Tree establishment along an ENSO experimental gradient in the Atacama desert

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Abstract

Questions: (1) What are the roles of regional climate and plant growth rate for seedling establishment during ENSO rainy pulses along the western coast of South America? (2) What is the water threshold for tree seedling establishment in these arid ecosystems?

Location: Atacama Desert, western South America: Piura (5°10' S, 80°37' W), Mejia (17°00' S, 71°59' W), Fray Jorge (30°41' S, 71°37' W).

Methods: We experimentally simulated a gradient of ENSO rainfall in three locations encompassing the total extent of the Atacama Desert to test the relative importance of regional climate for seedling establishment during rainy pulses. We also carried out a common garden experiment to test the role of potential interspecific differences in growth rate among two *Prosopis* tree species.

Results: Water threshold for seedling survival increased towards the south with less than 27 mm required in Piura, 100 mm in Mejia and 450 mm in Fray Jorge. We found that seedling survival and growth rate (shoots and roots) were much higher in Piura than in the other two sites for both *Prosopis* species.

Conclusions: Our results indicate that tree establishment during rainy pulses is more likely to be successful in regions where rain falls during warm months and stimulates fast plant growth, and where loose soil texture facilitates deep root growth and therefore access to more stable water sources.

Keywords: Afforestation; Arid; El Niño; Rainy pulse; Restoration; Seedling establishment; Semi-arid; Water threshold.

Abbreviations: ENSO = El Niño - Southern Oscillation; IPO = Interdecadal Pacific oscillation.

Introduction

Semi-arid and arid regions around the world have lost a major part of their original vegetation and ca. 20% of the dry lands have become degraded landscapes. Understanding the ecological mechanisms that can contribute to combat land degradation has become a global environmental priority (Anon. 2005).

Tree establishment plays a crucial role in the restoration of semi-arid shrublands and dry forests. In these systems, tree establishment usually occurs during rainy years such as those associated with the ENSO (El Niño Southern Oscillation) (Nicholls 1992; Brown et al. 1997; Holmgren et al. 2001, 2006 a, b) and is particularly successful when herbivory pressure is reduced during the rainy pulse (Austin & Williams 1988; Bowers 1997). These observations inspired the hypothesis that degraded semi-arid ecosystems could switch towards a more productive state during rainy ENSO years, especially when tree recruitment is also facilitated by controlling herbivores (Holmgren & Scheffer 2001). Because of positive feedback, a more productive state would tend to remain despite the short duration of the rainy pulse that triggered the initial increase in primary productivity. This hypothesis has large applied implications.

At present, ENSO events can be forecasted ca. six months in advance and model predictions are rapidly improving (Goddard et al. 2001), which could allow the coupling of reforestation programs to forecasted rainfall episodes. This could become increasingly relevant for management decisions. Although the effects of global climate warming on ENSO dynamics remain uncertain (Collins 2000), the analysis of ENSO patterns in recent centuries (Trenberth & Hoar 1997), as well as the results of recent high resolution climatic models, suggests that

the frequency of El Niño-like conditions should be expected to increase over the coming decades (Timmermann et al. 1999). Nevertheless, longer climatic cycles (e.g. interdecadal) have also been detected in the Pacific Basin (Zhang et al. 1997; Garreaud & Battisti 1999; Rutlland 2004). These correspond to periods where a series of El Niño-La Niña cycles are different in intensity than the following series. The strongest series of El Niño events during the last 20 years of the last century occurred during a positive phase of the Interdecadal Pacific Oscillation (IPO); the present time corresponds to a negative phase of IPO, where less intense El Niño events are to be expected (Salinger et al. 2001; Gosai et al. 2002).

An El Niño restoration approach (*sensu* Holmgren & Scheffer 2001) would need to be tailored to local environmental conditions. Not only ENSO events differ in intensity both spatially and temporally, but also how much rainfall is necessary for successful tree establishment would strongly depend on several ecological factors. In this paper, we study the relative importance of regional climate and interspecific differences between tree species – to tree establishment. We designed two field experiments in three locations across a latitudinal gradient of the Atacama Desert in western South America using two native *Prosopis* tree species (*Mimosaceae*). We designed a Water Threshold experiment to estimate the minimum rainfall needed for establishment of each species within the core of its distribution range. We also performed a Cross-Common Garden experiment to compare the growth rate of both species in each of the three locations. In both experiments we excluded herbivores to better understand the role of local climate and the intrinsic differences between the tree species. The latitudinal gradient covered northern Peru, southern Peru and north-central Chile. We used native species to Peru (*Prosopis pallida*) and Chile (*Prosopis chilensis*) that were previously very abundant and that are promising for afforestation programs (Pasiecznik et al. 2001).

