

Mediterranean pasture dynamics: the role of germination

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Abstract. Meteorological patterns have a decisive influence on the inter-annual dynamics of therophyte pastures under Mediterranean climatic conditions. The germination behaviour of annual pasture species was studied by subjecting two collections of seeds taken from plants and soil-seed banks to two phytotron-simulated weather patterns: early and late autumn rains. Species from these pastures were arranged along a gradient of sensitivity to temperature on the arrival of the first persistent rain. This sensitivity was manifested in both the total germination success of the species and the germination time profile. The different germination patterns of the species can provide competitive advantages depending on the autumn weather conditions.

Keywords: Autumn rain; Gradient; Phytotron; Seed bank; Temperature; Weather fluctuation.

Nomenclature: Tutin et al. (1964-1981).

Abbreviation: HMS = Hybrid Multidimensional Scaling.

Introduction

Research on permanent plots has revealed high inter-annual fluctuations in the floristic composition of mediterranean annual pastures (e.g. Austin, Williams & Belbin 1981; Peco et al. 1983; Pineda et al. 1987; Peco 1989). All of these studies point to the importance of total precipitation and autumn rain patterns in the dynamics of these pastures.

The influence of temperature and rainfall patterns on the floristic composition and biomass of mediterranean pastures is well known (e.g. Ratliff & Heady 1962; Hooper & Heady 1970; Murphy 1970; Duncan & Woodmansee 1975). Talbot, Biswell & Hormay (1939) differentiated grass, filarée and clover years, which are closely correlated with precipitation. Heady (1958) found that pasture composition is already determined before December. Talbot & Biswell (1942) observed that leguminous species are usually favoured by the late arrival of

autumn rains. Rossiter (1966) found that early rain followed by a long period of dry weather favours drought-tolerant species and leads to the death of annual grass and clover seedlings. Pitt & Heady (1978) correlated the yield of an annual pasture with 76 climatic variables, and found opposite responses of grasses and clovers to yearly weather patterns; they observed that consistent rainfall following autumn germination, and again during the period of rapid plant growth in spring, contributes to a 'grass year' in the California annual type, while clovers are favoured by good growing conditions during late autumn.

From these studies it is clear that the germination and establishment of seedlings is a key stage in determining the composition of annual pastures. In mediterranean annual pastures, germination is mainly concentrated in autumn and influenced by the time of arrival of the first persistent rains. Controlled tests on the influence of temperature on the germination of mediterranean annual species have focused on very few or a single species (e.g. Smith 1968; Young, Evans & Kay 1969, 1973). Inter-annual variations in germination timing are often attributed to differences in weather patterns (Bartolome 1979; Young et al. 1981; Ortega & Fernandez Alés 1988). Nevertheless, we know little about the factors controlling year-to-year fluctuations in composition (Pitt & Heady 1978; Bartolome 1989).

In this study we determine the germination response of conspicuous species from a Mediterranean pasture subjected to simulated early and late autumn rains. We test the hypothesis that autumn rain patterns are related to different germination patterns and success rates of species.

Material and Methods

The study area is a *Quercus rotundifolia* 'dehesa' or open woodland with therophyte pastures; it is situated on tertiary sands resulting from the erosion of the granitic massif of the Sierra de Guadarrama (central Spain). Intermittent ploughing is carried out to stimulate pasture

growth through the elimination of unwanted *Cistus ladanifer*, *Lavandula stoechas* and other thicket species. Each year after the summer drought, most species regenerate from the seed bank, whose composition has a high degree of similarity to the extant vegetation (Levassor, Ortega & Peco 1990). The climate is semi-arid Mediterranean, with a mean annual precipitation of ca. 400 mm and high inter-annual fluctuations.

Three weather patterns can be distinguished on the basis of monthly rainfall distribution in the study area, with early, intermediate and late autumn rains (Peco 1989). The first pattern is characterized by rains starting in September and continuing throughout the wet season. The second pattern includes rains in September, then a dry period of many weeks, and later rains again. The third pattern includes the first rains in November.

Precipitation in the following months did not have significant inter-annual differences.

