

Original article

Interference between perennial grassland and *Lavandula stoechas* subsp. *pedunculata* seedlings: a case of spatial segregation cause by competition

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Abstract

This paper analyses the relationship between *Lavandula stoechas* subsp. *pedunculata*, a common Mediterranean scrub species in central Iberia, and perennial grasslands. While *Lavandula* gives rise to almost monospecific formations in intermediate and upper hill zones, perennial grasses occupy the low areas. The proposed explanatory hypothesis for this spatial distribution is that the scrub is unable to establish itself in grasslands with heavy spatial occupation. We designed two experiments to test this hypothesis, one which analysed the effect of perennial grass cover on *Lavandula* establishment, and another which focused on its influence on previously implanted seedling survival and growth, distinguishing the effect of shoot and root interference. The results show negative interference during establishment and later in the use of light and nutrients. This results in a very low overall survival probability, with only 1.4% of seedlings surviving the first growth period. This low success rate explains the existence of a clear spatial segregation between scrub patches and perennial-dominated grasslands.

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Keywords: Labiatae; Mediterranean scrubland; Root and shoot interference; Seedling mortality; Survival analysis

1. Introduction

Competition between individuals for resources plays a widely accepted important role in plant community structure (Grime, 1977; Grace and Tilman, 1990; Goldberg and Barton, 1992). Although its influence on environments with low resource availability has been debated, there is now considerable evidence that competition also takes place in areas subject to heavy stress (Fowler, 1986; Vilá and Sardans, 1999).

In Mediterranean environments, irregular rainfall and summer drought often make water a limiting resource (Peco and Espigares, 1994; Tyler and D'Antonio, 1995). In addition, a lack of soil nutrients and the overlapping of different strata in the vegetation makes competition for nutrients and light also important (Callaway, 1992; Vilá and Terradas, 1995; Thébaud et al., 1996; Vilá, 1997). In microenvironments with a high level of vegetation cover, space availability is the first factor that limits the establishment of new individuals (Burke and Grime, 1996).

With all of these factors in play, interference between individuals may involve both the above and below-ground parts of the plant. Both types of interference are intimately related and may play an equally important role when there is competition for space (Casper and Jackson, 1997; McPhee and Aarssen, 2001; Cahill, 2002).

Finally, it should be noted that Mediterranean environments have a characteristically high heterogeneity associated with altitudinal gradients, topography and land use. This heterogeneity is evidenced in a wide diversity of environments that often arise at a small scale. In mountain areas of central Iberia, landscapes are often found with mosaic structures composed of small tessellates of scrub and grassland (Ramírez-Sanz et al., 2000). Traditionally, farmers have encouraged pasture at the expense of woody species to improve grazing conditions. This action has now ceased in most areas, which has led to the spread of shrubs in former grasslands and the colonisation of abandoned cropland.

In the following case, the spatial distribution of scrub and grassland seems to indicate the existence of clear spatial segregation. *Lavandula stoechas* subsp. *pedunculata* (Miller) Samp. ex Rozeira (Labiatae), henceforth *Lavandula*, occupies degraded, unproductive areas virtually lack-

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ing any perennial herbs. Their populations spread to low areas occupied by *vallicares*, Mediterranean grasslands over siliceous oligotrophic soils that are seasonally flooded and dominated by *Agrostis castellana* Boiss. & Reut. The aim of this research was to find out the mechanisms that bring on this distribution. The test hypothesis was that there is a process of competitive exclusion between the grassland and the scrub seedlings. We also tried to determine the stages during which this relationship becomes a restrictive interference on *Lavandula* colonisation.

Firstly, we studied the influence of interference on seedling emergence and establishment, regarded as the process via which the individual inserts its roots in the soil. Secondly, we planted *Lavandula* seedlings in a *vallicares* to observe the effect that interference with established species in the use of light and soil resources has on seedling growth and survival.