Methods

Study sites

The three experimental sites are within the Atacama Desert along a latitudinal gradient affected by ENSO events: Piura (northern Peru), Mejia (southern Peru) and Fray Jorge (north-central Chile) (Fig. 1).

Piura (northern Peru)

The experimental site was located within the University of Piura campus (5°10' S, 80°37' W, 30 m a.s.l.). Vegetation is dominated by a *Prosopis pallida* forest, associated with *Acacia* spp. and other shrubs (e.g. *Coldenia paronychioides*, *Apodanthera biflora*, *Lycopersicon* spp.), with scattered herbaceous species from the *Poaceae*. Soil texture is sandy (sand 95.7%, silt 2.6% and clay 1.6%). Soil is alkaline (pH = 8.4), nonsaline (electric conductivity = 0.5 mmho) and poor in organic matter (0.12%). Soils were low in available nitrogen (60 ppm) and phosphorus (5.7 ppm) and moderate in available potassium (84.7 ppm).

Rainfall is concentrated in the summer months (December-May) and strongly influenced by ENSO events (Ortlieb 2000). Mean annual precipitation is ca. 50 mm (1961-1983) (Bernex de Falen & Reves 1988), with high
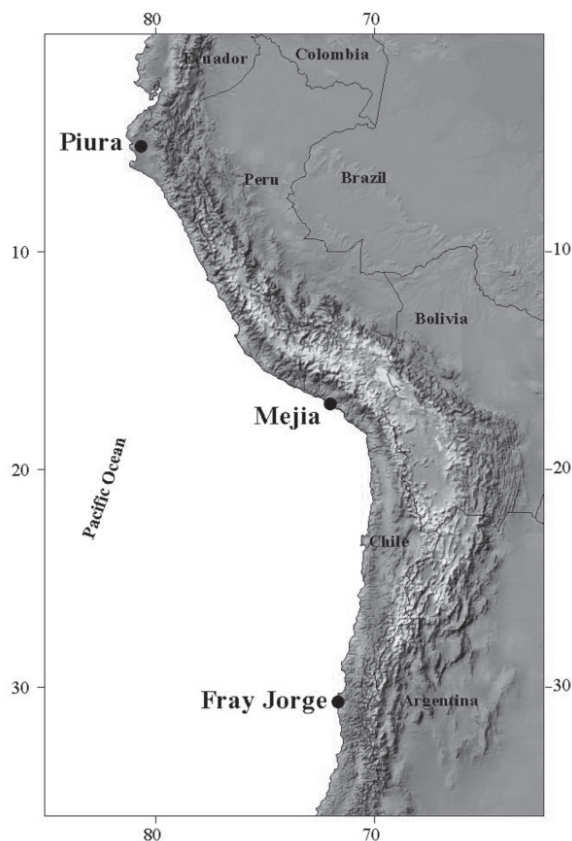

Fig. 1. Location of the three study sites in the Atacama Desert along a latitudinal gradient affected by ENSO events in western South America: Piura, Mejia and Fray Jorge.

interannual variation (e.g. ranging from 2.8 mm in 1996 to 1639 mm in 1998). Mean annual temperature is 24 °C, being warmest in February (27.9 °C) and coolest in August (21.1 °C). Annual potential evapotranspiration reaches 1825 mm. Precipitation during 2002 was 268 mm, with 98.4% of rain in March and April (263.8 mm). Precipitation in 2003 was 35.6 mm (Fig. 2).

