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Source: *Journal of Ecology*, Feb., 1995, Vol. 83, No. 1 (Feb., 1995), pp. 135-142

Published by: British Ecological Society

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*Journal of Ecology* 1995,
**83**, 135–142

# Mediterranean annual pasture dynamics: impact of autumn drought

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## Summary

**1** There are wide fluctuations in the floristic composition of pastures consisting mainly of annual species in Mediterranean climatic environments. This is attributed to variations in total precipitation and rainfall distribution patterns.

**2** In order to examine the effect of autumn drought on the floristic composition of Mediterranean annual pastures, soil samples with seed banks were taken from the upper and lower slopes of each of three pastures that differed in successional age. Half of each sample was subjected to a simulated autumn drought treatment while the other half received a continuous water supply (in both cases under controlled conditions). All germinations and deaths were recorded throughout the 2-month experimental period.

**3** Only five species had significantly different numbers of germinations between the two watering treatments, and in four of these germination was lower in the drought-simulated treatment. Re-watering of samples from this treatment did not result in a second wave of germination.

**4** Drought-induced mortality was greater in the samples with high seedling densities. A significant negative correlation was evident between seedling density and the water content of the pots at the end of the experimental drought.

**5** The least drought-sensitive species were those with stem or leaf hairs and those belonging to Crassulaceae, which show a particular adaptive metabolism.

*Keywords*: hybrid multidimensional scaling, phytotron, regrowth, successional stages, watering.

*Journal of Ecology* (1995) **83**, 145–152

## Introduction

The main characteristics of semiarid Mediterranean climates are the hot, dry summers and the unpredictable autumn rains (Noy-Meir 1973). Annual species that grow in Mediterranean grassland environments spend the summer in seed form, thus avoiding the period of high temperatures and lack of water. In autumn, the first rains initiate germination and regrowth of the grassland.

The study of species dynamics in annual grasslands has revealed large variations in the floristic composition. This has been attributed to fluctuations in total annual rainfall and its distribution during the year (Drury & Nisbet 1973; Austin *et al.* 1981; Peco *et al.* 1983, 1988; Pineda *et al.* 1987; Peco 1989; Figueroa & Davy 1991; Hobbs & Mooney 1991). Many studies also postulate the importance of weather conditions, particularly during germination and seedling establishment, for the species composition of the pasture in spring (Heady 1958; Pitt & Heady 1978; Marañón & Bartolome 1989).

The temperature at which seeds germinate is determined by the timing of the first autumn rains, while subsequent drought periods seriously affect seedling survival. Since both phenomena, i.e. the sensitivity of seed germination to temperature and seedling sensitivity to drought, are species-specific, they could affect the grassland floristic composition (Went 1949; Ashby & Hellmers 1955; Newman 1963; Rossiter 1966; Young *et al.* 1969, 1973; Young & Evans 1989; Gulmon 1992; Espigares & Peco 1993). However, very few studies analyse the consequences of autumn droughts on the survival of grassland species, and most use a phenomenological approach (Marañón & Bartolome 1989).

The aims of our study were to determine (i) whether a drought following the first autumn rains can change

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the floristic composition of annual Mediterranean pastures, and (ii) whether the effects are influenced by the successional age and topography of pasture communities. We therefore analysed the consequences of a phytotron-simulated drought on seed germination and seedling mortality of pasture species. We also tried to explain the species-specific seedling mortalities on the basis of their form/function traits. The working hypothesis was that drought causes higher mortality rates in drought sensitive species and in young seedlings, and that the gaps thus created may be occupied by seedlings resulting from a second wave of germination.

## Material and methods

### STUDY SITE

The study area is an estate covered by a *dehesa* (open woodland) of *Quercus ilex* ssp. *ballota* (Desf.) Samp. in Bol. (Holm oak) in central Spain. The zone is ploughed occasionally to impede invasion by maquis. The lower vegetation storey is an extremely species-rich annual pasture which changes successionally from pioneer stages (recently ploughed) to more-advanced stages under constant herbivore pressure. The climate has a mean annual rainfall of 450 mm, with high interannual fluctuations (Fig. 1). The rainfall distribution is typically Mediterranean, with a 2–3-month drought period that coincides with the summer.

### EXPERIMENTAL DESIGN

In the summer of 1991, 48 soil samples were taken from three pastures differing in the time since they were ploughed (3, 16 and 35 years, constituting the pioneer, intermediate and mature stages, respectively). Because the pastures grew on sloping ground, the samples were taken from both upper and lower regions of each pasture. The eight samples from each age and position were randomly divided into four pairs. Each pair was sieved and mixed, and it was divided into two halves. Each sample was placed in the upper part of a pot (~ 100 mm diameter) above a 5-cm-deep layer of vermiculite separated by a thin layer of gauze. Plastic mesh forming 1-cm$^2$ grids was placed on the surface of the pots to locate and monitor each seedling that emerged. The pots were kept in a phytotron. One pot from each pair of samples was subjected to a continuous watering treatment (keeping the soil at field capacity) while the other was subjected to continuous watering for the first 13 days, no watering for the next 18 days and re-watering thereafter until the end of the 2-month experimental period. These two watering treatments will be referred to as W (watered) and D (drought), respectively. Day and night temperatures were 20/15°C, which were the mean September temperatures for the last ten years in the area. Day length was 12 h, and light intensity was 205.2 $\mu$mol m$^{-2}$ s$^{-1}$. Air humidity was not monitored but was the same for all pots.

