

Floristic fluctuations in annual pastures: the role of competition at the regeneration stage

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Abstract. Many studies have shown the existence of large between-year fluctuations in the floristic composition of annual Mediterranean pastures, and these fluctuations have been linked to autumn rainfall patterns. It has been postulated that differing interannual weather patterns may play a decisive role in competitive processes, especially during the period of germination and seedling establishment. Removal experiments in conjunction with rainfall manipulation in a phytotron were conducted to test whether competition affects germination and seedling mortality under different autumn rainfall patterns, in pastures at three successional stages after last being ploughed.

Early and late autumn rains affect the floristic composition as certain species germinate better under certain conditions than others in each successional stage. In general, however, competition is not manifested through the inhibition of new germination once the space has been occupied, and density-dependent mortality is found only for a few species.

Keywords: Autumn rain; Germination; Phytotron; Seedling mortality.

Nomenclature: Tutin et al. (1964-1980).

Introduction

Mediterranean-type annual pastures are characterized by large fluctuations in floristic composition which overlap the successional processes and obscure any directionality (Austin et al. 1981; Peco 1989). Many studies have highlighted the relationships between characteristics of such pastures – floristic composition, structure, biomass – and meteorological parameters such as temperature and rainfall pattern (e.g. Talbot et al. 1939; Heady 1958; Ratliff & Heady 1962; Murphy 1970; Pitt & Heady 1978; Peco et al. 1983; Pineda et al. 1987; Peco 1989). Espigares & Peco (1993) found that two simulated patterns of autumn rainfall (early and late) influenced the germination of the 75 most abundant species in a Mediterranean pasture. Furthermore, late arrival of the autumn rains produced a differential delay in the species germination which provided advantages for species in occupying space.

We know that the relative competitive ability of species can be changed by variations in environmental factors. Rice (1989) postulated that fluctuations may play an important role in the competitive processes in meteorologically unpredictable environments such as Mediterranean areas. Rice & Menke (1985) found that two species of *Erodium* only coexisted in equilibrium when there was a drought at the time of flowering; if the drought occurred in the autumn, there was a reversal that gave competitive advantages to one of the two species.

Traditionally, studies of competition in plants have analysed the performance of one or a few species at different densities in the presence or absence of individuals of other species, or under natural conditions by means of species removal or addition (reviews in Schoener 1983; Keddy 1989; Aarssen & Epp 1990 and Goldberg & Barton 1992). Only a few studies on competition, however, have tackled the interaction between many species (Austin & Austin 1980; Austin 1982; Austin et al. 1985; Fowler 1981, 1982, 1986). Here, we use controlled (phytotron) conditions to investigate competition during the regeneration stage of a pasture, considering all species in the community. Despite the usual caveats about extrapolating results from greenhouse to field conditions, this is a good way to test the effects of single factors.

We tested two hypotheses on the mechanisms of competition during regeneration: (1) competition acts in the pre-germinative stage through induced dormancy in seeds available in the soil; or (2) it operates in the post-germinative stage, producing differential mortality of seedlings. The first hypothesis is supported by experiments showing enforced dormancy of seedlings due to inhibiting effects of light filtered through the leaves of other plants that have already germinated (Gorski et al. 1977; Silvertown 1980). Also, CO₂ produced by root respiration may reduce germination in the field (Mack & Harper 1977; Inouye 1980). As to the second hypothesis, Bartolome (1979) and Rice (1989) noted (but did not demonstrate) the possible importance of seedling mortality induced by competition at the seedling stage.

Either competition mechanism may lead to changes in the floristic composition and abundance relations in these pastures.

Specifically, our study deals with (a) competition at the time of regeneration of annual pastures with different successional stages since last ploughing, and (b) the influence of variations in the arrival time of autumn rains on these processes. There are also indications of a radius of interference that restricts competitive processes to the surrounding individuals (Mead 1966; Mack & Harper 1977; Goldberg 1987; Bonan 1991); also, the competitive ability of a species appears to be related to its biomass (Gaudet & Keddy 1988). Hence, a third aim of our study was to analyse the role of spatial distribution and death of seedlings during competition.

