Acta Bot. Barc., 45 (Homenatge a Oriol de Bolòs): 587–602 Barcelona 1998

AFTER SIGMATISM: WHAT WE LEARNED ABOUT SPATIOTEMPORAL CHANGES IN GRASSLAND COMMUNITIES AFTER 10 YEARS

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ABSTRACT

In this paper we summarize our findings on grassland communities after more than ten years of research on spatiotemporal patterns of vegetation, phenology, productivity and species richness. Grassland species from the Pyrenees and Cantabric mountains were organized in guilds, and coexistence was facilitated through vegetation stratification and temporal shifts in phenology between plant guilds. Graminoids were the most abundant group, developed earlier and grew taller than forbs. Most of the forbs were rare plants and acted as fugitives. Some of them were relatively abundant either in the seed rain or in the soil seed bank, although in general reproduction by seeds was scarce. Feedback processes and spatiotemporal changes of resources at different scales, including fertility and available space by gap opening, interacted to produce community structure in subalpine grasslands. At the landscape scale, fertility was the main factor structuring grassland communities, and although it varied gradually, two separated mesic and xeric community types resulted, as defined by plant species composition. Grazing was the main biotic disturbance and acted at several scales, increasing the space available for establishment and producing changes in composition. In montane grasslands there were changes in nitrogen fluxes in vole and mole mounds, resulting in an increase of ruderals, annuals and non-mycorrhizal plants, such as Caryophyllaceae. Only in subalpine ant hills, among the biotically formed mounds, was possible to find species not present in the surrounding pasture, such as *Festuca gautieri* and *Vicia pyrenaica*, usually found on unstable slopes. In conclusion, community organization is an extremely complex process, resulting from the action of different feedbacks and stochastic mechanisms operating at different spatial and temporal scales, and no simple mechanism explains the process.

Key words: Disturbance, Phenology, Plant diversity, Productivity, Vegetation structure.

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Introduction

If we are now aware of the richness of Catalan flora and the diversity of Catalan vegetation, it is in good part due to the studies of Oriol de Bolòs and his collaborators. The accurate catalogs of the plants from our territory (BOLÒS & VIGO, 1984), and the descriptive analysis of the communities through the Sigmatist method (BRAUN-BLANQUET & BOLÒS, 1957; BOLÒS, 1979; BOLÒS, 1987) have been extremely important to build a strong basis for environmental studies. The Sigmatist method describes plant communities, proposes an association nomenclature based on extensive community sampling methodology, and can be used in vegetation mapping.

But, beyond description, Prof. BOLÒS also sowed in his students the seed of curiosity on how plants live and communities function. In this paper we summarize our findings on grassland communities after more than ten years of research on spatiotemporal patterns of vegetation, phenology, productivity and species richness. The bulk of the data come from several studies we conducted on subalpine grasslands in the Eastern Pyrenees, and from montane grasslands there and in the Cantabric mountains: Vegetation surveys (mainly on limestones); productivity and phenological records on experimental plots; and laboratory experiments looking at plant responses to temperature, nutrients, and CO_2.

Plant species and guilds

The eight most abundant plants recorded in subalpine grasslands from Eastern Pyrenees were graminoids, six grasses and two *Carex* species (*C. caryophyllea* and *C. humilis*). The most abundant species was *Festuca nigrescens*, which occurred almost twice as frequently as *Nardus stricta*, the next most frequent plant (SEBASTIÀ, 1991a). *Agrostis vulgaris, Poa alpina, Koeleria macrantha, Avenula pratensis* were the other abundant grasses.

Most of the species were perennials (almost 99%), and mechanisms of vegetative propagation, mainly by tillers and rhizomes, were extremely common (70% of the species). Annuals increased their presence and abundance significantly in montane pastures (8% of the flora at Sant Jaume de Frontanyà, Eastern Pyrenees; 16% at the Urbasa-Andia ranges, Cantabric mountains).

We found two groups of morphologically and functionally differentiated plant guilds: graminoids and forbs (broadleaf herbs), as found in many grassland ecosystems (*see* BAZZAZ & PARRISH, 1982). Graminoids comprised only around 20% of the total recorded species, but made up more than half of the cover and up to 2/3 of the total biomass (SEBASTIÀ & CANALS, 1992). Forbs were highly diversified, but most occurred rarely (SEBASTIÀ, 1991a).

