REFERENCES

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POTENTIAL FOR USING FACILITATION BY GRASSES TO ESTABLISH SHRUBS ON A SEMIARID DEGRADED STEPPE

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Abstract. In arid and semiarid environments, isolated vegetative patches establish islands of fertility in which facilitation is a dominant interaction between plant species. These patches may provide favorable microsites for revegetation with desirable species in areas where traditional revegetation procedures fail. Alpha grass (*Stipa tenacissima*) steppes are widely distributed within the semiarid areas of southern Europe and northern Africa and represent a degraded stage of climax vegetation. In this study, we analyzed the effects of *S. tenacissima* tussocks on the survival, growth, and ecophysiological features of experimentally planted seedlings of *Medicago arborea*, *Quercus coccifera*, and *Pistacia lentiscus* in three sites in a semiarid region in southeastern Spain. Our main objective was to test whether *S. tenacissima* was able to facilitate shrub establishment in semiarid degraded steppes.

Soils under *S. tenacissima* tussocks had higher organic matter content and water availability than those from open areas. *Stipa tenacissima* significantly reduced photosynthetically active radiation and soil temperature. One year after planting, shrub survival was significantly higher near *S. tenacissima* ("tussock" microsite) than on the open areas ("open" microsite). Predawn water potentials of the shrub seedlings measured before and after the summer were significantly higher in the tussock microsites, with differences ranging from 22% to 33% and from 17% to 38% before and after the summer, respectively. Leaf biomass for seedlings harvested before and after the summer was significantly higher for seedlings planted on tussock microsites in comparison to the open microsites. Our results suggest a direct facilitative effect of *S. tenacissima* on introduced shrubs. This study indicates that positive interactions in semiarid steppes can be of particular importance for effective restoration in degraded semiarid ecosystems.

Key words: facilitation; island of fertility; Medicago arborea; Quercus coccifera; Pistacia lentiscus; *plant–species interactions; restoration; semiarid zones; southeastern Spain; steppes;* Stipa tenacissima.

INTRODUCTION

Degradation of arid lands by human activity is a major environmental problem throughout the world (Schlesinger et al. 1990). Degraded drylands often result in a decrease in plant cover, leading to a deterioration in the ecosystem composition and function and fostering physical and chemical soil loss to a point at which degradative trajectories may be sustained without further disturbance (Thornes 1995). In these cases, some form of remedial action is necessary (Aronson et al. 1993).

In arid and semiarid ecosystems, vegetation is sparse and spatial distribution of soil properties is markedly patchy, leading to the development of "resource islands" under the vegetative patches surrounded by relatively infertile soils (Schlesinger et al. 1996, Reynolds et al. 1999). These fertile patches are points of high biological activity where facilitation may be an im-

portant interaction between plant species (Callaway 1997). Positive interactions between plants is a widespread phenomenon (Callaway 1995) that has been mainly described in harsh conditions, such as those in arid and semiarid environments (Franco and Nobel 1989, Pugnaire et al. 1996, Moro et al. 1997). Positive interactions may become weaker as abiotic stress decreases and, as a result, competitive interactions often become more important (Bertness and Callaway 1994, Callaway 1997), even for the same species association (Callaway 1994).

Extensive areas of the world's semiarid zones are occupied by steppes (Soriano 1983, West and Young 2000). In the Mediterranean Basin they cover >400 000 km² (Le Houérou 1986), and many of them are dominated by alpha grass (*Stipa tenacissima* L.) tussocks (Puigdefábregas and Mendizábal 1998). These steppes are often structured in a spotted or banded spatial configuration (Puigdefábregas and Sánchez 1996) with patterns resembling features of the "tiger-bush" vegetation described for semiarid regions in Australia, the Sahel zone of Africa, Mexico, and USA (Valentin et al. 1999). It has been suggested that *S. tenacissima*

steppes resulted from the disturbance of Mediterranean open forests in northern Africa (Le Houérou 1986) and woodlands dominated by Quercus coccifera L. and Pistacia lentiscus L. in southwestern Europe (Rivas Martínez 1987). Moreover, these steppes have been progressively degraded by overexploitation, grazing, and later abandonment (Puigdefábregas and Mendizabal 1998). Spontaneous recolonization of woody species in alpha grass steppes may be unlikely or too slow because of the relative scarcity of remaining individuals, because the current soil and microclimate conditions may be unsuitable for their establishment (Le Houérou 1986), because of competition with established vegetation (Sánchez 1995), or because of the lack of appropriate dispersers and dispersal sites (Alcántara et al. 1997).

Recent studies have thoroughly described the effect of S. tenacissima tussocks on their own microenvironment through the amelioration of the microclimate (Valladares and Pugnaire 1999), the improvement in the soil structure (Bochet et al. 1999), and the increase in soil moisture (Puigdefábregas and Sánchez 1996), water infiltration (Cerdá 1997, Cammeraat and Imeson 1999), and carbon storage and nitrogen (Martínez-Sánchez et al. 1994, Sánchez 1995, Bochet et al. 1999) in relation to bare areas. At the hillslope and basin level, spatial patterning of S. tenacissima determines the distribution of water and sediment flows (Puigdefábregas and Sánchez 1996, Cammeraat and Imeson 1999). These changes may favor the establishment of therophytes (Sánchez 1995) and moss and lichen communities (Martínez-Sánchez et al. 1994).

Positive interactions can be used to improve restoration success (Bradshaw 1983, Franco and Nobel 1989, Mitchley et al. 1996). Restoration of degraded arid and semiarid ecosystems may be fostered with techniques that concentrate resources and ameliorate microenvironmental conditions (Whisenant et al. 1995, Ludwig and Tongway 1996, Tongway and Ludwig 1996). Existing vegetation may provide favorable microsites for the introduction of species of interest (Cortina and Vallejo 1999, Vallejo et al. 1999), especially in arid and semiarid areas where traditional revegetation procedures are highly mechanized, expensive, risky, and may promote further site degradation (Finkel 1986).

Facilitation has been incorporated into ecosystem management (Oliver and Larson 1996) and sometimes taken as a sine qua non condition for the establishment of late-successional species (Montero and Alcanda 1993). But despite the widespread importance of facilitation in arid and semiarid ecosystems, very few studies have conducted manipulative experiments including field plantings of potential beneficiary species and tested the role of positive interactions in restoration. In California oak woodlands, experimental plantings of Quercus douglasii H. and A. (Callaway 1992) and Quercus agrifolia Nee (Callaway and D'Antonio

1991) showed that no seedlings growing in the open survived 1 yr after planting, whereas survival of seedlings growing under shrubs was >30%. In the Great Basin and eastern Sierra Nevada, Callaway et al. (1996) found that survival of Pinus monophylla Torr. and Frém. and Pinus ponderosa Laws. was higher under the canopy of Artemisia tridentata Nutt. than on bare areas. In dry–subhumid Mediterranean conditions, plantings of Quercus ilex L. subsp. ballota (Desf.) Samp. seedlings performed better under the canopy of shrubs and Aleppo pine (Pinus halepensis Miller) individuals than in open areas (Vilagrosa et al. 1997).

Water use and rainfall interception by S. tenacissima could be offset by its ability to collect rainwater runoff coming from open areas, reduce evaporation due to shading, and increase the infiltration capacity of the soil. In addition, alpha grass tussocks may enhance soil nutrient content and improve soil structure by adding organic matter to the soil through litterfall and root turnover. We hypothesized that existing vegetation should facilitate the introduction of desirable plant species in degraded semiarid steppes. Our main objective was to test the effects of S. tenacissima tussocks on the survival, growth, and physiology of three Mediterranean shrub species (Medicago arborea L., Q. coccifera, and P. lentiscus). Pistacia lentiscus and Q. coccifera are long-lived species that play an important role in the succession of S. tenacissima steppes to climax woodland (Rivas Martínez 1987). They are of particular interest for their ability to withstand further disturbances and increase ecosystem resilience (Cortina and Vallejo 1999). Woody nitrogen-fixing legumes, such as M. arborea, can be used for the restoration of nutrient-depleted semiarid ecosystems due to their capacity to form symbiotic associations with both rhizobial bacteria and mycorrhizal fungi (Herrera et al. 1993) and to improve soil fertility (Jarrell and Virginia 1990).

