



SPECIAL FEATURE: VEGETATION RESTORATION

Irrigation, organic fertilization and species successional stage modulate the response of woody seedlings to herbaceous competition in a semi-arid quarry restoration

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Keywords

organic fertilization; irrigation; limestone quarry; woody-grass competition; semi-arid.

Nomenclature

Mateo & Crespo (2001).

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Introduction

Abandoned opencast quarries often have shallow soils and steep slopes as a result of logistic and economic constraints on their restoration. The priority in the restoration of these areas is soil protection (Bradshaw & Chadwick 1980), which is typically achieved by establishing a dense herbaceous cover (Andrés & Jorba

Abstract

Question: Is the response of woody plants to herbaceous competition affected by the level of irrigation and organic fertilization? Does the magnitude and the sign of this response depend on the successional status of woody species?

Location: A limestone quarry in a semi-arid Mediterranean area in SE Spain.

Methods: We studied seedling survival and growth of six woody species with contrasting ecological strategies (early-successional vs late-successional) and their associated herbaceous layer under different irrigation and organic fertilization levels

Results: Elevated water supply, but not organic fertilization, increased herbaceous cover. The response of woody seedlings and changes in herbaceous cover to a contrasting resource supply was species-specific. Seedling survival and growth of late-successional species increased at high levels of irrigation. Pioneer species showed the opposite trend, suggesting that increases in water availability may outweigh the deleterious effect of increased herbaceous competition in late-successional species but not in early-successional species.

Conclusions: Our study provides further insights into the role of techniques such as irrigation and organic fertilization, which are commonly used in conjunction with hydroseeding, in defining woody plant establishment and successional trajectories in semi-arid areas under restoration. Our results will contribute to improve restoration success by reconciling two major objectives of restoration: soil protection and secondary succession. We recommend a new approach for the restoration of limestone quarries. This approach comprises the planting of late-successional species on randomly distributed nutrient-rich patches of high availability of water and nutrients, and the use of pioneer species in the surrounding nutrient poor and drier matrix. This approach should promote optimal ecosystem functioning, including soil protection, while increasing biodiversity and fostering secondary succession.

2000). Hydroseeding with fast-growing herbaceous species, particularly grasses and legumes, is frequently used for this purpose (Wali 1999; Bochet & García-Fayos 2004; Tormo et al. 2007; García-Palacios et al. 2010). Few commercial hydroseeding plant species are adapted to low-quality substrates with poor water retention (Matesanz et al. 2006; Tormo et al. 2007). Thus, the results of hydroseeding have typically been poor in

semi-arid areas because seeds desiccate before germination (Bochet & García-Fayos 2004). Consequently, practices aimed at increasing soil fertility and water availability have been recommended to improve the success of hydroseeding (Bradshaw & Chadwick 1980).

Under semi-arid conditions, secondary succession is commonly slow (Bolling & Walker 2000; Bonet 2004). Various restoration practices, including planting late-successional species and improving soil conditions by fertilization and irrigation, have been recommended to enhance secondary succession (Booth et al. 1999; Cortina & Maestre 2005; Badia et al. 2007). In semi-arid areas, seedling establishment is mainly limited by soil moisture, especially during the first summer in the field, which is a major bottleneck for plant recruitment in these water-limited environments (Rey & Alcántara 2000; Cortina et al. 2004). It is not surprising, therefore, that irrigation enhances early plant survival and growth (Davis et al. 1999; Coyle & Coleman 2005; Sardans et al. 2005; Estrela et al. 2009). Organic amendments may also promote the establishment of planted species by improving soil fertility (Roldán et al. 1996; Querejeta et al. 1998; Fuentes et al. 2007a). In addition, irrigation and organic fertilizers may have synergistic effects on plant performance, as the increase in soil moisture may promote mineralization and increase nutrient availability (Coyle & Coleman 2005; Badia et al. 2007; but see Clemente et al. 2004 for contrasting results on the effect of organic amendments and irrigation).

In any restoration programme, the establishment of both herbaceous and woody species is desirable, and may be enhanced separately by increasing soil water and nutrients availability. While the addition of nutrients and water commonly enhance herbaceous cover and biomass (Moreno-Peñaranda et al. 2004; Jorba & Vallejo 2008), they may also hamper natural and artificial establishment of woody seedlings by increasing herb competition or limiting the number of suitable spaces for germination (Knoop & Walker 1985; Burke & Grime 1996; Eliason & Allen 1997). Although considerable research has been devoted to understanding the effects of biotic and abiotic factors on herbaceous communities in human-constructed ecosystems (e.g. Khater et al. 2003; Matesanz et al. 2006; García-Palacios et al. 2010; Alday et al. 2011), interactions among resource availability, herb cover and woody plant performance remain poorly understood. Some authors suggest that increasing resource availability may increase woody plant performance when competing with herbaceous species (Eliason & Allen 1997; Davis et al. 1999; Espigares et al. 2004). However, others have found, the opposite trend (Bush & Van Auken 1988; Sánchez & Peco 2004). Studies aimed at clarifying the reasons for

such conflicting results are crucial if we are to balance the need for soil protection with enhanced secondary succession.