Graminoids were often tall, caespitous and erect plants; they were wind-pollinated, and their propagules wind-dispersed. Forbs were usually insect-pollinated, and two subgroups were found. Plants from the first subgroup were short, prostrate or ascendent, and frequently rhizomatous. These species had flowers with complex showy corollas, brightly colored, in glomerules or vertical inflorescences; propagules were often water-dispersed. Species from the second subgroup (39% of the forbs) were relatively tall and erect, occasionally stoloniferous, with small flowers of pale colors, solitary or in horizontal inflorescences. Propagules had short-distance dispersal (SEBASTIÀ, 1991b).

Our hypothesis is that species coexistence is favored by spatial and temporal segregation of both guilds. The pasture is formed by a bulk of long-living graminoids that develop early and, because they are relatively tall and erect, with vertically disposed leaves, constitute an open canopy with relatively low light extinction coefficient (MONSI *et al.*, 1973; FLIERVOET & WERGER, 1984). This arrangement allows light to arrive to the plants present in lower layers of the canopy, many of which are forbs that develop late. This hypothesis has been partly confirmed by our results on biomass partitioning between guilds through time, and biomass stratification (SEBASTIÀ & CANALS, 1992).

Vegetation structure and structuring factors acting at different scales

Structural patterns of vegetation are an expression of the processes associated with plant community assemblage, and determine the matrix upon which ecological interactions between plants and animals take place. The search for patterns has to be considered in a spatiotemporal context, and at an appropriate scale of observation (LEVIN, 1992), because constraints and controlling factors are usually scale-dependent (ALLEN & HOEKSTRA, 1992).

At the landscape scale, the main factor structuring vegetation in subalpine grasslands on limestones at the Pyrenees was fertility (moisture and soil nutrient content; Fig. 1). We found this result consistently for other lithologies (CANALS *et al.*, 1995), altitudes (SEBASTIÀ, 1991c; CANALS *et al.*, 1994), and geographic areas (CANALS & SEBASTIÀ, 1996). We observed a relationship between physiography and community distribution as well, although the effect is probably mediated mainly through soil properties (SEBASTIÀ, 1991a).

In subalpine grasslands, there was a continuous variation in soil fertility, from shallow, carbonated, nutrient-poor rocky soils developed on raised sites to deep, decarbonated, nutrient-rich acid soils developed in depressions or on relatively level positions. Although the environmental properties varied gradually, the patterns of vegetation changed sharply. Recently, WILSON & NISBET (1997) have studied the possibilities of this paradox under the existence of positive interspecific recruitmemt. Two very clear-cut mesic and xeric community groups resulted, as defined by plant species abundance (Fig. 1). Two communities were recognized within each group. Within the mesic group *Nardus stricta* communities replaced *Festuca nigrescens* ones, when grazed by more selective livestock such as sheep. Within the xeric group *Festuca gautieri* communities replaced *Carex humilis* ones, when geomorphological processes such as solifluxion resulted in unstable substrates on rocky soils (MONTSERRAT & VILLAR, 1975; SEBASTIÀ, 1991a).