Material and Methods

The study area was in a 'dehesa' (open woodland) of *Quercus rotundifolia* on the granitic piedmont of the Sierra de Guadarrama (central Spain) near Madrid. Repeated ploughing is used to prevent the invasion of scrub and it permits the development of annual species-rich pastures. In August 1990, soil samples were collected from three slopes of different 'age' - time since last ploughing (2, 15 and 34 yr), representing the early, intermediate and late stages respectively. The slopes had the same type of substrate, exposition and angle. Four 10 cm × 10 cm × 6 cm soil cores were collected on each slope (two on the upper part and two on the lower part in order to cover the maximum amount of local variability). The four soil cores from the same slope were mixed and homogenized to avoid variation generated by spatial heterogeneity, and were subdivided in turn into 16 subsamples of soil. Each subsample was placed in the upper part of 10 cm deep and 80 cm² round pots on a 5-cm deep layer of vermiculate, separated by a fine layer of gauze. The 16 pots with soil from each slope with different successional ages were divided into two lots and subjected to two meteorological conditions: early and late autumn rains (Peco 1989). The first treatment started in September 1990 and the second in November 1990. In half of the replicates of each lot, we reduced competition by seedling removal (Fowler 1981), with a total of four replicates for each treatment.

The rainfall treatments included a constant supply of water at temperatures similar to average September or November day and night temperatures recorded over a 10-yr period in the area. The first treatment included abundant watering and a 20/15 °C day/night temperature regime, the second treatment included the same water supply at 10/5 °C day/night. Thus, in both treatments the difference between day and night tempera-

tures was kept the same to avoid potential favouring of germination, as many studies have revealed that exposure to fluctuating temperatures facilitates the rupture of seed dormancy (Thompson & Grime 1983; Khan & Akhtar 1989).

Plastic mesh divided into 1-cm² squares was placed on top of each pot. This system permitted the monitoring of all seedlings that germinated and the collation of information on their spatial distribution. The experiment lasted two months for each treatment, during which time each germination and death was noted every two days over the first three weeks, and weekly thereafter. Seedling removal was also performed at the same intervals.

For each successional stage, we used two-factor Anova to analyse differences between the treatments for total germination (g) and species germination (g_i). Semi-hybrid Multidimensional Scaling (SSH) (Belbin 1991) was also performed on the data of species germination in the replicates, to analyse global changes in the communities. Two-way Anova performed on the scores in the SSH spaces permitted differences between treatments (rainfall and removal) to be tested.

In subsamples with no seedling removal of each successional stage, scatter diagrams were plotted to explore non-linear responses. Afterwards, Pearson correlation coefficients were calculated between total (m) or species (m_i) mortality and total density (d), and also weighted density according to species size (d_s). Total density was the sum of species densities (d_i) while weighted density was the sum of species densities multiplied by weighted factors (0.5, 1 and 1.5), attributed to each species according to its allocation to a size class group (small, intermediate and large seedlings respectively). The above-mentioned population parameters were calculated in each pot on three scales: pot, 9 cm² and 1 cm², in order to analyse the role of seedling spatial distribution, and given that the association of variables can be influenced by the measurement scale. Individuals that germinated in the outermost squares were excluded from the analysis in order to avoid edge effects (Haefner et al. 1991).

The PATN package (Belbin 1987) was used to perform all multivariate analyses. Other statistical analyses (Anova and Pearson correlation coefficients) were performed with the BMDP package (Anon. 1985).

Results

Germination

In the set of 48 pots, 6216 seedlings emerged, of which 3078 corresponded to treatments without seedling removal. The total numbers of species found were

37, 34 and 50 in the early, intermediate and late stages, respectively. Species density per pot was significantly higher in the late stages (Confidence Level Test, $p < 0.05$), being the means 18.3, 19.2 and 27.8 in the early, intermediate and late stages respectively. The mean number of germinations found in each successional stage differed significantly (Confidence Level Test, $p < 0.05$) for the three stages. It reached its maximum in the mature stages (190.7 ± 31.1) and a minimum in the intermediate ones (89.5 ± 21.3).

The germination pattern over time is abrupt in the case of early autumn rains and more diffuse when the autumn rains arrive late (Fig. 1). In both cases germination is fast, as 90% occurs prior to day 10 in the former case and day 15 in the latter due to the delay caused by the low temperatures. No significant differences were found in the temporal patterns of germination between the two removal treatments. Neither autumn rainfall patterns nor seedling removal produced significant differences in total germination except the former at the early successional stage (Two-way Anova, $p < 0.000$) in which the number of germinations was greater when early autumn rains were simulated.