Differences in the response of woody species to resource-driven herbaceous competition could be explained by differences in ecological strategies among the species involved. Woody plants differ in the way that they respond to contrasting levels of radiation, water and nutrients (Grime 1979; Tilman 1988). Thus, their response to the presence of their neighbours will likely depend on changes in resource availability caused by irrigation and fertilization (Callaway 2007). In productive environments with abundant water and nutrients, late-successional plants have a competitive advantage over grasses because of their ability to capture and retain resources. Conversely, in environments with scarce water and nutrients, pioneer species are highly tolerant to disturbance, but are poor competitors when resource availability is high (Grime 1979; Tilman 1988). A lower performance can therefore be expected from pioneering species in response to a resource-driven increase in herbaceous competition. Considering the ecological strategy of the woody species may help, therefore, to understand successional trajectories, and design efficient restoration protocols (Prach 2003).

In this study, we aimed to assess the importance of soil resource availability and successional stage on the response of woody seedlings to herbaceous competition in a Mediterranean semi-arid area. We did this by evaluating the response of six woody species, and their associated herbaceous community, to irrigation and organic fertilization in a restored limestone quarry. Our main hypothesis were that: (1) organic fertilization and irrigation increase herbaceous cover; (2) increases in soil resources affect seedling response to neighbouring herbs; and (3) the magnitude and sign of this response depends on the successional stage of the woody species.

Methods

Study area

The study was conducted in a limestone quarry located in Sant Vicent del Raspeig, Alicante, SE Spain (38°22' N, 0°35' W). The site has a typical Mediterranean semi-arid climate, with mean annual temperature and rainfall of 17.8° C and 336 mm, respectively. Rainfall has an irregular distribution and a pronounced summer drought lasting 4–5 mo (Meteorological Station Ciudad Jardín, Alicante, 1971–2000). During the summer of 2005, a 20-m high quarry cliff was filled with sterile material, creating a 3000 m² area oriented N–NE with 14–17° slope. A 40-cm deep topsoil layer containing a high density of seeds of the

herbaceous species *Poa pratensis* L. and seeds and rhizomes of *Pennisetum clandestinum* Chiov. was deposited.

Experimental design

We applied two treatments – irrigation and organic fertilization – each of two levels, following a completely randomized, fully factorial design replicated three times (12 plots of 15 m × 15 m).

In Sep 2005, we applied composted sewage sludge (henceforth compost) from a nearby composting plant (SEARSA, Aspe, Alicante, Spain; see composition in the Supporting Information, App. S1) as an organic fertilizer on six randomly selected plots. Compost was applied at 4 kg dry weight (DW) m⁻², which is recommended for Mediterranean forest plantations (Fuentes et al. 2007a). Six control plots, without compost, were also established (hereafter C+ and C– plots, respectively). In the C+ plots, compost was mixed with the top 40 cm of soil by using a rotovator. The two levels of irrigation were achieved by using drip irrigation lines 0.8 m and 2.4 m apart, providing a water supply rate of 12 mm wk⁻¹ and 4 mm wk⁻¹, respectively (hereafter I+ and I– plots, respectively). Irrigation was maintained at this rate from Jan 2006 to Dec 2006, and doubled in Aug to account for the high evapotranspiration rates. A separation of 80 cm between drip irrigation lines is common in commercial roadside and quarry restoration (J. Fort, Projar SA, Spain, pers. com.).

Soil sampling and analyses

In Oct 2005, immediately after the organic amendment was applied and before irrigation, we took a soil core of 10 cm depth and 5 cm × 5 cm width in each of the 12 plots, and determined soil texture (Bouyoucos densitometer; Bouyoucos 1962), oxidizable organic carbon (Walkley–Black method), available phosphorus (Olsen bicarbonate extraction and colorimetric determination) and total nitrogen (NA-1500 elemental analyser; Carlo Erba Milan, Italy), as well as electrical conductivity of a saturated paste extract (see Peverill et al. 1999 for detailed descriptions of soil analyses).

Plantation and seeding

In Dec 2005, we planted 25 seedlings per plot of the species *Anthyllis cytisoides* L. (fam. Fabaceae), *Juniperus oxycedrus* L., *Pinus halepensis* Miller, *Pistacia lentiscus* L., *Rhamnus lycioides* L. and *Salsola genistoides* Juss. ex Poir. (hereafter *Anthyllis*, *Juniperus*, *Pinus*, *Pistacia*, *Rhamnus* and *Salsola*, respectively) in manually dug planting holes of 30 cm × 30 cm × 30 cm. The 1-year-old planted seedlings came from a local nursery (Santa Faz, Alicante, Spain; 38°23' N; 0°26' W; 80 m a.s.