Mejia (southern Peru)

The experimental site was located inside the experimental Station of Lomas de Mejía, province of Arequipa, Peru (17°00' S, 71°59' W, 760 m a.s.l.), 10 km from the coast. In normal, non ENSO years, the dominant species are suffrescents, such as *Grindelia glutinosa, Lippia nodiflora, Nicotiana paniculata* and *Heliotropium peruvianum*; during the fog season (August to November) dominant species are herbs such as *Palaua* spp., *Spergularia congestifolia, Erodium cicutarium, Lycopersicon peruvianum, Eragrostis* spp. and *Pennisetum clandestinum*. Trees (i.e. *Caesalpinia spinosa, Prosopis* spp.) are restricted to ravines or inaccessible areas. Soil texture is sand/loamy and silt/loamy. The concentration of organic matter at the uppermost soil level is almost 3%. The climate is subtropical arid with coastal fog influence and a non-seasonal rainfall pattern. Mean annual precipitation from 1996 to 2003 was 193.7 mm but excluding the mega ENSO event of 1997-1998 (715.4 mm from August 1997 to March 1998), mean annual precipitation was only 77.8 mm. Mean annual temperature in Mejia is 16.2 °C, with a summer maximum ca. 21.0 °C (January - February) and a winter minimum ca. 12.1 °C (July - September). The precipitation during 2002 was 69 mm and 148 mm in 2003 (Fig. 2).

Fray Jorge (north-central Chile)

The experimental site was located on a southeast facing gentle slope (10°), within a private farm (Fundo El Salitre), next to the Fray Jorge Forest National Park, 85 km south of La Serena (30°41' S, 71°37' W, 160 m a.s.l.). This old field is currently being used for livestock grazing. Vegetation is characterized by xerophytic shrubs: *Gutierrezia resinosa, Proustia cuneifolia, Senna cummingii, Bahia ambrosioides, Flourensia thurifera, Baccharis* spp., *Heliotropium stenophyllum, Haplopappus foliosus* and the cactus *Echinopsis skottsbergii*.

The soil profile at Fray Jorge shows a top organic layer of ca. 2cm, particularly prevalent under shrubs. Loamy soil material is found between 2-3 cm to 50-55 cm deep (gravimetric water contents were 5% at –0.03 MPa and ca. 2.5% at –1.5 MPa). The soil is rich in calcium carbonate, which makes it easily compacted. A calcarium layer with increasing clay (gravimetric water contents were 11.1% at –0.03 MPa and ca. 2.5% at –1.5 MPa) starts at 60 cm. Chemical analysis of the top soil layer indicated neutral
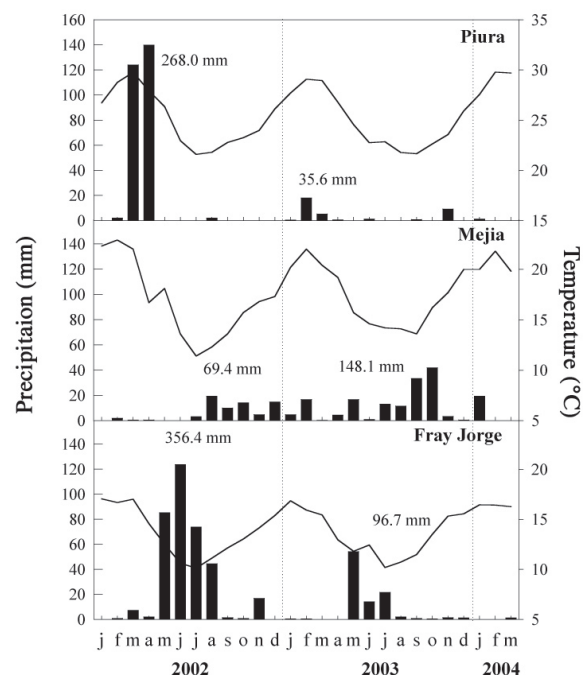

Fig. 2. Precipitation (mm) and monthly mean temperature (°C)between January 2002 and March 2004 in the three study sites.

pH (6.79 ± 0.03 SE), and relatively high concentrations of organic matter (3.12% ± 0.37%). Soils were low in electric conductivity (0.55 mS/cm ± 0.03 mS/cm) and available nitrogen (3.70 ppm ± 0.42), moderate inavailable potassium (176.4 ppm ± 10.1 ppm) and high in available phosphorus (20.63 ppm ± 1.03 ppm).