METHODS

Study area

Research was conducted at three experimental sites located in the province of Alicante, in southeastern Spain (Table 1). All three have a Mediterranean semiarid climate, with a 30-yr average annual precipitation ranging from 358 to 388 mm, falling mainly in autumn, and a mean annual temperature of 16–18°C (Pérez Cueva 1994). Soils are loamy–silty loam, Lithic Calciorthid, derived from marls and limestone (Ruiz 1993). The vegetation is an open steppe dominated by two perennial sprouting grasses, S. tenacissima and Brachypodium retusum (Pers.) P. Beauv., with dispersed shrubs such as Globularia alypum L., Ephedra fragilis Desf., and Rhamnus lycioides L. subsp. lycioides (see Appendix).

Experimental design

To investigate the effect of alpha grass tussocks on introduced seedlings we conducted experimental plant-

TABLE 1. Main characteristics of the experimental sites in southeastern Spain.

Site	Coordinates	Elevation (m)	Slope (°)	Aspect (°)	Plant cover (%)	Mean annual Temperature (°C)	Mean annual Rainfall† (mm)
Aguas	38°31′ N, 0°21′ W	460	12	160 SE	45	16	388
Campello	38°30′ N, 0°23′ W	380	18	140 SE	54	18	358
Ballestera	38°28′ N, 0°22′ W	140	21	170 S	59	18	358

† As measured at the nearest weather station: Relleu station (38°35′ N, 0°21′ W) for the Aguas site, and Alicante station (38°21′ N, 0°30′ W) for the Campello and Ballestera sites.

ings at three sites on south-facing slopes of moderate steepness representative of typical *S. tenacissima* steppes (Aguas, Campello, and Ballestera, Table 1). Density of *S. tenacissima* tussocks ranged between 940 and 1532 tussocks/ha in these sites, covering 35–85% of the vegetative area and 16–48% of the total surface. We selected two planting microsites near individual tussocks: the "tussock" microsite was located upslope and adjacent to *S. tenacissima* tussocks (<15 cm from the edge of the tussock); the "open" microsite was located in the intertussocks areas with sparse vegetation cover. We selected the upslope of the tussock because of better soil conditions as compared to any other side of the tussock (Sánchez 1995) and because the shading effect was expected to be higher. We used medium to large size tussocks, with individual diameter ranging from 80 to 200 cm. Within each site, we randomly selected 60 replicated planting points per microsite and species (360 planting points per site). The experiment was arranged in a combined factorial and blocking design where site was the blocking factor. We also studied microsite soil characteristics and microclimatic conditions in order to explore the potential mechanisms underlying interactions between *S. tenacissima* and introduced seedlings.

Seeds from the three species were collected from local provenances in the Valencia Region (eastern Spain) by the regional forest services (Generalitat Valenciana Forest Seed Bank). Before transplantation seedlings were grown in a nursery for 9 mo in 330 mL containers (Rootrainer Ash, Roxburghshire, UK) with a mixture of peat, coconut fiber, and sand (50 : 45 : 5). Slow-release fertilizer (Osmocote plus; Scotts, Columbus, Ohio, USA) was also included in the growing medium.

Site preparation was carried out manually. It consisted of digging a minimum hole (25 × 25 × 25 cm) to avoid soil disturbance as much as possible. We planted the seedlings in late autumn (December 1998). The experiment was conducted under natural conditions without any watering or weeding. We report seedling-response results for the first year after plantation. The first summer in the field is a key stage in plant establishment in Mediterranean areas (Vilagrosa et al. 1997, Rey Benayas 1998), and thus seedling response after transplanting can be a good indicator of the performance of management techniques such as the one discussed here.

Microsite characterization

Soil characterization.—Prior to site preparation for planting, we recorded the presence or absence of earthworm casts, litter, soil sealing crusts, cryptobiotic crusts (algae and lichens), and moss patches at each sampling site (25 × 25 cm surface area). We sampled five 20 cm depth soil cores per site and microsite. In each sample (<2 mm fraction) we determined total N content (Kjeldahl method, Bremner and Mulvaney 1982), organic C content (Walkley-Black method, Nelson and Sommers 1982), total carbonate content (Bernard calcimeter method, Nelson 1982), soil particle distribution (pipette method), and pH (pH meter, in a 1 : 2.5 mass : volume soil and water suspension).

Soil moisture.—We measured the soil moisture monthly from April 1999 by time-domain reflectometry (TDR; Topp and Davis 1985) using a Tecktronix 1502 metallic cable tester (Tecktronix, Beaverton, Oregon, USA). In randomly selected planting holes, we installed ten 20 cm long TDR probes per microsite and site. We applied a site-specific calibration factor for the soils of the experimental sites. After 1 yr of monthly measurements (March 2000), we measured soil moisture during a drying cycle at one of the experimental sites (Ballestera): all the microsites with TDR probes were irrigated until both tussock and open microsites reached similar initial soil moisture values; the soil moisture was recorded until the drying curve became stabilized. To complement these measurements, we collected 20 cm deep soil cores on the Ballestera site in June and November, coinciding with the ecophysiological measurements (see *Seedling measurements*), and we determined the gravimetric soil water content at three depths (0–5, 5–10, and 10–20 cm) per planting hole.

Soil temperature.—We measured the soil temperature with protected diodes buried at a 5 cm depth. The soil temperature was measured monthly from June 1999 at 10 points per microsite and sites located close to TDR probes.

Solar radiation.—We determined photosynthetic active radiation (PAR) by using a Sunfleck Ceptometer (Decagon, Pullman, Washington, USA). We randomly selected five tussock and five open microsites on each site and measured PAR as the average of 10 instanta-

TABLE 2. Frequency of measured soil surface characteristics at the two plantation microsites and results of hierachical log-linear analysis.

| Soil surface characteristic | Frequency (%) | | | | | | M × C | | S × C | | M × S × C | |
| | Aguas | | Campello | | Ballestera | | | | | | | |
	Tussock	Open	Tussock	Open	Tussock	Open	G^2	P	G^2	P	G^2	P
Soil crust	3.4	80.1	0.0	93.4	0.6	33.5	681.26	<0.001	162.89	<0.001	19.40	<0.001
Cryptobiotic crust	76.7	35.9	1.1	0.0	8.9	0.0	82.13	<0.001	471.66	<0.001	5.59	0.061
Moss	56.3	7.7	4.0	0.0	8.9	2.8	115.62	<0.001	178.25	<0.001	6.58	0.037
Earthworm casts	46.6	55.2	40.0	4.9	40.0	7.4	52.11	<0.001	88.25	<0.001	77.03	<0.001
Litter	96.6	51.1	92.0	82.4	96.1	18.9	323.50	<0.001	112.54	<0.001	48.83	<0.001
n	176	181	175	182	176	180						

Note: M = microsite (Tussock or Open), S = site (Aguas, Campello, or Ballestera), and C = diverse soil surface conditions (presence, in percentage).

† Results are for the unsaturated model containing two-order terms after backward elimination of the three-order nonsignificant term. Results for the saturated model in those cases are with the significant three-order term.

neous measurements at five heights (0, 20, 40, 60, 80, and 100 cm) from the surface soil. We measured PAR seasonally at the same points on all sites (20 April, 30 August, 5 November, and 30 December), between 1100 and 1300 Solar Time on clear days.

Seedling measurements

We used seedling survival, biomass increments, water status, and chlorophyll fluorescence as response variables to evaluate seedling performance. Prior to transplantation we characterized 15 seedlings of each species (shoot length, root collar diameter, above- and belowground biomass). We assessed seedling survival in January, May, October, and December 1999.

