Rethinking species selection for restoration of arid shrublands

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Abstract

Restoration is playing an increasingly important role in ecology as natural habitats become scarcer and chances to restore ecosystems damaged by human activities are more common. However, restoration of degraded Mediterranean arid ecosystems is hampered by drought and poor soils, which cause many establishment failures. To compare how species belonging to different successional stages establish in a very stressful site, we carried out a field experiment with 14 tree and shrub species differing in functional traits. After three growing seasons, mid-successional shrubs such as the leafless *Ephedra fragilis* and the C_4 *Salsola oppositifolia*, or green-stemmed legumes like *Coronilla juncea*, *Genista umbellata* and *Retama sphaerocarpa*, showed survival rates up to 93%, while late-successional species like *Tetraclinis articulata*, *Pinus halepensis*, *Olea europaea* and *Pistacea lentiscus*, frequently used and recommended in regular restoration projects, hardly reached 55%. We found that survival was highest for legumes, followed by leafless species, and C_4 shrubs, traits that are believed to maximize resource uptake in cleared and infertile areas while reducing water losses. Thus, selection of mid-successional species having such traits should be considered for successful restoration. These species would increase the success of restoration programs, but also would increase soil fertility, reduce soil erosion processes, and eventually facilitate establishment of other species, therefore accelerating secondary succession. We suggest a new approach for the restoration for arid shrublands in which species are carefully selected based on traits that best suit the environmental conditions.

Keywords: Sapling survival; Arid environments; Leafless shrubs; Legumes; Functional traits.

Introduction

Human impact on ecosystems is substantial and increasing, causing an enormous range of changes and direct and indirect effects. Indeed, between one third and half of the Earth's surface has been altered by human activities (Vitousek, Mooney, Lubchenco & Melillo 1997) and there is hardly any pristine area left.

Ecosystems in the western Mediterranean basin are amongst those which have undergone the most intense changes in land use in the last 500 years (Puigdefábregas & Mendizábal 1998). The expansion of crops, timber, and population growth until the beginning of the 20th century eroded almost completely the natural vegetation in many areas, while in others grazing and logging selectively harvested trees and shrubs from woodlands. In the second half of the twentieth century, population concentration in urban areas led to the abandonment of farm life and, consequently, of practices designed to control soil losses in steep hills, such as terraces. Indeed, one of the biggest challenges of restoration ecology lies particularly on abandoned land and old fields (Cramer, Hobbs & Standish 2008; Young 2000), as natural and seminatural habitats become scarcer and degraded territories are more common (Hobbs & Harris 2001; Prach, Bartha, Joyce, Pysek, van Diggelen et al. 2001).

Often the first step in restoration is the re-establishment of the local species pool by actively planting pre-disturbance species (Palmer, Ambrose & Poff 1997; Parker 1997). However, the success of community restoration in arid environments is especially at risk due to very stressful ecological conditions. Drought, together with high temperatures, high irradiance, grazing, and infertile soils, threaten the survival of planted saplings (García-Fayos & Verdú 1998; Maestre, Cortina, Bautista, Bellot & Vallejo 2003). To enhance the chance of sapling survival, research has focused on developing new procedures aimed at modifying sapling allometry (Pausas, Bladé, Valdecantos, Seva, Fuentes et al. 2004; Pemán, Voltas & Gil-Pelegrin 2006) and soil characteristics (Querejeta, Roldán, Albaladejo & Castillo 1998), and protecting saplings against limiting conditions (Jiménez, Navarro, Ripoll, Bocio & De Simón 2005; Padilla & Pugnaire 2009). However, much less attention has been paid to how species selection and plant traits determine restoration success (but see Pywell, Bullock et al. 2003).