2. Materials and methods

2.1. Study area

The study was conducted on a piedmont area with undulating relief in central Iberia (altitude 800–900 m; mean annual temperature 13.2 °C; annual rainfall 540 mm). The local lithology is gneiss covered by shallow acid soils. The potential vegetation of the zone is *Quercus ilex* subsp. *balota* grove, although little more than small fragments and isolated trees remain in rocky places. At present the predominant vegetation is *L. stoechas* subsp. *pedunculata* scrub. This species primarily appears in high and intermediate slope zones while the low zones are occupied by perennial grass communities, *vallicares*, in which *A. castellana* is the most common species (Rivas-Goday and Rivas-Martínez, 1963). *Vallicares* can grow to a metre in height, and their dry aerial biomass reach a mean weight of $322.5 \pm 159.0 \text{ g/m}^2$ (\pm S.D.) (Sánchez, 2001). The soil characteristics in the *vallicares* differ clearly from those in the scrub areas, showing a higher clay, silt, organic matter and nitrogen content and a greater water-retention capacity (Sánchez, 2001).

2.2. Experiment 1: seedling emergence and establishment

This experiment consisted of sowing *Lavandula* seeds in a bed of perennial grasses ($n = 50$) or bare earth ($n = 50$) in order to observe the seedling emergence and establishment in each environment. The study was conducted in plastic trays with $6 \times 5.5 \times 14$ cm pots, filled with soil collected in the study area. The grass layer was generated by sowing each pot with 0.2 g of seeds from a commercial mixture, which primarily includes *Festuca* spp. The grass was clipped twice with scissors to encourage a similar to natural community density. Before starting to sow the *Lavandula* seeds in May 1999, plots were visually observed and those showing inadequate growth were rejected. The *Lavandula* seeds were harvested from individuals chosen at random in five patches in the study area. The parasited or empty sterile seeds were then removed.

Ten *Lavandula* seeds were sown in each pot in order to observe the effect of grassland cover on seedling emergence and establishment. The trays were left outdoor near the study area and watered to keep the soil permanently moist. The number of seedlings and established plants were recorded 15, 30 and 50 days after sowing.

2.3. Experiment 2: seedling growth and survival

A total of 200 *Lavandula* seedlings were sown in a *vallicular* using a two-factor experimental design (shoot interference and root interference) with two levels each (suppression and control), in October 1997 (Fig. 1). *Lavandula* seeds were collected and sown (10 per pot) as in experiment 1. In cases where more than one seedling emerged, the first one was maintained and the rest immediately removed. The trays were kept in the open air as in experiment 1.

About 40 days after sowing, the emerged seedlings were transplanted to a *vallicular* and subjected to one of four treatments: only root interference, only shoot interference, no interference and control treatment, in which the seedlings remained exposed to the characteristic interference of this type of grassland.

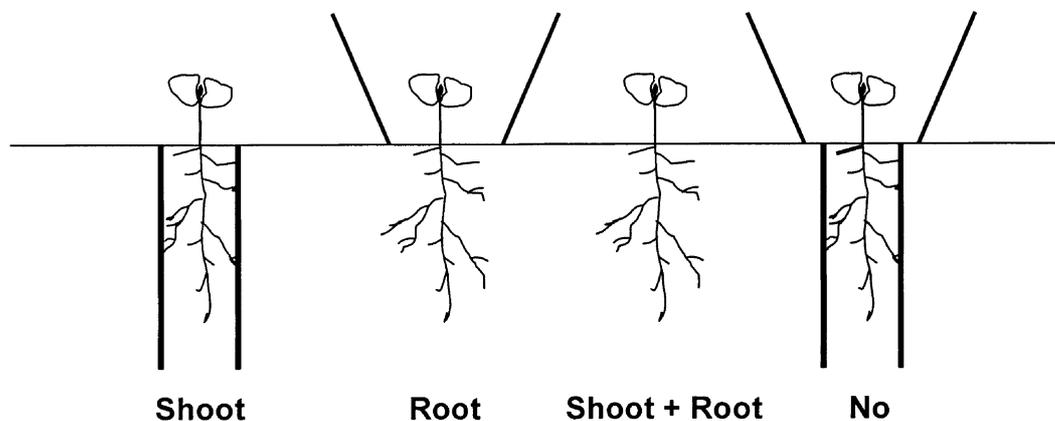


Fig. 1. Diagram of treatments in experiment 2 showing the type of interference between *Lavandula* seedlings and grassland in each case.