Soil-seed banks and collections of seeds taken from plants in situ were subjected to two phytotron-controlled temperature treatments which simulated the two extreme weather patterns (Peco 1989): early and late autumn rains. This was achieved by means of a constant supply of water at average September and November day/night temperature regimes (based on 10-yr records), i.e. 20/15 °C ('warm') and 10/5 °C ('cold') respectively. The difference between day and night (5 °C) was kept equal in order to avoid potential favouring of germination - exposure to fluctuating temperatures facilitates the rupture of seed dormancy (e.g. Thompson & Grime 1983; Khan & Akhtar 1989).

24 soil samples (10 cm × 10 cm × 6 cm cores) were collected in September 1989 to study germinable seed banks. These samples represent different extremes of geomorphological and successional (post-ploughing) variability previously detected in the area (Pineda et al. 1981). The homogeneity of seed banks from slopes with the same successional age is higher than amongst those with different successional ages (Levassor, Ortega & Peco 1990). For this reason, three slopes with different successional ages were chosen (1, 14 & 33 yr since last ploughing) as representatives of three successional stages: early, intermediate and late. From the upper and lower zones of each slope four random samples of soil were taken. Each of the 24 samples was homogenized and divided into two sub-samples, which were subjected to the above-mentioned treatments. Emerging seedlings were noted with the date of germination and removed after identification. The experiment was maintained for a 5-week period, i.e. the time difference between the weather patterns being compared. This period is sufficient to detect possible gradients in the responses of the species. 58 species from the seed bank were found.

More direct monitoring of the species was achieved in the spring of 1982, when seeds of the 75 most conspicuous pasture species in the study area were collected. The seeds were stored in a dark, dry place until October 1989. The storage may have affected the germination, but such an effect would have been the same for the seeds subjected to the two treatments; thus the experiment is valid for the establishment of germination differences in 'cold' and 'warm' regimes. Two sets of 20 seeds of each species were placed in Petri dishes on blotting paper and a 1.5 cm layer of hydrophyle cotton wool, and subjected to both treatments. The number of germinated seeds of each species in each treatment was noted every day over a period of 5 weeks.

Hybrid Multidimensional Scaling (HMS) (Faith, Austin & Belbin 1987) based on the Kulczynski similarity index (Hajdu 1981; Faith et al. 1985) was performed on the seedling composition in the different soil samples. A Correspondence Analysis of the same data was used to obtain a starting configuration for the HMS as this yielded minimum stress values (smallest differences between the inter-observation distance measured by the Kulczynski index and the Euclidian distance in the HMS space).

The experiments on seeds taken from plants yielded two germination characteristics for each of the most conspicuous pasture species: warm-cold emergence difference and difference profile. The warm-cold emergence difference is the difference between the number of seeds which germinated in the warm and cold treatments; the warm-cold difference profile represents the differences over time of the relative and accumulated percentage emergence in 'warm' and 'cold' treatments.

The species were classified according to the warm-cold difference profiles using a profile attributes index (Faith et al. 1985) and the UPGMA ('Unweighted Pair-Group Method using Asymmetric Averages') flexible sorting strategy ($\beta = 0.0$) as the clustering method. HMS was performed on the association matrix to obtain a quantification for the position of the species along the gradient of temporal sensitivity pattern detected in the analysis. This strategy permitted the objective quantification of the similarity between species in terms of their sensitivity to the two treatments, and enabled us to test differences between taxonomic groups and characteristic species of each successional stage, which were obtained from the seed-bank data, while assigning the species with the greatest relative abundance to each stage.

The PATN package (Belbin 1987) was used to perform all multivariate analyses. Other statistical analyses (Kruskall-Wallis one-way analysis by ranks, Wilcoxon's test for matched pairs, χ^2 and Pearson correlation coefficient) were performed with the BMDP package (Dixon 1985).

Results

Seeds-in-soil sensitivity

The seed banks were different on slopes with different successional ages (Fig. 1a); a geomorphological differentiation was obvious in the samples collected on the early and intermediate slopes, but not on the most mature slope.

There was a generalized downward movement in the paired samples from the ‘warm’ to the ‘cold’ treatment in the multivariate space (Fig. 1b) - 80% of the samples had higher coordinate values for axis 2 in the ‘warm’ treatment as compared to the ‘cold’ one. This movement indicates a change in floristic composition of the germinable seed banks when a soil sample was subjected to one of the treatments. In the analysis of species sensitivity to the treatment (Wilcoxon *T*-test), several species had a significantly higher germination percentage at high temperatures and no species appeared with a statistically higher germination rate at lower temperatures (Table 1a).

