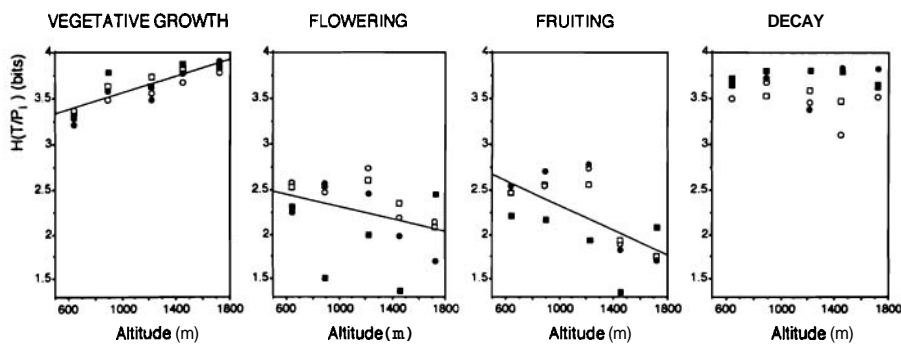

FIGURE 8.   Altitudinal variation of temporal distribution of each phenological state —H(T/Pᵢ)—. a) Vegetative growth; **b)** Flowenng; **c) Fruiting;** d) Decay. **Variance** analysis of regression lines is: a) **F=36.12 p<0.001, b)** F=4.38 p<0.05, **c)** F=14.42 p<0.01, **d)** F=0.09 ns. Symbols are as in Fig. 3.

FIGURA 8.   Variación **altitudinal** de la distribución temporal de **cada** estado **fenológico** —H(T/Pi)—. a) Crecimiento **vegetativo; b) Floración; c) Fructificación; d) Decaimiento.** El análisis de la **varianza** para la **línea** de regresión es: a) **F=36,12 p<0.001, b) F=4,38 p<0.05, c) F=14,42 p<0.01, d) F=0,09 ns. Símbolos como** en la **Fig.** 3.

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state of vegetative growth, although the reproductive phases are shorter. The phenology of lower localities on the gradient, however, is more dynamic, with a high phenological diversity and phenophases with a similar width. This indicates that there is a segregation of states as the annual cycle advances.

The altitudinal gradient represents a mesoclimatic type of variability which influences communities phenology. The limiting factors for plant development are different at either end of the gradient. In the lowest localities, control is primarily exercised by the summer drought, while low winter temperature is the fundamental limit to the phenological development of species in the higher localities.

There is also a gradient of rainfall predictability, linked to the altitudinal gradient, which may be related to the fall in species richness. The less predictable environments seem to prefer the coexistence of a greater number of species (GRUBB, 1977). The unpredictability of the intensity and duration of the drought also affects the evolution of adaptive responses in this type of climate (MOONEY & DUNN, 1970), which seems to favour the presence of annual plants that spend the period in seed form. Many of these species are known to invade and colonize xerophytic pastures of perennial grasses such as the Californian type (BARTOLOME, 1987; HEADY, 1977), probably due to their greater capacity to elude summer drought periods (JACKSON & ROY, 1986). In contrast, frosts favour perennials, capable of surviving the winter stress due to the prolonged union with the mother plant which reduces shoot mortality (GRIME, 1979). This type of regeneration is common in alpine environments (BILLINGS & MOONEY, 1968). Temperature also seems to be the prime controlling factor in flowering (MOONEY & KUMMEROW, 1977). This explains the delay and progressive abridgment of the reproductive period of the communities as altitude increases (see also KALIN et al., 1981).

In the perennial dominated communities of the higher altitudes, sexual reproduction is not the only way to ensure the persistence of the species. This explains the preponderance of the vegetative growth phase and the large number of species that do not flower (see Table 1). Conversely, on the lower sites of the altitudinal gradient there is an almost total domination of

annual species, which can only survive by means of sexual reproduction. This causes flowering and fruiting to acquire more relevance in the phenological organization of the latter pastures.

On a local level, the supply of water and matter from upper to lower slope zones temper the water stress in the latter areas. In contrast, the greater angle of solar incidence in the upper south-facing zones increases water stress (POPE & LLOYD, 1975). The greater predominance of perennials in the lower zones may be caused by these environmental differences, all of which seem to have a similar influence on phenological organization to that of the altitudinal gradient.

The construction of enclosures to prevent cattle grazing seems to have caused a change in the reproductive strategy of the pasture community. Cattle are one of the most influential factors in these communities along with the climatic regime. In the enclosures, biomass as litter reduces insolation. The resulting lower surface temperatures produce a delay in growth (FRENCH & SAUER, 1974). Enclosures also favour the development of perennial species (WILLIAMS, 1961; ELLIOT & WEHAUSEN, 1974; HEADY, 1977; WILLENS, 1983; NOY-MEIR et al., 1989; JACKSON & ROY, 1989; FOIN & PLOTENKAMP, 1989). These species would be more competitive than the annuals in the absence of cattle due to their greater height, their form of occupation of the belowground space and their tendency to deposit a layer of litter on the ground surface. These three characteristics coincide with Grime's (1973) proposals for competitive herbaceous species.

