J. Range Manage.
53: 277–281 May 2000

Effect of grazing on the population biology of *Phalaris aquatica*

MARÍA JOSÉ LEIVA AND ROCÍO FERNÁNDEZ ALÉS

Authors are assistant professor and full professor, Departamento de Biología Vegetal y Ecología, Universidad de Sevilla. Apartado 1095, 41080-Sevilla, Spain.

Abstract

To examine the effect of grazing and potential interactions among grazing and biological traits of plants, we studied patch dynamics, seed production, and seedling survival in a Mediterranean population of the perennial grass *Phalaris aquatica* L. in grazed and ungrazed plots in southern Spain. Grazing by cattle induced an important (70%) decrease in the abundance of plants over 4 growing seasons. In the ungrazed plots, abundance of plants remained stable. Within these plots there was some (30%) spatial replacement of plants. However, replacement was by tillering and not by genets, genetically different individuals produced from seeds. The lack of genet replacement within the ungrazed plots agrees with results on mortality of young plants that were obtained from an independent field experiment, in which 85–95% of plants in different cohorts died within 1 to 3 growing seasons. This mortality of seedlings and young plants was concentrated in summers, especially when drought was prolonged. In contrast, seed production was apparently not a limiting factor for plant recruitment in ungrazed plots as seed output of the perennial grass (25,312 ± 3,255 seeds m^{-2}) was of the same magnitude as seed output in annual grasses that were abundant in the study site. Intensive grazing limited tiller production, patch size, and a summer drought limited recruitment of new adult individuals. These factors resulted in a low tolerance to episodes of high stocking rates from which the perennial grass was unable to recover.

Key Words: mediterranean grassland, overgrazing, perennial grasses, plant recruitment, seedlings survival, summer-drought

Resumen

Para examinar el efecto del pastoreo y potenciales interacciones entre pastoreo y características biológicas de las plantas en una población del sur de España de la gramínea perenne *Phalaris aquatica* L, se ha estudiado la dinámica de manchas, la producción de semillas y la supervivencia de plántulas en parcelas pastadas y sin pastar. El pastoreo por ganado vacuno produjo importantes (70%) decrementos de abundancia a lo largo de 4 estaciones de crecimiento. En las parcelas no pastadas la abundancia de las plantas se mantuvo constante pero hubo algún (30%) recambio espacial de las plantas. Este recambio fue por ahijamiento y no por instalación de nuevos individuos. La fatia de reemplazamiento de individuos geneticamente distintos en las parcelas no pastadas concuerda con los resultados sobre mortalidad de plantas jóvenes obtenidos en un experimento independiente. Entre el 85 y el 95% de las plantas jóvenes de distintas cohortes murieron durante 1 a 3 estaciones de crecimiento. Esta mortalidad se concentró durante el verano, especialmente cuando le sequía fue prolongada. Por el contrario la producción de semillas no fue, aparentemente, un factor limitante en las parcelas no pastadas ya que dicha producción (25.3 ± 3.255 semillas m^{-2}) fue de la misma magnitud que la producción de semillas de varias gramíneas anuales abundantes en el área de estudio. El efecto del intenso pastoreo limitando el ahijamiento y el tamaño de las manchas y el efecto de la sequía estival limitando el reclutamiento, resultaron en una baja tolerancia a episodios de altas presiones ganaderas de los que la gramínea perenne no pudo recuperarse.

Mediterranean grasslands in Spain, California, Israel, and Australia are dominated by annuals (Rivas and Rivas 1963, Rossiter 1966, Gulmon 1977). In these grasslands perennial grasses are much less abundant. However, the latter species show potential for improving the value of grasslands for use by livestock because they have longer growing seasons than annuals (Joffre et al. 1987).

Much evidence supports the hypothesis that overgrazing and other human disturbances are major causes of scarcity of perennial grasses in these grasslands (Joffre et al 1987, Rossiter 1966, Stoddart et al. 1975). For instance, in Spain and elsewhere in the Mediterranean basin, grazing has been continuously important for at least 7000 years (Naveh 1987). In California, overgrazing by livestock and an exceptional drought in the 1860s promoted expansion of annuals at the expense of perennial bunchgrasses (Huenneke 1989, Heady et al. 1991). In Israel, perennial grasses consistently decrease in grazed areas compared with adjacent ungrazed plots (Noy-Meir et al. 1989). However, little is known about the mechanisms implied in the decrease of perennial grasses. In this study we analyzed effects of grazing on vegetative growth and reproduction of a perennial grass, *Phalaris aquatica* L., which occurs in Mediterranean grasslands of southern Spain. We also studied the inherent rate of recruitment of new individuals in the population.