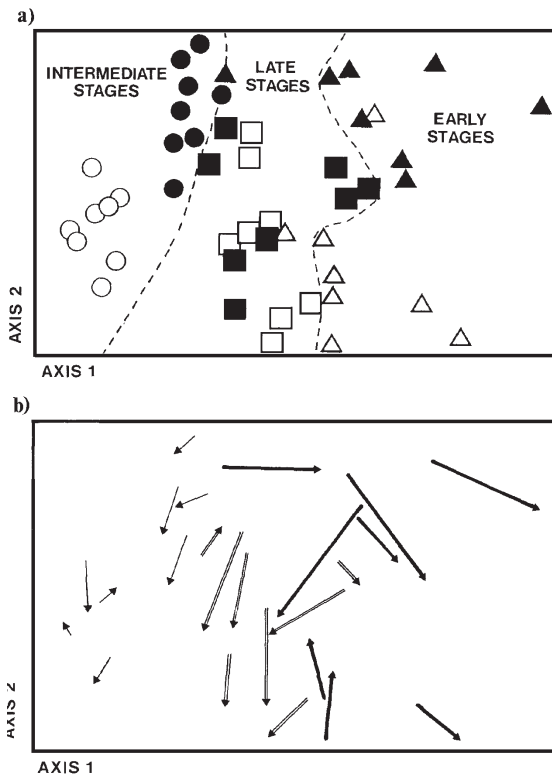


Fig. 1. Position of the samples in the HMS space. a: successional age and geomorphological position of the samples: early (triangles), intermediate (circles) and late stages (squares); upper slope zones (open) and lower slope zones (filled). b: arrows link the warm and cold treatments for the paired samples. The thickness of the line indicates successional age: early (solid thick line), late (double line) and intermediate stages (thin line).

The distance between paired samples was greater in the early stages (Kruskal-Wallis $H = 11.63$, $p < 0.005$), than the intermediate or late stages, in which the effect of the treatment was less obvious. The magnitude of change was not correlated to the number of species found in each sample ($r = 0.12$, n.s.). The relative number of shared species in paired samples was significantly lower in the early stage samples ($H = 10.33$, $p < 0.005$), although differences in the number of germinated seeds in species which germinated under both treatments did not differ significantly between successional ages ($H = 0.1949$, n.s.).

Seeds-in-Petri-dishes sensitivity

There was a gradient from cold-germinators such as *Bromus tectorum*, *Cerastium semidecandrum* and *Trifolium striatum* to warm-germinators such as *Campanula erinus*, *Mibora minima* and *Stellaria media* (Fig. 2). But only the latter species had significantly higher germination percentages in the warm treatment (Table 1b).

Three groups of species appeared to be based on the differential germination profile (Fig. 3): species with few differences (group 1), species affected by the lower temperatures (group 2) and species with delayed germination but ultimately higher germination percentages at low temperatures (group 3). In all cases there was a general delay in germination in the cold treatment, which was also found in the seed-bank experiments for species with immediately recognizable seedlings.

Through HMS applied to the species association matrix obtained from the differential germination profiles, the species could be arranged along a temporal gradient of sensitivity. Axis 1 is the best reflection of the gradient; there is scarcely any variation along axes 2 or 3. While some species seemed to prefer cold conditions and others germinated much better under warm conditions, the majority were indifferent or germinated slightly better under warm conditions (Fig. 4).

Once the germination behaviour of each species was quantified using the parameters of warm-cold emergence difference and temporal pattern of sensitivity (Axis 1 of HMS), a Kruskal-Wallis test was used to

Table 1. Species with significantly higher germination percentages in the ‘warm’ treatment (* $p < 0.05$, ** $p < 0.01$); a. Wilcoxon’s test for matched pairs for species from seed banks; b. χ^2 test for seeds taken from plants in situ. No significant differences found in the ‘cold’ treatment.

	a **	a *	b *
<i>Carduus tenuiflorus</i>		<i>Brassica barrelieri</i>	<i>Campanula erinus</i>
<i>Cerastium semidecandrum</i>		<i>Bromus madritensis</i>	<i>Mibora minima</i>
<i>Hypochoeris glabra</i>		<i>Crassula tillaea</i>	<i>Stellaria media</i>
<i>Sagina apetala</i>		<i>Geranium molle</i>	
<i>Trifolium suffocatum</i>		<i>Polycarpon tetraphyllum</i>	