In each pot, all germinations and deaths during the 2-month experimental period were recorded. All pots were also weighed every week. To assess their relative water contents, at the end of the experiment the pots were dried to a constant weight, and this was subtracted from each measurement made during the experiment. The wilting point and field capacity of each soil sample was measured by the method of Guitián & Carballas (1976).

### DATA ANALYSIS

Differences at the end of the experimental period in total germination, total mortality rates and species richness per pot between the paired samples from the two watering treatments were analysed using paired *t*-tests. When significant differences were detected, two-factor ANOVAs were used to test for differences in the effect of drought (W – D for each set of paired pots) between successional ages and topographic positions. Data that revealed heteroscedasticity was transformed logarithmically prior to analysis. Differences

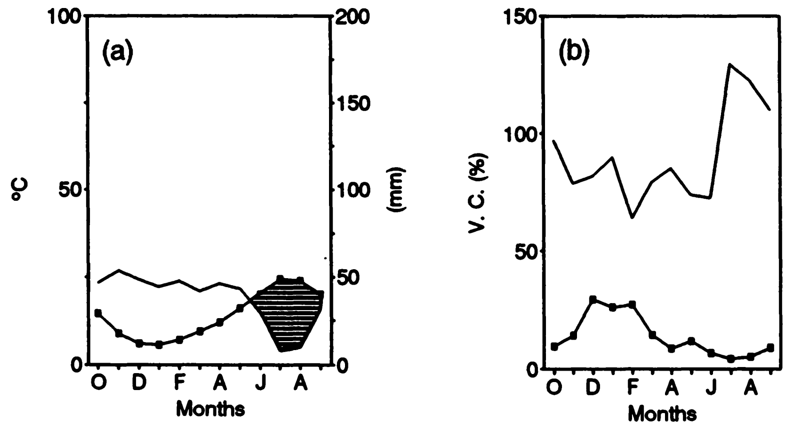

**Fig. 1** (a) Mean monthly values of precipitation and temperature in the study zone during the last 30 years. (b) Variation coefficient for monthly temperature (■) and precipitation during this period.

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in germination and mortality rates on a species level were analysed using nonparametric tests given the non-normal data distribution arising from the small number of cases. Wilcoxon Rank tests were used to test the differences in germination. The requirements of this test for checking significance allowed us to test differences only in those species which occurred in at least six sets of paired pots. Mann–Whitney tests were used to test the differences in mortality by species. In this case, the test requirements only permitted the use of species that were present in at least four paired samples.

The Pearson correlation coefficient was used to test for the existence of relations between total mortality per pot and seedling density. Given that 80% of the germinations occurred in the first 2 weeks, a $\chi^2$-test was performed to detect relations between emergence during the first or second week of the experiment and the survival or death of the individuals in each pot.

In order to answer the questions posed in our objectives, and given that the drought period is a key phase in this experiment, we also calculated the total germinations per pot in two specific periods: (i) between days 1 and 31 of the experiment, i.e. from the start to the end of the experimental drought, and (ii) from day 31 until the end of the experiment, i.e. the period following the experimental drought. We used the Pearson correlation coefficient to ascertain whether seedling density was linked to the relative amount of water in the pots at the end of the drought period. A Wilcoxon Rank test was also used to test for differences between total germinations in each of the watering treatments in the period after the experimental drought.

The floristic composition of each pot was calculated from the difference between germinated and dead individuals of each species. A Hybrid Multidimensional Scaling (HMS) (Faith *et al.* 1987) of these data was performed to analyse the overall differences in each community caused by the two watering treatments.

Finally, a $\chi^2$-test was used to detect any relationship between the drought-induced mortality and the presence in the species of mechanisms to reduce evapotranspiration, namely stalk or leaf hairs, or Crassulacean acid metabolism (CAM).

The difference between field capacity and wilting point of each soil sample can be considered as an approximate measure of the amount of water available for plants that each soil can hold. This was used in a two-factor ANOVA to test for differences between successional stages and topographic positions.

