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The Potential of Algarrobo (*Prosopis chilensis* (Mol.) Stuntz) for Regeneration of Desertified Soils: Assessing Seed Germination Under Saline Conditions

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Abstract Due to their multipurpose use, leguminous trees are desirable for the restoration of degraded ecosystems. Our aim was to investigate seed germination of the leguminous tree *Prosopis chilensis* in response to salinity, one of the major abiotic challenges of desertified soils. Germination percentages of seed from 12 wild *P. chilensis* populations were studied. Treatments included four aqueous NaCl concentrations (150, 300, 450, and 600 mM). In each population, the highest germination percentage was seen using distilled water (control), followed closely by 150 mM NaCl. At 300 mM NaCl or higher salt concentration, germination was progressively inhibited attaining the lowest value at 450 mM NaCl, while at 600 mM NaCl germination remained reduced but with large variation among group of samples. These results allowed us to allocate the 12 groups from where seeds were collected into three classes. First, the seeds from Huanta-Rivadavia showed the lowest percent germination for each salt condition. The second group was composed of moderately salt-tolerant seeds with 75 % germination at 300 mM NaCl, followed by 50 % germination at 450 mM NaCl and 30 % germination at 600 mM NaCl. The third group from Maitencillo and Rapel areas was the most salt tolerant with an impressive seed germination level of 97 % at 300 mM NaCl, 82 % at 450 mM NaCl, and 42 % at 600 mM NaCl. Our results demonstrate that *P. chilensis* seeds from these latter localities have an increased germination capability under saline stress, confirming that *P. chilensis* is an appropriate species to rehabilitate desertified soils.

Keywords Desertification · Aridity · Salinity · Seed germination · *Prosopis chilensis*

Introduction

Desertification is defined as "the land degradation in arid, semiarid and dry sub-humid areas resulting from various factors, including climatic variations and human activities" (UNEP 1992). In Chile, 49.1 % of the territory underwent some degree of soil erosion and in particular, the Coquimbo Region has 84 % of its soil affected by erosion, with 65.3 % of it categorized as extremely or severely degraded (CIREN 2011). The afforestation and reforestation program proposal using plant species adapted to arid and semiarid environments has been recognized as the best option to restore social, economic, and ecological value of impoverished lands (Koohafkan 1996; Ondrasek et al. 2011).

Among plants identified in affected lands, Algarrobo, or Chilean mesquite (*Prosopis chilensis* (Mol.) Stuntz), a tree belonging to Fabaceae family found naturally in dry regions of Peru, Bolivia, Chile, and Argentina (Galera 2000) is a good alternative for reclamation of degraded

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ecosystems, due to its nutritional value, capacity to fix nitrogen, resistance to drought, and ability to grow in saline soils (Serra 1997; Montandon et al. 2011). In Chile, wild Algarrobo forests are found in arid/semiarid regions from Copiapo River (Atacama Region; 27°S) to Maule River (Maule Region, 37°S) (Santibáñez et al. 2008). Unfortunately, current populations have been decimated to few fragmented forests located between marginal areas of the Intermediate Depression and Andean foothills (Fig. 1). Luebert and Pliscoff (2006) reported that the original forest of this species has been reduced from 3425 to 1316 km^2 (62 % loss). In man-occupied sites, trees are dispersed or form small patches, exposed to several abiotic stresses such as poor soil structure, human pressure exerted by agricultural activities, grazing, use of biomass as fuel, and one of the highest solar irradiances of the planet (Chapin et al.

2001; Peñuelas and Filella 2001; Parmesan and Yohe 2003; CNE 2009). In view of this lack of recruitment observed across the original habitat (personal observation) and recent evidence that current adult trees are in senescent stage with chances to disappear (Valdivia and Romero 2013), the prospect for survival is grim. Moreover, according to a recent report on the effect of global climate change on Chilean biodiversity, it is suggested that the Mediterranean Spiny Forest formed by *Acacia caven* and *Prosopis chilensis* species would be one of the three most affected ecosystems by 2050 (PAN 2014). Accordingly, *P. chilensis* is currently classified as a vulnerable species (Squeo et al. 2007; Avilés 2012).