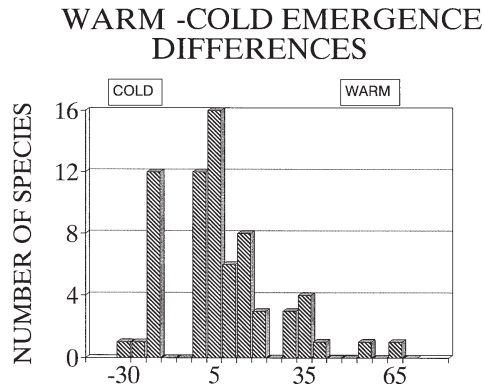


Fig. 2. Absolute frequencies of species for each value of the differences between the final percentages of germination in warm and cold treatments.

determine whether these factors differed amongst grasses (*Poaceae*), legumes (*Fabaceae*), composites (*Asteraceae*) or other groups. Neither absolute differences between warm and cold germination nor the temporal pattern of sensitivity revealed any significant relationship in the families analysed. The same analysis applied to groups of species that are characteristic of pioneer, intermediate and mature stages was also unable to provide any significant result.

Discussion

Germination from seed banks subjected to two temperature treatments simulating early and late autumn rains revealed differences in both total number of germinations and temporal distribution of germination for many of the species. These differences seem to depend on successional age. Differences were greater in early compared to intermediate and late stages, and were independent of the geomorphological position of the samples. This concurs with results obtained in previous studies in the same area (Peco et al. 1983; Pineda et al. 1987), which found greater fluctuations in inter-annual species composition related to weather conditions in early successional stages, and no differences in inter-annual fluctuations between upper and lower slope zones (Peco et al. 1991).

Changes in floristic composition produced by the treatment may be related to qualitative (different species germinating in each circumstance) or quantitative differences (different number of germinations for the same species). There were quantitative differences on all slopes in terms of the number of germinations in the species (normally lower in the cold treatment), and there were no significant differences between slopes. The time pattern of treatment sensitivity was not different in the characteristic species groups of the successional

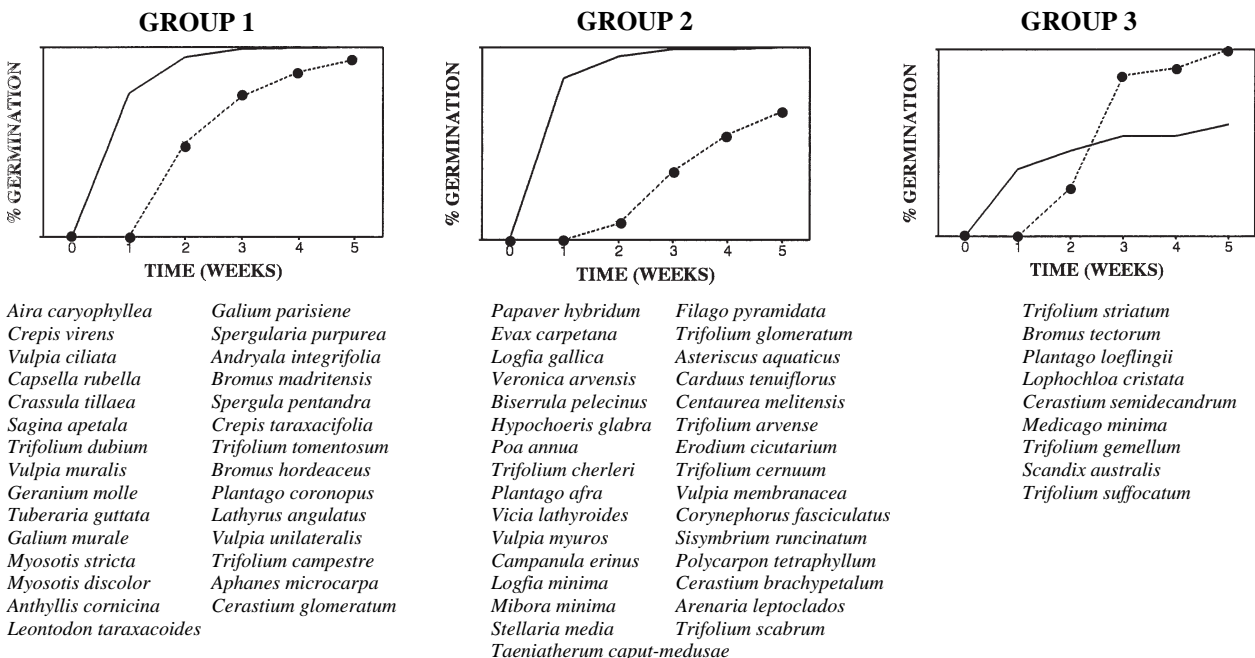


Fig. 3. Average germination profile in the warm (continuous line) and cold treatment (dotted line and filled circles) for three groups of species obtained by classification based on the difference between both profiles (differential profile of germination) - see text - and characteristic species in each group.