l.), and were grown in 300 cm³ plastic pots under optimal conditions (full sunlight, fertilized 1:1 peat–coco-peat substrate and regular irrigation). *Anthyllis* and *Salsola* are typically found in degraded or pioneer successional communities (Hensen 1999), sometimes accompanied by pioneer tree species such as *Pinus* (Cortina et al. 2006). Hence, we consider them to be early-successional species. In contrast, *Juniperus*, *Pistacia* and *Rhamnus* are common in more advanced stages of plant succession in the studied area (Maestre et al. 2004) and may be considered late-successional species. Additional support for this classification is that *Juniperus*, *Pistacia* and *Rhamnus*, but not the remainder of the species, have fleshy fruits. The presence of fleshy fruits is a highly conservative evolutionary trait typical of species that evolved during the Tertiary, under more benign and productive environments (Herrera 1984). In contrast, the lack of fleshy fruits, found in *Anthyllis*, *Pinus* and *Salsola*, is characteristic of species evolved during the Quaternary, under harsher and less productive conditions (Herrera 1984). Planting density was 7500 seedlings of all species per hectare. We assessed seedling growth parameters in 15 individuals per species by measuring root growth potential (RGP), root:shoot biomass ratio and stem height (see App. S2). All of these measures were taken before planting. Root growth potential was measured under controlled conditions in the laboratory, as the number of new roots growing beyond the root plug during 15 d under optimum growth conditions (for a detailed description of this procedure see Trubat et al. 2010). Once planting was completed (Dec 2005), the area was hydroseeded with a standard commercial mixture commonly used on these environments (Table 1). Hydroseeding is a restoration technique aimed to rapidly establish a dense herbaceous cover in degraded environments (Sheldon & Bradshaw 1997). Hydroseeding mixes fast-growing species, generally legumes and grasses, with water, fertilizer, mulch and stabilizing agents to promote the maintenance and germination of the seeds. The mixture is hosed onto the restoration site (Sheldon & Bradshaw 1997; Matesanz et al. 2006; García-Palacios et al. 2010). There is a general agreement on the need for an herbaceous layer to ensure soil protection in restored slopes (Andrés & Jorba 2000; Prach 2003). Hence, we did not establish an experimental control without hydroseeding. Rather, we focused our study on different resource availabilities and successional stages as drivers of woody seedling response to herbaceous cover.

Plant measurements

Herbaceous vegetation was measured, using the point-intercept method, every 10 cm along two 13-m transects per plot (260 sampling points per plot) in May and Aug 2006. Transects were randomly placed, parallel to the main

Table 1. Composition of the hydroseeding mix.

Hydroseeding component	Characteristics	
Wood fibre mulch (100 g m ⁻²)	Organic matter	95%
	Porosity	96%
	Water-holding capacity (volume)	40%
	Air content (volume)	55%
	pH	5.5
	Salinity (EC)	0.1 mS cm ⁻¹
	Total nitrogen (N)	0.12%
	Total phosphorus (P)	0.18%
	Total potassium (K)	0.14%
	Total calcium (Ca)	0.56%
	Total magnesium (Mg)	0.08%
Stabilizing agents (10 g m ⁻²)	From ground <i>Plantago</i> sp. seeds	100%
Humic acids (10 cm ³ m ⁻²)	Humic acids	10%
	Fulvic acids	6%
Added fertilizer (30 g m ⁻²)	NO ₃ -N	2.5%
	Urea-N	5%
	NH ₄ ⁺ -N	4.5%
	P ₂ O ₅ soluble in water and ammonium citrate	9%
	P ₂ O ₅ soluble in water	9%
	K ₂ O soluble in water	12%
	MgO soluble in water	2%
	Sulphur (S) soluble in water	4%
Commercial seed mixture (30 g m ⁻²)	<i>Dactylis glomerata</i>	30%
	<i>Lolium rigidum</i>	30%
	<i>Trifolium alexandrinum</i>	20%
	<i>Medicago lupulina</i>	5%
	<i>Agropyron cristatum</i>	15%

Data provided by J. Fort (PROJAR SA, Spain).

slope and separated at least 5 m apart with a buffer zone of 1 m around the entire plot to avoid edge effects. Dry and green herbaceous materials were sampled separately during this sampling period.

Seedling survival and growth were measured in Jan 2006 to assess transplant shock (i.e. possible initial elevated mortality owing to lack of acclimatization of the seedlings to field conditions), and again in May and Sep 2006. Measurements corresponded with the maximum growth period (May) and the end of the summer drought (Sep), a period of maximum mortality in Mediterranean environments (Cortina et al. 2004). On each sampling date, we monitored seedling survival, stem height and root collar diameter of every seedling planted (except for root collar diameter of *Salsola* seedlings, which could not be measured because of the excessive number of stems). Root collar diameter was measured where the stems joined the roots by removing soil from around the seedling. Relative growth rate in stem height and root collar diameter was calculated as $RGR = [\ln(X_2) - \ln(X_1)]/t$, where X_1 and X_2 correspond to stem height or root collar diameter in two

successive sampling dates separated by t months. With the final height and root collar diameter data, we calculated the slenderness coefficient (SC) for all species (except *Salsola*) as $SC = \ln(\text{height})/\ln(\text{root collar diameter})$. This coefficient may reflect competition for light (Kurashige & Agrawal 2005). Finally, on Sep 2006, we counted the number of *Salsola* seedlings flowering as an additional indicator of plant performance.