Spontaneous recruitment of *P. chilensis* in this habitat is associated with the occurrence of El Niño Southern Oscillation (ENSO) phenomenon (Holmgren 2006a; Squeo
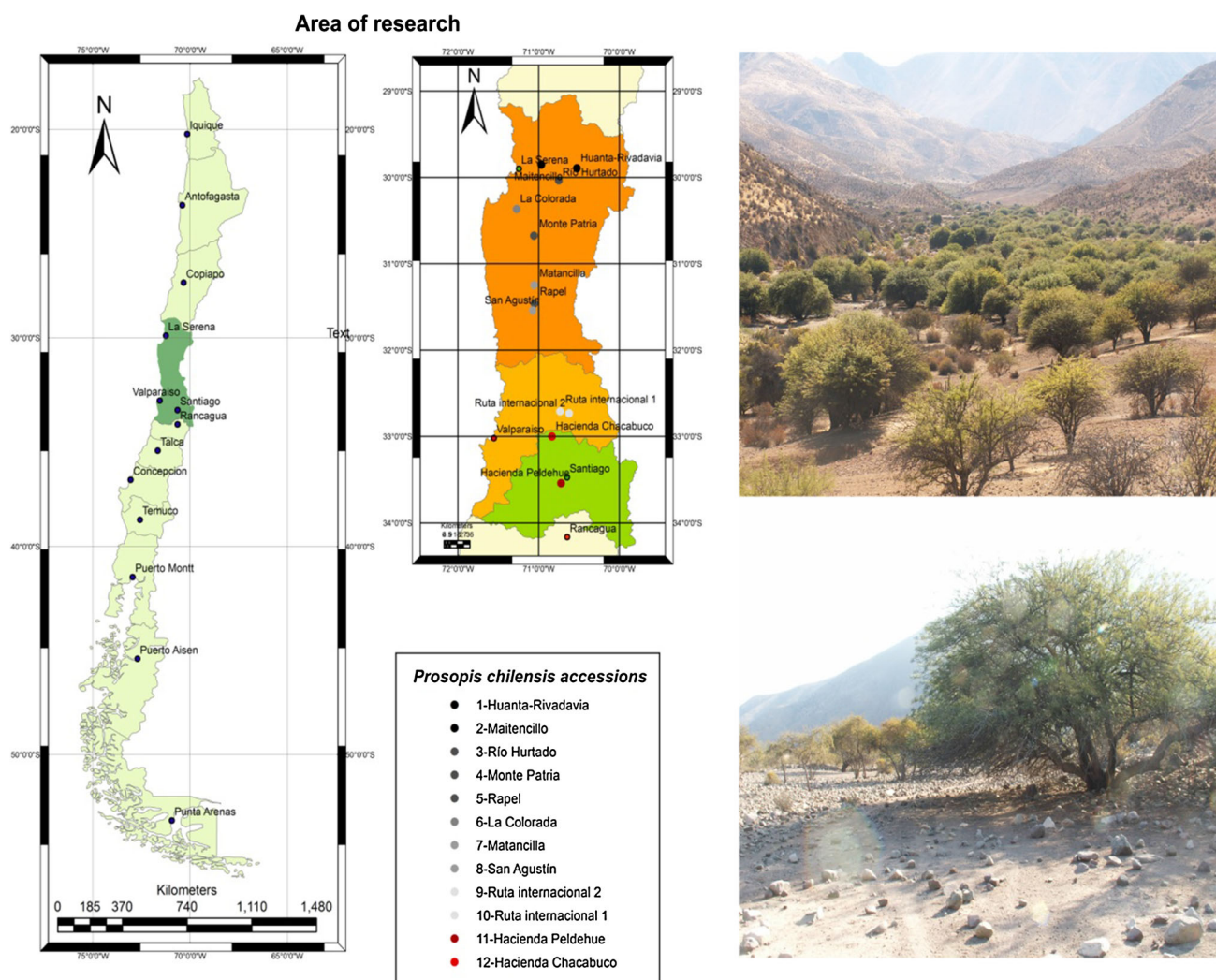

Fig. 1 Geographical distribution of *Prosopis chilensis* sampled in this study. The *green* area in the map (*left*) shows the natural distribution of *P. chilensis* in Chile. This area is part of the arid/semiarid climate in Chile. The zoomed map section (*upper center*) shows the geographical location of the 12 areas evaluated in this study. Pictures on the *right* show two of these 12 populations, corresponding to Maitencillo (*up*) and Matancilla (*down*), respectively (Color figure online)

et al. 2007). During the ENSO period, intense rainfalls triggered by anomalous heating of Pacific Ocean surface in the Northern coast of Chile (Rutland and Fuenzalida 1991; Montecinos and Aceituno 2003) increase soil water availability that stimulates germination of dormant seeds (Vidiella and Armesto 1989). The last ENSO event occurred in 1997 and, at least, 10 of these events happened during the last century (Holmgren and Scheffer 2001). Following ENSO rainfall period, strong sun irradiance increases soil evaporation and decreases water availability. As a consequence, salts deposited in deeper layers diffuse to the surface, induce ion accumulation, and exacerbate the $Na^+:Ca^{2+}$, $Na^+:K^+$, $Ca^{2+}:Mg^{2+}$, and $Cl^-:NO_3$ ratios, thus triggering salt stress to plants (Munns and Tester 2008). At seed level, the redistribution of toxic Na and Cl ions affects the embryo and impairs germination, and creates an osmotic imbalance affecting root growth and overall performance of new born plants (Grattan and Grieve 1999; Almansouri et al. 2001; Denby and Gehring 2005; Araújo et al. 2006; Adolf et al. 2013). In response to saline soils, germinating seeds modify their physiology to avoid the deleterious effects of toxic ions (e.g., Na^+ and Cl^-) (Gul and Khan 2002; Munns 2005; Läuchi and Grattan 2007). Meanwhile, salinity may decrease seed germination and seedling growth efficiency among halophytes (*P. chilensis*) tolerant to salinity (Felker et al. 1981; Cazebonne et al. 1999). In addition, leguminous plants are affected by saline stress reducing the ability to grow and fix nitrogen during subsequent developmental stage (Bekki et al. 1987; Dupont et al. 2012).