The climate is semi-arid mediterranean with 90% of the precipitation in winter months (May-September); summer months are warm and dry. Mean annual precipitation is 147 mm (1983-2003) and the annual potential evapotranspiration is close to 1000 mm. Longer meteorological records from La Serena (85 km north) report a mean precipitation of 114.4 mm (1878-1998, Soto & Ulloa 1997). High rainfall events are associated with the ENSO phenomenon (Aceituno & Montecinos 1992; Squeo et al. 2006 a, b) In rainy El Niño years, mean annual precipitation is 174 mm (1875-2000), with occasional strong events over 200 mm (e.g. in 1997: 233 mm, 1905: 487 mm, which is the strongest recorded event). Mean annual temperature is 13.6 °C (1998-2003), being warmest in January (ca. 17 °C) and coldest in July (ca. 10 °C) (López-Cortés & López 2004). Precipitation during 2002 was 356 mm and June was the wettest month (124 mm). In 2003, the accumulated rainfall was 97 mm. Monthly rainfall between January 2002 and March 2004 is shown in Fig. 2.

Experimental species

Prosopis pallida grows between 2°15' S and 16°15' S (northern Atacama Desert in Peru and Ecuador), but the most important *P. pallida* forests are found in northern Peru. *P. pallida* fruits are used to feed cattle and to prepare the honey mesquite 'algarrobina'. The wood is used mainly as fuel (logging reaches almost 20 000 ha/yr), and for making furniture. *P. pallida* grows well on sandy, loamy and sandy-loamy soils where it can develop a deep root system (J. Vilela pers. comm.), a pattern also found among other *Prosopis* species (Brock 1986; Salih 1998; Villagra & Cavagnaro 2000). *P. pallida* has been used for reforestation programs during El Niño years (Ferreyra 1987; Díaz 1995; Vilela 2002).

Prosopis chilensis is one of the most important trees in the semi-arid, arid and hyper-arid zones of northern Chile (22°54' S - 33°00' S, Arce & Balboa 1989). It has a very low natural regeneration and its wood is intensively used as fuel by rural communities. At present, it is considered to have a regionally vulnerable conservation state (Squeo et al. 2001). It is highly useful for rehabilitation programs because it grows easily in different climates (Arce & Balboa 1989) and adapts well to sandy, saline and alkaline soils (Riedermann & Aldunate 2001).

Experimental design

1. Water threshold experiment

This experiment was designed to estimate the water threshold for seedling establishment of both species. In each experimental site, we applied six water treatments in addition to natural rainfall (0, 50, 100, 200, 400, 600 mm) using drip irrigation. These six treatments were replicated eight times. Treatments were assigned in a randomized complete block design. The whole experimental set up was duplicated in order to harvest plants after six and 12 months. The experimental irrigation was given during the rainy season in each locality using the natural rainfall distribution pattern. The experimental setting was protected against predominant herbivores using a perimeter fence. Predominant large herbivores are goats and domestic livestock. Small mammals (rodents, rabbits and hares) are important herbivores in Chile, while large-medium lizards are particularly important in Peru. We used a 1 m high galvanized fence (0.5 cm mesh), buried 30 cm into the ground with 25 cm strip flashing at the top to exclude all main large and small herbivores. We removed all the woody shrubs from the experimental set to avoid either uncontrolled shading and/or hydraulic lift effects by shrubs (Squeo et al. 1999; León & Squeo 2004) or competition for water.

Soil water potential. We recorded soil water potential using a set of soil psychrometers (Wescor) installed at a depth of 50 cm, in three replicates of each experimental water treatment. Soil water potentials were recorded using a Dew Point Microvoltimeter (Wescor model HR-33T).

In Fray Jorge, soil water potential during the winter of 2002 (coinciding with a moderate ENSO event, McPhaden 2004), water potential was close to 0 MPa, whereas in winter 2003, it was close to –0.2 MPa. During the summer and fall of 2003, values became more negative (around –0.8 MPa) but there was no significant difference in water potential at 50 cm depth among water treatments ($P > 0.05$). Heavy rainfall in 2002 probably accounted for this similarity between treatments. In Mejia, there was a clear improvement in soil water potential at 50 cm with increasing water availability, ranging from near zero under the wettest treatment to less than –2 MPa under the driest treatments (0, 50 and 100 mm extra water treatments). In Piura, soil water potential was higher than -1 MPa in all treatments during the first three months.