According to the multivariate (SSH) analysis of the number of germinations of each species per pot for each of the three successional stages, the samples subjected to early and late autumn rain treatments could be differentiated in the multivariate spaces (Fig. 2). However, the seedling removal treatment did not appear to have a systematic effect on the species germination in any of the cases. Using the values of the coordinates of each pot for each of the three SSH axes, significant differences (Two-way Anova, $p < 0.008$) were found for the effect of the timing of the autumn rains in the three successional stages, while they did not do so for the removal effect.

Comparing the germination of each species under rainfall and removal treatments (Two-way Anova) in the three successional stages, there were many species with germination that were favoured significantly by the timing of autumn rains while only some species had significant germination differences between removal treatments (Table 1).

Seedling mortality

Total mortality differed significantly (Mann-Whitney U-test, $p < 0.01$) between the autumn rain treatments, with the lower level in the simulated late rain treatment, with a mean of 7.1% for early autumn rains and 2.9% for late autumn rains. Furthermore, the longevity of the seedlings that died in the September rain pots was shorter than that of those in the November rain pots (Mann-Whitney U-test, $p = 0$). In the former case, the

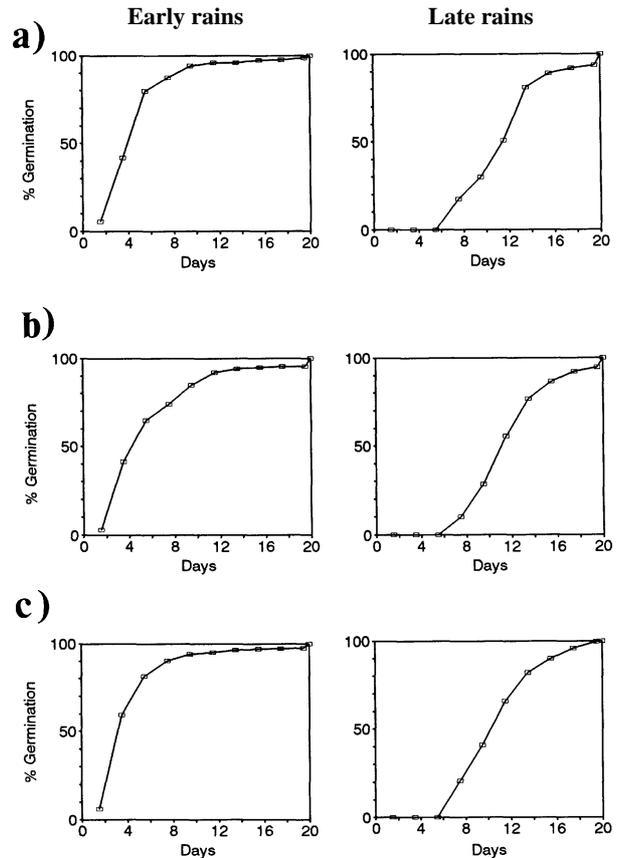


Fig. 1. Accumulative percentage of germination in pots without seedling removal of each successional stage. **a.** Early stages; **b.** Intermediate stages; **c.** Late stages.

mean longevity was 2 weeks, in the latter, it was 7 weeks.

The number of emerged seedlings per cm^2 for the set of all pots ranged between 1.0 and 10.0, 0.2 and 4.3, and 1.8 and 4.8 for the 1- cm^2 , 9- cm^2 and pot scales, respectively. For this range of densities, no significant correlations were found between total mortality (m) and density (d) or weighted density (d_s), except on the pioneer slope with early autumn rains (9- cm^2 scale: d/m , $p = 0.04$; d_s/m , $p = 0.01$) and the mature slope with late autumn rains (pot scale: d_s/m , $p < 0.02$).

Few species (17% of all 60 species germinated in the experiment) revealed significant correlations between their mortality (m_i) and density (d) or weighted density (d_s) (Table 2). In some cases, mortality increased with density (67%; positive correlations), while in others (33%), density appeared to favour the survival of seedlings (negative correlation). 83% of the detected cases of density-dependent mortality occurred under early autumn rain conditions. The majority of these cases corresponded to the early and late successional stages. Curvilinear or threshold responses were discarded on the basis of visual analysis of the scatter plots.