## Results

### EFFECTS ON GERMINATION

A total of 70 species germinated in the set of 48 pots. The mature stages had a significantly higher number of germinations per pot (300.81 ± 39.6) ($F_2 = 4.58$, $P = 0.01$) than the intermediate (217.31 ± 15.8) and pioneer stages (204.06 ± 24.7). The total number of germinations per pot at the end of the experiment did not differ significantly between the two watering treatments (paired $t$-test, $t = 0.43$). However, the total number of germinations per pot following the experimental drought period was significantly greater in the W pots (14.04 ± 1.63) than in the D pots (9.21 ± 1.48) (Wilcoxon Rank test, $T = 48$, $N = 22$, $P \leqslant 0.01$). There was also a significant negative correlation between the relative amount of water in the pots on the last day of the experimental drought and the density of germinations accumulated up to that point in each pot ($r = -0.4527$, $P \leqslant 0.02$).

Table 1 shows that 50% of the 70 species that germinated in the pots are not abundant: at the most, they appear in five of the 24 replicates of each watering treatment. With such a large number of rare species, we were unable to test for germination differences between treatments for each species. The Wilcoxon Rank Tests were used to test the differences in final germination between treatments in 40 species. Five species were found with final germination values that were affected by the watering treatment, and all but one showed more germinations in the continuous watering (W) treatment (Table 2).

### EFFECTS ON MORTALITY

The total mortality rate per pot differed significantly between the two watering treatments (paired $t$-test, $t = -8.81$, $P < 0.001$), with a higher rate in the D pots (Table 3). A two-factor ANOVA was applied to the values of mortality increase between each set of paired pots (D–W), revealing significant differences between successional stages ($F_2 = 4.89$, $P < 0.05$). The late stages showed the greatest effects of watering (Table 3). However, since there was a significant interaction ($F_2 = 5.73$, $P = 0.01$) between successional age and topographic position, these results should be approached with some caution.

A $\chi^2$-test revealed a link between mortality and the moment of emergence of the individuals in the pots subjected to the D treatment. The test showed that the individuals which emerged in the first week of the experiment had a greater tendency to survive than those that emerged in the second week ($\chi^2_1 = 159.3$, $P \leqslant 0.01$) (Table 4).

We used Mann–Whitney tests to compare species mortality rates between the two watering treatments in the 44 species that appeared in a sufficiently large number of pots. Mortality was significantly different between the two watering treatments for 19 species, all of which had a higher mortality in the D treatment (Table 5). One of the 44 species, *Crassula tillaea*, had CAM and 27 had stalk or leaf hairs. Of the 19 species with a significantly higher mortality rate in the D treatment, 14 lacked hairs or CAM: a $\chi^2$-test revealed

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**Table 1** List of species germinating during the experiment (nomenclature follows Tutin *et al.* 1964–81); *N*, number of pots in which each species appeared; *V* (variables that could be tested): *G*, total germination; *M*, mortality rate; *B*, both germination and mortality; –, none

| Species | *N* | *V* | Species | *N* | *V* | Species | *N* | *V* |
|---|---|---|---|---|---|---|---|---|
| *Aphanes microcarpa* | 48 | *B* | *Poa annua* | 18 | *B* | *Trifolium campestre* | 5 | – |
| *Vulpia muralis* | 48 | *B* | *Logfia minima* | 17 | *B* | *Apera interrupta* | 4 | – |
| *Sagina apetala* | 46 | *B* | *Myosotis stricta* | 15 | *B* | *Asteriscus aquaticus* | 4 | – |
| *Galium parisiense* | 46 | *B* | *Erodium cicutarium* | 14 | *B* | *Veronica persica* | 4 | – |
| *Spergularia purpurea* | 45 | *B* | *Trifolium glomeratum* | 14 | *B* | *Carduus tenuiflorus* | 4 | – |
| *Cerastium semidecandrum* | 43 | *B* | *Geranium molle* | 14 | *B* | *Cistus ladanifer* | 4 | – |
| *Arenaria leptoclados* | 42 | *B* | *Poa bulbosa* | 12 | *B* | *Medicago minima* | 4 | – |
| *Veronica arvensis* | 41 | *B* | *Filago pyramidata* | 12 | *B* | *Hordeum murinum* | 3 | – |
| *Biserrula pelecinus* | 41 | *B* | *Centaurea melitensis* | 12 | *B* | *Ranunculus parviflorus* | 3 | – |
| *Vulpia ciliata* | 40 | *B* | *Urtica urens* | 11 | *B* | *Teesdalia coronopifolia* | 3 | – |
| *Crassula tillaea* | 39 | *B* | *Trifolium arvense* | 11 | *M* | *Cardamine hirsuta* | 2 | – |
| *Trifolium suffocatum* | 37 | *B* | *Bromus hordeaceus* | 10 | *M* | *Heliotropium europaeum* | 2 | – |
| *Vulpia myuros* | 31 | *B* | *Cerastium glomeratum* | 10 | *G* | *Anthriscus caucalis* | 1 | – |
| *Herniaria hirsuta* | 30 | *B* | *Vulpia membranacea* | 10 | *B* | *Logfia gallica* | 1 | – |
| *Galium murale* | 29 | *B* | *Leontodon taraxacoides* | 9 | *B* | *Taeniatherum caput-medusae* | 1 | – |
| *Andryala integrifolia* | 27 | *B* | *Erophila verna* | 9 | *B* | *Trifolium repens* | 1 | – |
| *Polycarpon tetraphyllum* | 25 | *B* | *Veronica verna* | 8 | *B* | *Scandix australis* | 1 | – |
| *Lophochloa cristata* | 25 | *B* | *Tuberaria guttata* | 8 | *M* | *Schismus barbatus* | 1 | – |
| *Brassica barrelieri* | 23 | *B* | *Viola kitaibeliana* | 7 | *B* | *Sedum caespitosum* | 1 | – |
| *Bromus tectorum* | 22 | *B* | *Crepis virens* | 7 | *B* | *Trifolium retusum* | 1 | – |
| *Sisymbrium runcinatum* | 22 | *B* | *Arabidopsis thaliana* | 6 | *M* | *Trifolium tomentosum* | 1 | – |
| *Hypochoeris glabra* | 21 | *B* | *Isoetes histrix* | 6 | *M* | *Vicia lathyroides* | 1 | – |
| *Stellaria media* | 20 | *B* | *Asterolinon linum stellatum* | 5 | – | | | |
| *Geranium rotundifolium* | 19 | *B* | *Plantago afra* | 5 | *M* | | | |

