Plant Ecology **159:** 201–209, 2002. © 2002 Kluwer Academic Publishers. Printed in the Netherlands.

Early establishment of planted *Retama sphaerocarpa* seedlings under different levels of light, water and weed competition

José María Rey Benayas^{1,*}, Antonio López-Pintor¹, Carmen García², Nuria de la Cámara², Reto Strasser² and Antonio Gómez Sal¹

¹Departamento de Ecología, Universidad de Alcalá, Alcalá de Henares, 28871, Spain; ²Bioenergetics Laboratory, University of Geneva, Jussy-Geneva, CH-1254, Switzerland; *Author for correspondence (e-mail: Strasser@uni2a.unige.ch; fax: +41 22 7591945, phone: +41 22 7591944, http://www.come.to/bionrj)

Received 12 September 2001; accepted in revised form 12 April 2001

Key words: Abandoned Mediterranean cropland, Artificial shading, Fluorescence Performance Index, Irrigation, Shrub establishment, Weed biomass

Abstract

Large amounts of former cropland are being abandoned in developed regions. To formulate guidelines for land reclamation programmes, we explored the effects of artificial shading, irrigation, and removal of weed competition on the performance of Retama sphaerocarpa (L.) Boiss. seedlings in a factorial experiment located in an abandoned cropland in Central Spain. R. sphaerocarpa is of interest for revegetation because it is a drought tolerant leguminous shrub that is a major structural component of the native plant community. Seedling performance was evaluated in three ways: seedling survivorship, growth, and photochemical efficiency. We also measured soil moisture and weed biomass production and found that both increased under artificial shading conditions. Soil moisture increased very slightly where weeds were removed. Thus, increased transpiration from weeds outweighed reduced evaporation from soils due to shading by weeds. Artificial shading was the most effective treatment for seedling survivorship, followed by removal of competition by weeds. After summer, 34 % of the seedlings survived in the most favourable conditions (artificially shaded plots where weeds were removed), compared to ca. 1 % in full-light plots with no removal of weed competition. A positive effect of irrigation was found for growth of seedling cover and height in shaded plots. The analysis of photochemical efficiency pointed out the relevance of weed competition removal, and confirmed the usefulness of fast fluorescence transient techniques for the quantification of seedling performance. The data suggest that competition between seedlings and weeds was primarily for water rather than for light. We conclude that i) artificial shading improved seedling performance, but this is a little practical technique because of its cost; ii) as weeds compete with, rather than facilitate, planted seedlings, weed clipping around the seedlings is a feasible technique that would improve seedling survival; and iii) seedling performance could also considerably improve with a higher irrigation than was used in this experiment (75lm⁻² per growth period), provided that weeds are removed.

Introduction

Various social, economical and technological changes have resulted in the abandonment of extensive areas of former cropland in developed countries during the last few years (FAO 1998). This phenomenon has created considerable quantities of "empty" spaces in some regions of these countries. What can be done with these spaces? They can be devoted to a different use such as tree plantations (Lemieux and Delisle 1998); they can be left to undergo natural secondary succession (Debussche et al. 1996); or they can be managed to favour certain plant species which have specific environmental and ecological benefits such as soil erosion control, succession facilitation and increased biological diversity (Vieira et al. 1994; Whisenant et al. 1995; Bakker et al. 1998). However, the establishment of native woody plant species in Mediterranean environments is usually hindered by important abiotic and biological limitations such as radiation input, water stress and competition from herbaceous species. Thus, these constraints need to be identified and appropriate management practices must be developed to assure successful revegetation projects.

In this study we experimentally explored the effects of various factors limiting the performance of introduced seedlings of Retama sphaerocarpa (L.) Boiss in abandoned croplands in a Mediterranean region. R. sphaerocarpa is a xerophytic, nitrogen-fixing, leguminous shrub which ameliorates microclimatic conditions in its understory, thus increasing diversity and productivity of herbaceous species (Pugnaire et al. 1996; Moro et al. 1997a, 1997b). It is a pioneer species and a major structural component of the native plant communities in many old fields, being usually the only woody species, and functions as an "island" for the herbaceous plants in terms of nutrients, microclimate, and a refuge from livestock herbivory. It is a leafless shrub up to 4m tall which mostly occurs in the dry regions of North Africa and the Iberian Peninsula. Architecturally, it has multiple branches holding green cladodes rising from thick roots that can penetrate to soil depths of >25m (Haase et al. 1996a). These subterranean parts sprout easily when the aerial biomass is removed. Sexual reproduction is less successful because recently emerged seedlings are very susceptible to mortality due to abiotic factors, herbivory, and competition from herbs (Haase et al. 1996b; Gómez Sal et al. 1999).