Recent papers have discussed the advisability of different methods used to suppress aerial and root interference (McPhee and Aarssen, 2001), stressing the need to limit the effect of the chosen devices. Designs such as the one proposed to satisfy this aim require a large increase in the number of treatments. This increment, when time and resources are limited, can only be implemented at the cost of reducing the number of replicates per treatment. While this approach could be considered in greenhouse studies where mortality rates are low, it would not have been viable in our field study. The high summer mortality rate of *Lavandula* seedlings in the study area requires the use of a large number of replicates per treatment. Thus, we considered it more important to prioritise the design under natural conditions, taking into account the possible methodological implications when interpreting the results.

For the planting process, soil cores were extracted using a 10 cm deep \times 4 cm diameter metal extractor. For seedlings that had to grow without root interference, a PVC pipe of the same dimensions was inserted in the hole. All holes were re-filled with extracted soil along with a *Lavandula* seedling. The presence of the open PVC pipe prevented interaction with adjacent roots without interfering with the seedling root growth.

In the case of aerial interference, the vegetation in a 25 cm radius around the *Lavandula* seedling was clipped. In other papers, aerial biomass is withdrawn without being cut (Gill and Marks, 1991). The decision to clip in this study was due to the following considerations: (i) both methods can promote lower root growth rates due to a decrease in photosynthetic activity caused by clipping plant organs in one case, and by their agglomeration in the other. This possible effect was not quantified, but can be assumed to act in the same direction as the elimination of aerial interference, adding to but not countering, its effect; (ii) both clipping and the devices normally used to remove the surrounding vegetation cause microclimatic variations, however, those linked to clipping are more similar to those that a seedling would withstand under natural conditions with no interference; (iii) the installation of screens usually modifies both the quality and the direction of the light, which may affect growth; (iv) finally, we were convinced that clipping would be preferable because it makes the experiment less conspicuous in areas frequented by livestock and wild herbivores.

The seedlings and treatments were distributed at random in the nodes of a 50 \times 20 m grid, so the seedlings were spread over a 1000 m² total area, without any blocking and at a minimum distance of 1 m between seedlings. A nail was left in the ground alongside each seedling to find their location with a metal detector. Seedlings were monitored monthly in the spring and summer of 1998. In May 1998 growth was estimated on the basis of number of leaf verticils. After the first summer drought, the seedlings were monitored in May 1999 and 2000.

2.4. Statistical analysis

In experiment 1 the “number of emerged seedlings” and the “percentage and final number of successfully established seedlings” were analysed using a Mann–Whitney *U*-test, due to the difficulties found in normalising the variables.

In experiment 2, the effect of interference on seedling growth was subjected to a variance analysis after log transformation of the variable “number of verticils”. The “number of seedlings that survived in each treatment” was analysed using a χ^2 -test in which the expected values were the average percentage of surviving seedlings on each treatment. Survival functions were estimated by the Kaplan–Meier method for each treatment. Shape differences related to both shoot and root interference was tested by the Breslow test (Breslow et al., 1984).

3. Results

3.1. Experiment 1: seedling emergence and establishment

Total emerged seedlings were 231 and 134 in pots with perennial cover and bare earth, respectively, i.e. an average of 4.62 and 2.68 seedlings per pot. This difference in number of emerged seedlings was statistically significant ($n = 50$; $U = 626.5$; $P = 0.001$).