Over the past years, land managers have preferentially used late-successional species in restoration projects, especially trees and large shrubs based on the idea that these will accelerate succession and improve ecosystem resilience (Bonet 2004). On the other hand, the use of small shrubs such as mid-successional species is still rare for unknown reasons. The pace of colonization processes and secondary succession in Mediterranean arid environments is rather slow (Bonet & Pausas 2004; Pugnaire, Luque, Armas & Gutiérrez 2006), so we believe that introducing mid-successional, rather than late-successional species, may be more desirable for the restoration of arid shrublands for several reasons: (1) Mid-successional species are mostly more drought-tolerant species with their regeneration niche usually linked to open areas (Valiente-Banuet, Vital Rumebe, Verdú & Callaway 2006); This should help to increase restoration success. (2) They tend to root deeper at the seedling stage, which is critical in dry environments (Padilla & Pugnaire 2007); This will expedite establishment allowing for earlier protection against erosion. (3) Green-stemmed, leafless shrubs have a low ratio of leaf-to-total photosynthetic area, which is advantageous in dry, high irradiation habitats (Valladares, Hernández, Dobarro, García-Pérez, Sanz et al. 2003). (4) They facilitate the recruitment of drought-sensitive species under their canopies (Padilla & Pugnaire 2006) speeding up succession in a natural way towards a mature community.

To our knowledge, very few studies have simultaneously compared sapling survival of both late and mid-successional species during the first years of establishment in arid environments (but see a first attempt in Padilla, Pugnaire, Marín, Hervás & Ortega 2004). We compared sapling survival of both ecological groups, and we hypothesized that survival of mid-successional shrubs would be higher than that of late-successsional species because of their greater adaptation to cope with drought. We planted 14 tree and shrub species that potentially could be used in the restoration of Mediterranean arid shrublands in a very stressful environment in SE Spain and watered half of them in summer to look at drought effects on the survival of each species.

Materials and methods

Experimental site

The experimental area is located in the Sierra Alhamilla range (Almería, Spain, 37º99’N, 02º99’W, 650 m a.s.l.). Restoration of this deforested area had been attempted several times in the last years resulting in complete failure because of its very low rainfall and infertile soils. Here, we used this site as a representative case-study of limiting arid environments. We selected two 1-ha plots on opposite, moderate slopes to account for the different environmental conditions. Plant communities, soils, and slopes (<20%), were very similar in both plots, differing only in aspect. There was a relatively more humid, east-facing slope and a relatively drier, west-facing slope (see Appendix A: Table 1). The climate is Mediterranean arid with a mean annual temperature of 17.3 ºC, mild temperatures in winter and high temperatures in late spring and summer, and 282 mm of annual precipitation with a marked drought period from June to September. Soils are loamy-sandy, calcic regosols developed over a mica-schist bedrock with very low fertility and water-holding capacity.

The abandonment of human settlements in this range dates from the first part of the 20th century (National Statistics Institute, 2003). Until then, selective logging, grazing and cropping eroded the woodland canopy. Sixty years later, the extant plant community is a xeric scrubland dominated by species like *Anthyllis cytisoides*, *Artemisia barrelieri* and *Thymus hyemalis*, interspersed with individuals of the larger shrub *Retama sphaerocarpa*, annual grasses and herbs (see Appendix A: Figure 1). The potential vegetation of this area is a shrubland dominated by the large shrubs *Olea europaea* var. *sylvestris*, *Pistacia lentiscus*, *Quercus coccifera*, *Ziziphus lotus* and *Juniperus oxycedrus* (Peinado, Alcaraz & Martínez-Parras 1992), with dispersed *Pinus halepensis* and *Ceratonia siliqua* trees. The pace of plant succession in these environments is rather slow, with scant occurrences of mid-successional shrubs *Ephedra fragilis*, *Salsola* spp., and the legumes *Retama sphaerocarpa*, *Genista* spp. and *Coronilla juncea*.