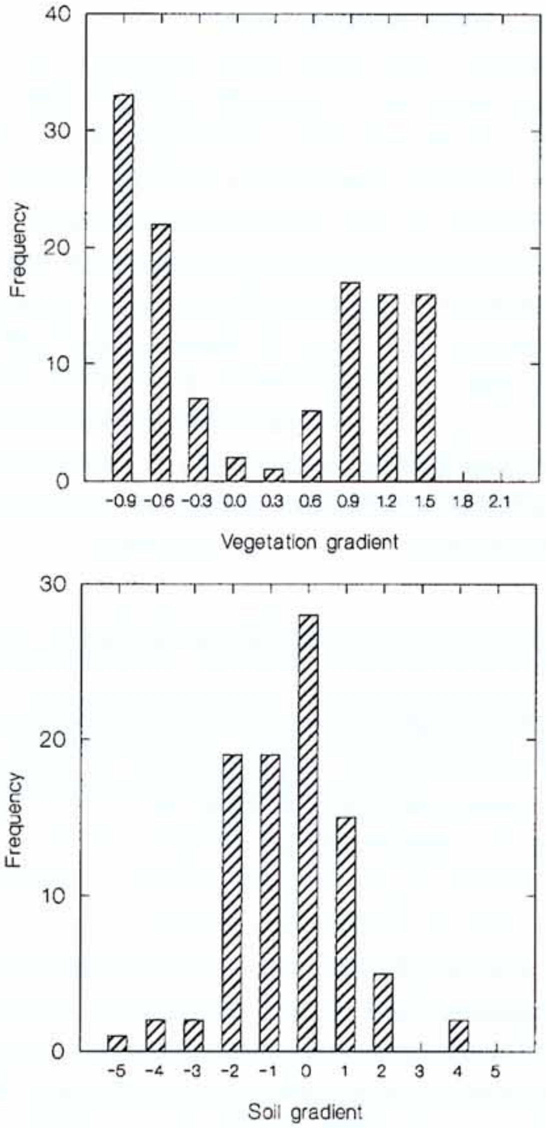


Figure 1. Comparison of sample frequency distribution along a fertility gradient defined by vegetation composition (above; frequency distribution of the coordinates on the first axis of a Reciprocal Averaging Analysis on plant species frequencies), and by environmental conditions (below; frequency distribution of the coordinates of the samples on the first axis of a Principal Component Analysis on soil parameters).

Nardus stricta communities (mainly on depressions and draining hollows) and *Festuca gautieri* communities (on steep unstable slopes) were found on a narrow range of environmental conditions, with no overlap, at opposite ends of the fertility gradient. In experiments conducted in controlled environments in a glasshouse at Harvard University, *Festuca gautieri* showed a threefold increase in biomass under high nutrient regimes (SEBASTIÀ & BAZZAZ, *in press*), indicating that this species responds positively to fertile conditions. In the field, we found *F. gautieri* in fertile sites only at the top of active, periodically disturbed ant hills. This result supports other studies showing that differences among species in competitive ability and niche breadth may play a role in their actual distributions (BAZZAZ, 1987; TURKINGTON & MEHRHOFF, 1990; TILMAN, 1994).

Festuca nigrescens communities had the ability to develop on a wide range of conditions and created a stable community type until a critical point on the mesic to xeric transition was reached, beyond which there was a dramatic change in plant composition (suggesting the existence of a breakpoint *sensu* MAY, 1977; SOLÉ & MANRUBIA, 1996; Fig. 2). Further analysis of our data is needed to find out whether the ability of the *Festuca nigrescens* community to develop under a broad range of environmental conditions is related to switches in the dominance of plants, or to minor changes in the relative abundance among its component species. Preliminary results suggest that *Festuca nigrescens* itself is always dominant in this community, and there is a consistent set of coocurring abundant species, although slight temporal segregation among them was observed. Further experiments are needed to determine the relationship between high species richness and the resilience of this community.

A different scenario appears when analyzing the *Carex humilis* community. Several species were relatively common, none of which was more abundant than the others at the community scale, but very often they constituted extensive monospecific patches at given locations. The lottery model may explain the dynamics of the dominant species in a particular patch (CHESSON & CASE, 1986). This model proposes a mechanism whereby a species becomes dominant by simply establishing before other possible species. The *Carex humilis* community is found on rocky places, where free soil is scarce and patchily distributed. Each patch of available space for plant establishment is isolated and may follow independent trajectories of species composition from the neighboring patches. Chance dispersal events seem to determine which plant species establishes first at a particular patch. Once established, their horizontal growth habit allows them to dominate the patch for a long time, difficulting the establishment of other species.

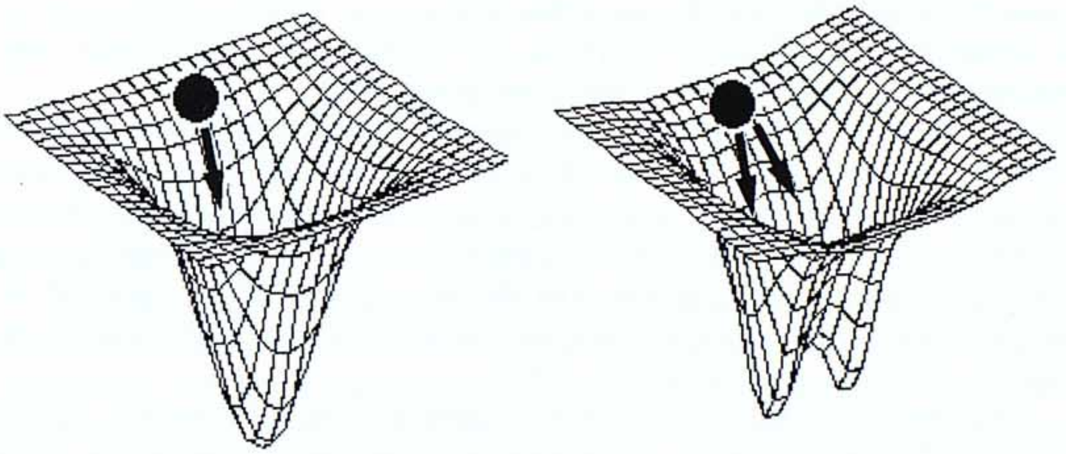


Figure 2. The environmental space can be expressed as a surface with the site behaving as a ball rolling towards more stable areas. Sometimes, a slight modification on the value of a controlling parameter (i.e. intensity of grazing) may give raise to the so-called "symmetry breaking", creating two or more local stable areas represented by different community types (modified from SOLÉ, 1995).