We carried out physiological measurements on the Ballestera site before and after the first summer (first week of June and second week of November), since the first summer is crucial for seedling establishment (Vilagrosa et al. 1997, Rey Benayas 1998, Fonseca 1999). We measured predawn water potential and maximum photochemical efficiency of photosystem II (PSII) in five randomly selected individuals per microsite. We measured water potential in situ on small terminal shoots using a pressure bomb (Soilmoisture Corporation, Santa Barbara, California, USA). We performed chlorophyll fluorescence measurements in situ on attached leaves using a portable, pulse-modulated

fluorometer (PAM-2000, Walz, Germany). We estimated the maximum efficiency of the photosynthetic energy conversion of PSII from the ratio of variable to maximum leaf fluorescence ($F_v/F_m = [F_m - F_0]/F_m$, where F_m, F_v, and F_0 are the maximum, variable, and initial fluorescence, respectively). Fluorescence determinations were performed under complete darkness before sunrise. We harvested the seedlings selected for ecophysiological measurements to assess changes in aboveground and belowground biomass. Seedlings were manually harvested and carried to the laboratory, where we separated roots, stems, and leaves. Roots were separated from soil with a water jet. Biomass fractions were dried at 60°C until constant mass, and dry mass was measured.

Statistical analyses

Analyses of attribute data were based on log-linear models. Frequency data for the surface characteristics of the planting sites were tested for independence in a three-way table (Surface Characteristics, Microsite, and Site). Survival was analyzed separately for each sampling period (January, May, October, and December), as each one represents relevant features for seedling survival: transplant shock, end of the first growing period, postsummer stress, and second growing period, respectively. Survival frequency data were first ana-

TABLE 3. Properties of soil (0–20 cm) at tussock and open microsites (means ± 1 SE; n = 5).

| Variable | Aguas | | Campello | | Ballestera | |
	Tussock	Open	Tussock	Open	Tussock	Open
pH	8.3 ± 0.1	8.4 ± 0.1	8.4 ± 0.1	8.5 ± 0.1	8.5 ± 0.0	8.5 ± 0.1
Organic matter (mg/g)	46.3 ± 5.0	37.7 ± 1.9	30.1 ± 1.5	25.7 ± 1.9	36.9 ± 3.6	30.2 ± 2.8
Total nitrogen (mg/g)	2.2 ± 0.3	1.9 ± 0.1	1.5 ± 0.1	1.5 ± 0.0	1.7 ± 0.1	1.5 ± 0.1
C : N	12.6 ± 0.4	11.4 ± 0.5	11.5 ± 0.4	10.1 ± 0.5	12.2 ± 0.7	12.0 ± 0.4
Total CO_3 (%)	85.2 ± 5.2	81.8 ± 3.0	69.8 ± 3.8	64.2 ± 1.2	59.2 ± 3.7	66.8 ± 6.1
Sand (%)	20.4 ± 1.5	19.5 ± 0.8	46.6 ± 2.1	34.1 ± 6.1	28.4 ± 2.2	28.4 ± 1.2
Silt (%)	52.0 ± 1.0	55.2 ± 1.2	36.31 ± 1.2	46.6 ± 4.9	45.0 ± 2.5	44.4 ± 1.1
Clay (%)	27.6 ± 1.0	25.2 ± 1.1	17.1 ± 1.0	19.4 ± 1.3	26.6 ± 2.0	27.1 ± 1.2
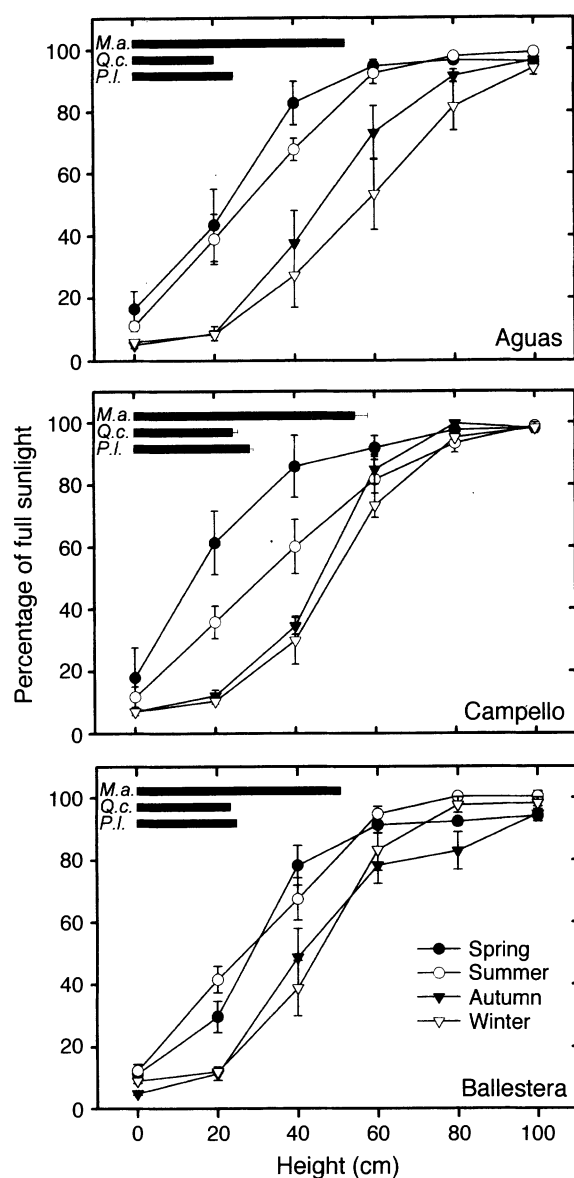
FIG. 1. Seasonal irradiance change at the tussock microsites expressed as percentages of irradiance at the open microsites at three experimental sites in southern Spain (means ± 1 SE; $n = 5$). Bar graphs show height of seedlings in the tussock microsites on the plantation date (December 1998; means + 1 SE; $n = 60$). M.a. = Medicago arborea; Q.c. = Quercus coccifera; P.l. = Pistacia lentiscus.

lyzed in a four-way table (Survival, Species, Microsite, and Site). Since the four-factor interaction term was significant for most of the sampling periods and exploratory analysis showed clear differences among species, we made separate three-way tests of independence (Survival, Microsite, and Site) for each species.

Soil data were analyzed by two-way (Site and Microsite) ANOVA, with Microsite as a fixed effect and Site as a random effect. Monthly TDR soil moisture and temperature measurements were analyzed by a
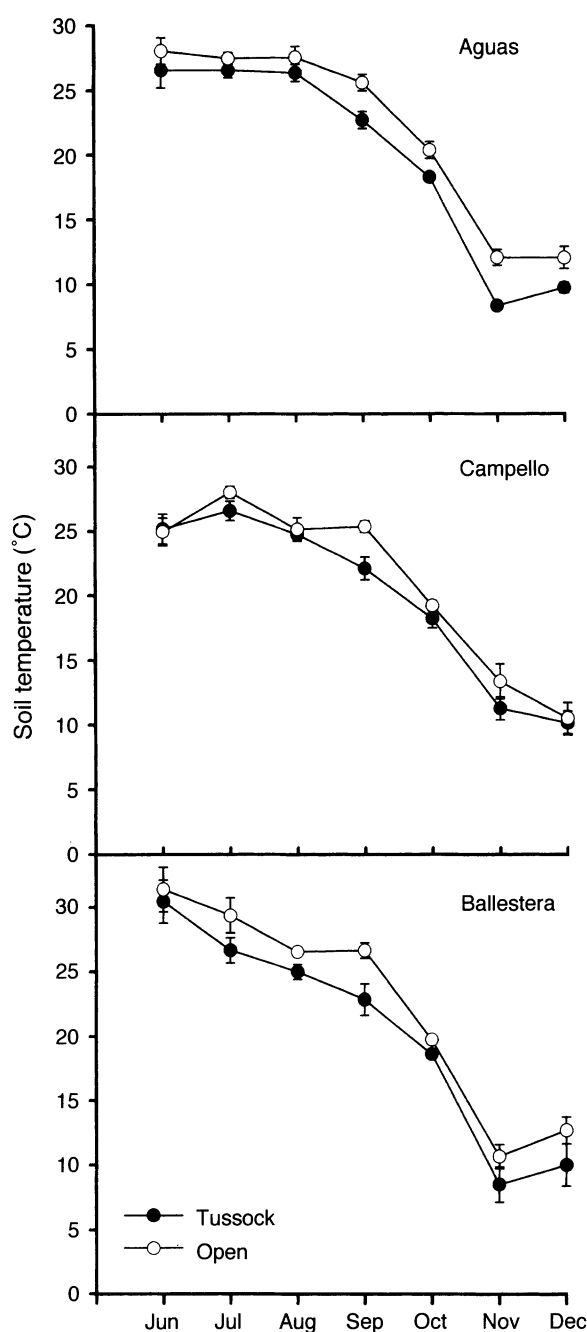