**Table 2** Species with significant differences (*$P \leqslant 0.05$, ** $P \leqslant 0.01$) in total germination between watering treatments (D: Drought, W: Without drought) (nomenclature follows Tutin *et al.* 1964–81). Mean (±1 SE) number of total germinations per pot in each treatment is indicated

| Species | W | D |
|---|---|---|
| *Aphanes microcarpa* | 42.58 ± 7.51 | * 38.30 ± 7.50 |
| *Galium parisiense* | 11.86 ± 4.21 | * 12.79 ± 2.51 |
| *Herniaria hirsuta* | 4.56 ± 0.95 | ** 3.92 ± 0.72 |
| *Polycarpon tetraphyllum* | 8.15 ± 1.73 | * 5.58 ± 0.92 |
| *Sagina apetala* | 19.33 ± 4.90 | ** 12.86 ± 3.23 |

**Table 3** Mean values (±1 SE) of total mortality rates for samples with the same successional age and topographic position (U, upper topographic position; L, lower topographic position) in each watering treatment (D, drought; W, without drought). Final column shows mean values (±1 SE) of the increment of total mortality rates between the two watering treatments (D–W) in the samples with the same successional age and slope position

| Succesional stage | | D | W | D–W |
|---|---|---|---|---|
| Early | U | 19.4 ± 2.7 | 2.3 ± 0.4 | 17.1 ± 2.5 |
| | L | 42.5 ± 3.0 | 3.2 ± 1.3 | 39.3 ± 2.1 |
| Intermediate | U | 23.0 ± 2.5 | 0.9 ± 0.2 | 22.1 ± 2.5 |
| | L | 58.1 ± 9.6 | 2.1 ± 1.2 | 56.0 ± 10.1 |
| Late | U | 67.0 ± 10.4 | 3.4 ± 1.3 | 63.5 ± 11.7 |
| | L | 51.4 ± 12.6 | 7.1 ± 3.2 | 44.3 ± 12.3 |

a significant relationship between the absence of hairs or CAM and the increased drought mortality ($\chi^2_1 = 12.99$, $P \leqslant 0.001$).

Finally, there was a significant correlation between density and total mortality rate in the D pots ($r = 0.6144$, $P \leqslant 0.001$) but not in the W pots.

### OVERALL EFFECTS

The HMS of the final floristic composition of each pot shows clear differences between the communities of the three pastures with differing successional ages and topographic positions (Fig. 2a). In Fig. 2(b), each W pot is linked by an arrow to its respective D replicate: autumn drought conditions produce a divergent distancing from the similar nondrought state, while the heterogeneity between the samples from the same successional stage and topographic position increases. The magnitude of the change in floristic composition, expressed as the distance between paired pots, differs significantly between samples from

**Table 4** Total number of individuals that died and survived when emerging in the first or the second week of the experiment in the pots subjected to drought

| | Died | Survived |
|---|---|---|
| Week 1 | 1678 | 2006 |
| Week 2 | 1278 | 751 |

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**Table 5** Species with significantly greater mortality under drought treatment. Mean ($\pm 1$ SE) total mortality rate per pot in each treatment is indicated