We have seen how changes in the initial conditions of a single factor, such as nutrient availability, in otherwise homogeneous environments can have a strong effect on the community structure (SEBASTIÀ, RAMSEIER & BAZZAZ, unpub.), and small initial differences in environmental parameters result in widely divergent trajectories in vegetation (HARTGERINK & BAZZAZ, 1984; CRAWLEY & MAY, 1987; INOUYE & TILMAN, 1995). We suggest that different sets of positive feedbacks would explain the formation and maintenance of the mesic and xeric vegetation types. These will be held in these states because of deep divergences in the multivariable environmental space (Fig. 2), unless an external force strong enough to disrupt these feedback connections operates (ROBERTS, 1987).

At the community scale, once the vegetation is established, the opening of available spaces for regeneration through time is the most important factor in the organization of the grassland. Gap opening through time has been said to be a random spatial process, generated by lottery mechanisms (CHESSON & CASE, 1986; CRAWLEY, 1986). Gaps play an important role in rare species dynamics for the whole grassland ecosystem, as it has been suggested for other calcareous grasslands (GRUBB, 1986), and for *Poa bulbosa* communities in grasslands from drier regions (MALO & LEVASSOR, 1996). The new free space behaves as a randomly available resource for perennial transient plants to compete in the regeneration process, and allows a great number of species to coexist, by increasing the environmental heterogeneity (TILMAN, 1982; TILMAN & PACALA, 1993, CANALS & SEBASTIÀ, 1996; GARCÍA-PÉREZ & SEBASTIÀ, 1996). In grasslands, many openings appear by grazing and other biotic disturbances.

Consequently, our results on plant community structure support the hypothesis that resource availability and disturbance are the two main factors determining the structure and the dynamics of grassland communities (HOBBS & MOONEY, 1991; ARNTHÓRSDÓTTIR, 1994). The nature of the disturbance, size, intensity, frequency, etc., together with the physiography of the disturbed site and the characteristics of the surrounding vegetation determine the nature of the response (BAZZAZ, 1983; COLLINS, 1987).

Disturbances increase the spatial heterogeneity of the rangelands at different scales. At the landscape scale, in the subalpine grasslands the recovering of the vegetation depended on physiography, as we found in a big area that was plowed 30 years ago to create terraces for a failed pine plantation. On steep slopes, with skeletal soils, only species tolerating substrate mobility (such as *Festuca gautieri*) established, while on level deep soils nearby pasture species rapidly revegetated the area; the poorly revegetated furrows were a reserve of rare species (BAÑERES & SEBASTIÀ, 1992).

At the same landscape scale, grazing was the main biotic component influencing grassland community structure (CANALS & SEBASTIÀ, 1992a). As a consequence of differences in grazing pressure (sometimes due to causes as arbitrary as water source location; SEBASTIÀ *et al., in press*), patches of heavily and lightly grazed vegetation coexisted, with substantial changes in species composition (COLLINS & GLENN, 1988). These changes can give rise to specific communities, such as eutrophic pastures of *Chenopodium bonus-henricus* (in overgrazed rest areas; CANALS & SEBASTIÀ, 1992a), and unpalatable swards of *Nardus stricta* (in areas intensely grazed by selective livestock, like sheep; SEBASTIÀ, 1991a).

At the community scale, small gaps originate through periodic, localized disturbances, such as grazing or vole mounds, or by random death of individual plants (BAZZAZ & PARRISH, 1982; TILMAN & PACALA, 1993; BAZZAZ & WAYNE, 1994; CANALS & SEBASTIÀ, 1996). Grazing is an important factor in gap formation (by removal of plants, excrement deposition, crushing by hoofs). The gaps opened by grazing within the community provide the opportunity for rare plants to colonize the newly available space, as discussed previously. Consequently, grazing produces heterogeneity at different scales, and the result is an increase of complexity and species richness at the community level, favoring rare species and increased patchiness within the community. Half of the species recorded in subalpine grasslands in the Pyrenees were found in less than 4% of the samples, and many of this rare species were forbs that acted as transient plants.