Three important factors limit the establishment and growth of woody plants in this type of habitat. These are excessive radiation inputs, low precipitation and water availability, and weed competition (Rey Benayas 1998). Strong radiation can limit plant survival in dry environments. However, the crown architecture of R. sphaerocarpa has been shown to achieve an optimal trade-off between radiation capture and avoidance of photo-damage, enabling this species to survive under high light conditions (Valladares and Pugnaire 1999). In our experimental design, radiation input was manipulated by artificial shading, water input by irrigation, and weed competition by clipping. These three factors have complex interactions (Berkowitz et al. 1995). Weeds may compete for resources with woody species, but they may also reduce radiation input and soil water evaporation thus favouring seedling establishment. Our objective is to ascertain the effects of these factors on the early establishment (first year) of *R. sphaerocarpa*, and then to develop management practices to aid survivorship. Performance of the seedlings can be assessed by measuring their survivorship and growth as well as by using eco-physiological methods. Here we use *in vivo* fluorescence to screen many samples rapidly and quantify the vitality of the planted seedlings (Hall et al. 1993).

Methods

The experimental design

The study was conducted in a 1-ha flat, homogenous plot that was formerly cropland. It had been cultivated for many years until *R. sphaerocarpa* seedlings were planted in the winter of 1998. This plot was located in the "El Encín" experimental estate in Alcalá de Henares, central Spain (Longitude $40^{\circ}35'$ N, Latitude $3^{\circ}25'$ W). Mean annual temperature is $13.5 \,^{\circ}$ C and annual precipitation averages 450mm, with a pronounced summer drought. In the year the experiment took place, the late spring and summer were drier than usual. The plot was fenced to exclude medium and large size herbivores. Nevertheless, at the end of summer we observed that rabbits damaged *R. sphaerocarpa* seedlings severely.

The experiment was laid out as a split-plot design with four replicate blocks. Each block contained four main-plot treatments and each plot was $7.5m \times 7.5m$ in size. The main plot treatments were factorial combinations of artificial shading (artificially shaded vs. full-light plots) and summer irrigation (irrigated vs. non-irrigated plots). These main-plot treatments were applied randomly within blocks. Each main-plot was split into two sub-plot treatments, namely clipping vs. no clipping of weeds. Twelve one-year-old seedlings were planted in winter with a regular distribution in each of the 32 sub-plots, being separated from each other by at least 1.5m. The seedlings were planted with 20-cm diameter plugs that were buried 40cm deep. All seedling death within the 4 first weeks of the experiment was attributed to transplanting problems, and these were replaced.

The treatments were the following:

- 1. Artificial shading: a black polyethylene net placed 1.8m above the ground, which reduced incident radiation by 68%.
- 2. Irrigation: providing water uniformly to 1m²

around the seedlings. This treatment was applied three times. The total amount of water added was 15 litres m⁻² at mid June, 30 litres m⁻² at the end of June and 30 litres m⁻² at the peak of the dry season (late July). Thus, the irrigated plots received "additional" water equivalent to 17% of the average annual precipitation in the area. We added this relatively small amount of water to simulate likely irrigation practice in large open fields.

 Clipping of weed aerial biomass around the planted seedlings. Weeds were clipped three times during the growth period (April, May and June) to continuously reduce competition by weeds, always within a 0.5m×0.5m quadrat centred on each seedling.

Measurements

We examined the performance of *R. sphaerocarpa* seedlings in the different treatments in three ways: 1) seedling survivorship, 2) growth and 3) effects on photochemical efficiency. We also measured 4) soil moisture and 5) weed biomass production.