P. chilensis is an allogamous plant (Pasiecznik et al. 2001) with high genetic variability (Mottura et al. 2005; Verga and Greogorius 2007) that can express different phenotypes in response to biotic or abiotic stress. In this context, the soil salt content must induce adaptive responses in seeds and/or seedlings of *P. chilensis* when facing salt stress (Blun 1998; IRRI 2006; Läuchi and Grattan 2007). We hypothesized that this adaptive response must be conserved but with some variability along its entire distribution range in Chile. This paradigm is supported by data from Plaza (2010) who reported by microsatellite analysis on *P. chilensis* across the Elqui, Limarí, and Choapa valleys (Coquimbo Region) the existence of allelic differences. Therefore, to use *P. chilensis* in afforestation or reforestation programs on desertified lands, a prior selection of seeds that can successfully withstand possible abiotic stress is appropriate .

This study aimed to compare the germination of *P. chile*nsis seeds from Chilean arid and semiarid areas to evaluate their response to saline stress. The data do not represent a comprehensive study among populations due to the scarceness of this species in their habitat; therefore, we provide a partial account of the germination rates of *P. chilensis* from 12 sites distributed along a 450 km transect that represents 80 % of its current distribution in Chile. We evaluated the seed germination response of these samples at different NaCl concentrations and discuss how these responses varied along its Chilean distribution and how this information could be useful to restore marginal zones with this species and as a model to implement sustainable agroforestry. We believe that our results can be used as a reference guide by the National Forestry Agency (CONAF) and/or private companies pursuing to restore marginal or desertified lands using seeds from the most salt-tolerant sites identified in this study.

Methods

Climatic Conditions and Soil Prevailing in the Area of Study

P. chilensis (Mol. (Stuntz)) trees naturally growing in the hinterlands between Coquimbo Region (29°S) to Metropolitan Region (33°S) were used in this study (Table 1). This area is located south of the Atacama Desert and spans an arid climate in Coquimbo to semiarid conditions in the Metropolitan Region (Luebert and Pliscoff 2006; Santibáñez 2014). A recent climatic study predicts that by 2050, the Metropolitan area will become an arid zone (Santibáñez 2014). The area of study is characterized by 8–11 months of a warm dry period, with relative humidity always below 78 % (Galera 2000). The rainy season is short and occurs during the winter period (May–August) (Santibañez et al. 2008). The annual rainfall averages 226 mm varying from 74–108 mm in the Elqui province (Coquimbo Region) to 344–378 mm in the Chacabuco province (Metropolitan Region) (Santibáñez 2014). A shortage of precipitation is frequent in the Coquimbo Region and under such condition evapotranspiration exceeds precipitation most of the year. Plants growing in this scenario frequently undergo hydric stress (Luebert and Pliscoff 2006). The annual mean temperature of the area of study is 17.6 °C. During winter (June–August), the minimum temperature varies from 4.9° C in the Elqui province (Coquimbo) to 4.0 °C in Chacabuco province (Metropolitan Region). In summer (January–March), the maximum temperature reaches 32 °C in the Elqui province (Coquimbo) and 30.4 °C in the Chacabuco province (Metropolitan Region). Another characteristic of *P. chilensis* habitat is the high prevalence of clear days which can sum up to 300 days per year and accumulate between 1600 and 1700 degree days (Santibañez et al. 2008). This high luminosity has been reported as necessary to obtain a good development of this species (Contreras 1983). The soils in areas where Algarrobo grows are aridisols, with

Table 1 Collection locations of *Prosopis chilensis* seeds

Accession	Province	Region	Latitude (S)	Longitude (W)	Elevation (m)	EC (dS/M)
1. Huanta-Rivadavia	Elqui	Coquimbo	29°54′	70°31′	953	–
2. Maitencillo	Elqui	Coquimbo	29°58′	70°46′	836	1.704
3. Río Hurtado	Limarí	Coquimbo	30°18′	70°43′	1051	0.468
4. Montepatria	Limarí	Coquimbo	30°44′	70°57′	490	0.935
5. Rapel	Limarí	Coquimbo	30°92′	70°52′	603	0.820
6. La Colorada	Choapa	Coquimbo	31°04′	71°03′	666	1.207
7. Matancilla	Choapa	Coquimbo	31°45′	70°56′	735	1.687
8. San Agustín	Choapa	Coquimbo	31°28′	71°04′	647	–
9. Ruta Internacional II	Los Andes	Valparaíso	32°53′	70°32′	1001	0.783
10. Ruta Internacional I	Los Andes	Valparaíso	32°53′	70°33′	949	0.541
11. Peldehue	Chacabuco	Metropolitana	33°11′	70°38′	771	0.934
12. Chacabuco	Chacabuco	Metropolitana	33°2′	70°41′	705	1.355

The electric conductivity (EC) value was determined as described by Rhoades et al. 1999

high presence of salts (such as sulfates and carbonates) or sodium, which in some places can form a petrocalcic horizon at the first meter (Luzio 1994; Casanova et al. 2004; CAAP 2010). These soils present limitations in salinity, sodicity, water availability, organic material, and compactivity limiting their arability without irrigation (Roshetko and Gutteridge 1996; Galera 2000; Casanova et al. 2004; Doussolin and Quezada 2006). Normally this tree occupies stony fluvial plain soils (Fig. 1) between 500 and 1500 masl with groundwater availability (Pasiecznik et al. 2001). It probably prefers mild alkaline soils (pH 7.6–8.9) since it is being proposed that acidic soils are a limiting factor for its distribution (Pasiecznik et al. 2001).