Both grazing and the formation of mounds by animals cause changes in the environment in addition to the creation of open space and increased light. Ruminants are vectors of fertility distribution through their excrements (MCNAUGHTON, 1979); and, in the montane grasslands of the Cantabric mountains, we found that revegetation of mole (*Talpa europaea*) hills seemed to be related to changes in nutrient fluxes and in the species competitive relationships (CANALS, 1997), as other authors have suggested (REICHMAN & JARVIS, 1989; DENSLOW, 1985). As a consequence of increased inorganic nitrogen availability, ruderals, annuals and non-mycorrhizal plants such as Caryophyllaceae species were favored at the first stages of establishment on mole hills (CANALS, 1997).

Specialized colonizers of mole hills were not found. The difference found in community vegetation between mole hills and surrounding grasslands was mainly quantitative, with some plants increasing their frequency at the hills, and some plants common in the pasture becoming rare or disappearing. In subalpine grasslands, the neighboring vegetation was also the main source for vole (*Microtus* sp.pl.) mound revegetation. Forbs such as *Achillea millefolium* and *Euphorbia cyparissias* were particularly common on the mounds. By contrast, in the same grasslands, the highest parts of functioning ant-hills supported species not found in the surrounding community. For instance, the xeric species *Festuca gautieri* and *Vicia pyrenaica*, commonly found in unstable slopes, grew on *Formica pressilabris* mounds in mesic grasslands. The bottom of the hills were recolonized vegetatively by nearby species, mainly by tillering and branching.

Patterns of diversity and abundance in a space-time perspective

So, what is the key for maintaining diversity in grasslands? Niche overlap (GRUBB, 1977)? Physical space as a soil resource (MCCONNAUGHAY & BAZZAZ, 1991)? Environmental fluctuations affecting competitive ability during regeneration (CHESSON & CASE, 1986)? Phenological asynchrony to avoid competition for pollinators (PARRISH & BAZZAZ, 1979; FAGERSTRÖM

& ÅGREN, 1980)? The answer seems to lie in a combination of explanations, a controlling parameter focusing on several factors simultaneously (ALLEN & HOEKSTRA, 1992).

Ongoing arguments on the influence of factors such as fertility (TILMAN, 1982; GRIME, 1985), physiography (SEBASTIÀ, 1991a), climate, historical use (forestry and grazing) and present livestock management (SEBASTIÀ *et al., in press*) have not solved the problem of the maintenance of species richness in these communities. Our field surveys in the Catalan Pyrenees and Cantabric mountains showed that species richness is not directly proportional to variation in soil fertility, and both extremes of the fertility gradient result in a reduction of species richness (SEBASTIÀ, 1991a; CANALS & SEBASTIÀ, 1996). Some studies find bell-shaped curves for species richness across a single factor gradient, due to the decrease of heterogeneity found at the highest and the lowest values of the factor (*see* TILMAN & PACALA, 1993; ROSENZWEIG & ABRAMSKY, 1993). In our case, we suggest a combination of several superimposed factors (Fig. 3; SEBASTIÀ, 1991a). Overall, low fertility sites had low species diversity; but we recorded both the highest and the lowest diversity rates at high to moderate fertility levels, depending on differences in disturbance by grazing. The invasion of *Nardus stricta* in selectively grazed pastures reduced plant species richness, as well as spatial heterogeneity, but a moderate exploitation by non selective grazers increased species richness, and probably spatial heterogeneity at small scales, at equivalent fertility values (up to 60 species per 10 m^2 recorded at some *Festuca nigrescens* plots). A further increase in disturbance as a consequence of high grazing pressure in pastures coincides with a high input of fertility through livestock manure; overall the result is a further decrease in species diversity (Fig. 4). Thus, a multidimensional approach seems to be needed for the understanding of the dynamics of these multispecies assemblages.