This study was supported with a grant from the Research and Development Program of the Spanish Government. The authors wish to thank Imanuel Noy-Meir and Maricruz Diaz-Barradas for useful comments and corrections on this manuscript. We also thank Manuel Ojedo, Isabel Roldán, Jose Laffarga and Ana Coca for field assistance.

Manuscript accepted 17 Aug. 1999.

Materials and Methods

Farm description and management

The study was conducted on a representative farm in Sierra

Morena, 30 km north of Seville, southern Spain (37°40'N, 5°59'W, 280 m above sea level), from 1988 through 1991. Climate was Mediterranean with 720 mm mean annual precipitation and 16°C mean annual temperature. Rainfall was concentrated from mid-September to mid-May and was usually negligible during the summer. However, the length of dry and wet periods varies greatly among years in this region (Ortega 1987). The vegetation was a holm oak savannah (40 trees ha^{-1}) with the understory dominated by annuals. The farm was dedicated to extensive beef cattle production with a total of 350 head of cattle on 1,200 ha of terrain. Cattle followed the breed composition of the major beef cattle of the region. Cows were of a local land race called Retinta and bulls were Retinta and Charolais. Cattle management followed the usual practices of the region. Animals were divided in lots with different composition (cows in pregnancy or lactation, dry cows, bulls, heifers) that moved rotationally among the 10 paddocks of different size (20–200 ha) in which the farm was divided. The number and kind of grazing animals in each paddock and the time they remained in them during each year did not depend on grassland offer but on other criteria such as facility for handling animals (Daza 1997). As a consequence, these parameters varied greatly among paddocks and from year to year. The paddocks that were closer to the headquarters often had high grazing intensity at peak intervals and were grazed by cows in late pregnancy and lactation because these paddocks were equipped with feedings troughs and animal health-care installations. Calves were born from September until January and the off-spring were usually sold at weaning.

Study site

The study was conducted in a paddock about 31 ha in size that was close to the headquarters. The terrain was flat and soils, derived from granite rock, were slightly acid. Grassland was composed of an annual sward dominated by the grasses *Bromus hordeaceous* L., *Agrostis pourretii* Willd, and *Vulpia geniculata* (L.) Link, the legume *Trifolium glomeratum* L., and the forbs *Chamaemelun mixtum* (L.) All. and *Leontodon longirrostris* (Finch & P.D. Sell) Talavera. There were also interspersed patches of the perennial grass *Phalaris aquatica* L. This perennial grass was re-seeded in the paddock in 1968 with seeds collected from scattered individuals naturally occurring in the surrounding area (Joaquin Terceño personal comm. 1987). There was also a 0.25 ha fenced plot, which excluded grazing, in the middle of the paddock. This plot was established 3 years before the beginning of our study. At this time, species composition inside and outside the fence was very similar (Joffre 1987).

Grazing treatment

The fenced plot continued ungrazed during the years of our study. For the rest of the paddock, information on the number and kind of animals, grazing season, supplementary feedings and animal care was obtained from the farmer (Miguel Huges personal comm. 1991 and 1999) and from personal observations during our visits to the field. From these data we calculated Cattle Units (C.U.) following recommendations of the French Institute of Agronomic Research (INRA), which are based on energy requirements of the animals (Jarrige 1990). A dry cow (500 kg) corresponded to 1 C.U., a cow in late pregnancy or lactation to 2 C.U., and a heifer (200 Kg) to 1.3 C.U. The stocking rate per month was calculated as the number of C.U. that grazed the paddock each month (during the grazing season) divided by the size (in ha) of the paddock. We also calculated the mean stocking rate per year as the stocking rate per month multiplied by the length (in months) of the grazing season and divided by 12 (number of months per year; Table 1).