Sowing and planting. At the beginning of September (Fray Jorge and Mejia) and December 2002 (Piura), we planted six two week old seedlings of *P. chilensis* (Fray Jorge) and *P. pallida* (Mejia and Piura) in each experimental unit. Seeds were germinated in sterilized soil from the site and transplanted when seedlings were 2 cm tall and the cotyledons had emerged.

Field measurements. We monitored survival, plant height and soil water potential at weekly intervals during the first month, every 15 days during the second and third months and monthly thereafter. Plant biomass, root length and root:shoot ratio were determined on six and 12 month old seedlings by excavation. This material was oven dried at 70 °C until a constant weight was reached.

2. Transplantation experiment

This field experiment compared the potential intrinsic differences in growth rate and survival of *P. pallida* and *P. chilensis* under the same environmental conditions, and evaluated their responses to the different environments of our three study sites. In each site, we installed 20 1-m² experimental plots, each containing 25 seedlings of either *P. chilensis* or *P. pallida* (i.e. ten replicate plots per species in each site). We used the same sowing and planting techniques previously described, and irrigated only once to field capacity at planting time. The experiment was carried out between March and September 2003 in Piura and between September 2003 and March 2004 in Mejia and Fray Jorge.

Statistical analyses

In the water threshold experiment, survival and plant growth at six and 12 months were analysed using one-way ANOVAs for each species. Differences between treatment means were assessed by *post hoc* Tukey tests. Treatment differences in survival through time were analysed by ANCOVAs, using posthoc *t*-tests to look for differences between slopes. The Common garden experiment was analysed as a two-factor ANOVA with species and sites as main factors. In both types of experiments, survival percent data were square-root arcsin transformed prior to statistical analyses.

Results

1. Water threshold experiment

Survival of *Prosopis pallida* seedlings in Piura was very high under all water conditions (Fig. 3a, $F_{(5,90)}$ = 1.27, P = 0.29). With only 27 mm natural rainfall (no extra irrigation), survival was over 85% at six months. After one year, seedling survival decreased to around 60% under 90 mm of water availability ($F_{(5,42)}$ = 4.56, P = 0.002) but remained constant at more than 90% under the higher water treatments (Fig. 3b).

In contrast, seedling survival was very low in Fray Jorge. At six months, survival was only 20% at the highest water treatment (around 950 mm) and near 10% at 450 mm (Fig. 3a, $F_{(5,90)}$ = 6.67, P < 0.001). After one year, no seedlings survived below the 500 mm water treatment and reached only 8% at higher water levels, with no statistical differences among the higher water treatments (Fig. 3b, $F_{(5,42)}$ = 0.91, P = 0.48). The slopes of the survival curves for each water treatment clearly show a higher mortality at decreasing water availability (Table 1).

In Mejia, survival of *P. pallida* seedlings showed a different pattern. After six months, survival reached around 20% at 90 mm natural rainfall (no extra irrigation), and increased to 40-60% over 100 mm of water (Fig. 3a, $F_{(5,90)}$ = 4,30, P = 0.0015). This pattern is also reflected in the analysis of the survival curves for each water treatment (Table 1). Mortality at high irrigation levels was caused by a complex of several fungi species. The same pattern was maintained at the end of the first year, although no statistical differences were found among water treatments (Fig. 3b, $F_{(5,42)}$ = 2.25, P = 0.07).

Shoot height, root depth and biomass

We did not find treatment differences in plant growth (shoot height, root depth and biomass) at either six or 12 months in each of the experimental sites. Clearly, seedlings grew much faster in Piura. After one year,
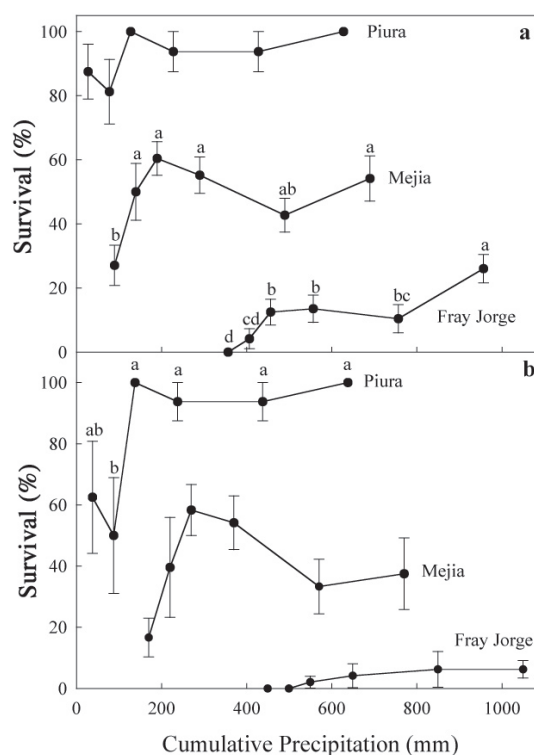