- 1. Seedling survival was assessed three times: early summer (beginning of July), end of summer (October) and 1 year after planting. One year after planting, we also counted any new shoots from apparently dead seedlings for an additional period of 5 months.
- 2. Growth was estimated in all living seedlings by measuring the following biometric parameters: straightened seedling height, stem diameter (2cm above the ground level), and seedling volume. The volume was the product of the crown projected area -the elliptical surface of the crown projected onto the ground- and seedling height. All biometric parameters were measured right after planting took place (before treatments were applied) and at the end of the growth period (October, after treatments were applied). To avoid the effect of initial biometric differences in seedlings, growth was evaluated as relative growth (initial biometric measure-minus final biometric measure/initial biometric measure).
- 3. Fast chlorophyll-a fluorescence induction kinetics was measured with a Plant Efficiency Analyser (PEA Hansatech Instruments Ltd. King's Lynn GB). We took the average of two fluorescence

measures per live seedling in the field in early summer. The fast fluorescence rise has been described earlier (Strasser et al. 1995) as OJIP-rise due to the intermediate steps J (at 2ms) and I (at 30ms) between the initial fluorescence O (Fo, measured at $50\mu s$) and the maximal fluorescence $P(F_{M}, which appears between 200 and 1000ms).$ The experimental data were analysed according to the equations of the OJIP-test (Strasser et al. 1996). We inferred a Performance Index (PI_{ABS}) which is an overall value that combines parameters related to photosynthetic activity. The PIABS was defined according to the Nernst equation and can therefore be considered in the logarithmic form as an estimation of a potential or a photosynthetic force of the sample (Strasser et al. 1999, 2000). More details about the Performance Index can be found in the cited publications.

- 4. Soil moisture was measured at 0–20cm depth. Measurements were taken in early spring (May), late spring (June) and mid summer (end of July) using the TRIME-method, an specially designed TDR technique (IMKO, Micromodultechnik company).
- 5. Above ground weed biomass was clipped, dried at 80 °C and weighed for one third of the 0.5×0.5m quadrats. Clipping was practised always in the same quadrats.

Data analysis

Statistical analyses of data were based upon ANOVA to detect the effects of treatments and treatment interactions on the above mentioned measures. The general structure of the ANOVA is shown in Table 1. Seedling survival was so low under some treatment combinations that we did not have sufficient replicates to test the effects of treatment interactions on seedling growth. We used STATISTICA for the analyses (Statsoft, Inc. 1993).

Table 1. General structure of the ANOVAs –degrees of freedom for the different sources used to detect treatment effects on the various measures analysed in the experiment.

Term	Df
Total	31
Main plots	15
Blocks	3
Shading	1
Irrigation	1
Shading×Irrigation	1
Error I	9
Clipping	1
Clipping×Shading	1
Clipping×Irrigation	1
Clipping×Shading×Irrigation	1
Error II	12

Results and discussion

Treatment effects on soil moisture, weed biomass production and R. sphaerocarpa seedling performance

Overall, we found significant differences for R. sphaerocarpa seedling survivorship and fluorescence Performance Index PIABS, i.e. photochemical efficiency, and for soil moisture and weed biomass production among treatments (Table 2). The rank of importance for the treatments was artificial shading, removal of weed competition, and irrigation; irrigation had very little effect on the various variables analysed. Soil moisture increased under artificial shading conditions (Figure 1, Table 2A). Soil moisture averaged 16.9 \pm 1.15 % in late spring and 4.44 \pm 0.59 % in mid summer in full-light plots, and $21.06 \pm 2.63 \%$ and 5.1 ± 0.32 %, respectively, in shaded plots. Weed removal had only minor effects on soil moisture when water was a limiting factor $(4.63 \pm 0.65 \%$ in nonclipped plots vs. 4.9 ± 0.49 % in clipped plots in mid-summer) (Figure 1, Table 2A). Total weed biomass production also increased in the plots under artificial shading treatment (63.89 \pm 15.39g/m² in fulllight plots vs. 83.98 ± 19.47 g/m² in shaded plots) (Figure 2, Table 2B)

Artificial shading greatly affected seedling survivorship, followed by removal of weed competition (Table 2C). After summer, only 34.4 % of the seedlings survived under the most favourable conditions (artificially shaded plots with removal of competition), compared to ca. 1 % that survived in full-light

plots without the removal of competition (Figure 3). For the rest of the year, mortality was insignificant. We did not observe any new shoots sprouting from apparently dead seedlings during the following growing season. For R. sphaerocarpa seedling growth, the only significant effect we found was that irrigation increased volume under artificial shading conditions $(-0.48 \pm 0.53 \text{ in irrigated plots } vs. - 0.57 \pm 0.36 \text{ in}$ non-irrigated plots) (Table 1D). We found only one significant interaction effect at P < 0.05: weed removal and irrigation increased stem diameter growth in shaded plots ($F_{1,6} = 8.31$). Actually, these growth parameters were slightly negative, i.e. seedling volume and stem diameter shrank rather than expanded, meaning that seedling performance was extremely poor even under favourable treatments.