| Species | Without drought | *P* | Drought |
|---|---|---|---|
| *Aphanes microcarpa* | $0.04 \pm 0.01$ | ** | $0.65 \pm 0.06$ |
| *Arenaria leptoclados* | $0.08 \pm 0.05$ | ** | $0.40 \pm 0.09$ |
| *Biserrula pelecinus* | $0.15 \pm 0.04$ | * | $0.44 \pm 0.09$ |
| *Bromus hordeaceus* | $0.00 \pm 0.00$ | * | $0.56 \pm 0.19$ |
| *Cerastium semidecandrum* | $0.08 \pm 0.02$ | ** | $0.59 \pm 0.08$ |
| *Galium murale* | $0.08 \pm 0.08$ | ** | $0.73 \pm 0.09$ |
| *Galium parisiense* | $0.19 \pm 0.06$ | ** | $0.87 \pm 0.04$ |
| *Hypochoeris glabra* | $0.00 \pm 0.00$ | * | $0.54 \pm 0.14$ |
| *Polycarpon tetraphyllum* | $0.00 \pm 0.00$ | * | $0.41 \pm 0.13$ |
| *Sagina apetala* | $0.01 \pm 0.01$ | ** | $0.77 \pm 0.05$ |
| *Spergularia purpurea* | $0.04 \pm 0.02$ | ** | $0.51 \pm 0.07$ |
| *Trifolium arvense* | $0.00 \pm 0.00$ | ** | $0.70 \pm 0.18$ |
| *Trifolium glomeratum* | $0.00 \pm 0.00$ | ** | $0.86 \pm 0.01$ |
| *Trifolium suffocatum* | $0.02 \pm 0.02$ | ** | $0.56 \pm 0.09$ |
| *Veronica arvensis* | $0.02 \pm 0.01$ | ** | $0.52 \pm 0.09$ |
| *Vulpia ciliata* | $0.04 \pm 0.01$ | * | $0.33 \pm 0.07$ |
| *Vulpia membranacea* | $0.00 \pm 0.00$ | ** | $0.80 \pm 0.05$ |
| *Vulpia muralis* | $0.02 \pm 0.01$ | ** | $0.34 \pm 0.07$ |
| *Vulpia myuros* | $0.03 \pm 0.01$ | * | $0.48 \pm 0.10$ |

$*P \leqslant 0.05$, $**P \leqslant 0.01$.

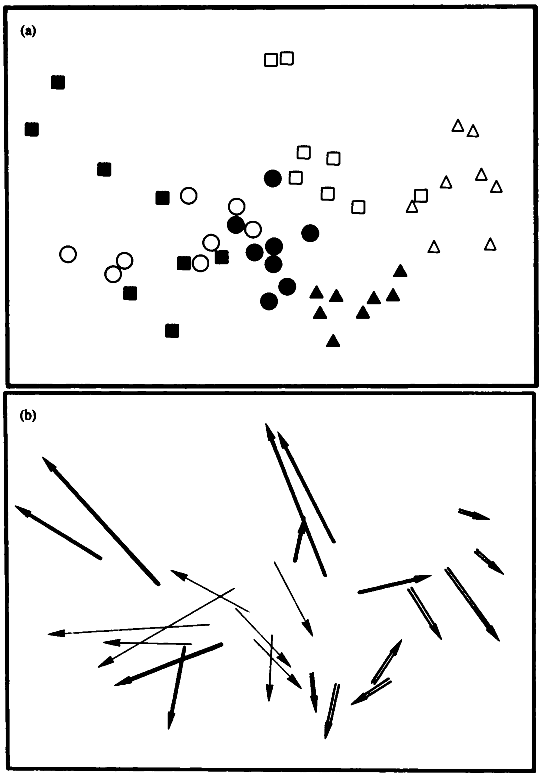

**Fig. 2** Ordination (Hybrid Multidimensional Scaling) illustrating differences in final floristic composition of all samples. (a) early stage, upper zone (△), early stage, lower zone (▲), intermediate stage, upper zone (○), intermediate stage, lower zone (●), mature stage, upper zone (□) and mature stage, lower zone (■). (b) arrows link each sample in the continuous watering treatment to its homologue in the drought treatment. Line thickness indicates successional age (double line: early successional stage, thin line: intermediate successional stage, thick line: late successional stage).

different pastures, without any influence from their topographic position (two-way ANOVA, $P \leqslant 0.01$). These distances are greatest in pots with soil from the late successional pasture and least in pots with soil from the pioneer stage (Confidence Level test, $P \leqslant 0.05$). Furthermore, these distances are significantly correlated with the increase in total mortality from W to D treatments ($r = 0.742$, $P \leqslant 0.001$).

The number of species per pot was lower in the D pots ($17.7 \pm 1.0$) than in the W pots ($22.9 \pm 0.8$) (paired *t*-test, $t = 3.80$, $P < 0.001$). Successional age and topographic position did not affect number of species per pot.

We used a Kruskal–Wallis test on each of the 20 species that indicated drought sensitivity of germination, mortality or both, in order to analyse the differences in the total number of germinations per pot between the pastures with different successional stages. Of 16 species with significant differences (Table 6), one has highest abundance in the early, four in the intermediate and 11 in the late pasture. There was also an increase with successional age of the percentages of drought-sensitive species with respect to the number of species that could be tested (Table 6).

Differences between field capacity and wilting point (Table 7) were higher in the late successional pastures ($F_2 = 12.3$, $P < 0.01$), while no differences were detected between the topographic positions ($F_1 = 2.7$, $P \geqslant 0.05$).