Seed Collection

In 2011, seeds of *P. chilensis* were collected from eight locations in Coquimbo Region (29°S–31°S), two locations from Valparaíso Region (32°S), and two locations from Metropolitan Region (33°S) (Table 1). In each locality, pods from several trees were collected and then seeds pooled in one sample. Seeds were placed in polypropylene tubes and stored at 4 ± 2 °C, as recommended by Pompelli et al. (2010) for a minimum of 2 months. Seed masses from each locality are presented in Supplemental Table 1.

Soil Collection

At least five samples from the top 25 cm of soil were collected in each locality and soil samples from the same locality were pooled into one sample. The soil salinity, determined as electrical conductivity, (EC total concentration of ionized solutes in aqueous sample; Rhoades et al. 1999) was measured at the Centro Tecnológico de Suelos y Cultivos, Universidad de Talca, Chile. Content of Na, Ca,

Mg, K, Cl, P, N–NO_3, HCO_3, and SO_4 was also determined (see Supplemental Table 4).

Preliminary Seed Germination Assay

As in many others salt-stress studies, we used NaCl as a surrogate for saline conditions (Felker et al. 1981; Katembe et al. 1998; Khasa et al. 2001; Khan and Gulzar 2003). The experimental design adopted from a preliminary study incorporated six concentrations of NaCl from 100 to 600 mM, using seeds, with or without sulphuric acid. Results of this preliminary study are presented in Supplemental Tables 2 and 3. Initially, seeds from healthy adult specimens in 18 localities were collected, but trees near villages, highly transited routes, seeds heavily infected by bruquids or planted trees were excluded. In the end, 6 of these sites were excluded and the study pursued at the remaining 12 sites. The scarification protocol was evaluated after separation of pooled seeds into two groups, (treated with H_2SO_4 vs. non-treated) followed by soaking in water. The germination observed on day 21 (Supplemental Table 2) indicates that non-treated seeds afforded lower germination (22 %) than those subjected to acid scarification. Consequently, subsequent germination experiments included an acid scarification step. Next, seeds from each locality were pooled into one sample and evaluated using six NaCl concentrations (100, 200, 300, 400, 500, and 600 mM) during a 14-day interval. Since no germination was observed above 400 mM NaCl (data not shown), the assay was replicated during a 21-day interval, as shown in Supplemental Table 2. Using this condition, similar germination percentages occurred at 100 and 200 mM, and also at 500 and 600 mM NaCl, as confirmed by one-way ANOVA (Supplemental Table 3). Based on these data, we selected an intermediate salt concentration (150 mM) in lieu of the 100 and 200 mM NaCl conditions.

Also, because no statistical germination differences were seen between 300 mM NaCl and 400 mM NaCl, but, a difference was evident between 300 and 500 mM NaCl (Supplemental Table 3), we kept the 300 mM NaCl condition and adjust the second concentration to 450 mM NaCl (between 400 and 500 mM NaCl). In short, the adopted protocol included a sulphuric acid scarification procedure and four saline concentrations (150, 300, 450, and 600 of NaCl). Two germinations assays were carried out independently.

Seed Germination Assay

In germination assays, 30 seeds from each locality were scarified in concentrated H_2SO_4 (Miranda et al. 2011) for 3 min and rinsed thoroughly with distilled water for 2 min. Then, the seeds were dried out on tissue paper, placed into polypropylene tubes, and stored at 4 ± 2 °C for 24 h. Then, the seeds were placed into three Petri dishes (10 seeds/plate) covered with sterile filter paper (Whatmann 603) moistened with distilled water (control, 100 % humidity) and incubated in a growth chamber at 21 °C, 50–60 % relative humidity and photoperiod of 16 h day/8 h night using 120 μE/m²/s (where $E = 1$ mol of photons) provided by Sylvania cool-white fluorescent lamps. Germination was monitored every 24 h and at the same time (midday) for 21 days. A seed was considered "germinated" when its radicle was ≥ 2 mm (Cazebonne et al. 1999; Miranda et al. 2011). The salt treatment included four conditions: 150 mM ($\psi = -0.99$ MPa), 300 mM ($\psi = -1.64$ MPa), 450 mM ($\psi = -2.33$ MPa) and 600 mM ($\psi = -3.11$ MPa) NaCl. Sea water concentration is ~ 500 mM; 30,000 mg/L (Kim et al. 2010). The NaCl concentration that reduced seed germination by 50 % at the end of the assay (21th day) was termed as LD_{50} (Djanaguiraman et al. 2006; Delatorre-Herrera and Pinto 2009; Li et al. 2013). The LD_{50max} term represents the same value but obtained in the most tolerant population (Delatorre-Herrera and Pinto 2009). In summary, a total of 30 seeds from each locality were germinated using four saline concentrations plus a water control, totaling 1800 samples. The complete germination assay was repeated twice. Then, the average of these two independent germination assays (3600 seeds in total) was compared and analyzed following a logistic regression model analysis.

Statistical Analysis

Statistical analysis is based on a multiple logistic regression model, considering the germination status at day 21 as response, and both accession and saline treatment as predictor variables. Model selection was based on likelihood ratio tests and Akaike information criterion. Final conclusions are based on an additive model, considering Huanta-Rivadavia accession and control treatment as reference

cells. A baseline shift parameter was considered to adjust for any difference between the first and second experiment. Results are expressed as odds ratios (OR) with 95 % confidence intervals. The OR is defined as the quotient between the probability that any event occurs and the probability that it does not occur (Agresti 2002). In this case, the event is "germination in response to salinity". The OR compares the "odds" between two populations, typically exposed to two different treatments. Normally, it is considered as an approximation to the relative risks, it means, the probability of an event to occur in a population compared to another event. All statistical analysis was performed with R version 2.15.3 (R 2013).