Species and experimental design

We tested sapling survival of a wide range of native shrub and tree species that potentially can be used in the restoration of these dry environments. We selected species that usually occur in mid-successional stages as well as late-successional species. Early-successional species, such as scrub, were not selected because they were already present in the experimental site. Among the mid-successional species we selected the shrubs *Coronilla juncea* L., *Ephedra fragilis* Desf., *Genista umbellata* (L'Hér.) Dum. Cours., *Lycium intricatum* Boiss., *Retama sphaerocarpa* (L.) Boiss. and *Salsola oppositifolia* Desf. These species usually occur in open environments, and exhibit morphological and physiological adaptations to cope with very dry environments; *Ephedra*, *Coronilla*, *Genista* and *Retama* are green-stemmed or leafless shrubs, the latter three being legumes, and *Salsola* is a C_4-xero-halophyte shrub. Most of them are able to root deep (Padilla & Pugnaire 2007) and establish well in very dry environments (Padilla et al. 2004). Late-successional species were the trees *Ceratonia siliqua* L., *Pinus halepensis* Mill. and *Tetraclinis articulata* (Vahl) Mast., and the large shrubs *Juniperus oxycedrus* L., *Juniperus phoenicea* L., *Olea europaea* L. var. *sylvestris* Brot, *Pistacia lentiscus* L. and *Ziziphus lotus* (L.) Lam. These tend to occur in undisturbed areas, and under less stressful conditions.

In January 2004, one-year-old saplings of each species, provided by local nurseries and of local provenance, were transplanted to the east- and west-facing slopes, in gaps previously selected at random, distant at least 3 m from any perennial species. Before transplanting, the soil was dug up to a depth of 0.5 m using an auger (BT 120 C, Stihl AG & Co. KG, Germany) to increase aeration, and planted saplings were covered with piled branches of the shrub *Anthyllis cytisoides*. These branches provided saplings protection against radiation and extreme temperatures, and presumably also against herbivory (Padilla & Pugnaire 2009). To test the relative effect of drought on survival, watering was supplied to half the saplings every 20 days on average (six times a year) during the summers of 2004 and 2005. Water supply was discontinued in 2006 to evaluate the effect of normal drought on previously irrigated saplings. Water was supplied through the micro-irrigation technique (Sánchez, et al. 2004), which consisted of a water tank and a network of polyethylene pipes of different diameters distributed along the experimental plots that allocated water to the rooting zone of each sapling. Micro-tubes, 5 mm in diameter and 35 cm in length, connected to pressure-compensate drippers were buried into the soil at a depth of 25 cm. Previous tests showed that around 1.5-3.0 L of water were released from each drip into the soil per watering event (J. Sánchez, *pers. comm.*).

Plant survival and statistics

Since summer drought is the major threat to saplings in Mediterranean environments, sapling survival was recorded before and after the summers of 2004, 2005, and 2006. Since we registered some deaths soon after transplant, cumulative survival rate on each date was calculated as a ratio of plants living in the spring of 2004. Preliminary tests showed no significant effect of aspect on survival, so data from east and west-facing plots were pooled. Cumulative survival in the field after three years was analyzed by simple binary logistic regression where survival in autumn was the dependent variable, and species and watering were the predictor factors. Since we detected a very significant species x watering interaction (χ^2_{13}=40.731, P<0.001), and exploratory analysis showed clear differences among species, we made separate one-factor (watering) logistic regression for each species. Sample size of treatments was 15-47 saplings due to different mortality following transplantation. Analyses were conducted with the statistical package SPSS v15.0 (SPSS Inc., Chicago, IL, USA) and differences were set significant at P< 0.05.

Results

A very rainy spring in 2004 was followed by a summer with negligible rainfall (see Appendix A: Table 2). *Ephedra*, *Genista*, *Retama*, *Salsola* and *Coronilla* maintained survival rates above 70% without irrigation (Figure 1). On the other hand, the mortality of unwatered *Juniperus* spp., *Ceratonia*, *Olea*, *Tetraclinis* and *Ziziphus* was remarkable. In this case, watering managed to enhance sapling survival.