FIG. 2. Monthly evolution of soil temperature in the tussock and open microsites at the three experimental sites (means ± 1 SE; $n = 10$).

three-way (Site, Microsite, and Time) ANOVA with repeated measures of one of the factors (Time). Drying rates at the Ballestera site were compared using the nonparametric Mann-Whitney U test. Gravimetric soil moisture data collected at the Ballestera site in June and November were analyzed by three-way (Microsite, Depth, and Planting hole) nested ANOVA, with Microsite and Depth as fixed effects and Planting hole (nested within Microsite) as the random effect.
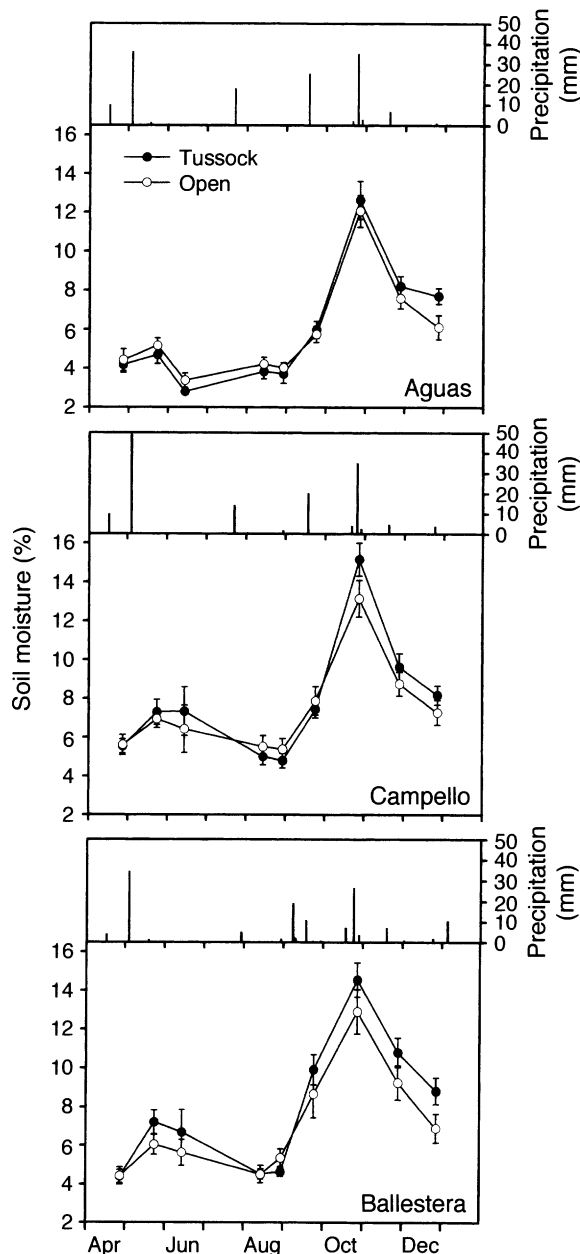
FIG. 3. Monthly evolution of soil moisture in the tussock and open microsites at the three experimental sites (means ± 1 SE; $n = 10$). Bar graphs show rainfall events as measured by an on-site meteorological station.

Water potential, chlorophyll fluorescence, and seedling biomass at the Ballestera site were analyzed separately for each sampling period by two-way (Species and Microsite) ANOVA, with both factors as fixed effects. Biomass variation with time was analyzed separately for each species and microsite by one-way ANOVA, considering two different periods, nursery–June and June–November. Biomass data required log transformation to correct departures from the normal distribution.

All the statistical analyses were performed using the SPSS 9.0 package (SPSS, Chicago, Illinois, USA).

RESULTS

In 1999, the precipitation at the study sites was 192–220 mm, ~45% below the 30-yr average (Table 1). The previous year was also very dry (179 mm). Drought years of this kind are common in the study area, where long-term rainfall analyses show that >60% of all years have below-average annual precipitation values (Pérez Cueva 1994).

Microsite characteristics

All of the soil surface properties that were measured showed significant differences between microsites (Table 2). The presence of cryptobiotic crusts, mosses, and litter was more frequent at tussock microsites, whereas soil crusts were more frequent at open microsites. All properties that were measured showed significant differences between sites (Table 2). Soils in tussock microsites showed more organic matter than those in open microsites (Table 3, two-way ANOVA, $F_{microsite} = 29.77$, df $= 1, 2, P = 0.03$). Total nitrogen, carbon-to-nitrogen ratio, pH, carbonate content, and texture did not show any microsite effect (two-way ANOVA, $P > 0.09$ in all cases). The experimental sites differed in organic matter content (two-way ANOVA, $F_{site} = 46.25$, df $= 2, 2, P = 0.02$) and total nitrogen content (two-way ANOVA, $F_{site} = 28.03$, df $= 2, 2, P = 0.03$), with the highest values found in Aguas.

Quercus coccifera and P. lentiscus seedlings planted in tussock microsites received between 30% (autumn) and 70% (summer) less radiation than those planted in open microsites (Fig. 1). Only the lower parts of the M. arborea seedlings were effectively shaded all year round, since the mean height for M. arborea seedlings

TABLE 4. Gravimetric soil moisture measured at the Ballestera site in June and November during ecophysiological measurements (means ± 1 SE; $n = 15$) and results of a three-way (microsite, depth, and planting hole) nested ANOVA showing the significance of the microsite and depth effects and the interaction between microsite and depth.

	Soil moisture (%)					
	0–5 cm		5–10 cm		10–20 cm	
Period	Tussock	Open	Tussock	Open	Tussock	Open
June	3.57 ± 0.30	2.67 ± 0.30	5.75 ± 0.45	5.46 ± 0.66	8.84 ± 0.39	6.87 ± 0.43
November	9.38 ± 0.48	7.58 ± 0.29	10.67 ± 0.27	8.76 ± 0.31	11.52 ± 0.37	9.43 ± 0.19

Note: M = microsite (Tussock or Open), and D = depth (0–5, 5–10, or 10–20 cm).

was ~60 cm and above this height radiation was >80% of full sunlight.

The three experimental sites were significantly different in surface soil temperature (Fig. 2, repeated measures ANOVA, F_{site} = 7.04, df = 2, 2, P = 0.002), and soil temperature was consistently higher in open microsites (mean ~2°C, repeated measures ANOVA, $F_{microsite}$ = 71.77, df = 1, 2, P < 0.001).