Results

Soils Analysis

None of the soil samples gathered at the same sites where seeds were collected had EC higher than 4 dS/m (equivalent to 40 mM NaCl, Table 1, Supplemental Table 4), a value considered as low for saline soils (Munns 2005). pH averaged 7.86, varying from 8.16 (Peldehue site, Metropolitan Region) to 7.15 (Ruta Internacional site, Los Andes province) (Supplemental Table 4). It means that at levels sampled during 2011, seeds were not exposed to salt levels or pH levels considered detrimental for germination in the field. Nevertheless, no single seedling was found in any of the locations where soils were collected.

Germination Potential of *Prosopis chilensis* Seeds

Regardless of the location, acid-scarified seeds exhibited the largest germination (92.9 % in average; $P < 0.0001$), (Table 2). This successful germination demonstrated that seed dormancy was properly broken by the stratification and scarification protocol and that embryo viability was not affected by this treatment.

Also, regardless of the location, germination was impaired by various concentrations of NaCl ($P < 0.0001$). This adverse effect was marginal at 150 mM NaCl (72–100 % range, 91 % mean), minor to moderate at 300 mM NaCl (47–100 % range, 88 % mean), moderate to significant at 450 mM (22–95 % range, 67 % mean), and robust at 600 mM NaCl (6.7–57 % range, 34 % mean), (Table 2). At 150 mM NaCl, seed germination maxima occurred on day 5 similar to the control without salt treatment (Fig. 2). Germination was delayed until day 9 in seeds incubated with 300 mM NaCl. At 450 mM NaCl and 600 mM NaCl, maximal germination was observed on day 15th, with large variability within each population (Fig. 2).

Table 2 The effect of salt on seed germination in collecting sites

Accession	Province	Saline concentration (mM)				
		0	150	300	450	600
Huanta-Rivadavia	Elqui	81.7	71.7	46.7[a]	21.7	11.7
Maitencillo	Elqui	85.0	93.3	81.7	71.7	50.0[a]
Río Hurtado	Limarí	86.7	76.7	80.0	66.7	20.0[a]
Montepatria	Limarí	96.7	93.3	93.3	83.3	38.3[a]
Rapel	Limarí	91.7	90.0	96.7	76.7	55.0[b]
La Colorada	Choapa	98.3	98.3	93.3	75.0	38.3[a]
Matancilla	Choapa	96.7	100.0	100.0	95.0	56.7[b]
San Agustín	Choapa	100.0	100.0	98.3	76.7	30.0[a]
Ruta Internacional II	Los Andes	91.7	91.7	90.0	60.0	15.0[a]
Ruta Internacional I	Los Andes	98.3	100.0	96.7	75.0	50.0[a]
Peldehue	Chacabuco	100.0	88.3	90.0	55.0	6.7[a]
Chacabuco	Chacabuco	88.3	83.3	83.3	48.3[a]	41.7
Average		92.9	90.6	87.5	67.1	34.4

Seed germination values represent the mean of two repetitions. Each repetition evaluated 30 seeds per treatment. Each treatment was evaluated in the 12 accessions, totaling 3600 seeds analyzed by this study

[a] LD_{50} which represents the concentration that reduced seed germination by 50 %

[b] LD_{50max} which represents the LD_{50} but in the most salt-tolerant population

Influence of Geographical Location on Seed Germination in Response to Saline Conditions

Overall, no large differences in germination were observed among seeds from different localities. The exception was the seeds from Huanta-Rivadavia, the germination of which was decreased at 150 and 300 mM NaCl (Table 2).

At 450 mM NaCl, seeds from Huanta-Rivadavia and Chacabuco showed germination below 50 % (21.7 and 48.3 %, respectively), while seed germination from remaining locations remained above 50 %. At 600 mM NaCl, the overall germination processes was affected, however, four populations were less affected, as their germination level remained above 50 % (Matancilla,