## Discussion

The results show that many species have higher mortality rates in the D treatment, while very few species show differences in germination between the two watering treatments. This suggests that a drought following the first autumn rains can have a considerable effect on the floristic composition of annual grasslands, mainly due to its differential effect on seedling mortality. Given that Heady (1958) found that the definitive composition of annual pastures was always determined prior to the third month after the start of germination, and that we found notable differences in floristic composition imposed by the drought after the first 2 months, we may assume that these differences in floristic composition are a reflection of the differences that would exist in the grassland in the following spring.

Nevertheless, the drought effect is probably underestimated in this experiment. We were unable to test for differences in germination or mortality rates for all the germinated species due to the fact that approximately half of the species comprising these pastures are rare. The collection of a larger number of replicates or the analysis of germination in seed lots and a subsequent analysis of seedling survival would probably facilitate the assessment of the impact of drought on a larger number of species.

Multidimensional scaling reveals that the changes

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**Table 6** Mean number of germinations per pot (± 1 SE) of the drought-sensitive species with significant differences in their abundance in the samples of each pasture. The value of the $K$ statistic is also indicated. The last row shows the percentage of sensitive species (from the total of species that could be tested) in each pasture

| | Successional stage | | | |
|---|---|---|---|---|
| Species | early | intermediate | late | $K$ |
| *Biserrula pelecinus* | 5.9 ± 1.7 | 2.1 ± 1.0 | 11.3 ± 3.0 | 11.5** |
| *Bromus hordeaceus* | 0 | 7.0 ± 5.0 | 0.1 ± 0.1 | 13.6** |
| *Galium murale* | 2.6 ± 1.3 | 0.2 ± 0.2 | 9.6 ± 6.2 | 7.6* |
| *Galium parisiense* | 11.6 ± 4.5 | 3.0 ± 0.8 | 18.0 ± 11.0 | 8.6** |
| *Herniaria hirsuta* | 4.4 ± 1.0 | 5.0 ± 2.1 | 0.9 ± 0.3 | 8.3** |
| *Hypochoeris glabra* | 0.1 ± 0.1 | 1.7 ± 0.7 | 1.6 ± 1.2 | 28.3** |
| *Polycarpon tetraphyllum* | 3.9 ± 1.8 | 0.1 ± 0.1 | 9.2 ± 2.6 | 9.1** |
| *Sagina apetala* | 7.9 ± 1.6 | 39.7 ± 12.1 | 10.4 ± 2.8 | 16.0** |
| *Spergularia purpurea* | 8.0 ± 1.7 | 2.1 ± 0.6 | 9.0 ± 2.7 | 8.8** |
| *Trifolium glomeratum* | 0.2 ± 0.2 | 0.7 ± 0.5 | 1.0 ± 0.5 | 14.3** |
| *Trifolium suffocatum* | 4.7 ± 2.7 | 2.9 ± 1.2 | 7.2 ± 1.2 | 19.0** |
| *Veronica arvensis* | 17.8 ± 3.6 | 5.2 ± 2.5 | 6.4 ± 3.0 | 20.0** |
| *Vulpia ciliata* | 3.2 ± 1.3 | 13.0 ± 3.9 | 27.7 ± 10.5 | 12.5** |
| *Vulpia membranacea* | 0 | 0.1 ± 0.1 | 0.7 ± 0.4 | 19.2** |
| *Vulpia muralis* | 8.0 ± 3.4 | 25.1 ± 6.2 | 48.6 ± 17.6 | 18.4** |
| *Vulpia myuros* | 0.4 ± 0.3 | 7.2 ± 3.4 | 8.7 ± 4.0 | 13.0** |
| Percentage of sensitive species | 7% | 12% | 29% | |

*$P \leqslant 0.05$, **$P \leqslant 0.01$.

in floristic composition stimulated by autumn drought become greater as the successional age of the pastures increases. The fact that the magnitude of these changes correlates with the increased mortality in the D pots is further evidence that the mechanism affecting floristic composition is seedling mortality and not differential species germination: differences in total germination between both watering treatments were only detected in five species. This higher seedling mortality in the D pots is also the cause of the lower species richness found in these pots. These results coincide with those of Loria & Noy-Meir (1979) in desert annuals, who found that the floristic composition of mature grassland in dry years is quite different from the initial seedling composition because of changes produced by differential seedling mortality.

In contrast to our expectations, there was no second wave of germination after the drought. Furthermore, the total number of germinations in this period was significantly higher in the W pots, which were in turn the pots with lowest mortality and hence had generated the fewest gaps. This might have been due to the less-favourable conditions for germination in the D pots, and also because of the irreversible loss of the germinative capacity of some seeds due to desiccation. Previous studies have highlighted the disastrous consequences of desiccation for germinative capacity when the seed has already begun cell division (Berrie & Drennan 1971; Bewley 1979).