Statistical analyses

Changes in soil properties after compost application were analysed by one-way ANOVA, using presence–absence of compost as a fixed factor. Two-way ANOVA, with compost and irrigation as fixed factors, was used to assess their effects on herbaceous cover.

Mean values of RGR in stem height and root collar diameter of each species and plot were significantly positively correlated among them, and correlated among successive sampling periods. We therefore conducted a multivariate analysis of variance (MANOVA) using species, irrigation and compost as fixed factors and the average RGR for all individuals of a given species in each plot as response variable. This procedure is recommended to avoid Type I errors when dealing with multiple correlated response variables (Zar 1998). Because of the significant species \times treatments interactions (see below), we performed MANOVA analyses for each species separately, using irrigation and compost as fixed factors. All data met normality and homoscedasticity assumptions and no transformations were required.

Non-parametric ANOVA (PERMANOVA; Anderson 2001; McArdle & Anderson 2001) was used to analyse treatment effects on the mean slenderness coefficient for each species and plot as it was not possible to homogenize the variance of this variable. We used Bray–Curtis distance and performed no data transformations or standardisations. PERMANOVA analyses multivariate and univariate datasets on the basis of any distance measured using permutation methods, with no data distribution assumptions. This test was performed first for all species, and where species \times treatment interactions were significant, separate analyses were performed for each species.

Mean values of seedling survival per species and plot, and the frequency of flowering *Salsola* individuals, were analysed using hierarchical log-linear models. The analysis of seedling survival was performed using the whole set of species first, and then separately for each species, where the species \times treatments interactions were significant. We studied the relationship between herbaceous cover and initial seedling stem height and seedling survival (the latter combining all the species) by using linear regression analyses, with survival as dependent variable. All statistical anal-

yses were performed using SPSS 12.0 for Windows (Chicago, Illinois, USA). All analyses involving woody seedlings were performed for three different periods: pre-summer (Jan–May), summer (May–Sep) and the entire study period (Jan–Sep), except for the analysis of the slenderness ratio (conducted only for the two latter periods).

Results

Soil properties and herbaceous cover

Soil properties were not significantly affected by compost application (Table 2). Herbaceous cover was high in all plots (> 76% cover; data not shown), and increased with irrigation [ANOVA (water): $F_{1,11} = 12.79$; $P = 0.009$, and $F_{1,11} = 15.59$; $P = 0.006$ for herbaceous cover in May and Aug 2006, respectively]. Herbaceous cover increased from $76 \pm 6\%$ and $83 \pm 4\%$ in I– plots to $91 \pm 1\%$ and $96 \pm 0.5\%$ in I+ plots in May and Aug, respectively. Conversely, compost and the interaction irrigation \times compost had no significant effect on herbaceous cover either in May ($F_{1,11} = 2.5$; $P = 0.16$ and $F_{1,11} = 0.28$; $P = 0.6$ for compost and irrigation \times compost, respectively) or in Aug ($F_{1,11} = 0.08$; $P = 0.8$ and $F_{1,11} = 0.08$; $P = 0.8$ for compost and irrigation \times compost, respectively).

Seedling survival and flowering

Log-linear analyses revealed a significant species \times compost interaction before summer (LOG-LINEAR: $G^2 = 11$; $df = 5$; $P = 0.05$), and species \times irrigation before and during summer ($G^2 = 12.53$; $df = 5$; $P = 0.03$, and $G^2 = 47.7$; $df = 5$; $P < 0.0001$, respectively). These results suggest a species-specific response to compost addition and irrigation.

Compost had a marginally positive effect on pre-summer survival of *Salsola* ($G^2 = 2.75$; $df = 1$; $P < 0.1$; Fig. 1). In May 2006, irrigation had a negative effect on the survival of all species except *Pistacia*, which was unaffected. Compost had a negative effect on seedling

survival of all species ($P < 0.05$ in all cases) except *Salsola* and *Juniperus*. No synergistic effect between compost and irrigation was observed in the survival of any of the species studied. The largest pre-summer survival rates were found in control plots (I–C–) in all species, whereas the lowest rates were found in I+C+ plots, with the exception of *Pistacia*.

Seedling survival after the first summer in the field varied strongly among species, ranging from 18% in I+C+ *Rhamnus*, to a maximum of 80% in I+C– *Juniperus* ($G^2 = 120.3$; $df = 5$; $P < 0.0001$). The increase in water supply benefited *Rhamnus*, *Juniperus* and *Pistacia* but not *Pinus*, *Anthyllis* or *Salsola*. The positive response of *Rhamnus*, *Juniperus* and *Pistacia* decreased when compost was added. In addition, we found a negative effect of compost on post-summer survival of *Pinus*, *Pistacia* and *Rhamnus* ($P < 0.05$ in all cases). This effect was marginally significant in *Anthyllis* ($P < 0.1$). *Juniperus* and *Salsola* were not affected by compost (Fig. 1).