Soil moisture, as measured with TDR probes, remained <8% for the three sites during spring and summer and reached maximum values (~15%) in autumn (Fig. 3). We did not find significant differences in the monthly measurements between microsites (repeated measures ANOVA, $F_{microsite}$ = 1.01, df = 1, 2, P = 0.32). However, significant differences occurred among the sites (repeated measures ANOVA, F_{site} = 7.35, df = 2, 2, P = 0.002). Gravimetric water content was significantly higher at tussock microsites than open microsites for the June and November measurements. There were slightly higher differences between microsites in the 10–20 cm soil layer, but there was no significant interaction between microsite and depth (Table 4). The drying pattern obtained in the Ballestera site showed that water was lost faster from the open microsite than from the tussock microsite (Fig. 4), as drying rates were significantly higher in the open microsite (Mann-Whitney U test, U = 9.00, P = 0.002). Nevertheless, the water content of the two microsites became similar at low moisture values, when the drying curve stabilized.

Survival of seedlings

Seedling survival was dependent on the species, but for all of them we found higher survival rates at the tussock microsites (Fig. 5). One year after transplantation, *M. arborea* had the highest survival rates (77–93% at the tussock microsites and 30–89% at the open microsites), greatly differing from *Q. coccifera* (7–33% at the tussock microsites, and 4–7% at the open microsites), and *P. lentiscus* (8–25% at the tussock microsites, and 3–11% at the open microsites). Differences in survival between microsites were significant for *M. arborea* in both October and December, for *Q. coccifera* in May, October, and December, and for *P. lentiscus* in January, October, and December (Table 5).

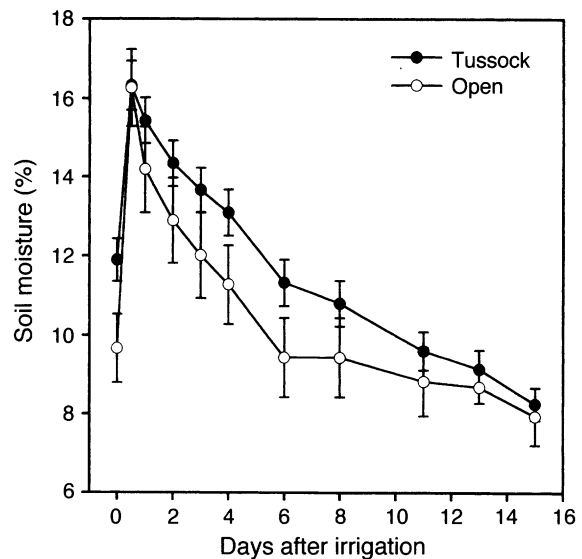At Campello, 68% of the seedlings planted in the

Fig. 4. Drying curves after irrigation at the tussock and open microsites at the Ballestera site (means ± 1 SE; n = 10). See *Methods* for details.

tussock microsite and 85% of those planted in the open microsite were excavated during the summer by rabbits (*Oryctolagus cunniculus*). They harvested roots and green tissues for food, leaving intact only the coarse woody parts of shoot and stems. The November and December survival rates for this species in Campello were estimated from the seedlings that were not excavated, and thus they must be considered with caution.

Ecophysiological status

Predawn water potentials were low in June, particularly for *Q. coccifera* seedlings (Fig. 6). After the autumn rainfall, water potential increased for all three species. Seedlings established close to *S. tenacissima* tussocks showed higher predawn water potential in June (two-way ANOVA, $F_{microsite}$ = 15.44, df = 1, 24, P < 0.001), and November (two-way ANOVA, $F_{microsite}$ = 27.10, df = 1, 24, P < 0.001), with higher water potentials at the tussock microsites. We found a significant interaction between microsite and species in June (two-way ANOVA, $F_{microsite \times species}$ = 3.9, df = 2, 24, P = 0.03), which reflected the different responses

TABLE 4. Extended.

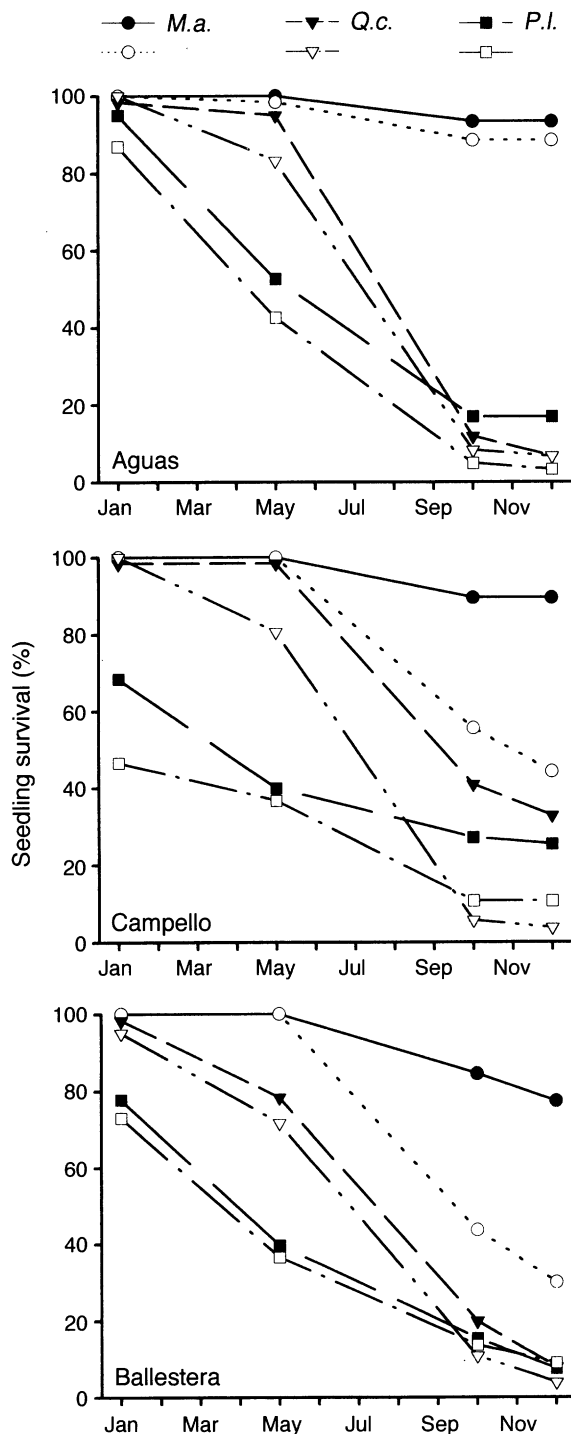| ANOVA results								
M			D			M × D		
F	df	P	F	df	P	F	df	P
4.74	1,28	0.038	75.03	2,56	<0.001	1.65	2,56	0.202
23.27	1,28	<0.001	43.06	2,56	<0.001	0.16	2,56	0.850

FIG. 5. Survival of 1-yr-old, planted seedlings at tussock microsites (black symbols) and open microsites (white symbols). For all species and microsites, initial n = 60 seedlings. Abbreviations: M.a. = Medicago arborea; Q.c. = Quercus coccifera; P.l. = Pistacia lentiscus. At the Campello site, 68% of the M. arborea seedlings planted in tussock and 85% of those planted on open microsites were eaten by rabbits during the summer (see Results: Survival of seedlings for details). At the Ballestera site, 5 seedlings per species and microsite were harvested in June and November.
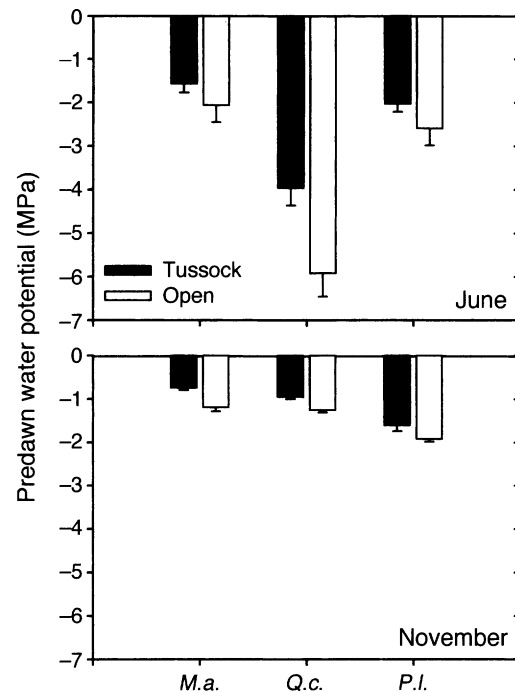

FIG. 6. Predawn water potential for seedlings planted at tussock and open microsites at the Ballestera site (means + 1 SE; n = 5). Abbreviations: M.a. = Medicago arborea; Q.c. = Quercus coccifera; P.l. = Pistacia lentiscus.

of the three species to microsite conditions in a relatively dry period. All the species showed lower predawn water potential in the open microsites, but differences were particularly marked for Q. coccifera. Maximum photochemical efficiency of PSII (F_v/F_m) was low in the three species in both June and November (Table 6). Despite the significant reduction in PAR reaching the plants on the tussock microsites, the maximum photochemical efficiency of PSII did not differ among microsites in June (Table 6). In November, seedlings in tussock microsites showed higher values of F_v/F_m (Table 6).