Very low rainfall characterized year 2005, which was also marked by a very dry spring and summer. In this dry year, sapling survival decreased compared with 2004, but our leguminous shrubs and the C_4 *Salsola* showed rates above 50% even if unwatered (Figure 1).

In autumn 2006, an average year in terms of annual and spring rainfall, saplings that had been irrigated in preceding summers kept showing higher survival rates than non-irrigated plants, although species like *Ceratonia* and *Lycium* suffered from the overall low water availability and equalled survival of controls.

On the whole, survival data after three years showed that water supply during summer did increase sapling performance of mid-successional species such as *Coronilla*, *Ephedra*, *Genista*, *Retama* and *Salsola* (Figure 2), but very high survival rates were reported even for unirrigated saplings of these species. They clearly survived best, attaining establishment rates close to 50% without water supply, and generally well above this number if watered: 93% for *Genista*, 83% for *Retama*, and 75% for *Ephedra*.

Survival of late-successional species was notably lower than that of mid-successional species, and in some cases survival of unirrigated, mid-successional species was higher than that of irrigated, late-successional species. Water supply boosted establishment rates of most late-successional species, particularly those of *Juniperus* spp., *Tetraclinis*, *Ziziphus*, *Olea* and *Pistacia*, but these species mostly died without irrigation (i.e., survival <25%). As an extreme case, we recorded very low survival (<10%) for irrigated *Ceratonia* trees, suggesting that in this species more watering should be provided to secure establishment.

Discussion

Unirrigated mid-successional shrubs attained much higher survival rates than late-successional shrubs and trees. Since usually, late successional species dominate in restoration programs, our data provide more evidence for critically reconsidering species selection for dryland management. Indeed, Padilla et al. (2004) had already showed in a very stressful site that legumes and chenopodiaceous shrubs attained high survival, whereas large casualties were recorded for the traditional late-sucessional trees and shrubs.

We believe that at least three suits of morpho-physiological traits might be involved in the responses of mid-successional species. First, these species tend to colonize disturbed, open habitats whereas late-successional species occur frequently in less limiting sites (Peinado, Alcaraz & Martínez-Parras 1992; Pugnaire et al. 2006). For instance, *Retama sphaerocarpa* and the halophytic C_4 shrub *Salsola oppositifolia* root much deeper than the late-successional *Pinus halepensis* under very dry soil conditions (Padilla & Pugnaire 2007) indicating a better adaption to drier and more disturbed habitats at least at the seedling stage. It is thus likely that these species are better suited to cope with drier climate predicted by global change scenarios. Second, mid-successional species having the highest survival, except *Salsola*, had green stems and remained leafless for most of the year. This low ratio of leaf to total photosynthetic area prevents water losses and injuries from high irradiance in high irradiation habitats. Thus, leaflessness seems a trait involved in high sapling survival in arid environments. In *Salsola*, however, the C_4 photosynthetic pathway is an advantage under high irradiance and temperature. Third, the best survivors were mostly leguminous shrubs. Valladares, Villar Salvador et al. (2002) found that *Rhizobium* inoculation enhanced the early performance of *Retama* saplings in very poor soils, so N-fixing bacteria likely favoured endurance of leguminous shrubs in these unfertile sites.

In ecological terms, restoration of arid shrublands should not only aim to install a number of desired species, but should also speed up succession and restore ecosystem functioning to pre-disturbance levels (Aronson, Floret, Le Floc'h, Ovalle & Pontanier 1993; Palmer et al. 1997; Parker 1997; Prach et al. 2001). In this sense, we believe that using colonizers, legumes and/or leafless species in restoration of very stressful habitats may contribute to ecosystem restoration in several ways.

Chenopodiaceous shrubs are able to successfully establish in cultivated pastures, and hence have potential to develop a perennial woody canopy in the landscape in the long term (Wong, Dorrough, Hirth, Morgan & O'Brien 2007). Mid-successional species establish more easily in degraded habitats that late-successional species, as their regeneration niche is often linked to open areas (Valiente-Banuet et al. 2006). Thus, better plant establishment can lead to more successful restoration, in terms of binding organic matter, reducing soil erosion, and providing microsites for other species to establish.