The fluorescence measurement allows an estimation of the efficiency of these treatments. Figure 4 represents the effects of environmental manipulations on seedling photosynthetic performance (PI_{ABS}). The highest and lowest PI_{ABS} values were obtained under conditions of maximal and minimum (control) environmental manipulation, respectively. This figure and Table 2E show that the removal of weeds increased the PI_{ABS} under full light, artificial shade, no irrigation, and irrigation conditions.

Interpretation and management implications

The positive effects of artificial shading on the performance of R. sphaerocarpa seedlings are attributed to the reduction of abiotic stress. Abiotic stress amelioration has two major components in our study: a reduced soil moisture evaporation that may increase water availability to plants (Figure 1, Table 2A) and a likely reduction of direct photo-inhibition. We did not assess direct photo-inhibition. R. sphaerocarpa has been reported to be able to cope efficiently with strong radiation (Valladares and Pugnaire 1999), but our results suggest that this is only true for adult, well-established plants, since we obtained a very low survivorship rate for seedlings under full-light conditions. The surplus of available water provided by artificial shading was also used by weeds (seedling competitors) throughout the growth period, since artificially shaded plots exhibited a greater total weed biomass production (Figure 2, Table 2B). Weed cover in our study little affected soil moisture, although clipped plots exhibited slightly moister soils than non-clipped plots (Figure 1, Table 2B).



Figure 1. Changes in soil moisture under different treatment conditions (see Table 2A for overall statistical comparisons). Pair-wise comparisons resulted in not different means at P < 0.05 according to a Tukey's test. Bars are standard errors. Environmental conditions are: FL = full light, AS = artificial shade, NI = no irrigation, I = irrigation, WP = weed presence, WR = weed removal.



Figure 2. Total weed biomass production under different treatment conditions (see Table 2B for overall statistical comparisons). Pair-wise comparisons resulted in not different means at P < 0.05 according to a Tukey's test. Bars are standard errors. Environmental conditions are: FL = full light, AS = artificial shade, NI = no irrigation, I = irrigation.

We found one marginally negative effect of irrigation on seedling performance; fewer seedlings survived in irrigated plots at mid-summer (Figure 3, Table 2C). This effect can be attributed to increased competition by weeds in irrigated plots rather than to negative effects of the water itself. In fact, at this time weed biomass production was greater in irrigated plots than in non-irrigated plots. Removal of competition by weeds improved seedling performance. Our fluorescence analysis pointed to this treatment as the most efficient. Weed layer was very dense and taller than the seedlings, a feature of vegetation cover in recently abandoned cropland. Is weed competition primarily for space and light or for water? Our data suggest that competition is primarily for water for two reasons: 1) increased transpiration

Table 2. Effects of artificial shading, irrigation, and removal of weed competition on A) soil moisture, B) weed biomass production, C) R.
sphaerocarpa seedling survivorship and D) growth, and E) fluorescence Performance Index. (*) P < 0.1, * P < 0.05, ** P < 0.01, ***P < 0.001.
Note: if for a given measure a treatment had not been applied yet or was not considered, the general structure of the ANOVA reported in
Table 1 does not remain.