The fall in species richness in the enclosed pastures, also observed by several authors, e.g. BAKKER et al. (1980); WILLENS (1983, 1985); NOY-MEIR et al. (1989); MONTALVO et al. (1993) is due in this case to the competitive exclusion of the annual species by the perennials (HARPER & WHITE, 1974; WILLENS, 1983). The annuals are not totally excluded from the community, probably because of their ease of accumulating dormant seeds on the ground. Although these effects are primarily manifested in the medium and long term, the results obtained two years after the enclosure establishment indicate a dif-

Altitude		GRAZED			INGRAZED		
		Ft	Fnf	%nf	Ft	Fnf	%nf
642 m	U	1	0	0	2	2	100
	L	2	1	50	1	1	100
891 m	U	3	0	0	8	4	50
	L	17	2	12	12	4	33
1215 m	U	16	9	56	12	7	58
	L	13	4	31	16	10	63
1449 m	U	10	6	60	9	4	44
	L	17	11	65	19	15	79
1719 m	U	17	9	53	15	9	60
	L	15	6	40	14	8	57

TABLE 1. Frequency of perennial species that did not flower during the study period in relation to total number of perennials. Ft= absolute frequency of perennials; Fnf= frequency of perennials that did not flower; %nf= relative frequency of perennials that did not flower; U= high slope zones; L= low slope zones.

TABLA 1. Frecuencia de especies perennes que no florecen durante el período estudiado en relación con el número total de perennes. Ft= frecuencia absoluta de perennes; Fnf= frecuencia de perennes que no florecen; %nf= frecuencia relativa de perennes que no florecen; U= zona alta de ladera; L= zona baja de ladera.

ferent phenological organization from the corresponding grazed control plots. The differences appear to be in the same line as those found in the altitudinal rise and the geomorphological fall, coinciding with the increase in perennial species detected in the enclosures.

The phenology of Mediterranean pastures is thus influenced not only by abiotic factors of the climatic type (temperature, soil moisture, climatic fluctuations), but also by biotic factors such as cattle that can alter the competitive ability and the reproductive habit of the species. Other biotic factors such as pollinators probably have little influence in these predominantly anemophilic communities. All of these factors determine the organization of the phenological states in the vegetative cycle.

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APPENDIX I. List of species found in 80 plots

Agrostis castellana Boiss. et Reut.
Aira cariophyllea L.
A. praecox L.
Alopecurus pratensis L.
Alyssum minutum Schlecht.
Andryala integrifolia L.
Anthemis arvensis L.
Antoxanthum odoratum L.
Apera interrupta (L.) Beauv.
Aphanes microcarpa (Boiss. et Reuter) Rothm.
Arenaria leptoclados (Reich.) Guss.
Asteriscus aquaticus (L.) Less.
Bartsia trisago (L.) All.
Bellis perennis L.
Biserrula pelecinus L.
Brasica barrelieri (L.) Janka
Briza minor L.
Bromus hordeaceus L.
B. madritensis L.
B. maximus Desf.
B. tectorum L.
Capsella bursa-pastoris (L.) Med.
Cardus picnocephalus L.
C. tenuiflorus Curtis
Carex divisa Hudson
C. flacca Schreb.
Centaurea melitensis L.
Cerastium glomeratum Thuill.
C. gracile Dufour
C. semidecandrum L.
Chondrila juncea L.
Conopodium bourgaei Cosson
Convolvulus arvensis L.
Conyza bonaerensis (L.) Cronq
Crassula tillaea Lester-Garl.
Crepis capillaris (L.) Wallr.
C.taraxacifolia Thuill.
Crocus nevadensis Amo
Cruciata pedemontana (Bell.) Ehrend.
Cynodon dactylon (L.) Pers.

Dactylis glomerata L.
Dianthus lauricifolius Boiss. et Reuter.
Echium plantagineum L.
Elaeoselinum gummiferum (Desf.) Tutin
Erodium cicutarium (L.) L'Hér.
E. moschatum (L.) L'Hér.
Erophila verna (L.) Chevall.
Eryngium campestre L.
Evax carpetana Lange.
Festuca ampla Hackel
F. arundinacea Schreber
F. costei (St-Yves) Mark., Danne.
F. iberica (Haekel) K. Richter
F. rothmaleri (Litard) Mark., Dann.
Filago piramidata L.
Gallium murale (L.) All.
G. parisiense L.
G. verum L.
Gaudinia fragilis (L.) Beauv.
Geranium molle L.
G. rotundifolium L.
Hedypnois cretica (L.) Dum. Courset.
Helianthemum aegyptiacum (L.) Miller.
Heliotropium europaeum L.
Herniaria hirsuta L.
Hieracium pilosella L.
Holcus setosus Trin.
Holosteum umbellatum L.
Hordeum murinum L.
Hypochoeris glabra L.
Lactuca serriola L.
Lamium amplexicaule L.
Leontodon taraxacoides (Vill.) Merát.
L. tuberosus L.
Linum bienne Miller
Logfia minima (Sm.) Dumort.
Lolium perenne L.
Lophocloa cristata (L.) Hyl.
Lotus corniculatus L.
Luzula campestris (L.) DC.