Abundant literature has shown that early- and mid-successional shrub canopies reduce irradiance and temperature at the soil surface, thus facilitating the recruitment of more drought-sensitive species (see review in Padilla & Pugnaire 2006). This nurse plant effect has not only been found in very harsh environments, but also in highly polluted and degraded grasslands in Central Europe between a forb and other forb species and grasses (Temperton & Zirr 2004). Therefore, as facilitation and nurse plants often play a key role in succession (Walker & del Moral 2003), mid-successional shrubs may accelerate secondary succession in a natural way (Li, Fang, Jia & Wang 2007), which is essential in ecosystem restoration (Prach et al. 2001). In addition, some shrubs flower very soon after plantation (like *Genista* and *Coronilla, pers. obs.*; De Mei and Di

Mauro 2006), and may accelerate succession in neighbouring areas by forming a new source of seeds.

Finally, leguminous shrubs may increase soil fertility (Pugnaire, Haase, Puigdefábregas, Cueto, Clark et al. 1996; Rodríguez-Echeverría & Pérez-Fernández 2005), and the improvements in the physico-chemical and biological properties of the rhizosphere of these species could facilitate the establishment of new species in the surrounding area, which would help revegetation of arid ecosystems (Caravaca, Alguacil, Figueroa, Barea & Roldán 2003). In addition, the use of mid-successional shrubs would help restore soil fertility as these species tend to reduce erosion processes (Bochet, Rubio & Poesen 1998; De Baets, Poesen, Knapen, Barber & Navarro 2007).

In conclusion, we underline a new approach in the restoration of arid sites,which the ecology of the site and the appropriateness of the initial species restored play a pivotal role. In this framework, species selection is a critical step that should be carefully considered. Early colonizers, legumes, and leafless species should be preferred to late-successsional species in arid regions. Selection of species with these traits is key for successful restoration of arid ecosystems. In practical terms, using these species would save an enormous amount of money and manpower as no watering would be needed to ensure establishment, and enhanced survival of implanted saplings would reduce costs of replanting.

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Appendix A: Supplementary Material

The online version of this article contains additional supplementary data. Please visit