An inverse relationship was found in some species between herbaceous cover and seedling survival (see Table 4). Spring and summer herbaceous cover reduced summer survival of *Anthyllis*, *Juniperus* and *Salsola*, explaining from 35% to 51% of the variance in seedling survival. In contrast, herbaceous cover had a positive effect on survival in summer, after leaves dried out. The trend in the survival of the six species studied in relation to dry herbaceous cover in Aug was always positive, although only statistically significant for *Pinus* (see Table 4). A significant positive relationship between seedling initial height and survival was found, regardless of the treatments applied (Fig. 2).

Increased water availability substantially reduced the number of *Salsola* individuals flowering (LOG-LINEAR: $G^2 = 12.22$; $df = 1$; $P < 0.001$). For example, 29% of *Salsola* individuals flowered in I– plots during the first spring, whereas this number was reduced to 11% in I+ plots. Compost did not affect *Salsola* flowering.

Seedling growth

Growth in stem height showed a significant increase with increased water availability in *Pistacia* (1.7 ± 0.3 vs 1.8 ± 0.3 and 2.4 ± 0.5 vs 2.6 ± 0.5 [I– vs I+, respectively]; MANOVA: $F_{1,8} = 13.19$; $P = 0.007$ and $F_{1,8} = 9.25$; $P = 0.016$ for pre-summer and total height growth, respectively; Table 3), and a positive trend in two of the six species studied (*Juniperus* and *Pinus*). Compost positively affected height growth for the whole study period in *Rhamnus* ($F_{1,8} = 5.41$; $P = 0.053$) and *Pistacia* ($F_{1,8} = 21.41$; $P = 0.002$), but had no effect on other species. Marginal interactions between compost and irrigation were found in *Rhamnus* stem height ($F_{1,8} = 4.76$; $P = 0.065$ and

Table 2. Properties of unamended soil (C–) and soil amended with composted sewage sludge (C+).

	C–	C+
Clay (%)	12.6 \pm 0.8	14.0 \pm 1.0
Silt (%)	4.2 \pm 0.6	4.7 \pm 0.7
Sand (%)	83.2 \pm 0.7	81.3 \pm 0.7
Oxidizable carbon (%)	1.6 \pm 0.1	1.6 \pm 0.1
Total nitrogen (%)	0.19 \pm 0.01	0.22 \pm 0.02
Available phosphorus (mg kg ⁻¹)	101 \pm 16	109 \pm 11
Electrical conductivity (dS m ⁻¹)	6.0 \pm 1.0	7.0 \pm 1.0

Data are means \pm standard errors of $n = 6$ samples in all analyses but available P ($n = 3$).

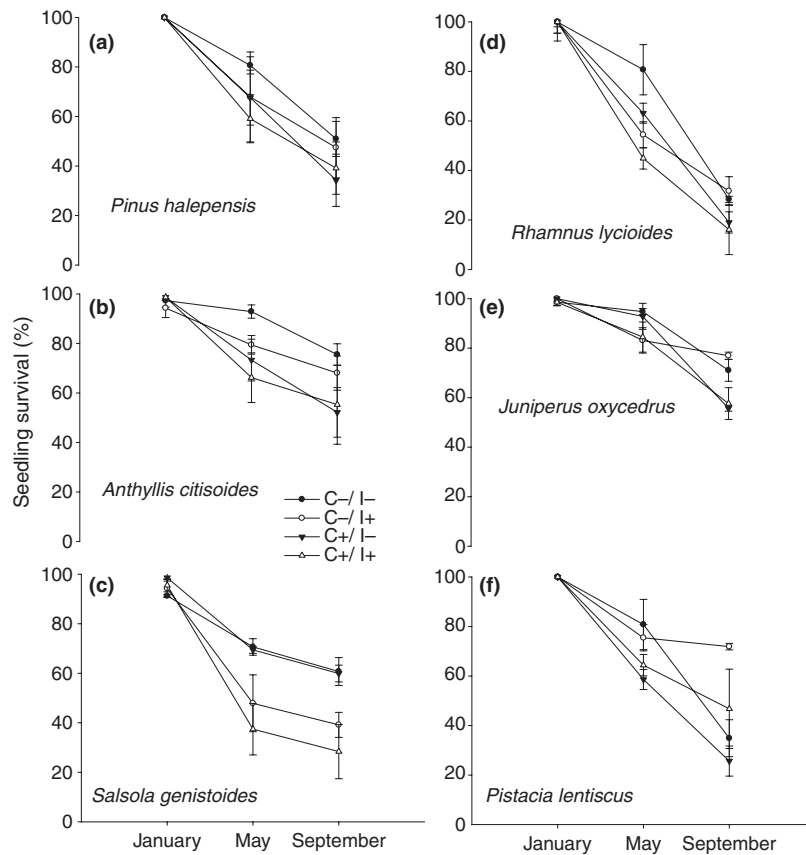


Fig. 1. Survival of Mediterranean woody seedlings as affected by irrigation and compost application. Mean \pm standard error of $n = 3$ plots per treatment combination are shown. Transplant shock was measured in January 2006, 1 mo after planting, and pre-summer and summer survival were measured in May 2006 and September 2006, respectively. C+/C– = seedlings with/without compost; I+/I– = seedlings with/without irrigation. (a) *Pinus halepensis*; (b) *Anthyllis cytisoides*; (c) *Salsola genistoides*; (d) *Rhamnus lycioides*; (e) *Juniperus oxycedrus*; (f) *Pistacia lentiscus*.