Fig. 3. Survival (%) of *Prosopis pallida* (Piura and Mejia) and *P. chilensis* (Fray Jorge) at (**a**) six and (**b**) 12 months. Same letters indicate no statistical differences between means. Cumulative precipitation combines the irrigation treatments (0, 50, 100, 200, 400, 600 mm) with the natural rainfall. (a) for six month old plants, natural rainfall includes the six months before and after plantation (Piura = 27.4 mm, Mejia = 89.5 mm and Fray Jorge = 356.2 mm). (b) the one yr old plants natural rainfall adds the precipitation of the next six months (35.6, 169.8, and 449.1 mm, respectively). Data are mean ± 1 SE.

Table 1. Slopes of the first year survival curves for seedlings growing under the six experimental water treatments (0, 50, 100, 200, 400, 600 mm irrigation). Slopes of each treatment were calculated as the log-log relationship between water amount (+1) and survival (+1). Same letters in a column indicate no significant differences between slopes. Piura is not shown because there were no significant differences between treatments.

Treatments	Mejia		Fray Jorge	
0 mm	–0.34	a	–1.19	a
50 mm	–0.17	b	–0.71	ab
100 mm	–0.10	c	–0.65	ab
200 mm	–0.12	c	–0.58	b
400 mm	–0.22	b	–0.53	b
600 mm	–0.19	b	–0.49	b

Table 2. Plant height and root depth, total dry biomass and root:shoot ratio (biomass R:S) of *Prosopis pallida* (Piura and Mejia) and *P. chilensis* (Fray Jorge) at six and 12 months. Data are mean ± 1 SE.

	Piura	Mejia	Fray Jorge
6 months			
Height (cm)	33.0 ± 3.4	6.4 ± 0.4	4.2 ± 0.2
Depth (cm)	-	40.2 ± 3.8	34.5 ± 1.6
Total biomass (g)	-	0.491 ± 0.072	0.082 ± 0.008
R : S	-	0.99 ± 0.08	2.27 ± 0.22
12 months			
Height (cm)	39.0 ± 5.2	7.2 ± 0.5	4.1 ± 0.2
Depth (cm)	101.1 ± 8.2	48.0 ± 4.1	55.9 ± 4.9
Total biomass (g)	9.584 ± 3.086	1.255 ± 0.213	0.373 ± 0.073
R : S	0.61 ± 0.04	1.73 ± 0.18	3.30 ± 0.67

plant height was around ten and five times higher in Piura than in Fray Jorge and Mejia, respectively, and root depth was twice as deep in Piura than in the other two study sites (Table 2). Growth differences were even more pronounced in terms of total biomass. After one year, plants in Piura were more than 25 times heavier than in Fray Jorge and more than seven times heavier than in Mejia (Table 2). We found the opposite latitudinal pattern for relative carbon allocation. Although total plant biomass increased towards north, the root:shoot ratio decreased, and in Fray Jorge, relative carbon allocation to roots compared to shoots was more than five times larger than in Piura.

2. Transplantation experiment

We found no differences in growth rate between both species when planted together in each site (Table 3, $F_{(1,26)}$ = 1.06, P = 0.3133). There was a clear site effect since, in Piura, seedlings of both tree species grew taller (Table 3, $F_{(1,26)}$ = 11.29; P = 0.0024) and there was no interaction effect between species and site ($F_{(1,26)}$ = 1.16; P = 0.2916). Seedlings survival was higher in northern and southern Peru than in Fray Jorge (Table 3).