The percentage of seedlings that successfully survived the establishment stage was significantly higher in pots with bare earth than in pots with perennials, 78.36% versus 7.36%, ($U = 116.5$; $P < 0.0001$).

The total count of seedlings that survived until 30 June, i.e. survival after both the emergence and the establishment stages in bare soil ($n = 105$), was significantly higher than in the grass treatment ($n = 17$) ($U = 390.5$; $P < 0.0001$).

3.2. Experiment 2: seedling growth and survival

Seedlings with the highest average number of verticils were those for which both types of interference were prevented (Fig. 2). However, only the effect of root interference was significant, and thus growth was greater in seedlings that were not exposed to root competition from their surroundings. The interaction between the two types of interference showed no significant effect on growth (Table 1).

Thirty-seven out of 190 seedlings survived the first summer drought, i.e. 19.47% of the total. Approximately 26% of the seedlings died in the winter, before March, some presumably due to the transplant from the pots to the *vallicar*. The highest mortality rate, 49.51%, was recorded in July and August, most probably caused by water stress during summer.

No significant effects were detected between the different interference treatments on numbers of seedlings that survived the first summer drought ($\chi^2 = 6.70$; $df = 7$; $P < 0.46$). Shoot interference caused significant differences on the

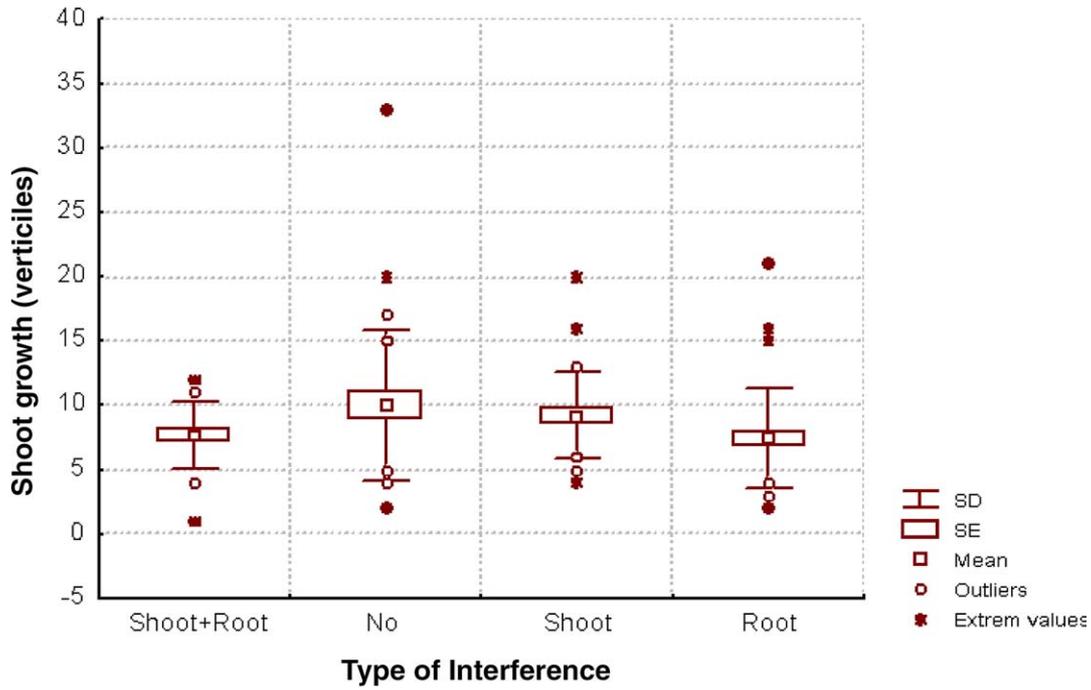


Fig. 2. Number of *Lavandula* seedlings verticiles in each treatment.