**Table 7** Mean values (± 1 SE) of water available (difference between field capacity and wilting point) of the soil samples from the different successional stages and topographic positions

| Successional stage | Topographic position | |
|---|---|---|
| | upper | lower |
| Early | 3.00 ± 0.22 | 3.64 ± 0.83 |
| Intermediate | 3.74 ± 1.02 | 4.14 ± 0.68 |
| Late | 4.92 ± 1.94 | 5.42 ± 2.11 |

Drought-induced mortality is a mechanism that triggers changes in floristic composition. Marañon & Bartolome (1989) found that an autumn drought following the first September rains causes the death of 77% of the seedlings in a Californian annual grassland. These levels were reached in some of our pots, although the total mortality rates tended to be lower, probably because Marañon & Bartolome (1989) worked in the field, where conditions may be less benign.

Whatever the case, it must be stressed that drought sensitivity differs among species. The possession of leaf or stem hairs or CAM is effective in reducing plant water loss, and species such as *Crassula tillaea* probably owe their insignificant mortality in an autumn drought to possession of CAM. Similarly, the mortality rate of *Erodium cicutarium* is also unaffected by drought, as found in California, where years of low rainfall are described as 'filaree years', in which *Erodium* species are very abundant (Talbot *et al.* 1939; Rossiter 1966). On the other hand, in our experiment, clovers (which have neither CAM nor hairs) are characterized by a higher seedling mortality rate that coincides with observations of other authors (Gerakis *et al.* 1975).

There is a relationship between time of emergence and individual survival. The last seedlings to ger-

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minate have a higher mortality rate than the earlier germinators. This indicates that seedling survival is related not only to the presence of hairs or CAM, but also to the greater vigour of the individuals that have had more time to develop, giving the individuals a greater competitive ability. This result coincides with those of Black & Wilkinson (1963) who found that delays in germination of only a few days caused a significant fall in the survival of pure mixtures of *Trifolium subterraneum*. Harper (1961) also induced competitive reversals in competition between *Bromus diandrus* and *Bromus madritensis* by manipulating the timing of emergence. Differential species mortality also leads to a loss of species richness. This agrees with Tilman & El Haddi's (1992) results, who found that drought reduced the species richness of a mixed annual–perennial grassland in Minnesota by 37%, with the annual species being the most disadvantaged.

The positive correlation between mortality and density and the negative correlation between density and relative amount of water at the end of the simulated drought period, suggests that water is an increasingly limiting factor as seedling density increases. This coincides with Gordon & Rice's results (1993) for competition between annuals and blue oak seedlings (*Quercus douglasii*), where the lowest water potentials occur with the highest density of annuals. Piemeisel (1951) suggested that in communities of annuals, the amount of water available for an individual is a function of overall plant density.

Differences between field capacity and wilting point of the soils are bigger in the late successional pastures, indicating a greater water-retention capacity of these soils. In our estimate of water content, we are measuring the water contained in three compartments: water in the plant tissue + hygroscopic water + water available in the soil. It is thus only an approximate measure of the amount of water available in the pots for the plants. Nevertheless, the relative amount of water in the pots at the end of the experimental drought period correlates negatively with seedling density. The seedling densities are significantly higher in the successionally mature pasture. For this reason, although the gravimetric water content is not an accurate indicator of water potential when comparing soils of different texture, our results suggest that high seedling densities aggravate the limiting effect of water, which is translated into a higher seedling mortality.

The decline in species richness caused by the autumn drought has a similar magnitude in pastures with different successional ages and topographic positions. On the other hand, the differences in drought-induced mortality are greater in the late successional pastures, although this result should be approached with caution because of the significant interaction between the factors of successional age and topographic position.

The HMS shows that the most successionally mature pastures undergo the greatest change in their floristic composition in an autumn drought. This might be explained by the large number of individuals that germinated in several of the pots containing this pasture soil. On the other hand, the greater abundance of drought-sensitive species in mature pasture, would produce this result. However, because only 40% of species could be tested for drought sensitivity, it is difficult to detect possible successional trends in the abundance of drought-sensitive species.

## Acknowledgements

The authors are grateful to Catherine Levassor and Marta Ortega for their invaluable help in the field work and plant identification, Laparanza S.A. for providing access to the property, and the CICYT for Project Grant No. PB91-0020 which partially funded the study. We thank Dr A. H. Fitter, Dr L. Haddon and two other referees for their comments and corrections of the manuscript.

## References

Austin, M.P., Williams, D.B. & Belbin, L. (1981) Grassland dynamics under sheep grazing in an Australian mediterranean type climate. *Vegetatio*, **47**, 201–211.

Ashby, W.C. & Hellmers, H. (1955) Temperature requirements for germination in relation to wildland seeding. *Journal of Range Management*, **8**, 80–83.

Berrie, A.M.M. & Drennan, D.S.H. (1971) The effect of hydration-dehydration on seed germination. *New Phytologist*, **70**, 135–142.

Bewley, J.D. (1979) Physiological aspects of dessiccation tolerance. *Annual Review of Plant Physiology*, **30**, 195–238.