Medicago minima (L.) Bartal
Melica ciliata L.
Merendera bulbocodium Ramond
Mibora minima (L.) Desv.
Moenchia erecta (L.) P. Gaert., Meyer et scherb.
Molineriella laevis (Brot.) Rouy
Montia fontana L.
Myosotis discolor Pers.
M. stricta Link ex Roemer et Schul.
Narcisus bulbocodium L.
Nardus stricta L.
Neatostema apulum (L.) I. M. John.
Ononis repens L.
Ornithogalum umbellatum L.
Ornithopus perpusillus L.
Parentucelia latifolia (L.) Caruel.
Petrorhagia nanteuillii (Burnat.) P. W. Ball. et Heyw.
Phleum pratense L.
Plantago afra L.
P. coronopus L.
P. lagopus L.
P. lanceolata L.
P. loeflingii L.
P. subulata L.
Poa annua L.
P. bulbosa L.
Polycarpon tetraphyllum (L.) L.
Ranunculus bulbosus L.
R. paludosus Desf.
Rumex angiocarpus Murb.
Sagina apetala Ard.
Sanguisorba minor Scop.
Saxifraga granulata L.
Scandix australis L.
Scleranthus annuus L.
Scolymus hispanicus L.

Sedum caespitosum (Cav.) DC.
Senecio jacobaea L.
S. vulgaris L.
Sisymbrium officinale (L.) Scop.
S. runcinatum Lag. ex DC.
Spergula arvensis L.
S. pentandra L.
Spergularia purpurea (Pers.) G. Don fil.
Stellaria media (L.) Vill.
Teesdalia coronopifolia (J. P. Berg.) Thell.
T. nudicaulis (L.) R. Br.
Tolpis barbata (L.) Gaertner.
Tribulus terrestris L.
Trifolium arvense L.
T. campestre Schreber
T. cherleri L.
T. dubium Sibth.
T. glomeratum L.
T. leucanthum Bieb.
T. micranthum Viv.
T. repens L.
T. resupinatum L.
T. retusum L.
T. squarrosum L.
T. striatum L.
T. strictum L.
T. subterraneum L.
T. suffocatum L.
T. tomentosum L.
Tuberaria guttata (L.) Fourr.
Urtica urens L.
Veronica arvensis L.
V. verna L.
Vicia lathyroides L.
V. sativa L.
Viola kitaibeliana Schultes
Vulpia spp.
V. unilateralis (L.) Stace

APPENDIX II.

From a matrix with c times (columns) and r states (rows):

$$\begin{array}{ccccc|c}
u_{11} & u_{12} & u_{13} & \cdots & u_{1c} & u_{1.} \\
u_{21} & u_{22} & u_{23} & \cdots & u_{2c} & u_{2.} \\
u_{31} & u_{32} & u_{33} & \cdots & u_{3c} & u_{3.} \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
u_{r1} & u_{r2} & u_{r3} & \cdots & u_{rc} & u_{r.} \\
\hline
u_{.1} & u_{.2} & u_{.3} & \cdots & u_{.c}
\end{array}$$

the following expressions are used with the Shannon-Wiener formula for the u_{ij} values ($i = 1, 2, 3, \ldots r; j = 1, 2, 3, \ldots c$):

$$\text{W0lH(P)} = -\sum_{i=1} p_{i.} \log_2 p_{i.} =$$

$$= -\sum_{i=1} \frac{u_{i.}}{\sum_i \sum_j u_{ij}} \log_2 \frac{u_{i.}}{\sum_i \sum_j u_{ij}}$$

which may be expressed as follows for computer calculation:

$$H(P) = -\sum_{i=1} \left(\sum_{j=1} p_{ij} \right) \log_2 \left(\sum_{\substack{\text{W0lj} \\ =1}} p_{ij} \right)$$

and equally,

$$H(T/P) = \sum_{i=1} \left[-\sum_{j=1} p_{ij} \log_2 p_{ij}/p_{i.} \right]$$

$$H(T) = -\sum_{j=1} \left(\sum_{i=1} p_{ij} \right) \log_2 \left(\sum_{i=1} p_{ij} \right)$$

$$H(P/T) = \sum_{j=1} \left[-\sum_{i=1} p_{ij} \log_2 p_{ij}/p_{.j} \right]$$

$$H(P.T) = -\sum_i \sum_j p_{ij} \log_2 p_{ij.}$$