Fig. 2 Cumulative mean germination in *Prosopis chilensis* influenced by NaCl concentration. Each curve is a mean of two independent seed germination assays and it represents the mean of the cumulative germination observed in the 12 populations during a 21-day period. Each curve represents the performance of 760 seeds ($n = 60$ seeds per population) at each NaCl concentration, totalling 3600 seeds analyzed. *Error bars* show 25 and 75 % percentiles
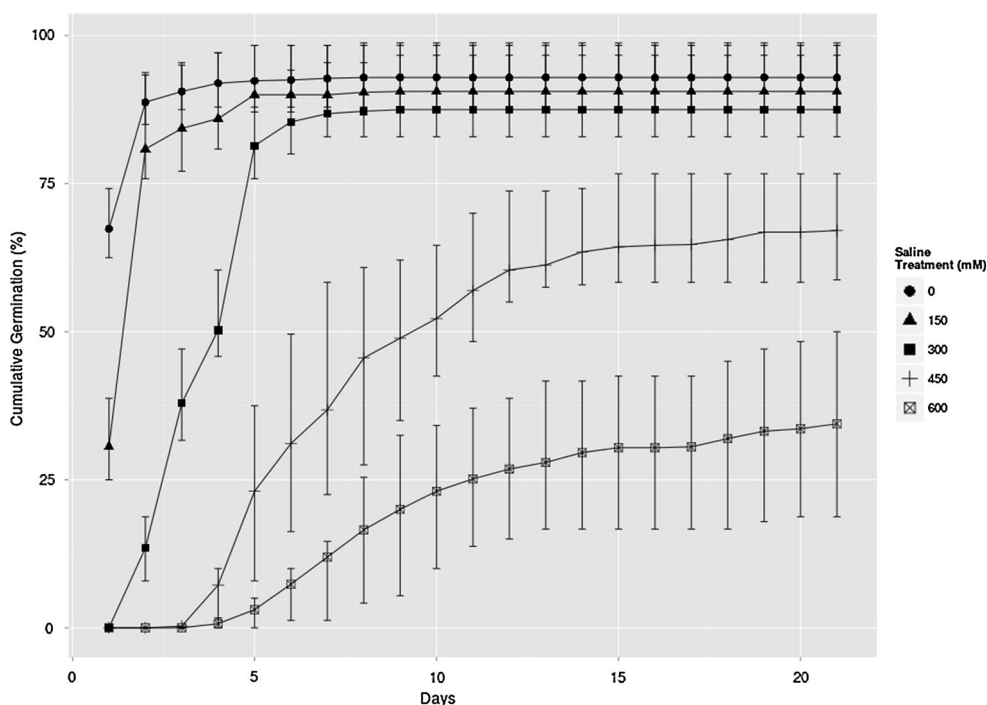
Rapel, Maitencillo and Ruta Internacional I) (Table 2). Assuming that germination levels correlate with the competence of seeds, we establish the LD_{50} as germination set at 50 %. The LD_{50} doses for seeds from Huanta-Rivadavia was 300 mM NaCl, for Chacabuco seeds was 450 mM NaCl and for the remaining locations was 600 mM NaCl. The exception was Maitencillo and Rapel whose germination percentages remained above 50 % (56.7 and 55 %, respectively, Table 2). Consequently, the most salt-tolerant population were Matancilla (Choapa Region, 56.7 %) followed by Rapel (55 %).

Probability of Seed Germination in Response to Salinity

In this study, we applied a model that determined the OR of germination in *P. chilensis* seeds exposed to four NaCl conditions from several populations and compare them with one population used as reference. In this case, Huanta-Rivadavia was chosen as reference because it showed the lowest germination level throughout different conditions. Analysis of every population included in this study was highly significant (Table 3). The Matancilla population with an OR of 33.3 (19.4; 19.1) (95 % CI) and the sample from Ruta Internacional I with an OR of 16.4 (10.1; 26.5) showed the highest germination probability relative to the reference population. In other words, Matancilla seeds afforded approximately 33-fold higher chance of germination than seeds from Huanta-Rivadavia. In contrast, seeds from

Río Hurtado (OR of 3.5) and Peldehue (OR of 4.0) had a 3.5- and 4-fold higher chance of germinating compared to Huanta-Rivadavia, respectively.

When comparing each salt concentration with the control condition, all ORs were <1 indicating that every salt condition impaired the probability of germination relative to the control (Table 3). Nevertheless, the OR at 150 mM NaCl is 0.7 (0.5; 1.1) which is barely significant ($P < 0.08$). Above 300 mM NaCl, the reduction in germination was statistically significant with "odds" of 48, 11, and 2 %, for 300, 450, and 600 mM NaCl, respectively.

Discussion

Seeds Viability and Lack of Recruitment

The initial evaluation of seed viability using sulphuric acid to break physical dormancy (Catalán and Balzarri 1992) demonstrates that scarification is required to stimulate germination in *P. chilensis* (Supplemental Table 2). All the seeds treated with sulphuric solution attained 100 % of germination by the third day, while 17 % of non-scarified seeds germinated during the same interval and increased to 22 % by the end of the assay on day 21 (Supplemental Table 2). In summary, using the sulphuric acid protocol, germination (48 h for radicle emergence) was similar to that reported by Cony and Trione (1998) and Villagra (1995) in other *Prosopis* species.

Table 3 The probability of seed germination on day 21

	Province	OR (95 % CI)	P
Accession			
Maitencillo	Elqui	7.79 (4.99; 12.14)	<0.0001
Río Hurtado	Elqui	3.48 (2.3; 5.26)	<0.0001
Montepatria	Limarí	11.97 (7.52; 19.07)	<0.0001
Rapel	Limarí	13.23 (8.26; 21.19)	<0.0001
La Colorada	Choapa	11.59 (7.29; 18.42)	<0.0001
Matancilla	Choapa	33.25 (19.44; 56.89)	<0.0001
San Agustín	Choapa	11.97 (7.52; 19.07	<0.0001
Ruta Internacional II	Los Andes	4.55 (2.98; 6.94)	<0.0001
Ruta Internacional I	Los Andes	16.35 (10.08; 26.51)	<0.0001
Peldehue	Chacabuco	4.02 (2.64; 6.11)	<0.0001
Chacabuco	Chacabuco	4.32 (2.84; 6.59)	<0.0001
Saline treatment (compared to control group)			
150 mM NaCl		0.7 (0.47; 1.05)	0.08
300 mM NaCl		0.48 (0.33; 0.71)	<0.001
450 mM NaCl		0.11 (0.07; 0.15)	<0.0001
600 mM NaCl		0.02 (0.01; 0.03)	<0.0001