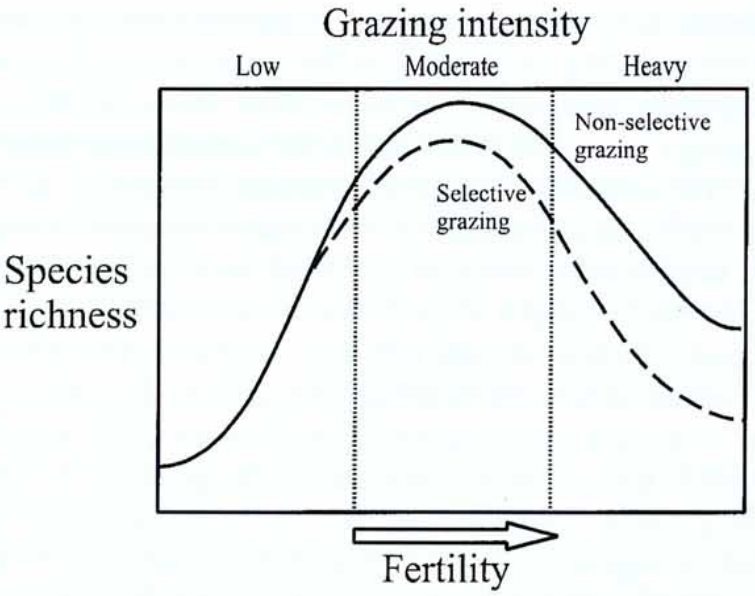
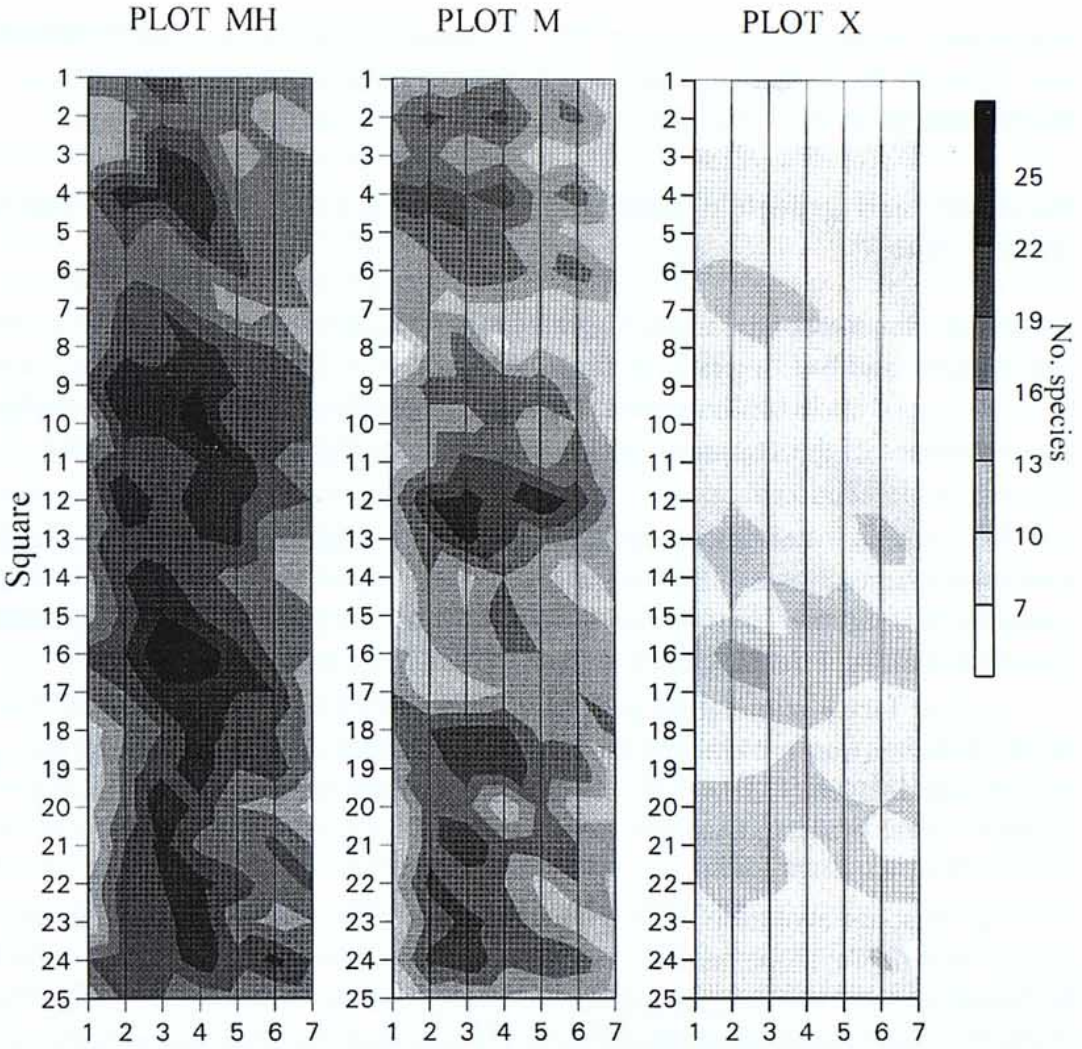


Figure 3. Relationship between plant species richness and soil fertility at different disturbance regimes by grazing.