Most animals that grazed our paddock were cows in late pregnancy and lactation, especially during the first 2 years of the study. This was due to the proximity to the headquarters and the facilities for supplementary feeding and vaccination of the offspring in the site. The herd size was similar in 1988 and 1989 but it was increased in 1990 and 1991 by adding 10 replacement heifers. Animals were usually moved to the paddock in early-winter, except for the year 1990 when they were moved in mid-autumn. This year, cattle remained in the paddock for 8 months instead of the 3 or 4 months of the other years (1987, 1988, and 1991). As a result mean stocking rate per year was 3-fold higher in 1990 than in the other years. Animals were supplemented yearly with straw and dry fodder from November until February and were provided with salt.

Patch dynamics and seed production in Phalaris aquatica.

In December of 1987, 4 permanent transects, 0.6 m x 10 m, were established in the grasslands. Each transect was divided into 150, 20- x 20-cm cells. Transects were placed on a mixed sward with patches of *Phalaris* and some patches of annuals. Two transects were inside the fence and the others were outside it, about 30 m apart from the former transects. In winter of 1988, a presence-absence map of each transect was recorded by hand, based on visual observations. Cells in which 1 or more shoots of *Phalaris* occurred were considered as present, and cells with no shoots of the species as absent. Mapping was conducted twice a year (in winter and spring) until winter of 1991.

To study seed production, in summer of 1988 we chose at random 15 presence-cells within each transect. All the spikes of *Phalaris* produced inside each cell were marked and were measured for length. The number of seeds per spike was estimated using a regression equation of the number of seeds and the length of the spike (seeds/spike = 1.43 *length of the spike (in mm) + 26.23) ($r = 0.67$, $p < 0.01$). This equation was obtained on a set of 20 spikes that were collected close to the transects inside the fence. In the grazed transects, all spikes that were marked were

Table 1. Grazing treatment. The length of the grazing seasons, the number and kind of animals that grazed the paddock each year and the calculated stocking rates are indicated.

Year	Grazing season	Herd composition	Stocking rate per month[1]	Mean stocking rate per year[1]
			-------------($C.U. ha^{-1}$)---------------	
1988	Jan. - April	17 Lp.[2] and lactation cows 10 dry cows	1.4	0.47
1989	Jan. - April	18 Lp. and lactation cows 8 dry cows	1.4	0.47
1990	Oct.- May	23 Lp. and lactation cows 4 dry cows 10 replacement heifers	2	1.35
1991	Jan.- March	21 Lp and lactation cows 5 dry cows 10 replacement heifers	1.9	0.47

[1]Cattle Units, calculated by procedure of Jarrige (1990)
[2]Late pregnancy.

eaten by cattle before seed ripening. Thus, there was no seed input into the soil's seed bank in these transects, and the spikes produced within them were not considered in our study.

Plant recruitment

In November 1987, eight, 50 cm x 50 cm plots were established at regular intervals inside the fence. Plots were sown at 5,000 seeds m^{-2} with seeds of *Phalaris* that had been collected in spring at the site described above. Plots were free of patches of *Phalaris* or any other perennial before sowing and were about 30 m apart from the closest patches of the perennial grass. To avoid competition among young plants of *Phalaris* and annuals, we removed all seedlings of annuals by hand in early autumn, before sowing the perennial grass (treatment annuals-). In the other 4 plots, annual seedlings were not removed (treatment annuals +). At the end of the first growing season (May 1988), the number of individuals of *Phalaris* that were established in each plot was recorded (the 1988 cohort). The censuses were repeated at the beginning and at the end of the growing seasons of the next 3 years (1989–1991). Individuals of *Phalaris* occurring inside each plot were assumed to belong to the initial seedling cohort because the newly established plants did not produce seeds during our study, presumably because they were too young. Moreover, seed drop from nearby patches of *Phalaris* inside the plots was unlikely to occur because of the long distance. Inside the annuals- plots, competition among plants was assumed to be of low intensity because of the low density (100 seedlings m^{-2}) of the established individuals of *Phalaris* from the beginning of the study.

Most annuals + plots were destroyed by rodent mounds during the first winter and we had to discard these plots from the experiment. A new experiment was performed in autumn of 1990 using 8 new plots that were assigned to identical treatments as in the first experiment, and the individuals established from this sowing (the 1990 cohort) were similarly monitored.