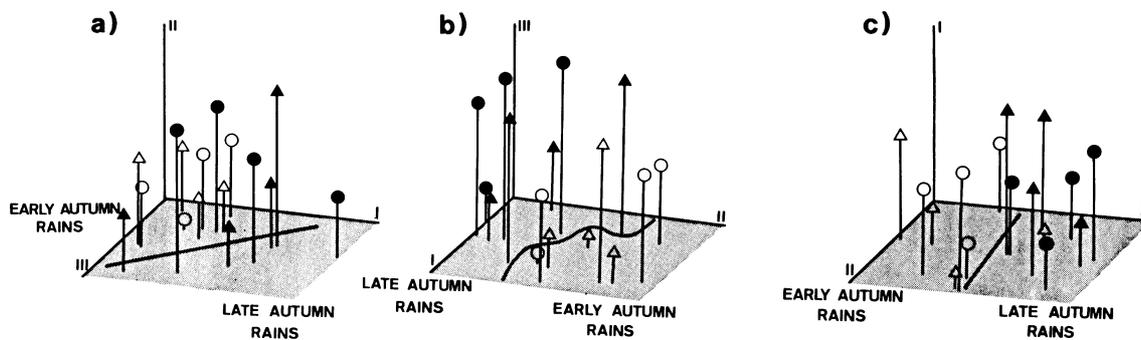


Fig. 2. Position of pots of each successional stage in ordination space. **a.** Early stages. **b.** Intermediate stages. **c.** Late stages. Black: pots with late autumn rains; white: with early autumn rains; circles: pots with seedling removal; triangles: without seedling removal.

Discussion

Differential germination of species, as depending on the time of arrival of the first autumn rains, is one of the causes of interannual fluctuations in the floristic composition of our annual pastures: the germination of some species is favoured by the early arrival of the rains while others are favoured by a late arrival – compare the effect of autumn rain patterns on the germination of annual pastures (Espigares & Peco 1993).

Competition at the regeneration stage, however, does not seem to have an important effect on the floristic composition through its influence on germination. The differences in germination between removal treatments were never significant on the community level, and seldom on the species level. Competition did not seem to act through an enforced dormancy of some seeds once

the space had been occupied. These results agree with those of Aguiar et al. (1992) on the recruitment of seedlings in Patagonian steppes, where a partial reduction of competition had no significant effect on the number of emerged *Bromus pictus* seedlings.

Inouye (1980) observed germination inhibition produced by high densities of seedlings in desert annuals. He postulated that these species are favoured by delaying germination until periods of greater water availability – the species have long-lived seeds and the water deficit stress is much more extreme than in the Mediterranean. Moreover, most species in our pastures have a transient seed bank (Levassor et al. 1990); thus, delayed germination is a less appropriate strategy. Evidence for enforced dormancy due to the presence of a leaf canopy in herbs was presented by Gorski et al. (1977), but in that experiment seeds had to germinate under a dense

Table 1. Species with a significantly higher germination rate in one of the autumn rain or removal treatments (* = $p < 0.05$, ** = $p < 0.01$) for each successional stage. R: rainfall treatment; RE: removal treatment; R*RE: interaction; E and L: early and late autumn rain treatments; Y: with seedling removal; N: without seedling removal.

Species	Early			Intermediate			Late		
	R	RE	R*RE	R	RE	R*RE	R	RE	R*RE
<i>Andryala integrifolia</i>	n.s.	n.s.	n.s.	**E	* Y	n.s.	n.s.	n.s.	n.s.
<i>Aphanes microcarpa</i>	n.s.	n.s.	n.s.	* L	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Arenaria leptoclados</i>	**E	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Brassica barrelieri</i>	**E	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Crassula tillaea</i>	* E	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Galium parisiense</i>	* L	n.s.	n.s.	**L	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Herniaria hirsuta</i>	**E	n.s.	n.s.	**E	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Leontodon taraxacoides</i>	-	-	-	n.s.	n.s.	n.s.	* E	n.s.	n.s.
<i>Logfia minima</i>	n.s.	n.s.	n.s.	* E	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Lophochloa cristata</i>	* E	n.s.	n.s.	n.s.	n.s.	n.s.	**E	n.s.	n.s.
<i>Poa annua</i>	**L	n.s.	n.s.	-	-	-	**E	n.s.	n.s.
<i>Polycarpon tetraphyllum</i>	**E	n.s.	n.s.	**L	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Sagina apetala</i>	* E	n.s.	n.s.	**E	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Spergularia purpurea</i>	**E	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Trifolium arvense</i>	-	-	-	**E	n.s.	n.s.	n.s.	n.s.	n.s.
<i>Tuberaria guttata</i>	-	-	-	* L	n.s.	n.s.	-	-	-
<i>Veronica arvensis</i>	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	* E	n.s.	n.s.
<i>Vulpia ciliata</i>	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	* L	* Y	n.s.
<i>V. membranacea</i>	-	-	-	-	-	-	**L	**N	**
<i>V. myuros</i>	n.s.	n.s.	n.s.	* L	n.s.	n.s.	**L	n.s.	n.s.