Table 1
Analysis of variance for seedling growth measured as number of verticiles

	Type III sum of squares	df	Mean square	F	Sig.
Root interference	0.318	1	0.318	6.620	0.011
Shoot interference	5.351E-03	1	5.351E-03	0.111	0.739
Root × shoot	3.808E-03	1	3.808E-03	0.079	0.779

shape of seedlings survival functions (Breslow statistic = 5.52; df = 1; $P = 0.188$). On the contrary, root interference did not cause such an effect (Breslow statistic = 1.45; df = 1; $P = 0.228$) (Fig. 3).

A total of 25 seedlings successfully survived the second summer drought, 20 of which were still alive in May 2000.

4. Discussion

The main idea arising from this study is that the spatial distribution of the studied communities is more closely related to the biotic component of the ecosystem than to the abiotic component. A species that is potentially able to live in a given area is displaced by species that take more advantage

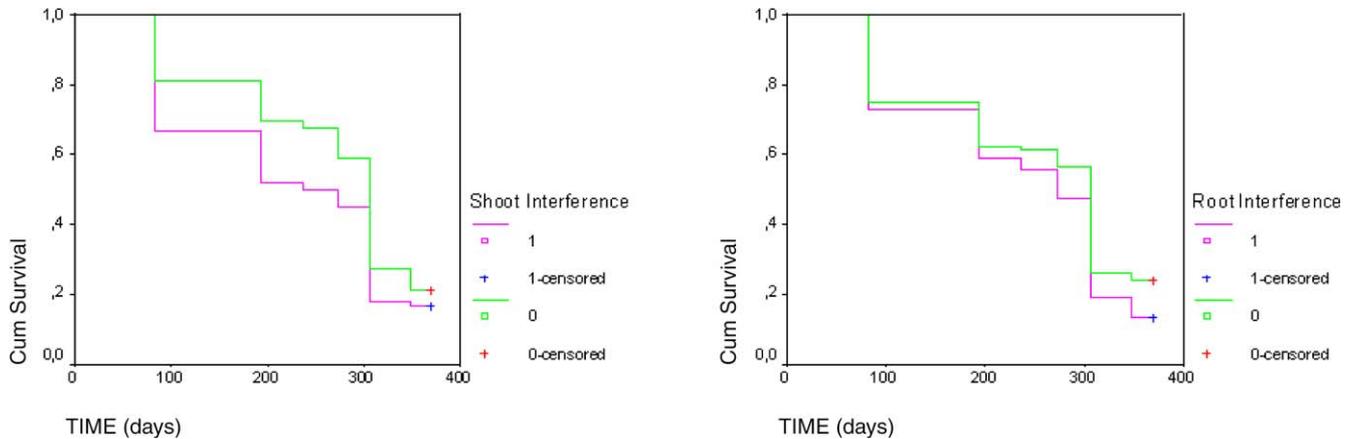


Fig. 3. Seedling survival functions showing the effect of root and shoot interference (1, interference; 0, no interference) during the seedlings' first vegetative period (November 1997–October 1998).

of the local environmental conditions. This is proven by the fact that several *Lavandula* seedlings survived for at least 2 years in the *vallicar* after their establishment was facilitated. Thus, the initial hypothesis to explain the spatial distribution of *Lavandula* seems to point in the right direction.

The most restrictive process for *vallicar* colonisation by *Lavandula* was establishment. The degree of cover in a community has often been linked to the probability of new seedling establishment and consequently its invasibility (Tilman, 1993, 1997; Burke and Grime, 1996; Davis et al., 2000). Some studies also show, specifically, how the presence of a blanket of perennial grasses prevents the establishment of woody species seedlings (O'Connor, 1995; Smit and Olf, 1998). Their roots are incapable of penetrating the layer of established vegetation and reach the soil if there are no gaps that create a discontinuity in the community (Brown and Archer 1990; Bush and Van Auken, 1991; Burke and Grime, 1996). The results of our paper provide evidence in the same direction.