Each accession was compared to Huanta-Rivadavia

CI credibility interval

Like in many Fabaceas, *P. chilensis* seeds are released by endozoic dispersion following animal ingestion. Animal digestion weakens the wax endocarps that protect seeds from a number of environmental factors facilitating germination when excreted on soils with appropriate water supply (Campos and Ojeda 1997; Peinetti et al. 1993). This strategy aids *P. chilensis* seeds to gain temporal and spatial opportunity for germination in adverse conditions, similar to what has been reported in other *Prosopis* species (Villagra et al. 1995). It is assumed that grazing herbivores ate tree pods and spread the seeds, as signs of depredation were detected on visited sites, although no new plants were detected across the sampled area. Excess of grazing after ENSO events can also be another fact putatively effecting establishment of new plants. The overall mean germination was 93 %, with extreme values between 82 % in Huanta-Rivadavia to 100 % in Montepatria, Matancilla, and Peldehue sites. This yield is considerably higher than that reported in other woody plants (Khasa et al. 2001; Beritognolo et al. 2007; Li et al. 2008) but it is similar to that described in other species of the genus *Prosopis* (Rohdes and Felker 1988; Cazebonne et al. 1999; El-Keblawy and Al-Rawai 2005; Villagra and Cavagnaro 2006). In this case, the unaffected viability of *P. chilensis* seeds was confirmed during germination assays when the physical coat-imposed dormancy had been interrupted by acid treatment. Therefore, the absence of recruitment in almost every site searched along the latitudinal transect (personal observation) is not a consequence of dysfunctional germination imposed by defective embryo development, but it is a result of forced dormancy in seeds where the presence of rearing herbivores feeding on plant pods is inefficient to warrant adequate germination that could contribute to ameliorate afforestation. Another factor that may be influencing the lack of recruitment is allied to the abiotic stress imposed mainly by water deficit. It is a fact that a diminishing of precipitation and increment in the index of aridity has occurred in north and central regions of Chile since 1950 (Santibáñez and Santibáñez 2007; PAN 2014; UDP 2012; Santibáñez 2014), and that 17 out of 18 of these dry periods (3–6 years of extension) occurred in the area where *P. chilensis* is distributed (Meza et al. 2010). This aridness is influenced by the less frequent ENSO phenomenon (Wang et al. 2012; PAN 2014) whose precipitation events are vital to recruit new plants (Holmgren et al. 2006b; Squeo et al. 2007). Lack of recruitment worsen by unrestrained animal breeding and/or wild animal predation (Valdivia and Romero 2013), poor soil structure, and reduced organic matter, with less *P* and other essential minerals that are vital for facilitating germination and establishment of new plants (Miranda et al. 2013).

Effects of NaCl on Germination Response

As seen in many plant species, stress impairs germination and several other physiological traits (Hu and Schmidhalter 2005; Beritognolo et al. 2007; Ríos-Gómez et al. 2010; Zolla et al. 2010; Mane et al. 2011; Bui 2013; Jamil et al. 2014). *Prosopis chilensis* is not the exception but interestingly, seeds of this tree are capable of germinating under adverse conditions when seeds from other woody plants fail (Fang et al. 2006; Li et al. 2008; Hosseini et al. 2012). In fact, it is demonstrated here that germination of *P. chilensis* was not affected at 150 mM NaCl and became marginally affected at 300 mM NaCl (CI ≥ 99 %) (Fig. 2; Table 2). The salt tolerance of *P. chilensis* confirms observations by Villagra and Cavagnaro (2005) in seeds of *Prosopis argentina* (80 % at 300 mM), Al-Ansari (2002) for *Prosopis tamarugo* (57 % at 18,000 ppm of salts), and Sosa et al. (2005) for *Prosopis strombulifera* (60 % at −1.2 MPa). These germination efficacies contrast with those observed in glycophytes like Arabidopsis (Vallejo et al. 2010), *Lupinus albus* (Jeschke 1984), and Solanaceas (Bojovic et al. 2010) where seeds hardly germinate at concentrations higher than 200 mM NaCl. The inability to germinate in these latter cases is being linked to an increase of reactive oxygen species (ROS) triggered by toxic levels of NaCl that deplete the activity of relevant antioxidant enzymes such as catalase (CAT), peroxidase (POX), and polyphenol oxidase (PPO) (Dash and Panda 2014) leading to severe damage of proteins and nucleic acid (Miller et al. 2010).