canopy of *Rheum*, while in our case all the plants were allowed to germinate in the absence of any other plants that might interfere. Silvertown (1980) also found leaf-canopy induced seed dormancy in grassland species but, as in the case of Gorski et al. (1977), the experiment was based on the existence of a dense leaf canopy. In the annual pasture of the present study, where most germination occurred in a short period of time, this type of dormancy in the regeneration stage is highly unlikely.

At the same time, competition does not seem to have an important effect on seedling mortality. Seedling mortality was very low (< 10 %) in all successional stages and rainfall treatments. Seedling mortality for almost all species does not seem to be related to density or weighted density according to the size of neighbours. These results agree with those of Silander & Pacala (1985) on the mortality of the annual *Arabidopsis thaliana* which occurred mostly in the seedling stage and was density-independent. Kadmon & Shmida (1990) found that in the annual *Stipa capensis*, in different habitats and water regimes, with competition (with all neighbours) and without (absence of neighbours in a radius of 50 cm) competition did not influence seedling mortality, but it did influence fecundity through seed production. As to the possible importance of mortality induced by competition at the seedling stage, our results contradict those of Bartolome (1979) and Rice (1989) in Californian annual pastures. The high seedling mortality detected there during the first month after autumn germination, is influenced mainly by abiotic (meteorological) factors and density-independent biotic factors.

Table 2. Species with significant correlations between mortality m_i and density d or weighted density d_s . Significance and correlation sign indicated; * $p < 0.05$, ** $p < 0.01$. Successional stage and autumn rain treatment indicated as E = early, L = late, Int. = intermediate. Scale of treatment: Pot, 1 cm², 9 cm².

	Corr.		Succ. stage	Aut. rains	Scale
	d/m_i	d_s/m_i			
<i>Arenaria leptocladus</i>	* -	-	E	E	Pot
<i>Brassica barrelieri</i>	** +	-	E	E	1
“ “	* +	-	Int.	E	Pot
“ “	-	** +	E	E	1
<i>Cerastium semidecandrum</i>	** -	-	L	E	Pot
“ “	-	* +	E	E	Pot
<i>Herniaria hirsuta</i>	-	* +	E	E	9
<i>Poa bulbosa</i>	-	* +	L	L	Pot
<i>Polycarpon tetraphyllum</i>	-	* +	L	E	Pot
“ “	-	** +	L	L	9
<i>Sagina apetala</i>	** -	-	E	E	Pot
<i>Spergularia purpurea</i>	** +	-	E	E	1
“ “	* -	-	L	E	Pot
“ “	* -	-	L	E	9
“ “	-	** +	E	E	1
“ “	-	* -	L	E	9
<i>Veronica arvensis</i>	-	* +	L	E	Pot
<i>Vulpia muralis</i>	-	* +	L	L	Pot

Perhaps, our results are due to the very favourable moisture conditions included in our experiments. Competition might have been stronger under conditions of water stress. On the other hand, Grime (1979) assumed that competition is weaker under stress conditions, and Kadmon & Shmida (1990) found strong competition to be associated with high resource availability.

It should also be borne in mind that the year prior to the collection of our soil samples was extremely dry, and that the seed production had therefore probably dwindled (Young et al. 1981). Therefore, we do not discard the possibility that, for other densities, competition at the regeneration stage might induce seed dormancy or produce more density-dependent mortality. Furthermore, the lower density-dependent mortality found under late autumn rain conditions could be related to the fact that low temperatures produce a delay in germination and a lower seedling growth rate, which might reduce their mutual interference. This might explain the greater average seedling longevity under this treatment than in the early rain treatment.

On the basis of the present experiment we conclude that the interannual fluctuations in the floristic composition observed in the field are related to the time of arrival of the first rains, because of their influence on the differential germination of the species. Competition does not, however, appear to result in an inhibition of germination under any of the autumn rain conditions in any of the successional stages. Few cases of density-dependent mortality were detected, probably due to the favourable moisture conditions in the experiment. The specific effect of the timing of autumn rain arrival on this self-thinning could not be fully assessed, however, given the possibility that the two-month experimental period was not long enough to detect the entire seedling mortality for the case of simulated late autumn rains.

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