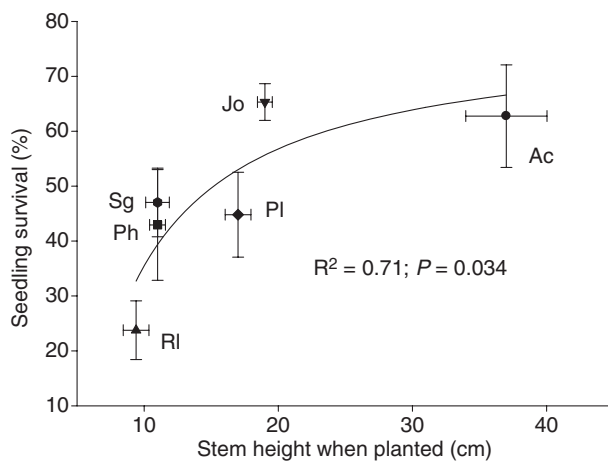


Fig. 2. Relationship between mean seedling height before planting and summer survival, regardless of the resource level supplied. Ac = *Anthyllis cytisoides*; Jo = *Juniperus oxycedrus*; Ph = *Pinus halepensis*; PI = *Pistacia lentiscus*; RI = *Rhamnus lycioides*; Sg = *Salsola genistoides*.

$F_{1,8} = 4.19$; $P = 0.08$, after the summer and during the whole year, respectively). While irrigation slightly increased *Rhamnus* seedling height in the absence of compost, this effect waned when both compost and increased water availability were applied together (App. S3).

Treatment effects on root collar diameter were less evident than those found in stem height (App. S3). We found no significant effect of irrigation on root collar diameter growth of any of the species studied. In contrast, compost had a marginally significant and negative effect on root collar diameter growth in *Pinus* [0.9 ± 0.2 vs 0.7 ± 0.3 and 1.0 ± 0.3 vs 0.9 ± 0.3 (C– vs C+, respectively); $F_{1,8} = 4.42$; $P = 0.069$ and $F_{1,8} = 4.43$; $P = 0.067$ for summer and total growth, respectively], but a positive effect on *Pistacia* total diameter growth (2.4 ± 0.4 vs 2.6 ± 0.5 [C– vs C+, respectively]; $F_{1,8} = 9.883$; $P = 0.014$). Marginally significant effects of the interaction compost \times irrigation were found in root collar diameter growth of *Juniperus* after the summer, with compost decreasing root collar diameter growth under the

Table 3. Slenderness coefficient (unitless) of Mediterranean woody species as affected by irrigation and compost application.

Species	Treatments			
	C– I–	C+ I–	C– I+	C+ I+
<i>Anthyllis cytisoides</i>	3.2 ± 0.2	2.6 ± 0.2	3.0 ± 0.2	2.7 ± 0.1
<i>Juniperus oxycedrus</i>	2.6 ± 0.1	3.0 ± 0.2	3.0 ± 0.2	2.7 ± 0.1
<i>Pinus halepensis</i>	2.5 ± 0.1	2.5 ± 0.1	2.6 ± 0.1	3.0 ± 0.3
<i>Pistacia lentiscus</i>	2.4 ± 0.2	2.6 ± 0.1	2.4 ± 0.1	2.4 ± 0.1
<i>Rhamnus lycioides</i>	6.1 ± 1.3	6.8 ± 1.3	6.4 ± 1.4	4.0 ± 0.8

C+/C– = seedlings with/without compost; I+/I– = seedlings with/without irrigation. Mean ± standard error of $n = 3$ plots per species and treatment level are shown. The number of plants measured per plot and species ranged from 3 to 20, depending on survival rate.

low watering treatment but not under the high watering treatment ($F_{1,8} = 4.75$; $P = 0.061$). No interactions were found for the other species.

Treatment effect on seedling slenderness depended upon the species tested (PERMANOVA: species × compost × irrigation: $F_{4,40} = 6.84$; $P < 0.001$, Table 3). While the slenderness coefficients for *Anthyllis*, *Pinus* and *Pistacia* were not affected by the treatments, a compost × irrigation interaction affected *Juniperus* and *Rhamnus* slenderness coefficients ($F_{1,8} = 4.5$; $P = 0.06$ and $F_{1,8} = 11.28$; $P < 0.05$, respectively). Compost amendment and irrigation promoted seedling slenderness when applied separately, but their effect virtually disappeared when applied simultaneously.