Sampling date

Figure 4. Spatiotemporal variation of species richness through the growing season represented in a 3D contour plot, for three transects made up of 25 subplots of 10 × 20 cm, and arranged along a toposequence on subalpine grasslands at Eastern Pyrenees. Plot, MH: mesohygrophytic; M: mesic; X: xeric. Sampling dates, 1: 21 June; 2: 10 July; 3: 29 July; 4: 17 August; 5: 5 September; 6: 20 September; 7: 11 October.

Another component of diversity, besides species richness, is specific abundance. In a rank-abundance plot (MACARTHUR, 1984) made on different subalpine grasslands, dominance increased from mesic (broken-stick model for species abundances distribution) to xeric communities (log-normal model; *see* MAY, 1975; MAGURRAN, 1989; SEBASTIÀ, 1991a), except when considering *N. stricta* grasslands, that showed the strongest dominance.

We have addressed this problem recently to assess possible constraints in the spatiotemporal dynamics of subalpine grasslands (GARCÍA-PÉREZ & SEBASTIÀ, 1996). We measured the temporal dynamics (as an expression of processes of colonization, development and mortality) and spatial variability (space-sharing) of species richness in three plots located along a topographic gradient. We found a high temporal variation in the number of species through the growing season in mesic plots. This may be a way to partition resources requirements through time in a densely occupied environment (Fig. 4). Spatial variability in species richness was higher in the xeric plot, and could be related to the high spatial patchiness in the distribution of available soil in xeric communities (SEBASTIÀ, 1991a).

Phenology and growth dynamics: coping with environmental harshness through time

Harsh climatic conditions at high elevations, such as long-lasting snow cover, cold weather and freezing risk, favor the dominance of long-lived perennials with mechanisms of lateral colonization. These factors and the secular grazing explain the dominance of the vegetative phase in these areas (VIGO, 1976; BAÑERES & SEBASTIÀ, 1992).

Total biomass and its accumulation during the growing season depended mainly on macroclimate (SEBASTIÀ, 1992). Year to year variations in snow melt, temperatures, summer rainfall and episodic hail storms greatly affected grassland growth dynamics. Phenological patterns also reflected these variations.

Another factor stimulating grassland productivity was grazing. When livestock pressure was prevented, necromass accumulated. The following spring growth was delayed (CANALS & SEBASTIÀ, 1992b), decreasing the global productivity of the grassland, as shown in other studies (SALA *et al.*, 1986; ALONSO *et al.*, 1994).

The seasonal evolution of the vegetation has been related to physiographic factors (soil depth, slope, aspect, rockiness, etc.) and evapotranspiration, at both the landscape and the community scales (BAÑERES & SEBASTIÀ, 1992). The productive and phenological responses to climate varied among communities according to their ability to cope with climatic fluctuations. In general, in convexities with shallow rocky soil, soil water reserves may decrease rapidly in summer, and physiological drought is a risk many years. In concavities with deep fertile soil, this restriction may exist only in severely dry years. Consequently, we found important spatial variations on productivity and seasonal growth dynamics. Mesic pastures were more productive and less affected by the climate of the year than xeric communities. In xeric communities, biomass showed a clear bimodal distribution many years, with a decrease at the peak of the summer, reflecting Mediterranean influences in both montane and subalpine grasslands (SEBASTIÀ, 1992).

Slope, hydric status and aspect determined duration, intensity and beginning of flowering, producing earlier and more explosive patterns in xeric, steep and South-exposed plots (SEBASTIÀ & CANALS, 1992; BAÑERES & SEBASTIÀ, 1992), where the plants usually have higher reproductive costs (SCHEMSKE *et al.*, 1978; VENABLE, 1984). Fruiting seemed to be less driven by the environmental factors, while senescence was controlled mainly by ontogenetic causes.

Seedling establishment was anecdotal, due to the dominance of asexual colonization (BAÑERES & SEBASTIÀ, 1992). The grasslands showed stochastic fluctuations in pulses of seedling dynamics, which may be related to local disturbances (SEBASTIÀ, 1991a; CANALS & SEBASTIÀ, 1996).

Seed biology

Our studies on soil seed bank, seed rain, seed set, and seed germination indicated that sexual reproduction is, in subalpine grasslands, a risky event for most of the species most of the years. Gramineae, the most abundant family in the extant vegetation, had the highest number of seeds in the seed rain (50 to 70%, depending on the year and the plot); three of the most frequent grasses –*Koeleria macrantha, Poa alpina* and *Festuca nigrescens*– made up almost 3/4 of the seed rain from mesic grasslands in 1992. Other families, such as Compositae (20-40%), and growth forms, such as therophytes, were over-represented.