Biomass growth

In June 1999, seedlings in open microsites showed less foliar biomass than those planted in tussock microsites (Table 7). This was the only morphological trait that was significantly affected by the microsite at this time (Table 8). We obtained similar results, i.e., significantly higher foliar biomass accumulation in tussock seedlings in November 1999 (Table 8).

In the field, total biomass, root biomass, and stem biomass increased in M. arborea after the first spring in both tussock and open microsites as compared to nursery seedlings (Table 9). Root-to-shoot ratio was also higher in seedlings located in open microsites. We found no significant differences in Q. coccifera seedling size between December (nursery seedlings) and June (Table 9). Pistacia lentiscus seedlings partially

TABLE 5. Partitioned likelihood ratio statistic (G^2) and P values of the hierarchical log-linear analysis describing seedling survival.

Period	Species	M × U		S × U		M × S × U	
		G^2†	P	G^2	P	G^2	P
January 1999	Quercus coccifera	0.20	0.651	6.08	0.047	2.29	0.318
	Pistacia lentiscus	6.97	0.008	37.99	<0.001	1.64	0.441
	Medicago arborea	0‡	···	···	···	0‡	···
May 1999	Quercus coccifera	10.64	0.001	12.28	0.001	6.26	0.043
	Pistacia lentiscus	1.92	0.166	4.65	0.098	1.07	0.587
	Medicago arborea	0‡	···	···	···	0‡	···
October 1999	Quercus coccifera	16.62	<0.001	8.53	0.014	7.92	0.030
	Pistacia lentiscus	7.22	0.007	3.12	0.211	2.71	0.258
	Medicago arborea	21.83	<0.001	45.52	<0.001	3.24	0.072
December 1999	Quercus coccifera	11.85	0.001	11.89	0.003	6.54	0.038
	Pistacia lentiscus	7.07	0.008	5.59	0.061	4.02	0.134
	Medicago arborea	21.83	<0.001	45.52	<0.001	3.24	0.072

Notes: For each site × microsite combination, $n = 60$ cases. Total n per species = 360. M = microsite (Tussock or Open), S = site (Aguas, Campello, or Ballestera), and U = survival (percentage). Analyses of *M. arborea* in October and December were made only with data from two sites (Aguas and Ballestera) due to the high seedling predation at the Campello site (see *Results: Survival of seedlings* for details).

† Results are for the unsaturated model containing two-order terms after backward elimination of the three-order nonsignificant term. Results for the saturated model in those cases are with the significant three-order term.

‡ In January and May 1999 *M. arborea* survival was 100% in both tussock and open sites.

shed their leaves after transplanting due to drought stress, although only significantly in the open microsites, resulting in an increase in the root-to-shoot ratio on both the tussock and the open microsites (Table 9). We found no significant differences in *M. arborea* biomass accumulation between June and November 1999. In contrast, *Q. coccifera* and *P. lentiscus* still showed the effects of the first summer in November 1999. The foliar biomass of *Q. coccifera* seedlings significantly decreased between June and November for both tussock and open microsites, as did the stem biomass in the open microsites (Table 9). Accordingly, root-to-shoot ratios increased for this species for the two microsites. Root-to-shoot ratios also increased in *P. lentiscus* seedlings between June and November for the two microsites (Table 9). Foliar biomass and total biomass decreased between spring and autumn in this species, although this decrease was only significant in the open microsites (Table 9).

DISCUSSION

Stipa tenacissima tussocks appeared to directly enhance seedling survival by favorably altering soil-surface properties, soil fertility, microclimate, and moisture availability. Tussocks improved soil characteristics, enhancing the presence of cryptobiotic crust, mosses, and litter, and reducing soil sealing crust. Litter favors soil surface porosity and increases infiltration capacity (Janeau et al. 1999). Cryptobiotic crusts play an important role in semiarid environments by promoting soil stabilization, enhancing moisture content, and increasing the amount of available nutrients by concentrating essential elements such as nitrogen,

which is fixed by cyanobacteria (West 1990). On the contrary, soil crusts decrease the hydraulic conductivity of the soil surface and promote runoff (Bromley et al. 1997). The higher organic matter contents found in the tussock microsites are probably caused by the litterfall and root growth of tussocks, and our results agree with other observations of *S. tenacissima* steppes (Puigdefábregas and Sánchez 1996, Bochet et al. 1999). In spite of the differences between both microsite types, the organic matter content was relatively high as compared to other degraded soils under similar climatic conditions and on similar bedrock types (García and Hernández 1996). These results indicate that soils in alpha grass steppes are not so degraded as those resulting from other land uses, and thus restoration of these ecosystems may be less limited by soil properties. It has been suggested that *S. tenacissima* is a good soil improver (Bochet et al. 1999). The relatively small difference in organic matter content found between alpha grass tussocks and open areas suggests that aboveground and belowground carbon inputs (including *S. tenacissima* roots) may be enough to maintain soil organic matter levels in open areas. The relatively high contrast found in previous work between tussock microsites and open areas (Puigdefábregas and Sánchez 1996, Bochet et al. 1999) may reflect higher intertussock soil losses and lower productivity. On the other hand, the organic matter content was lower in *S. tenacissima* steppes than in other communities such as those dominated by *Q. coccifera* and *P. lentiscus* (Arevalo et al. 1993, De la Torre and Alías 1996), two of the species introduced in this study. Thus, if successful, restoration of *S. tenacissima* steppes to thorn shrub-

TABLE 6. Predawn measurements of photochemical efficiency of PSII (F_v/F_m) for seedlings at the Ballestera site (means ± 1 SE; $n = 5$) and results of a two-way (microsite and species) ANOVA.

| | Photochemical efficiency of PSII (F_v/F_m) | | | | | |
| | Medicago arborea | | Quercus cocifera | | Pistacia lentiscus | |
Period	Tussock	Open	Tussock	Open	Tussock	Open
June	0.67 ± 0.03	0.54 ± 0.10	0.45 ± 0.07	0.51 ± 0.04	0.53 ± 0.03	0.53 ± 0.05
November	0.68 ± 0.04	0.68 ± 0.02	0.67 ± 0.03	0.58 ± 0.02	0.64 ± 0.04	0.56 ± 0.04

Note: M = microsite (Tussock or Open), and S = species (*Medicago arborea, Quercus coccifera,* or *Pistacia lentiscus*).

lands could represent an additional store of carbon in soils and an overall improvement in soil properties.