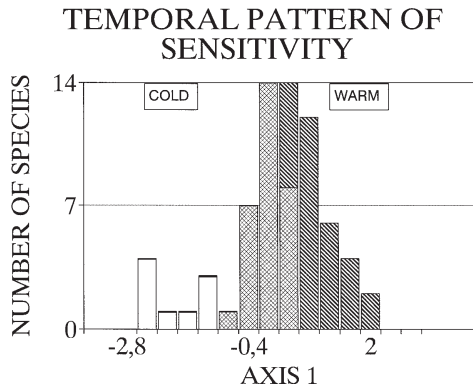


Fig. 4. Absolute frequencies of species for each value of axis 1 from the HMS of time profiles of the differences in germination between warm and cold treatments. Species groups presented in Fig. 3 are identified by: crossed bars (group 1), striped bars (group 2) and open bars (group 3).

stages, either. The early stage samples, however, had a smaller number of shared species. The greater change found in the pioneer slope samples seems to be due to a substitution of species rather than a quantitative variation in the percentages of germination with different autumn rain patterns.

Some species performed better in the warm treatment, but none had a higher % germination in the cold treatment. The overall delay in germination under the cold treatment could indicate that the experimental period of 5 weeks was not long enough for all seeds to germinate, especially in species in which this delay was more pronounced. The right-skewed shape of the warm-cold emergence differences (Fig. 2) could be evidence of this, and might explain the lack of statistical significance for the species under the cold treatment. Nonetheless, only a few species need to be favoured by high temperatures for this to be manifested in an alternation of communities in years with early and late autumn rain.

It is possible that no species 'preferred' the most adverse conditions in the experiment. Nevertheless, species can be arranged along a gradient of treatment sensitivity. While some responded positively to the warm treatment, others performed less badly in the cold. This sensitivity was manifested in terms of both germination success and the distribution of germination over time.

The early or late arrival of autumn rains is a factor which may also affect the survival of the seedling cohorts. Seedlings which have sprouted early in the growth season, with a consequently longer time for development, have a lower risk of mortality under subsequent adverse environmental factors (Ross & Harper 1972; Harper 1977). If early autumn rains are followed by a period of well distributed rains, seedlings which sprout at this point will have a higher probability of survival

than those which sprout if the autumn rains arrive late.

Neither absolute nor profile differences in germination between both treatments function consistently in grasses, legumes, composites or other families. Although previous studies (e.g. Talbot, Biswell & Hormay 1939; Talbot & Biswell 1942; Pitt & Heady 1978) have shown that the abundance of some taxonomic groups (mainly grasses and legumes) depends on rainfall and its annual distribution, we were unable to find that this relationship is linked to germination success under different autumn-rainfall patterns. Previous seed-bank analyses have demonstrated that a transient seed bank is characteristic of therophytic vegetation (Grubb 1988; Young & Evans 1989), and that annual legumes have a tendency to establish more or less permanent seed banks (Bartolome 1979). Grime et al. (1981) noted rapid germination in annual grasses and forbs. In Mediterranean ecosystems, where the dry season leaves the ground practically bare, a crucial factor is occupation of space. Although high germination rates are adaptive for occupying space, species which prolong their period of germination may have other advantages - fast germinators can die if a catastrophe occurs (Grubb 1977; Marañón & Bartolome 1989). Probability of drought in periods following germination, or advantages of some species in the occupation of space during seedling establishment, may also explain differences in floristic composition which were found among different types of years.

We may conclude that the temperature at the time of arrival of persistent autumn rains affects the configuration of the pasture, because species in these communities have a different germination behaviour related to different autumn weather conditions. The wide variety of germination behaviour might be one of the factors which permits the coexistence of a large number of Mediterranean pasture species subject to fluctuating environmental conditions at the time of regeneration (Grubb 1977).

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