Black, J.N. & Wilkinson, G.N. (1963) The role of time of emergence in determining the growth of individual plants in swards of subterranean clover. *Australian Journal of Agricultural Research*, **14**, 628–638.

Drury, W.H. & Nisbet, I.C.T. (1973) Succession. *Journal of Arnold Arboretum of the Harvard University*, **54**, 331–368.

Espigares, T. & Peco, B. (1993) Mediterranean pasture dynamics: the role of germination. *Journal of Vegetation Science*, **4**, 189–194.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57–68.

Figueroa, M.E. & Davy, A.J. (1991) Response of mediterranean grassland species to changing rainfall. *Journal of Ecology*, **79**, 925–941.

Gerakis, P.A., Guerrero, F.P. & Williams, W.A. (1975) Ground water relation and nutrition of three grassland annuals as affected by drought. *Journal of Applied Ecology*, **12**, 125–135.

Gordon, D.R. & Rice, K.J. (1993) Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology*, **74**, 68–82.

Guitián, F. & Carballas, T. (1976) *Técnicas de Ana'lisis de Suelos*. Pico Sacro, Santiago de Compostela.

Gulmon, S.L. (1992) Patterns of seed germination in Californian serpentine grassland species. *Oecologia*, **89**, 27–31.

Harper, J.L. (1961) Approaches to the study of plant competition. *Society of Experimental Biology Symposium*, **15**, 1–39.

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Heady, H.F. (1958) Vegetational changes in the California annual type. *Ecology*, **39**, 402–416.

Hobbs, R.J. & Mooney, M.A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology*, **72**, 59–68.

Loria, M. & Noy-Meir, I. (1979) Dynamics of some annual populations in a desert loess plain. *Israel Journal of Botany*, **28**, 211–225.

Marañón, T. & Bartolome, J.W. (1989) Seed and seedling populations in two contrasted communities: open grassland and oak (*Quercus agrifolia*) understory in California. *Acta Oecologica*, **10**, 147–158.

Newman, E.I. (1963) Factors controlling the germination date of winter annuals. *Journal of Ecology*, **51**, 625–638.

Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–52.

Peco, B. (1989) Modelling mediterranean pasture dynamics. *Vegetatio*, **83**, 269–276.

Peco, B., Levassor, C., Casado, M.A., Galiano, E.F. & Pineda, F.D. (1983) Influences météorologiques et géomorphologiques sur la succession de pâturages. *Ecologia Mediterranea*, **9**, 63–76.

Peco, B., Olmeda, C., Casado, M.A., Levassor, C. & Pineda, F.D. (1988) Différentiation entre les effets des oscillations météorologiques et le processus successionel dans un pâturage méditerranéen. *Time Scales and Water Stress* (eds F. Di Castri, Ch. Floret, S. Rambal & J. Roy), pp. 441–445. *Proceedings of the 5th. International Conference on Mediterranean Ecosystems*. The International Union of Biological Sciences, Paris.

Piemeisel, R.L. (1951) Causes affecting change and rate of change in a vegetation of annuals in Idaho. *Ecology*, **32**, 53–72.

Pineda, F.D., Casado, M.A., Peco, B., Olmeda, C. & Levassor, C. (1987) Temporal changes in therophytic communities across the boundary of disturbed-intact ecosystems. *Vegetatio*, **71**, 33–39.

Pitt, M.D. & Heady, H.F. (1978) Responses of annual vegetation to temperature and rainfall patterns in Northern California. *Ecology*, **59**, 336–350.

Rossiter, R.C. (1966) Ecology of the mediterranean annual-type pasture. *Advances in Agronomy*, **18**, 1–56.

Talbot, M.W., Biswell, H.M. & Hormay, A.L. (1939) Fluctuations in the annual vegetation of California. *Ecology*, **20**, 394–402.

Tilman, D. & El Haddi, A. (1992) Drought and biodiversity in grasslands. *Oecologia*, **89**, 257–264.

Tutin, T.G. *et al.* (1964–81) *Flora Europaea*. Cambridge University Press, Cambridge.

Went, F.W. (1949) Ecology of desert plants. II. The effects of rain and temperature on germination and growth. *Ecology*, **30**, 1–13.

Young, J.A. & Evans, R.A. (1989) Seed production and germination dynamics in California annual grasslands. *Grassland Structure and Function*: *California Annual Grassland* (eds L.F. Huenneke & H. Mooney), pp. 39–45. Kluwer Academic Publishers, the Hague.

Young, J.A., Evans, R.A. & Kay, B.L. (1969) Germination characteristics of range legumes. *Journal of Range Management*, **23**, 98–103.

Young, J.A., Evans, R.A. & Kay, B.L. (1973) Temperature requirements for seed germination in an annual-type rangeland community. *Agronomy Journal*, **65**, 656–659.

*Received 4 February 1994*
*Revised version accepted 8 July 1994*

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