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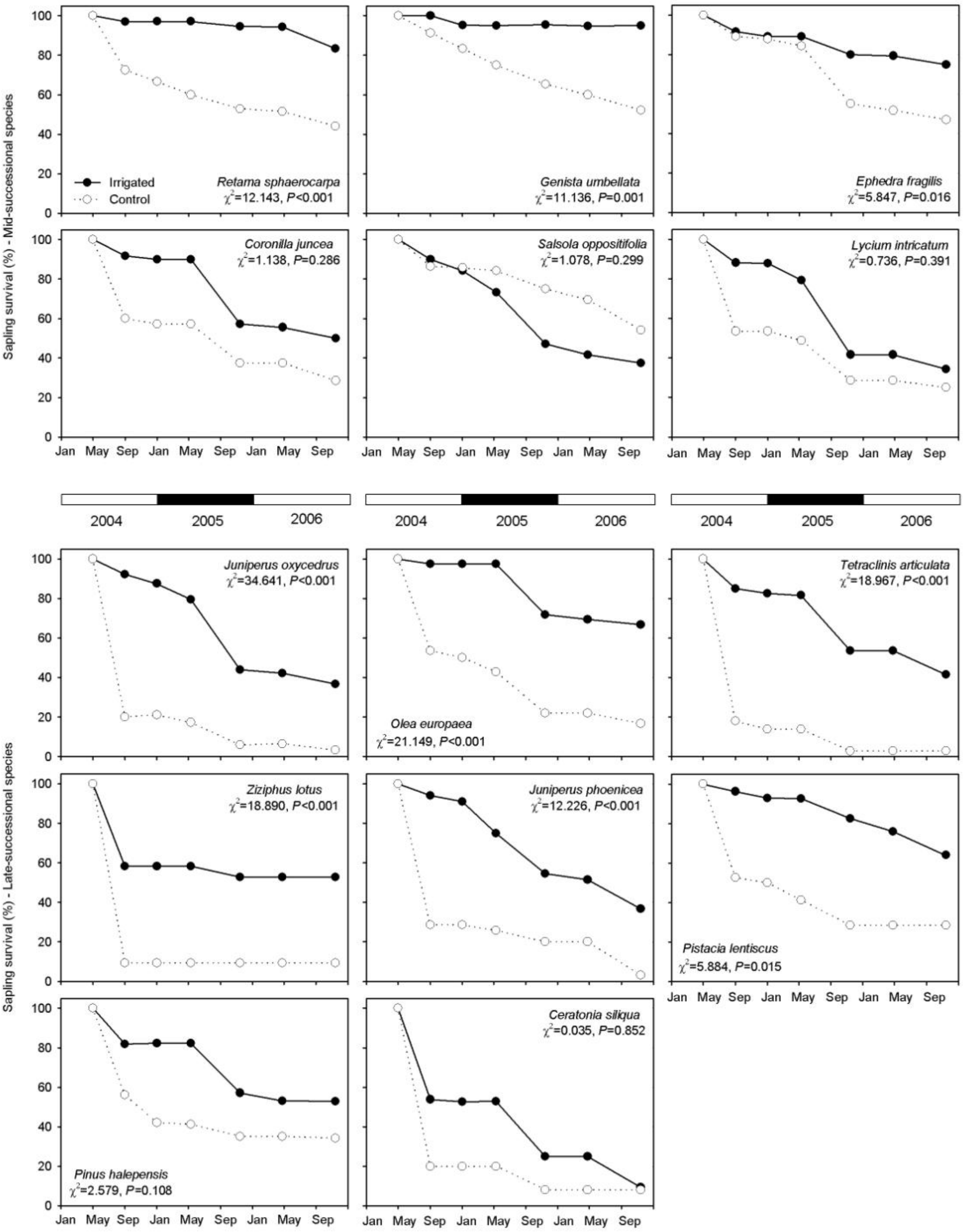
Figure legends

Fig.1. Sapling survival of 14 shrub and tree species with summer irrigation (solid dots) and without watering (open dots) in a degraded semiarid shrubland in SE Spain. χ^2 and significance of the watering treatment (logistic regression) in autumn 2006 are shown below each species name.



Appendix A: Supplementary Material

Table 1. Air temperature, soil temperature and relative air humidity in the east and west-facing plot, in the experimental site, on a six-day period of summer 2004. Soil temperature was measured at 5 cm depth (Hobo, Onset Computers, Pocasset, MA, USA) and relative air humidity and air temperature at 20 cm height (Hobo Pro).

		East	West
Air temperature (ºC)	Mean	29.8±0.6	30.0±0.6
	Max	45.9±0.8	46.7±0.8
	Min	18.7±0.4	19.1±0.5
Soil temperature (ºC^1)	Mean	35.5±0.3	36.1±0.4
	Max	46.5±0.7	47.1±0.8
	Min	26.9±0.4	27.5±0.4
Relative air humidity (%)	Mean	52.7±4.6	28.5±1.1
	Max	93.6±6.0	41.7±5.1
	Min	24.1±0.1	23.4±0.0

Table 2. Seasonal and annual rainfall (in mm) in the years 2004, 2005, and 2006, and average of the 1950-2000 period in the experimental site.

Year	Season				Annual
	Winter	Spring	Summer	Autumn	
2004	90	205	2	18	315
2005	73	35	6	30	145
2006	113	90	26	52	281
Average	91	82	16	92	281

Fig.1. Experimental area, located in the Sierra Alhamilla range, SE Spain. In the past years, intense pressure from human activities deforested the woody canopy. Recurrent restoration with late-successional species resulted unsuccessful because of severe drought.