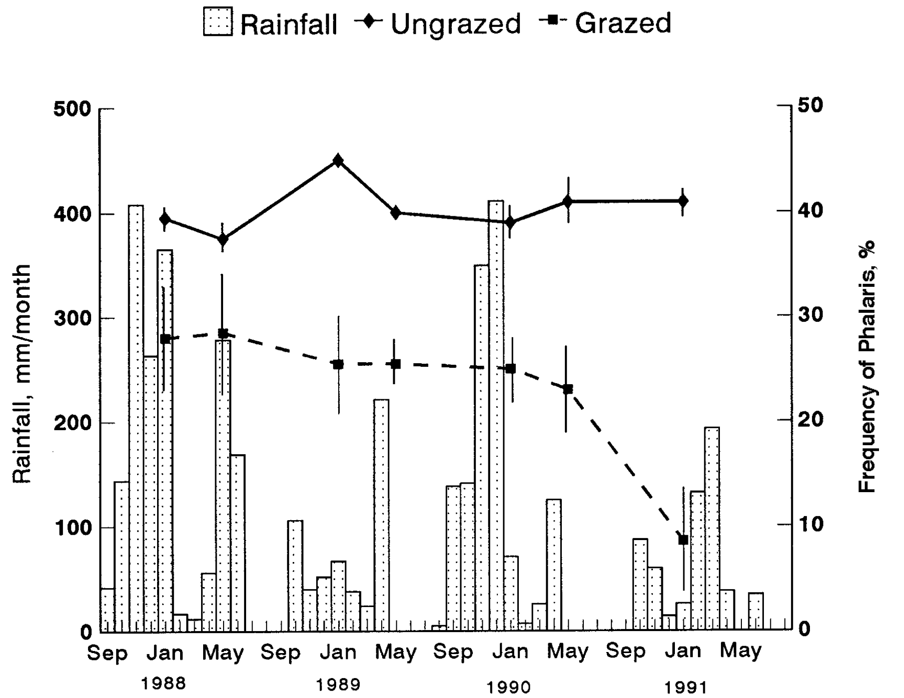

Fig. 1. Frequency of Phalaris (presence cells/total number of cells) in grazed and ungrazed transects (each point represents the mean of 2 transects (SE bars). Bars indicate monthly rainfall.

Results

Annual rainfall and its distribution varied greatly among years (Fig. 1). Both 1988 and 1990 were wet years with 1454 and 1268 mm rainfall, respectively. However, in 1988, the dry season was very short (112 days), while in 1990 it was very long (169 days). The other 2 years, 1989 and 1991 were dry, with 553 and 585 mm of rainfall, respectively. The length of the dry season in 1989 was intermediate (130 days).

In the grazed transects, frequency of *Phalaris* (i.e., presence cells/total number of cells) decreased slowly from the beginning of the study until spring of 1990 (Fig. 1). However, frequency of the species decreased more rapidly (62% losses) in winter of 1991, after the intensification of grazing. In the ungrazed transects, frequency of *Phalaris* changed very little during the years of this study (Fig. 1). The majority (67%) of cells in which the species occurred in autumn of 1989 (class 1 cells) contained it also at the end of the study (Table 2). We called these cells "permanents." Losses of *Phalaris* from the rest of class 1 cells were compensated by colonization of new cells (class 2 to 7 cells). However, colonization was ephemeral and the species disappeared again from most of these cells. Similar patterns (i.e., ephemeral colonization of some cells) were found in the grazed transects. However, in the latter transects, colonization did not compensate losses of the species from class 1 cells and net changes in frequency were negative. Cell colonization took place in the border of permanent cells and was due to spread of vegetative tillers. No seedlings of *Phalaris* were observed in the transects during our study.

Protected transects of *Phalaris* produced 25,312$\pm$3,255 seeds m^{-2} (mean $\pm$ standard deviation) in 1988. Although seed output varied greatly among years and production in 1988 cannot be taken as an absolute value, we observed significant spike and seed production in *Phalaris* during the 4 years of this study.