Photosynthetically active radiation and soil temperature results indicated that *S. tenacissima* tussocks produced significant changes in light intensity and soil temperature. Shading significantly reduced soil temperatures, which has an important bearing on evapotranspiration and plant water status. *Stipa tenacissima* has a dense canopy that maintains its dead leaves and avoids excessive radiation by structural photoprotection, including moderate self-shading (Valladares and Pugnaire 1999). Indeed, soils on the tussock microsites were observed to retain moisture longer than those in the open areas, as can be seen by the drying pattern obtained in the Ballestera site and other experiments carried out in different *S. tenacissima* steppes (Puig-defábregas and Sánchez 1996, Cerdà 1997, Cammeraat and Imeson 1999). Differences in drying rates promoted the improvement of soil water conditions on the tussock microsites provided that the soils were not too dry, since the differences in water content disappeared when the drying curve stabilized at low values. Thus, monthly data did not reveal an overall microsite effect on soil moisture, as most of the data corresponded to relatively low moisture values, particularly on the Aguas site. Only in autumn and on some spring days when the soil moisture exceeded ~6% (volume : volume) was more water available in the tussock than in the open microsite. Gravimetric moisture measurements in June and November also showed these differences between microsites. It is worth noting that the differences were maintained even in the 10–20 cm layer, which was probably the main zone exploited by the roots (Fonseca 1999).

Higher soil water availability and reduced evaporative demand near the *S. tenacissima* tussocks in June improved the water status of the three test species. Predawn water potential measured at this time was low, which was probably due to transplant shock accentuated by a dry winter and spring. The contrast in water status of the seedlings planted on the two microsites was still significant in November when the soil moisture content was already relatively high. Thus, despite the low values of water availability at both microsites in midsummer, shrub seedlings at tussock microsites were probably capable of using the excess moisture content observed during the autumn and early summer.

Tussock seedlings may also be able to make more efficient use of the short water pulses that occur when soils are dry.

Several authors suggest that the maximum photochemical efficiency of PSII may be close to 0.8 in unstressed plants (Mohammed et al. 1995). We measured F_v/F_m values ranging from 0.45 to 0.68, indicating that seedlings were subjected to stress, even when predawn water potentials had recovered. Species that may be more sensitive to water stress than those used in the present study, such as *Quercus ilex* and *Q. pubescens,* have predawn F_v/F_m values that do not fall below 0.7 until the predawn water potential is lower than −4.0 MPa (Damesin and Rambal 1995, Méthy 1999). Furthermore, in *Q. petraea* the maximum photochemical efficiency was maintained until the water was almost depleted from the leaf (Epron and Dreyer 1992). Only *Q. coccifera* in June reached predawn water potentials below −4.0 MPa and, indeed, those were reflected in the lowest F_v/F_m values measured (mean of 0.45). These values are considerably lower than the ones measured by Werner et al. (1999) in adult individuals of the same species (0.80 ± 0.02 in summer [means ± 1 SD]). In November, when water potentials were above −2.0 MPa for all seedlings and radiation was probably not as intense as in the summer, predawn F_v/F_m values were still relatively low, particularly for *Q. coccifera* and *P. lentiscus* seedlings planted at open microsites (0.58 and 0.56, respectively). This could have been due to low temperatures (Mohammed et al. 1995), although decreases in F_v/F_m generally do not seem to occur in Mediterranean sclerophyllous species at temperatures above freezing (Méthy et al. 1997). The maximum photochemical efficiency of PSII measured at dawn tended to increase in tussock seedlings, as suggested by significant differences found in November, when seedlings were suffering from a long-term drought. During June, the F_v/F_m of the *Q. coccifera* seedlings planted in open microsites decreased significantly during the day (data not shown), but not for seedlings planted at the tussock microsites. This suggests that the shade provided by *S. tenacissima* may attenuate the diurnal photoinhibition caused by high light intensities (Long et al. 1994). The lack of differences between the two microsites during the summer suggests that the diurnal component in the decline of F_v/F_m is fully reversible overnight even under drought stress. This has been reported for *Q. coc-*

TABLE 6. Extended.

ANOVA results								
M			S			M × S		
F	df	P	F	df	P	F	df	P
0.13	1,24	0.721	2.19	2,24	0.134	1.26	2,24	0.303
5.14	1,24	0.033	3.25	2,24	0.057	1.14	2,24	0.337

cifera (Werner et al. 1999) and for other Mediterranean evergreen shrubs like *Arbutus unedo* L. (Werner et al. 1999) and *Q. ilex* (Méthy 1999).

All shrub seedlings planted upslope of *S. tenacissima* tussocks maintained a higher foliar biomass than seedlings in open microsites. *Pistacia lentiscus* planted in open microsites showed a gradual reduction in leaf biomass. Foliar senescence may be an adaptation to drought (Davis et al. 1989), and it has been previously reported for adult and seedlings of *Q. coccifera* (Ksontini et al. 1998, Fonseca 1999, Werner et al. 1999). During the first year after transplanting, Fonseca (1999) found no significant changes in the foliar biomass of *P. lentiscus* seedlings planted on degraded semiarid ecosystems close to the experimental sites used in our study. The contrast with our results may be related to a lower water availability, but probably more specifically to the greater foliar biomass of the seedlings used in the present study. Thus Fonseca (1999) reported a root-to-shoot ratio in nursery *P. lentiscus* seedlings of 0.6, whereas in the present study it was 0.19 and gradually increased after transplanting. The biomass of *M. arborea* seedlings sharply increased during the first spring in the field. During summer they suffered from an almost complete defoliation in August (data not shown). However, the similarity in the leaf biomass values obtained in June and November show that the *M. arborea* seedlings recovered the biomass they had lost during the summer. This is an indication of the remarkable capacity of this species to withstand water stress. In a pot experiment, Noitsakis et al. (1991) found that *M. arborea* seedlings were active throughout the summer; but in this experiment leaf biomass also substantially decreased in midsummer, even when irrigated. There was a general trend for all species towards increasing root-to-shoot ratio with time, which may be related to drought (Romero et al. 1986).

One year after planting, survival of *Q. coccifera* and *P. lentiscus* was low regardless of the microsite considered. The low precipitation during 1999 may explain

TABLE 7. Aboveground and belowground biomass (g) for (A) nursery and (B) harvested seedlings at the Ballestera site (means ± 1 SE; *n* = 5 [June and November] or 15 [nursery]).

Measure	Medicago arborea	Quercus coccifera	Pistacia lentiscus
A) Nursery			
LB	0.40 ± 0.07	1.77 ± 0.29	3.86 ± 0.45
SB	1.98 ± 0.32	1.14 ± 0.25	2.19 ± 0.30
RB	1.00 ± 0.16	3.51 ± 0.65	1.15 ± 0.16
TB	3.38 ± 0.53	6.42 ± 1.13	7.30 ± 0.94
R : S	0.43 ± 0.03	1.29 ± 0.11	0.19 ± 0.01

B) Harvested

Measure	Tussock	Open	Tussock	Open	Tussock	Open
June						
LB	0.48 ± 0.04	0.41 ± 0.05	2.39 ± 0.43	1.36 ± 0.13	2.23 ± 0.33	1.85 ± 0.31
SB	3.51 ± 0.31	3.97 ± 1.32	1.74 ± 0.35	1.43 ± 0.17	1.56 ± 0.17	1.23 ± 0.10
RB	1.98 ± 0.20	2.34 ± 0.60	5.57 ± 0.66	3.96 ± 0.55	1.21 ± 0.28	1.05 ± 0.16
TB	5.97 ± 0.49	6.72 ± 1.92	9.69 ± 1.42	6.76 ± 0.82	5.01 ± 0.67	4.13 ± 0.47
R : S	0.49 ± 0.02	0.56 ± 0.03	1.41 ± 0.10	1.41 ± 0.13	0.32 ± 0.07	0.34 ± 0.04
November						
LB	0.63 ± 0.09	0.64 ± 0.23	0.45 ± 0.18	0.19 ± 0.04	1.55 ± 0.48	0.70 ± 0.28
SB	4.05 ± 0.40	4.91 ± 0.89	1.41 ± 0.15	1.00 ± 0.05	1.36 ± 0.28	0.88 ± 0.14
RB	2.07 ± 0.12	3.19 ± 0.46	4.61 ± 0.67	3.10 ± 0.05	1.73 ± 0.33	0.87 ± 0.09
TB	6.74 ± 0.54	8.74 ± 1.56	6.47 ± 0.72	4.30 ± 0.13	4.64 ± 0.92	2.44 ± 0.21
R : S	0.45 ± 0.03	0.61 ± 0.05	2.55 ± 0.39	2.63 ± 0.16	0.61 ± 0.06	0.60 ± 0.11

Note: LB = leaf biomass, SB = stem biomass, RB = root biomass, TB = total biomass, R : S = root-to-shoot ratio (belowground : aboveground biomass).