After establishment, mortality until and during the first summer period was also very high. The first drought is the critical period in the population dynamics of *Lavandula* (Sánchez, 2001) and other Mediterranean shrubs that depend on seed-based propagation (Herrera, 1997; García-Fayos and Verdú, 1998; Paynter et al., 1998). After the first summer period, mortality declines. Probably, after passing this critical period, *Lavandula* roots should be able to pass through the soil horizon occupied by the established vegetation. This implies a niche separation or spatial stratification of resource exploitation according to functional groups, as described elsewhere for other communities (Manning and Barbour, 1988; Sala et al., 1989; Scholes and Archer, 1997).

Light availability appears to influence survival and cause the early death of seedlings subjected to shoot interference. The greater availability of resources in the *vallicar* is linked to a higher level of cover, which leads to a more intense interference in light use (Davis et al., 2000) than in the middle and upper slope zones. Furthermore, this interference is asymmetric (Casper and Jackson, 1997; Cahill and Casper, 2000), i.e. larger individuals enjoy an advantage that is disproportionate to their biomass from the moment when they begin to shade the smaller individuals. This was the case of perennial grasses, shoots and leaves on *Lavandula* seedlings which, when transplanted to the *vallicar*, only had two cotyledons measuring no more than 2 cm in height. This clear imbalance between the size of the woody seedlings and perennial grasses, together with the clear heliophyte feature of *Lavandula*, are the major factors that possibly explain the existence of a negative interference in light use.

At the same time, below-ground interference has a negative effect on growth, implying that exclusion of roots facilitates access to resources by *Lavandula* seedlings. This type of interference has been mentioned elsewhere (Reichenberger and Pyke, 1990; Van Auken and Bush, 1997) and frequently for pioneer successional stages (Fowler, 1986; Casper and Jackson, 1997). In this type of community, the

nutrient level is usually decisive and may even determine the degree of success of different functional types (Burke and Grime, 1996; Smit and Olf, 1998).

The lack of significant differences in the number of surviving seedlings between treatments suggests that the existing level of competition, both root and aerial is not strong enough to have an influence at this level. However, the high mortality rate makes it necessary to use a larger sample size in order to confirm this.

5. Conclusion

In this study, different short term effects of interference between *Lavandula* seedlings and perennial grass communities were found to be strong enough to influence the medium-term performance of *Lavandula* in *vallicares*. We, therefore, conclude that the difficulty during establishment and subsequent negative interference in the use of light and nutrients influences the viability of *Lavandula* in these areas, with a very low overall probability of survival (1.4%) until and during the first drought. This low success rate in surviving the first growth period explains the existence of a clear spatial segregation between shrub patches and perennial-dominated grasslands. The colonisation of these environments under the present conditions thus seems unlikely. At a larger temporal scale, however, the presence of disturbances that reduces grass cover might facilitate the process. These disturbances could be related to herbivores, ants or other agents, which at the same time can act as seed dispersers (Sánchez and Peco, 2002).

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References

- Breslow, N.E., Edler, L., Berger, J., 1984. A two-sample censored-data rank test for acceleration. *Biometrics* 40, 1049–1062.
- Brown, J.R., Archer, S., 1990. Water relations of a perennial grass and seedling vs. adult woody plants in a subtropical savanna, Texas. *Oikos* 57, 366–374.
- Burke, M.J.W., Grime, J.P., 1996. An experimental study of plant community invasibility. *Ecology* 77 (3), 776–790.
- Bush, J.K., Van Auken, O.W., 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (Leguminosae) seedlings in the presence of C4 grass. *Am. J. Bot.* 78 (12), 1732–1739.
- Cahill, J.F., 2002. What evidence is necessary in studies which separate root and shoot competition along productivity gradients? *J. Ecol.* 90, 201–205.