Dependent variable	Treatment Effects				
	Artificial shading	Weed competition removal	Irrigation	Block effects	
A) Soil moisture					
In early spring	$F_{1,3} = 3.82$	$F_{1,6} = 6.56^*$	NOT APPLIED	$F_{1,3} = 10.94^{**}$	
In late spring	$F_{1,3} = 12.72^*$	$F_{1,6} = 0.09$	NOT APPLIED	$F_{1,3} = 0.58$	
In mid-summer	$F_{1,9} = 12.37^{**}$	$F_{1,12} = 3.89(*)$	$F_{1,9} = 0.73$	$F_{1,9} = 1.43$	
B) Weed biomass					
In early spring	$F_{1,3} = 1.6$	NOT CONSIDERED	NOT APPLIED	$F_{1,3} = 0.91$	
In late spring	$F_{1,3} = 4.61$	NOT CONSIDERED	NOT APPLIED	$F_{1,3} = 0.62$	
In mid-summer	$F_{1,9} = 0.28$	NOT CONSIDERED	$F_{1,9} = 4.24$	$F_{1,9} = 0.28$	
Total	$F_{1,9} = 10.23^{**}$	NOT CONSIDERED	$F_{1,9} = 0.51$	$F_{1,9} = 5.53^*$	
C) Seedling survivorship					
In mid-summer	$F_{1,9} = 0.89$	$F_{1,12} = 3.08$	$F_{1,9} = 4.45(*)$	$F_{1,9} = 0.25$	
Early autumn	$F_{1,9} = 24.4^{***}$	$F_{1,12} = 16.31^{**}$	$F_{1,9} = 1.27$	$F_{1,9} = 0.25$	
After 1 st year	$F_{1,9} = 23.23^{***}$	$F_{1,12} = 8.57^*$	$F_{1,9} = 0.52$	$F_{1,9} = 0.99$	
D) Seedling growth after the growing s	season ⁽¹⁾				
Straightened height	NOT CONSIDERED	$F_{1,6} = 0.57$	$F_{1,3} = 2.71$	$F_{1,3} = 3.47$	
Stem diameter	NOT CONSIDERED	$F_{1,6} = 0.02$	$F_{1,3} = 0.22$	$F_{1,3} = 0.33$	
Volume	NOT CONSIDERED	$F_{1,6} = 0.03$	$F_{1,3} = 11.44^*$	$F_{1,3} = 22.19^{**}$	
E) Fluorescence Performance Index	NOT CONSIDERED	$F_{1,12} = 24.85^{***}$	$F_{1,9} = 0.33$	$F_{1,9} = 10.04^{**}$	

⁽¹⁾ For these measurements analyses apply to shaded plots only. See *Data Analysis* for further explanations.

from weeds outweighed reduced evaporation from soils in the soil moisture loss balance, and 2) artificial shading improved seedling survival (light was not limiting). A number of studies have demonstrated that herb competition reduces survival and growth of different woody species, either planted or naturally established (Gordon et al. 1989; Morris et al. 1993; Owens et al. 1995; Kollmann and Reiner 1996; Geyer and Long 1998; Lemieux and Delisle 1998). Henkin et al. (1998) found that soil water depletion during the spring-summer transition period left very little available water in the rooting zone of the herbaceous vegetation to maintain shrub seedlings throughout the summer. The difference in the success of shrub seedling establishment mainly reflected the accessibility of water below the rooting zone of the herbaceous vegetation. Early succession weeds are capable of rapidly developing their biomass and exploit resources, particularly water, more efficiently than R. sphaerocarpa seedlings (Alon and Kadmon 1996).

It is remarkable the enormous mortality of planted 1-year old *R. sphaerocarpa* seedlings. A later examination of the seedlings within their nursery bags made us suspect that part of this mortality could be due to the curvature acquired by the main root. Thus, a conclusion of this experiment is that the choice of this age seedlings for revegetation projects is clearly not the best. This does not invalidate our experimental results since all seedlings were produced under equal conditions in the same nursery and randomly picked out to be planted among different treatment plots. An alternative is the introduction of pre-germinated *R. sphaerocarpa* seeds. Espigares et al. (under review) did so and also found an enormous competition effect of herb seedlings. Survival of seedlings, either planted or not, in early establishment has been found to be a bottleneck in the recruitment process of many woody species (García-Fayos and Verdú 1998; Rey Benayas 1998).

Since weeds proliferate more intensively during the first two years right after cropland abandonment, introduction of *R. sphaerocarpa* seedlings should take place later, when weeds proliferate less and perennials are still little abundant. In this way, excessive weed competition can be avoided. Actually, our field observations indicate that natural re-establishment of *R. sphaerocarpa* usually does not occur before 4–5 years after cropland abandonment. The management practices of artificial shading, irrigation, and weed re-



Figure 3. Survival counts of planted *R. sphaerocarpa* seedlings under the 8 treatment combinations (see Table 2C for overall statistical comparisons). Bars are standard errors. Environmental conditions are: FL = full light, AS = artificial shade, NI = no irrigation, I = irrigation, WP = weed presence, WR = weed removal. Data for significant differences according to ANOVAs are the following. At mid-summer: $NI = 77.08 \pm 14.43$ %, $I = 64.12 \pm 20.37$ %. In early autumn: $FL = 5.2 \pm 9.06$ %, $AS = 29.81 \pm 18.54$ %; $WP = 10.54 \pm 14.35$ %, $WR = 24.48 \pm 20.97$ %. After one year: $FL = 3.64 \pm 5.24$ %, $AS = 24.48 \pm 17.6$ %.