TABLE 8. Results of a two-way ANOVA to assess the significance of the microsite and species effect on seedling biomass.

Period	Fraction	Species			Microsite			Microsite × Species		
		F	df	P	F	df	P	F	df	P
June	Leaf biomass	74.28	2,24	<0.001	7.02	1,24	0.014	1.05	2,24	0.366
	Stem biomass	19.11	2,24	<0.001	1.16	1,24	0.292	0.16	2,24	0.854
	Root biomass	32.94	2,24	<0.001	0.65	1,24	0.426	0.73	2,24	0.493
	Total biomass	7.12	2,24	0.004	2.10	1,24	0.160	0.67	2,24	0.523
	R : S ratio	113.25	2,24	<0.001	0.17	1,24	0.681	0.09	2,24	0.917
November	Leaf biomass	7.36	2,24	0.003	5.02	1,24	0.035	0.68	2,24	0.515
	Stem biomass	31.80	2,24	<0.001	0.93	1,24	0.346	0.80	2,24	0.461
	Root biomass	29.01	2,24	<0.001	2.03	1,24	0.168	5.50	2,24	0.011
	Total biomass	14.72	2,24	<0.001	3.27	1,24	0.084	3.00	2,24	0.070
	R : S ratio	76.38	2,24	<0.001	0.23	1,24	0.636	0.11	2,24	0.897

this high mortality rate. In arid and semiarid environments, seedling survival is primarily a function of moisture availability (Fowler 1986, Lonsdale and Abrecht 1988), and high mortalities in semiarid afforestations have been recorded when the first year after planting was exceptionally dry (Grantz et al. 1998, Alloza and Vallejo 1999, Fonseca 1999). In Mediterranean shrublands, recruitment is strongly limited by climatic constraints, as seedling mortality is coupled with drought periods (Herrera et al. 1994, García-Fayos and Verdú 1998). High mortality rates associated with unfavorable climatic conditions may partly explain the lack of substantial spontaneous colonization of woody sprouters in *S. tenacissima* steppes. *Medicago arborea* showed the highest survival rate after 1 yr and also the clearest microsite effect. For this species, *S. tenacissima* tussocks appeared to have a negative effect on biomass accumulation but a positive effect on survival. Similar contrasting results for survival and growth were obtained by Callaway et al. (1996) with *Pinus monophylla* seedling plantings under the canopy of *Artemisia tridentata*.

We did not set out to study the effects that small

herbivores had on seedling establishment, but it is interesting to note the differential predation between microsites of *M. arborea* seedlings observed in Campello. This species was the only one harvested by rabbits, probably due to its high palatability (Noitsakis et al. 1991). The differences observed suggest that *S. tenacissima* could provide protection against herbivores, a common mechanism of facilitation (Callaway 1995). However, the high density of rabbits at the Campello site with respect to the Aguas and Ballestera sites, as suggested by visual observations of individuals and fecal pellets, may have overemphasized the effects of predation. As we did not conduct predator-exclusion experiments, the importance of *S. tenacissima* tussocks in the reduction of predation still remains uncertain. This is a factor that should be explored in order to choose suitable species for the restoration of areas with important herbivore populations.

Taking advantage of the soil and microenvironmental variations within a landscape to recreate naturally occurring vegetation patterns is an ecologically sound approach (Whisenant et al. 1995). Despite the importance that "fertile islands" can play in the restoration

TABLE 9. Results of one-way ANOVA to test the significance of the microsite effect on seedling biomass accumulation between December 1998 (nursery) and June 1999 and between June 1999 and November 1999.

Species	Fraction	Nursery–June						June–November					
		Tussock			Open			Tussock			Open		
		F	df	P	F	df	P	F	df	P	F	df	P
Medicago	Leaf biomass	1.64	1,18	0.217	0.36	1,18	0.559	2.14	1,8	0.182	0.29	1,8	0.605
arborea	Stem biomass	7.26	1,18	0.015	4.89	1,18	0.040	1.13	1,8	0.319	0.81	1,8	0.394
	Root biomass	8.25	1,18	0.010	8.36	1,18	0.010	0.25	1,8	0.633	1.81	1,8	0.216
	Total biomass	7.49	1,18	0.014	5.89	1,18	0.026	1.13	1,8	0.319	1.08	1,8	0.330
	R : S ratio	1.56	1,18	0.228	5.02	1,18	0.038	1.29	1,8	0.289	0.79	1,8	0.401
Quercus	Leaf biomass	1.76	1,18	0.201	0.03	1,18	0.866	22.01	1,8	0.002	82.52	1,8	<0.001
coccifera	Stem biomass	2.63	1,18	0.122	1.65	1,18	0.215	0.64	1,8	0.448	4.69	1,8	0.067
	Root biomass	3.90	1,18	0.064	0.85	1,18	0.369	1.31	1,8	0.286	1.19	1,8	0.311
	Total biomass	3.03	1,18	0.099	0.56	1,18	0.466	5.01	1,8	0.056	7.78	1,8	0.027
	R : S ratio	0.72	1,18	0.408	0.61	1,18	0.445	11.60	1,8	0.009	29.02	1,8	0.001
Pistacia	Leaf biomass	2.39	1,18	0.140	4.87	1,18	0.041	2.26	1,8	0.172	8.26	1,8	0.021
lentiscus	Stem biomass	0.25	1,18	0.623	1.36	1,18	0.259	0.59	1,8	0.464	4.83	1,8	0.059
	Root biomass	0.09	1,18	0.762	0.01	1,18	0.919	0.84	1,8	0.385	0.68	1,8	0.435
	Total biomass	0.64	1,18	0.434	1.91	1,18	0.184	0.26	1,8	0.624	13.69	1,8	0.006
	R : S ratio	7.48	1,18	0.014	19.47	1,18	<0.001	8.67	1,8	0.019	5.57	1,8	0.046

of degraded semiarid environments (Allen 1988), their possibilities still have not been fully developed. Initiating dynamic vegetation changes by introducing shrubs to these resource islands may gradually benefit adjacent parts of the landscape, although successional processes will require considerable time in these regions. The use of microsites in the restoration of semiarid degraded ecosystems represents a cost-effective approach to reduce degradation and initiate rehabilitation. Current approaches based on the extensive use of heavy machinery result in profound changes in the ecosystem and the landscape and have proved to be largely ineffective and unaffordable. Although 1 yr is insufficient time to evaluate long-term successional changes, this study reveals the important role that facilitation can play during the first stages of restoration in these ecosystems.

To our knowledge there are no previous works reporting tussock grass facilitative effects on tall shrub species establishment. Our study provides basic information on positive interactions in semiarid steppes and can be used to design effective restoration strategies for degraded semiarid ecosystems. Our hypothesis, that *S. tenacissima* tussocks could facilitate the introduction of tall shrub species, was supported by field experiments. The microsite provided by the *S. tenacissima* tussocks enhanced survival, promoted an increment in leaf biomass, and improved the ecophysiological status of seedlings of the three shrubs assayed, indicating the presence of a positive interaction between *S. tenacissima* and these species. Facilitation seems to have been mediated by microclimatic and surface modifications, as well as by other related effects on water availability, rather than by any microsite effect on soil fertility. Further manipulative experiments are needed to clarify the relative importance of the different mechanisms involved in the facilitation observed.

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APPENDIX

Two photographs of the experimental sites showing the structure of vegetation and the two microsites used in the study are available in ESA's Electronic Data Archive: *Ecological Archives* A011-019.