- Cahill, J.F., Casper, B.B., 2000. Investigating the relationship between neighbour root biomass and belowground competition: field evidence for symmetric competition belowground. *Oikos* 90, 311–320.
- Callaway, R.M., 1992. Effect of shrubs on recruitment of *Quercus douglassii* and *Quercus lobata* in California. *Ecology* 73, 2118–2128.
- Casper, B.B., Jackson, R.B., 1997. Plant competition underground. *Annu. Rev. Ecol. Syst.* 28, 545–570.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Fowler, N., 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17, 89–110.
- García-Fayos, P., Verdú, M., 1998. Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. *Acta Oecol.* 19 (4), 357–366.
- Gill, D.S., Marks, P.L., 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Monogr.* 61 (2), 183–205.
- Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* 139, 771–801.
- Grace, J.B., Tilman, D., 1990. *Perspectives on Plant Competition*. Academic Press, Inc., San Diego, CA.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111 (982), 1169–1194.
- Herrera, J., 1997. Effects of disturbance on the reproductive potential of *Lavandula stoechas*, a Mediterranean sclerophyllous shrub. *Ecography* 20, 88–95.
- Manning, S.J., Barbour, M.G., 1988. Root systems, spatial patterns, and competition for soil moisture between two desert subshrubs. *Am. J. Bot.* 75 (6), 885–893.
- McPhee, C.S., Aarssen, L.W., 2001. The separation of above- and below-ground competition in plants. A review and critique of methodology. *Plant Ecol.* 152, 119–136.
- O'Connor, T.G., 1995. Acacia karoo invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103, 214–223.
- Paynter, Q., Fowler, S.V., Memmott, J., 1998. Factors affecting the establishment of *Cytisus scoparius* in southern France: implications of managing both native and exotic populations. *J. Appl. Ecol.* 35, 582–595.
- Peco, B., Espigares, T., 1994. Floristic fluctuations in annual pastures: the role of competition at the regeneration stage. *J. Veg. Sci.* 5, 457–462.
- Ramírez-Sanz, L., Casado, M.A., de Miguel, J.M., Castro, I., Costa, M., Pineda, F.D., 2000. Floristic relationship between scrubland and grassland patches in the Mediterranean landscape of the Iberian Peninsula. *Plant Ecol.* 149, 63–70.
- Reichenberger, G., Pyke, D.A., 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85, 159–166.
- Rivas-Goday, S., Rivas-Martínez, S., 1963. Estudio y clasificación de los pastizales españoles. Ministerio de Agricultura, Madrid.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A., 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81, 501–505.
- Sánchez, A.M., 2001. Colonización y regeneración de *Lavandula stoechas* subsp. *pedunculata* en un paisaje agrario abandonado de la Sierra de Guadarrama. Ph.d. Thesis, Universidad Autónoma de Madrid.
- Sánchez, A.M., Peco, B., 2002. Dispersal mechanism in *Lavandula stoechas* subsp. *pedunculata*: autochory and endozoochory by sheep. *Seed Sci. Res.* 12, 101–111.
- Scholes, R.J., Archer, S.R., 1997. Tree–grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28, 517–544.
- Smit, R., Olf, H., 1998. Woody species colonisation in relation to habitat productivity. *Plant Ecol.* 139 (2), 203–209.
- Thébaud, C., Finzi, A.C., Affre, L., Debussche, M., Escarré, J., 1996. Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean old fields. *Ecology* 77, 791–804.
- Tilman, D., 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74, 2179–2191.
- Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78 (1), 81–92.
- Tyler, C.M., D'Antonio, C.M., 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. *Oecologia* 102, 255–264.
- Van Auker, O.W., Bush, J.K., 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology* 78 (4), 1222–1229.
- Vilá, M., 1997. Effect of root competition and shading on resprouting dynamics of *Erica multiflora* L. *J. Veg. Sci.* 8, 71–80.
- Vilá, M., Terradas, J., 1995. Effects of nutrient availability and neighbours on shoot growth, resprouting and flowering of *Erica multiflora*. *J. Veg. Sci.* 6, 411–416.
- Vilá, M., Sardans, J., 1999. Plant competition in Mediterranean-type vegetation. *J. Veg. Sci.* 10 (2), 281–294.