moval have an economic impact. From our experiment, we suggest the following for introduction of R. sphaerocarpa in Mediterranean abandoned croplands: 1) Artificial shading improves seedling performance because it increases soil water availability and, probably, because it ameliorates photo-inhibition damage. 2) Weeds hinder, rather than facilitate, the implantation of seedlings, competition being primarily for water. 3) The irrigation scheme adopted in this experiment did not improve seedling performance. 4) Weed removal favoured photosynthetic activity as measured by OJIP fluorescence rise. We highlight the following associated conclusions for management of R. sphaerocarpa plantations. 1) Unfortunately, artificial shading is not a practical technique because it is very costly, unless plantations are concentrated into small

plots scattered in the target lands. 2) Clipping of weeds around the seedlings, particularly in late spring and early summer, is an inexpensive technique that would greatly improve seedling survival. 3) A larger amount of water than was used in this experiment $(75 \text{Im}^{-2} \text{ per growth period})$, added by irrigation, could also considerably improve seedling performance, as long as weeds are removed. 4) *In vivo* fluorescence techniques are a rapid and useful method to quantify the actual vitality of planted seedlings. Overall, our results demonstrate the importance of experimental approaches, together with empirical field observations, to understand factors explaining woody seedling performance and, as a consequence, to improve the success of revegetation efforts.



Figure 4. Fluorescence performance indexes PI_{ABS} of *R. sphaerocarpa* cladodes grown under eight different experimental field conditions. Field conditions are represented at the eight corners of a cube. The size of the spheres is proportional to the PI_{ABS} value under the different field conditions. The diameter of the sphere was plotted as the square of the calculated PI_{ABS} . Each line on the cube indicates an environmental transition due to a management practice (artificial shading: Full Light to Artificial Shade; irrigation: Non-Irrigated to Irrigated; weed removal: Weed Presence to Weed Removal). All parallel lines of the cube correspond to the same management practice. The non-manipulated field conditions (control) correspond to the corner FL-NI-WP; and maximal management conditions correspond to the corner AS-I-WR. Abbreviations in the figure correspond to the above bolded initials.

Acknowledgements

This research was chiefly funded by the CICYT project "Determinantes de la diversidad biológica en ecosistemas mediterráneos. Papel de los procesos locales y regionales" (AMB 96-1161). Additional support from the projects "Factores limitantes de la revegetación con especies leñosas autóctonas de áreas degradadas en ambientes mediterráneos. Rendimiento distintas actuaciones de manejo" (CICYT de REN2000-0745/GLO) and "Estrategias para la restauración de paisajes degradados en zonas secas" (UA), the Swiss National Foundation (to R. J. Strasser) and by an Erasmus-Socrates Mobility Grant (to Carmen García and Nuria de la Cámara). We are indebted to Rafael Muñoz Box for his input on the statistical analyses, and to P. Castro, D. Milchunas, F. Valladares, P. Villar, and two reviewers for their comments on a preliminary version of this manuscript.

References

- Alon G. and Kadmon R. 1996. Effect of successional stages on the establishment of *Quercus calliprinos* in an East Mediterranean maquis. Israel Journal of Plant Science 44: 335–345.
- Bakker J.P., van Andel J. and van der Maarel E. 1998. Plant species diversity and restoration ecology: Introduction. Applied Vegetation Science 1: 3–8.
- Ball M.C., Butterworth J.A., Roden J.A., Christian R. and Egerton J.J.G. 1995. Applications of chlorophyll fluorescence to forest ecology. Australian Journal of Plant Physiology 22: 311–319.
- Berkowitz A.R., Canham C.D. and Kelly V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology 76: 1156–1168.
- Debussche M., Escarré J., Lepart J., Houssard C. and Lavorel S. 1996. Mediterranean plant succession: Old-fields revisited. Journal of Vegetation Science 7: 519–526.
- Espigares T., López-Pintor A., Rey Benayas J.M. and Gómez Sal A. Effects of phenology and water availability on competition between *Retama sphaerocarpa* seedlings and the understorey herbaceous vegetation. Journal of Vegetation Science under review.
- FAO 1998. The State of Food and Agriculture, Rome.
- García-Fayos P. and Verdú M. 1998. Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. Acta Oecologica 19: 357–366.