Seedlings of *Phalaris* that were established in experimental plots in spring of 1988 (i.e., 1988 cohort) comprised 2% of the sown seeds. Seedlings that were established in spring of 1990 (i.e., 1990 cohorts) comprised 1.5% and 0.9% of the seeds that were sown in the annuals - and annuals + plots. Seedling survival was very low in the 2 cohorts (Fig. 2). About 91% of the individuals of the 1988 cohort had died by the end of the experiment. The highest mortality (57%) was suffered during the first summer, when seedlings were very young. Mortality was lowest (7%) in the second summer when plants were older and drought length was intermediate. Mortality increased again (22%) the third summer when drought was the longest during the study period. During the last dry season, the majority of seedlings of the 1990 cohort died also. In this cohort mortality was moderately lower (83%)

Table 2. **Number of cells in which Phalaris occurred at different times (presences). Class 1 are cells in which the species occurred at the beginning of the study. Class 2 are cells that were colonised by the species in spring of 1988 and so on. Values are total number of cells in fenced and grazed transects.**

Cell class	1988		1989		1990		1991
	Winter	Spring	Winter	Spring	Winter	Spring	Winter
Fenced transects	(N)						
1	119	104	104	98	94	86	80
2	—	7	7	4	4	4	2
3	—	—	23	14	8	8	2
4	—	—	—	4	0	0	0
5	—	—	—	—	11	5	4
6	—	—	—	—	—	20	8
7	—	—	—	—	—	—	25
Grazed transects							
1	80	74	65	53	52	44	20
2	—	7	2	1	1	1	0
3	—	—	6	4	4	2	0
4	—	—	—	7	5	0	0
5	—	—	—	—	11	10	1
6	—	—	—	—	—	7	1
7	—	—	—	—	—	—	2

when annuals were removed from plots (annuals - plots) than when annuals were not removed (95% mortality in the annual + plots).

Discussion and Conclusions

The substantial decrease of *Phalaris* in grazed transects vs. the small changes that occurred in transects protected from grazing (Fig. 1) are in agreement with patterns found in other Mediterranean grasslands where perennial grasses consistently decreased in areas grazed by cattle (Noy-Meir et al. 1989). Our results also agree with studies on the effect of general disturbances in grassland reducing locally the cover of perennial grasses (Gomez-García et al. 1995, McIntyre et al. 1995, Milton et al. 1997). The delayed response to overgrazing in *Phalaris*, which decreased in abundance in the year after grazing intensification, has been also found in other perennial grasses in Mediterranean and semiarid grasslands. This delay is probably related to a decrease of energy reserves stored by plants which decrease regrowth of new tillers in autumn (Trlica and Cook 1972, Singh et al. 1980).

During the years of this study, there was some (30%) spatial replacement of plants of *Phalaris* within the transects, with ephemeral colonization of cells adjacent to permanent cells (i.e., cells in which the species occurred from the beginning of the study until the end). This replacement was among ramets, the vegetative tillers that were presumably produced from below-ground plant parts (rhizomes and crowns) rooted in permanent cells. However, there was no replacement associated with new genets, the genetically different individuals produced from seeds, because no seedlings of *Phalaris* were found in any transect.

In the grazed transects, lack of seedlings could be explained by almost complete consumption of *Phalaris* spikes by cattle before seed dispersal, effectively preventing seed input to the soil. However, seedlings were also abscent in protected transects although *Phalaris* plants produced and dispersed abundant seeds each year. In 1988, seed output of *Phalaris* (25,312 ± 3,255 seeds m^{-2}) was similar to seed output of representative annual grasses abundant in the study site. For instance, *Bromus hordeaceus*, an annual grass of similar seed size as *Phalaris*, produced 53,434 ± 2,138 seeds m^{-2} and *Vulpia genic - ulata* 30,308 ± 2,150 seeds m^{-2} (Leiva 1992). Lack of seedlings and young plants of *Phalaris* in protected transects disagree with results of our experiment on plant recruitment, in which we did find 1- to 3-year old plants of this species (Fig. 2). Thus, seedlings and young plants of *Phalaris* could have been understimated in protected transects because of accumulated litter and green biomass, which made it difficult to find tiny plants. Potential underestimation of young plants, however, does not substantially change our conclusion on the scarcity of genet replacement even in protected transects, since the summer mortality (85-95%) of young plants of *Phalaris* observed in the plant recruitment experiment indicated a low probability for individuals to reach maturity (Fig. 2). The low tolerance to summer drought that we found in young *Phalaris* plants is in agreement with observed influence of summer