Discussion

Approaches using multiple species are often needed to properly assess the overall usefulness of management or restoration techniques (Padilla et al. 2011). Our study, by using this multiple species approach, highlights the role of resource management and the ecological strategy of woody species involved as drivers of secondary succession. The presence of an herbaceous layer is recommended in

order to protect the soil surface during the restoration of degraded slopes (Andrés & Jorba 2000; Prach 2003). Hence, management techniques aimed to foster secondary succession need to take into account the interactions between woody and herbaceous vegetation. Our results suggest that the response of woody seedlings to herbaceous vegetation under variable irrigation and fertilization is species-specific. Thus, while positive responses were found under higher resource levels for late-successional species, the opposite was found for pioneer species. Unfortunately, the lack of a control treatment (without herbaceous neighbours) and soil water availability measurements prevented us from disentangling the effects of herbaceous competition from the effects of irrigation or organic fertilization. However, the negative effect of irrigation and fertilization on the performance of early-successional woody seedlings likely resulted from an increase in competition from herbaceous species (Table 4). This negative effect might sometimes be partly compensated by the positive mulch effect, which increased summer survival of *Pinus*. Our conclusions should be viewed with caution because they are based on only three replicates by treatment combinations. However, these three replicates account for the results of a total of 75 individuals by species and treatment, a much larger number of individuals than most previous studies on the topic, adding some more confidence to our results and conclusions. Our study should help to reconcile the contrasting results found in the literature regarding the response of woody–grass interactions to different resource levels. It suggests that the outcome of these interactions under different resource levels depends on the balance between the capacity of woody species to use soil resources and their ability to compete with herbaceous vegetation.

In contrast with other studies (Ros et al. 2003), organic fertilization did not affect our measurements of soil fertility. However, we did not measure changes in micronutrient availability, which could explain the increase in seedling height growth for most species promoted by fertilization. Previous research has demonstrated significant

Table 4. Relationships between herbaceous cover in May and Aug and seedling summer survival.

Herbaceous Cover		Summer Survival					
		<i>Anthyllis</i>	<i>Juniperus</i>	<i>Pinus</i>	<i>Pistacia</i>	<i>Rhamnus</i>	<i>Salsola</i>
May	R^2	0.46	0.20	0.03	0.00	0.33	0.35
	P	0.015	0.149	0.610	0.964	0.052	0.041
August (green cover)	R^2	0.51	0.35	0.02	0.08	0.44	0.16
	P	0.009	0.043	0.699	0.364	0.019	0.204
August (dry cover)	R^2	0.08	0.13	0.39	0.06	0.11	0.18
	P	0.386	0.242	0.031	0.446	0.284	0.167

Note that cover in summer included standing biomass and necromass. Linear regression coefficients and P -values are shown for each pair of variables ($n = 12$). Significant results ($P < 0.05$) are in bold type. All the relationships found were negative.

increases in micronutrients that are fundamental for plant development, after organic fertilization (Fuentes et al. 2007a). The lack of difference in macronutrients between amended and unamended soils can be explained by the fact that the recommended dose of 4 kg m^{-2} represents a small input (0.6%) compared with the original soil organic matter content. In this study, the topsoil was of higher quality than commonly used in quarry or roadside restoration (Badia et al. 2007; Tormo et al. 2007), which probably reduced the response to compost addition in our study. The high quality of the topsoil most likely contributed to the high herbaceous cover observed (Alday et al. 2011). Following previous research conclusions (Andrés & Jorba 2000), plant cover was sufficient to ensure soil protection, regardless of the treatment applied. However, it may be considered that in many other studies, organic amendments have been very useful to improve physical and chemical properties and reduce erosion of less fertile soils (Caravaca et al. 2002; Ros et al. 2003).

Although the effect of compost on soil properties was weak, it slightly improved plant performance. Overall, we found a generally positive response in growth, but a negative effect on survival – a common response of plants to organic fertilization on calcareous soils and under semi-arid climates (Fuentes et al. 2007a; Valdecantos et al. 2011). While the increase in biomass accumulation is likely caused by an increase in micronutrient availability (Caravaca et al. 2002; Fuentes et al. 2007a), the reduction in survival could be explained by two different mechanisms. First, the most plausible explanation is that lower survival reflects an increase in water stress caused by increased salinity resulting from rapid nutrient mineralization – a response commonly found under semi-arid conditions (Kozłowski 1997; Ingelmo et al. 1998; Fuentes et al. 2007a). Second, an alternative explanation could be that there is a slight increase in toxicity caused by the increase in heavy metals content promoted by organic fertilization (App. S1). Although most heavy metals were in concentrations lower than those specified in the current legislation (Valdecantos et al. 2004), zinc concentration was slightly higher (1012 cf. 1000 mg kg^{-1}). We believe, however, that this scenario is unlikely because compost negatively affected four of the six species, including *Pistacia* and *Pinus*, which are known to be resistant to high zinc concentrations (Fuentes et al. 2007b). Conversely, *Salsola*, a species highly resistant to soil salinity, was not significantly affected by compost application, supporting the salinity explanation. Unfortunately, our experimental design does not allow us to disentangle both possible mechanisms. Regardless of the mechanism involved, these results suggest that composted sewage sludge may help to increase biomass accumulation, but not to improve seedling survival when applied to nutrient-rich

soils in semi-arid areas (Fuentes et al. 2007a,c; Valdecantos et al. 2011).