- Geyer W.A. and Long C.E. 1998. Weed management in plantings of tree and shrub seedlings with sulfometuron methyl (Oust). Transactions of Kansas Academy of Science 101: 120–124.
- Gómez Sal A., Rey Benayas J.M., López Pintor A. and Rebollo S. 1999. Role of disturbance in maintaining a savanna-like pattern in Mediterranean *Retama sphaerocarpa* shrubland. Journal of Vegetation Science 10: 365–370.
- Gordon D.R., Welker J.M., Menke J.W. and Rice K.J. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. Oecologia 79: 533–541.
- Haase P., Pugnaire F.I., Fernández E.M., Puigdefábregas J., Clark S.C. and Incoll L.D. 1996a. An investigation of rooting depth of the semi-arid shrub *Retama sphaerocarpa* (L.) Boiss. by labelling of ground water with a chemical tracer. Journal of Hydrology 177: 23–31.
- Haase P., Pugnaire F.I., Clark S.C. and Incoll L.D. 1996b. Spatial patterns in a two-tiered semi-arid shrubland in south-eastern Spain. Journal of Vegetation Science 7: 527–534.
- Hall D.O., Scurlock J.M.O., Bolhar-Nordenkampf H.R., Leegood R.C. and Long S.P. 1993. Photosynthesis and Production in a Changing Environment: a Field and Laboratory Manual Chapman & Hall, London.
- Henkin Z., Seligman N.G., Kafkafi U. and Prinz D. 1998. End-ofseason soil water depletion in relation to growth of herbaceous vegetation in a sub-humid Mediterranean dwarf-shrub community on two contrasting soils. Plant and Soil 202: 317–326.
- Kollmann J. and Reiner S.A. 1996. Light demands of shrub seedlings and their establishment within scrublands. Flora 191: 191–200.
- Lemieux C. and Delisle C. 1998. Using cover crops to establish white and black spruce on abandoned agricultural lands. Phytoprotection 79: 21–33.
- Moro M.J., Pugnaire F.I., Haase P. and Puigdefábregas J. 1997a. Effect of the canopy of *Retama sphaerocarpa* on its understory in a semiarid environment. Functional Ecology 11: 425–431.
- Moro M.J., Pugnaire F.I., Haase P. and Puigdefábregas J. 1997b. Mechanisms of interaction between a leguminous shrub and its understory in a semi-arid environment. Ecography 20: 175– 184.
- Morris L.A., Moss S.A. and Garbett W.S. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. Forest Science 39: 166–187.

- Owens M.K., Wallace R.B. and Archer S.R. 1995. Landscape and microsite influences on shrub recruitment in a disturbed semiarid *Quercus-Juniperus* woodland. Oikos 74: 493–502.
- Pugnaire F.I., Haase P., Puigdefábregas J., Cueto M., Clark S.C. and Incoll D. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semiarid environment in south-east Spain. Oikos 76: 455–464.
- Rey Benayas J.M. 1998. Growth and mortality in *Quercus ilex* L. seedlings after irrigation and artificial shading in Mediterranean set-aside agricultural lands. Annales de Sciences Forestieres 55: 801–807.
- Strasser R.J., Srivastava A. and Govindjee 1995. Polyphasic chlorophyll a fluorescence transient in plants and cyanobacteria. Photochemistry and Photobiology 61: 32–42.
- Strasser R.J., Eggenberg P. and Strasser B.J. 1996. How to work without stress but with fluorescence. Bulletim de la Societe Royale des Sciences de Liége 65: 330–349.
- Strasser R.J., Srivastava A. and Tsimilli-Michael M. 1999. Screening the vitality and photosynthetic activity of plants by fluorescence transient. In: Behl R.K., Punia M.S. and Lathers B.P.S. (eds), Crop Improvements for Food Security. SSARM, Hisar, India, pp. 79–129.
- Strasser R.J., Srivastava A. and Tsimilli-Michael M. 2000. The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yurus M., Pothe U. and Mohanty P. (eds), Probing Photosynthesis: Mechanism, Regulation and Adaptation. Taylor and Fransis, London, pp. 445–483.
- Valladares F. and Pugnaire F. 1999. Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. Annals of Botany 83: 459–469.
- Vieira I.C.G., Uhl C. and Nepstad D. 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. Vegetatio 115: 91–99.
- Whisenant S.G., Thurow T.L. and Maranz S.J. 1995. Initiating autogenic restoration on shallow semiarid sites. Restoration Ecology 3: 61–67.