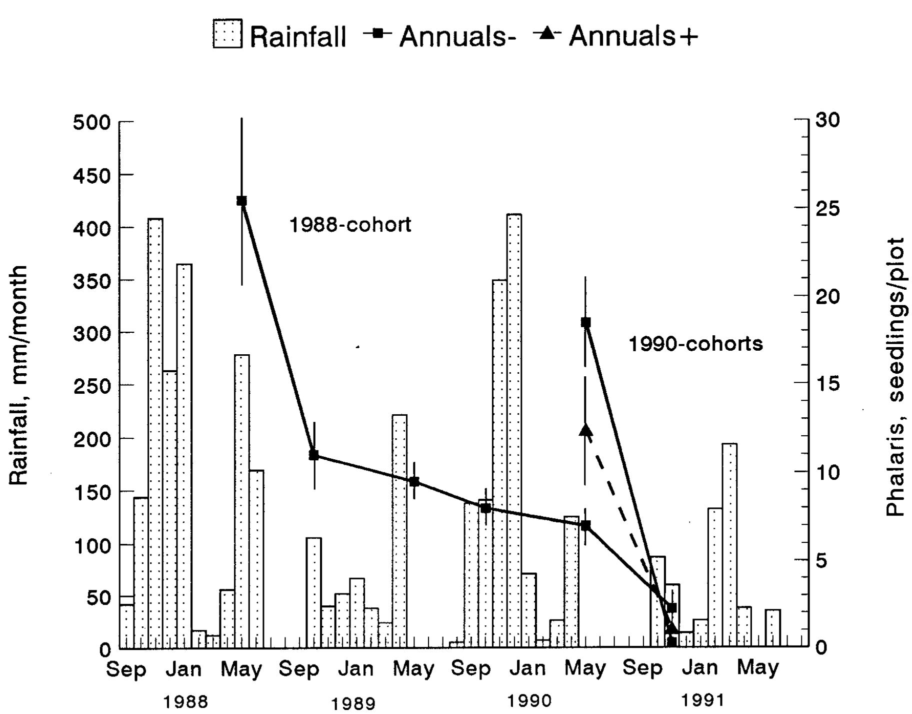

Fig. 2. Survival curves of cohorts of seedlings of *Phalaris* (each point represents the mean of 4 replicates (SE bars). Annuals - and annuals + indicate treatments for 1990-cohorts. Monthly rainfall as in Figure 1.

drought on seedling survival in many species in other Mediterranean ecosystems (Horton and Kraebel 1955, Keeley and Zedler 1978, Aschman 1984, Frazer and Davis 1988). Populations of herbaceous perennials have been considered to be at a regressive stage when they have lost their ability to produce seeds and replace genets (Harper 1977). This stage can also be reached if, as in our case, mortality of young plants is very high and there is a lack of recruitment of adult plants. Mediterranean populations of some endangered plants that fail in recruitment of new individuals also show high sensitiviy to grazing (Aparicio and Guisande 1997).

We conclude that in the Mediterranean population of *Phalaris* studied, grazing decreased tiller production and patch size. Summer drought limited recruitment of new adult individuals, resulting in a low tolerance to episodes of heavy grazing from which the perennial grass was unable to recover. Recovery could have been higher under more favorable climatic and edaphic conditions. We propose that, in any given habitat, a grazing intensity should be considered as overgrazing if it promotes irreversible declines in populations. Thus, the threshold level of overgrazing is species and habitat dependent.

Literature Cited

Aparicio, A. and R. Guisande. 1997. Replenishment of the endangered *Echinospartum algibicum* (Genisteae, Fabaceae) from the soil seed bank. Biol. Conserv. 81:267–273.

Aschmann, H. 1984. A restrictive definition of Mediterranean climates. Bull. Soc. Bot. Fr., Actual. Bot.131:21–30.