Table 3. Survival and height of *Prosopis chilensis* and *P. pallida* at six months growing in the transplantation experiment in the three study sites. Data are mean ± 1 SE).

	P. chilensis		P. pallida	
	Survival (%)	Height (cm)	Survival (%)	Height (cm)
Piura	67.5 ± 9.3	15.2 ± 3.8	71.7 ± 8.5	23.5 ± 5.6
Mejia	46.7 ± 8.0	5.3 ± 0.4	75.8 ± 5.8	5.5 ± 0.2
Fray Jorge	16.0 ± 2.5	4.0 ± 0.3	2.4 ± 1.6	4.2 ± 1.0

Discussion

We experimentally simulated a gradient of ENSO events from moderate to strong precipitation. Because ENSO events tend to be stronger in northern Peru, we expected to find higher water thresholds for seedling establishment in Piura than in Fray Jorge. Our results showed exactly the opposite trend. After one year, seedling establishment in Fray Jorge was less than 10% at more than 450 mm of water availability, while survival was 60% with only 90 mm in Piura.

Since our threshold experiments were not performed with both species at each site, we broadly estimated the potential survival using the results of the Common garden experiment. Expected survival at six months when water availability is above the water threshold would be for a hypothetical *P. pallida* 92.7%, 52.5% and 2.3% in Piura, Mejia and Fray Jorge, respectively (and 87.3%, 32.3% and 15.6% for a hypothetical *P. chilensis*).

Although water is probably the most limiting resource for plant recruitment in drylands, rainfall seasonality, and therefore its interaction with temperature, could be crucial for successful tree seedling survival. In northern Peru, rainfall is concentrated in the summer when temperatures are also favourable for plant growth. Fast root growth could allow water extraction from deeper soil layers and its subsequent use for plant growth. This could explain the paradoxical high survival at very low water availability. In contrast, rainfall is concentrated in the cold winter months in Fray Jorge, making plant growth slow and reducing seedling survival even in very wet conditions. Indeed, tree-ring analysis among natural populations clearly indicates a higher recruitment and growth of *P. pallida* during strong ENSO years in northern Peru while no signal was found for *P. chilensis* in north-central Chile (Holmgren et al. 2006 b; López et al. 2006).

Our study sites differ in soil texture and this could reinforce differences in plant growth rate. Piura is characterized by more sandy soils with low resistance for root growth. Here, root depth after one year was over 100 cm, compared with nearly half that in the other two sites. Since desert sandy soils have high infiltration rates and lower evaporation rates compared to heavier soils, this could further favour root development (Noy-Meir 1973). Soil texture also strongly mediates plant water availability through its control on soil hydraulic characteristics (Sperry & Hacke 2002). Hultine et al. (2006) showed that *Prosopis* trees on loamy-clay soil probably respond only to intense precipitation inputs that occur much less frequently than moderate events. Conversely, trees on sandy-loam soils are highly sensitive to small precipitation pulses reflected by uptake of pulse water and carbon gain (Fravolini et al. 2005).

Warm deserts are the natural habitat of *Prosopis* species. In northern Peru and Argentina, as in warmer North American deserts, *Prosopis* spp. dominate extensive flat landscapes, with sandy soil and groundwater recharged by summer rains (Díaz 1995; Ferreyra 1987, 1993; Pasiecznik et al. 2001). Between north-central Chile and southern Peru, smaller forests are restricted to microhabitats such as ravines and foothills where water accumulates or where soils are more sandy. In this southern portion of the Atacama Desert, several *Prosopis* species have a vulnerable conservation status (Del Carpio 1996; Squeo et al. 2001). Populations in these colder deserts probably represent the margins of the species distribution ranges where environmental conditions are suboptimal for growth and resilience to disturbances is much lower.

Reforestation experiences with *Prosopis* spp. in the Atacama Desert have been partially successful. Large areas have been reforested with *P. alba* in Pampa del Tamarugal in north Chile (Anon. 1999) and with *P. pallida* in Piura (Díaz 1995; Vilela 2002).Our results indicate that, when herbivores have been controlled (Gutiérrez et al. 2007; Holmgren et al. 2006 b), reforestation during rainy pulses is more likely to be successful in regions where rain falls during warm months and stimulates fast plant growth, and where loose soil texture facilitates deep root growth and access to more stable water sources.

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