All species, irrespective of their successional stage, had higher pre-summer survival in the control plots. These results indicate that woody seedlings do not always show positive responses to increases in irrigation or fertilization, likely because of increases in herbaceous competition. We note that irrigation significantly increased herbaceous cover, but this changed after the onset of summer drought. Although the three pioneer species *Anthyllis*, *Pinus* and *Salsola* had greater survival in control plots, *Pistacia*, *Juniperus* and *Rhamnus* had greater survival in the I+ plots. Mulch provided by dry herbaceous vegetation increased the survival of *Pinus* seedling over summer. The negative effects of herbaceous plants on the performance of woody seedlings during spring probably outweighed any positive effects resulting from the accumulation of herbaceous litter.

Overall, our results suggest a species-specific response, which is dependent on soil resource level, which we believe might help to reconcile contrasting results found in the literature. Increases in the amount of resources may compensate for greater herbaceous competition in more competitive (late-successional) woody species (Eliason & Allen 1997; Davis et al. 1999). Conversely, the contrary may happen with less competitive (early-successional) species, where the presence of neighbours determines seedling performance above resource availability (McDonald 1986; Bush & Van Auken 1988; Sánchez & Peco 2004). This was particularly evident in *Salsola*, as not only survival and growth, but flowering was also reduced by irrigation. However, the survival of some species was unrelated to herbaceous cover (Table 4). This could be explained by the contrasting heights of the plant species at the commencement of our study (Fig. 2; see below).

The intensity of competition along gradients in resource availability depends on the response variables measured (Goldberg & Novoplansky 1997; Maestre et al. 2005a). This is particularly true for plants growing under water-limited conditions (e.g. Mediterranean environments) where contrasting results for growth rate under benign conditions or survival under water stress have been often found (Goldberg & Novoplansky 1997; Castro et al. 2004; Gómez-Aparicio et al. 2008). Larger plants lose more water during droughts and therefore have lower survival (Trubat et al. 2008). It is expected that different measures of plant performance (e.g. survival or growth), vary in their response to resources availability or to the presence of neighbouring plants (Goldberg & Novoplansky 1997; Castro et al. 2004; Valdecantos et al. 2011). In our study, treatment effects on growth were weaker than the effects on survival for all species studied. We found positive treatment effects on growth for four of the species examined, in

accordance with previous studies (Rey-Benayas & Camacho-Cruz 2004; Coyle & Coleman 2005; Sardans et al. 2005), but these effects were discontinuous and their intensity was lower than previously found with similar species (see Badia et al. 2007 and references therein). The increase in the slenderness coefficient under the compost and irrigation treatments for *Juniperus* and *Rhamnus* can be interpreted as an indicator of competition for light between woody seedlings and herbaceous vegetation (Eliason & Allen 1997; Davis et al. 1998; Soliveres et al. 2010). The positive relationship between seedling height and field survival may reflect a stronger ability of taller seedlings to compete for light, which has been identified as an important limiting resource that plants compete for even in water-limited systems (Eliason & Allen 1997; Soliveres et al. 2010). Indeed, competition between woody and herbaceous plants for both light and water are likely to interact, with lower shade tolerance under dryer conditions (Valladares & Pearcy 2002). Therefore, an alternative explanation for the positive response to higher water levels in late-successional but not in early-successional species might be related to the relative shade and drought tolerances of the species involved (Hastwell & Facelli 2003; Saccone et al. 2009; Soliveres et al. 2011). An increase in water availability might benefit more shade-tolerant and water-demanding (late-successional) species (Fahey et al. 1998) but not early-successional species. In early-successional species the increase in water availability may be insufficient to compensate for low light levels because they are less shade-tolerant and water-demanding than late-successional species (Marañón & Bartolomé 1993; Hastwell & Facelli 2003; Soliveres et al. 2011).

Contrary to our expectations (Coyle & Coleman 2005), we found no synergistic effect of water and compost application on the performance of herbs and woody plants. Response to simultaneous changes in various levels of resources depends on climatic and soil conditions (Coyle & Coleman 2005), and may range from synergistic to antagonistic (Clemente et al. 2004), depending on initial conditions. Resource management should aim at improving community condition, ecosystem function and the provision of services while minimizing costs (Cortina et al. 2006; Rey-Benayas et al. 2009). In semi-arid Mediterranean ecosystems, this may be better accomplished by establishing heterogeneous patches of high resources (water and nutrients) within a resource-poor matrix (Booth et al. 1999), simulating natural mosaics (Maestre et al. 2005b; Badia et al. 2007). This heterogeneous matrix could be optimised by planting species with contrasted ecological traits, associated with their successional stage, on specific microsites. While late-successional species can be introduced into resource-rich patches, pioneer species could be more successfully

established in the nutrient-poor matrix. This heterogeneous matrix could meet the multiple goals of soil protection, enhancing secondary succession, and increasing the diversity of vascular plants, ultimately contributing to improved efficiency of restoration practices in degraded slopes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Composition of the compost used in the experiment.

Appendix S2. Morphological and environmental features of studied seedlings.

Appendix S3. Relative growth rate in root collar diameter and stem height of the studied species.

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