Daza, A. 1997. Sistemas de producción de vacuno de carne en zonas de dehesa, p. 193–211. *In*: C. Buxadé-Carbó (ed.), Vacuno de Carne: aspectos clave. Mundiprensa. Madrid, Spain.

Frazer, J. M. and S. D. Davis. 1988. Differential survival of chaparral seedlings during the first summer drought after wildfire. Oecologia 76:215-221.

Gomez-García, D., C. E. Borghi, and S. M. Giannoni. 1995. Vegetation differences caused by pine vole mound building in subalpine plant communities in the Spanish Pyrenees. Vegetatio 117:61–67.

Gulmon, S.L. 1977. A comparative study of the grassland of California and Chile. Flora 166: 261–278.

Harper, J.L. 1977. Population biology of plants. Academic Press. London, England.

Heady, H. F., J.W. Bartolomew, M.D. Pitt, G. D. Savelle, and M.C. Stroud. 1991. California Prairie, p. 313-335. *In*: Coupland R.T. (ed.), Ecosystems of the world, Natural Grassl. Elsevier, Amsterdam, The Netherlands.

Horton, J. S. and C. J. Kraebel. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecol. 36:244–262.

Huenneke, L. F. 1989. Distribution and regional patterns of Californian grasslands, p. 1-12. *In*: L. F. Huenneke and H. A. Mooney (eds.), Grassland structure and function: California annual grassland. Kluwer Academic Publisher, Dordrecht, So. Africa.

Jarrige, J. 1990. Alimentación de bovinos, ovinos y caprinos. Mundiprensa. Madrid, Spain.

Joffre, R. 1987. Contraintes du milieu et réponses de la végétation herbacée dans les dehesas de la Sierra Norte (Andalousie Espagne) Thèse de doctorat USTL Montpellier, France.

Joffre, R., M. J. Leiva, S. Rambal, and R. Fernandez Alés. 1987. Dynamique racinaire et extraction de l´eau du sol par des graminées pérennes et annuelles méditeranéennes. (Ecol. Plant. 8:181-194.

Keeley, J. E. and P. J. Zedler. 1978. Reproduction of chaparral scrubs after fire: A comparison of sprouting and seeding strategies. Amer. Midl. Nat. 99:142–161.

Leiva, M. J. 1992. Factores que limitan a las comunidades de gramineas perennes en los pastos mediterráneos de la Sierra norte de Sevilla. Tesis Doctoral Univ. Seville, Spain.

McIntyre, S., S. Lavorel, and R. M. Tremont. 1995. Plant life history attributes: Their relationship to disturbance response in herbaceous vegetation. J. Ecol. 83: 31-44.

Milton, S.J., W.R.J., Dean, and S. Klotz. 1997. Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. J. Veget. Sci. 8: 45-54.

Naveh, Z. 1987. Landscape ecology, management and conservation of European and levant Mediterranean uplands, p. 641-657. *In:* J. D. Tenhunen, F. M. Catarino, O. L. Lange, and W. C. Oechel (eds.), Plant response to stress. Functional analysis in Mediterranean ecosystems. Springer-Verlag, Berlin, Germany.

Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of mediterranean grassland plants to grazing and protection. J. Ecol. 77: 290–310.

Ortega, F. 1987. Cambios temporales de los pastos anuales mediterráneos de la Sierra Norte de Sevilla en relación con el régimen de precipitación. Tesis Doctoral. Univ. Seville, Spain.

Rivas, S. and S. Rivas. 1963. Estudio y clasificaciún de los pastizales españoles. Publicaciones del Ministerio de Agricultura. Madrid, Spain.

Rossiter, R C. 1966. Ecology of the mediterranean annual-type pasture. Advan. Agron. 18:1–56.

Singh, J. S., M. H. Trlica, P. G. Risser, R. E. Redmann, and J. K. Marshall. 1980. Autotrophic subsystem, p. 60-190. *In*: A. I. Breymeyer and G. M. Van Dyne (eds.), Grasslands, systems analysis and man. Cambridge Univ. Press. Cambridge, England

Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. Range management 3rd ed., McGraw-Hill, New York, N.Y.

Trlica, M. J. and C. W. Cook. 1972. Carbohydrate reserves of crested wheatgrass and Russian wildrye as affected by development and defoliation. J. Range Manage. 25:430-435.