Some rare species showed a strong contagious distribution from the source, such as *Linum catharticum*. This plant constituted the main component of the seed rain in 1990, although it was present only in a few samples, indicating a possible explanatory mechanism for persistence in the pasture. However, in 1992 another annual, *Euphrasia minima*, was an important element in the same grasslands, suggesting among-year variability. This species was also very abundant in the soil seed bank, while Gramineae and Compositae decreased.

Seed density in both the seed rain and the soil bank was low, as stated in similar studies (MCGRAW & VAVREK, 1989). The bank was less diverse than the rain, and there were substantial qualitative and quantitative differences between them. Rosaceae were the main representatives in the soil bank, particularly *Potentilla neumanniana*, suggesting perpetuating mechanisms in non-dominant forbs. Some annual, eutrophic plants from lower altitudes, such as *Stellaria media*, were also extremely abundant, probably transported by cattle, and absent from the vegetation (*see* REINÉ & CHOCARRO, 1994; RICE, 1989). The importance of vernalization in germination experiments with seeds from plants and from the soil bank showed that there are security mechanisms to avoid germination at the wrong time and the wrong place (SEBASTIÀ *et al.*, 1994).

And the future?

It is difficult to predict the effects of global change on plant communities, particularly scaling from experiments made on ecophysiological responses of individually grown plants. However, the results from such experiments, such as the ones we carried on at the glasshouse at Harvard University under atmospheres with varied CO_2 concentrations, should help us understand possible future scenarios. From a study on six species, three regularly found on fertile (*Trifolium repens, Dianthus hyssopifolius, Nardus stricta*) and three on unfertile subalpine grasslands (*Festuca gautieri, Sideritis hyssopifolia, Globularia cordifolia*), we concluded that the response to a double-ambient CO_2 atmosphere is species-dependent, unconstrained by the species original habitat, and variable within and across environments (SEBASTIÀ & BAZZAZ, *in press*). Also, the response of a plant to a particular resource does not predict its response to another resource. *Festuca gautieri*, from resource-poor grasslands, almost tripled its biomass under high nutrients regime, but showed low response to elevated CO_2. *Globularia cordifolia*, from similar environments, doubled its biomass with doubling CO_2, but did not respond to the nutrient regime. A third species from the same habitats, *Sideritis hyssopifolia*, responded highly to both treatments. This individual behavior probably will imply significant shifts in the structuring and dynamics of future grassland communities, as past changes in climate and grassland management did for the present.

Final remarks

Community organization is an extremely complex process, resulting from the action of different feedbacks and stochastic mechanisms operating at different spatial and temporal scales, and no trivial answer responds the most basic questions.

Nevertheless, a significant amount of evidence was found which helped us to understand better how these complex systems operate. At a large scale, fertility and grazing intensity seem to be the main factors structuring the landscape, and giving raise to different communities. At a smaller scale, gap opening by disturbances affecting spatial and temporal arrangement of species, such as grazing or biotically formed mounds, combined with a limiting similarity of life history traits among different species and guilds (such as resource needs for colonization and establishment, and dispersal ability) could play a crucial role in the dynamics of plant metapopulations in grasslands.

Further explorations in grassland dynamics will raise new ways to address and answer questions on community dynamics and spatiotemporal scales. New insights, maybe through a link with the science of complexity, could bring us closer to the understanding of structuring patterns and community function.

Acknowledgements

We thank F.A. Bazzaz, G. Berntson and R. Stromberg for useful comments on the manuscript. Mentxu Arandia, Tete Bañeres, Montse Casals, Ester Castelló, Sonia Guri, Pep Pintó and Laura Puig were involved in this project in different ways. To the Cadí-Moixeró Natural Park (Generalitat de Catalunya), Institut d'Estudis Ilerdencs, CIRIT (Generalitat de Catalunya), Caixa de Barcelona, Servei d'Agricultura i Ramaderia (Diputació de Barcelona), Depto. Agricultura y Pesca (Gobierno Vasco), and Univ. Politècnica de Catalunya (PRE8924 project), for several grants and material support along these years. The Univ. Pública de Navarra rewarded several Ph.D. fellowships to RMC. The Dept. Biologia Vegetal from the Univ. Barcelona contributed with advice and some instrumentation. A grant for a visit to the Centre Louis Emberger-CNRS (CIRIT), and a postdoctoral fellowship at Prof. Bazzaz' Laboratory at Harvard University (FPU, Ministerio de Educación y Ciencia) to one of us (MTS) helped to develop many of our arguments.

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Rebut / Received: XI-1996