At higher salt concentrations, *P. chilensis* delays germination, a similar finding was observed during the culture of quinoa (Adolf et al. 2013); however, following this delay germination remains successful (Fig. 2). In fact, germination above 450 mM NaCl is remarkable for plants and not many of them succeed (Munns 2002; Villagra and Cavagnaro 2005). For instance, a wild wheat species considered resistant to abiotic stress (*Aegilops* spp.) held as gene reservoir with potential to improve commercial wheat (*Triticum*) species, attains LD_{50} at 450 mM NaCl, becoming unsuitable for saline soils (Yildiz et al. 2006). At a similar NaCl concentration, we observed a mean germination of 67 %, for the large majority of studied samples (Table 2). Finally, at 600 mM NaCl, we obtained a sizable germination mean of 34 % (Fig. 2; Table 2). This percentage is similar to that obtained in other *Prosopis* species incubated at 600 mM NaCl, such as *P. flexuosa* (40 %, Catalán et al. 1994) and *P. tamarugo* (85 %, Arce and Balboa 1988) and approximates the germination of extreme halophytes such as some species of *Chenopodium, Atriplex,* and *Casuarina* (Rhodes and Felker 1988; Cushman 2001; Khan et al. 2001; Araújo et al. 2006; Kachout et al. 2009; Zurita-Silva et al. 2014). Adolf et al. (2013) analyzed the

germination capability and seedling establishment of quinoa genotypes populating the Andes Altiplano arid environment. They proposed that tolerance of quinoa to salt stress at germination is the result of a significant gradient limiting the distribution of potential toxic (Na^+ and Cl^-) ions and essential ions such as K^+, Mg^{+2}, Ca^{+2}, PO_4^{2-}, and SO_4^{2-}, across the protecting seed coat and to a reallocation of elements in the embryo. Hariadi et al. (2011) suggested that seed viability of quinoa was dependent on its ability to exclude toxic Na^+ from the developing embryo to avoid ion toxicity. In summary, it seems that the high salt tolerance of quinoa seeds is associated to structural and physiological protective features in the seeds. It is possible that *P. chilensis* adopted a similar strategy to avoid salt toxicity. This notion gain supports now following the observation that high salt concentrations in *P. chilensis* delayed seed germination (Fig. 2), similar to what has been observed in quinoa genotypes (González and Prado 1992; Prado et al. 2000; Delatorre-Herrera and Pinto 2009).

Seed Germination in Different Locations

The results show that *P. chilensis* seeds display enhanced germination especially under salt levels considered as toxic (Table 2). The results also show that seeds from the central section encompassing Limarí and Choapa provinces (see Table 1 for georeference details) displayed increased germination under saline conditions relative to seeds collected at bordering sites (Elqui Valley and Chacabuco province, see Table 1 for georeference details). A possible explanation for this unexpected difference comes from Plaza (2010) who found that *P. chilensis* trees growing in Choapa valley display five "rare" alleles only found in these populations. In addition, in Elqui populations they described two specific alleles, one of them in locus Mo05 (213 bp) and the second in locus Mo13 (236 bp), while in the Limarí populations a specific allele in locus Mo09 (214 bp) was detected. In summary, eight polymorphic sites were described, two in Elqui valley, one for Limarí valley, and the remaining five alleles found in algarrobos growing in Choapa valley. Based on these genetic differences, it can be argued that the *P. chilensis* populations along its geographical distribution display specific genetic determinants involved in tolerance to saline stress. While the altered expression of several genes has been associated with abiotic stress, in leguminous species the enzyme betaine aldehyde dehydrogenase responsible for the synthesis of the osmotic regulator glycine betaine appears as candidate to tolerate stress (Yu et al. 2014). Because of the limited number of samples collected due to insufficiency of available trees and because the sampling procedure represented a single year of collection (2011), new assays

circumventing these limitations are required. Under similar conditions, Cazebonne et al. (1999) reported 68 % seed germination at 500 mM NaCl using seeds collected in 1993 at the same location (Peldehue) we reported in this study. After eighteen years (2011), we observed a 13 % reduction in germination (55 %, Table 2) at 450 mM NaCl. In view of these data, it is suggested that the germination capacity at Peldehue site has declined during this period. Since we have no explanation that accounts for this difference, it is felt that further studies are required to confirm this difference and to investigate possible factor (s) influencing the decreased seed competence.

Finally, it is remarkable that in this study two populations of *P. chilensis* (Matancilla and Rapel) successfully withstand salt stress, as their germination rate remains superior to the LD_{50} (Table 2) at 600 mM NaCl (sea water salt concentration is $\sim$500 mM; 30,000 mg/L, Kim et al. 2010). For the purpose of seed selection, seeds from these two places are good candidates to be used during recovery of degraded or marginal zones, and it would be of interest to learn if seedlings from these two localities tolerate irrigation with sea water. More importantly, the utilization of *P. chilensis* for afforestation becomes desirable considering countless experiences where afforestation in degraded soils using non-native species caused undesirable effects such as uncontrolled propagation, loss of biological diversity, changes in composition and structure of wild vegetation, poisonous fodder for livestock and wild animals among others (Mc Neely 2001; Andrade et al. 2009). In the Chilean situation, local programs should encourage enrichment of *P. chilensis* reforestation due to the imminent process of extinction recently detected (Valdivia and Romero 2013) and for recovery of marginal lands thus contributing to the development of a more sustainable world.

Conclusion

The results showed that the absence of recruitment of *Prosopis chilensis* observed along its natural Chilean habitat is a consequence of physical seed dormancy, a prolonged drought affecting north and central Chile since 1950 and inefficacious herbivory unable to release the protective dormancy of seed. Also, it is demonstrated that germination of *P. chilensis* seeds is highly tolerant to salt stress and that this adaptation remains effective in most naturally growing trees in Chile. We found that seeds from Limarí and Choapa valley remain able to germinate when challenged by extreme salt stress. The effort to screen the Chilean *P. chilensis* populations represents a valid approach not only to find candidate locations to collect seeds, but also to perform further detailed studies aimed to recover degraded and marginal soils in arid and semiarid regions.

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