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RESEARCH ARTICLE

From seed germination to established seedlings: a comparative evaluation in five shrub species and implications for seed-based restoration in arid lands

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In a context of global desertification, direct seeding of native species is emerging as a hopeful technique to achieve large-scale arid land restoration. Although low percentages of establishment have been reported for direct seeding in arid lands, it has been more cost-effective than outplantings for some species. Therefore, in order to determine the most suitable species for direct seeding we evaluated potential germination in laboratory trials (ex situ), and seedling emergence and establishment in the field (in situ) for five shrub species from the most arid region of Argentina called "*Monte*." Direct seeding was performed in three alternative environmental conditions: (1) abandoned oil-drilling platforms, (2) bare soil patches, and (3) under the canopy of shrubs patches in cattle ranching areas. In the three cases, four soil treatments were applied: hydrogel, soil enrichment with arbuscular mycorrhizal fungi, and clay pot irrigation. Seedling emergence and establishment after the first period of extreme weather conditions (summer) were higher in severely degraded sites (oil-drilling platforms). In this particular condition, seedling emergence and establishment presented the highest values for *Ephedra ochreata* (64.8–82.8% and 26.8–46.4%, respectively) and the lowest values for *Larrea divaricata* (6.78–24.8% and 2.8–6.4%, respectively). These results show that direct seeding offers potential possibilities to restart processes of assisted succession in arid lands and that species selection is a key stage/phase in direct seeding success.

Key words: direct seeding, ecological restoration, *Monte*, oil-drilling platform

Implications for Practice

- Seedling emergence results are not definitive for direct seeding performance and require careful analysis in conjunction with seedling establishment after at least the first year.
- Several treatments can reach the same seedling establishment values by direct seeding.
- In arid lands, some species are more suitable for direct seeding because they can achieve higher establishment values.

Introduction

Seed-based restoration is emerging worldwide as a hopeful technique for large-scale application (Pérez et al. 2019, 2020; Shackelford et al. 2021). For a long time, a great limitation for seed-based restoration was addressed by the lack of knowledge about seed dormancy, especially in drylands where more than 80% of the plant species produce seeds with some form of this syndrome that prevents germination (Baskin & Baskin 2014). This obstacle has been partly overcome in the last decades through fundamental research contributions in dormancy alleviation treatments in different continents (Erickson et al. 2016; Kildisheva et al. 2020; Rodriguez Araujo et al. 2021). Even when the most effective dormancy alleviation treatments are known, the transition from seeds to established seedlings in natural environmental conditions represents a critical filter for dryland ecological restoration (James et al. 2011; Gerlein-Safdi et al. 2020). An example of extreme difficulties for direct seeding can be seen in arid lands (Abella et al. 2012; Huebner et al. 2022). These extensively distributed regions around the world are water limited ecosystems characterized by low and unpredictable rainfall (Noy-Meir 1973) where recruitment flushes are infrequent and can lead to low levels of plant regeneration (Arkle et al. 2014; Abella et al. 2020). This limitation for ecological succession development determine that arid lands are considered highly susceptible to degradation (Cherlet et al. 2018).

The heterogeneity of germination sites imposed by land use, different degradation levels or soil surface manipulation is

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closely related to success or failure outputs, as it has been demonstrated in studies that focused on soil-seeds interaction (Chambers 2000; Bosco et al. 2015). Research on seedling emergence and establishment from direct seeding show a clear benefit of soil amelioration through ripping, holes, or adding materials, including rocks, litter or top-soil (Chambers 2000; Commander et al. 2019; Cross et al. 2021). Thus, improvements in microsite conditions such as temperature and water availability seem to be key determinant factors for seedling recruitment (Kildisheva et al. 2016; Lewandrowski et al. 2021; Veblen et al. 2022). For instance, Lewandrowski et al. (2021) found that temperatures affect seedling emergence and survival after emergence. Meanwhile, Muñoz-Rojas et al. (2016) reported that, depending on the species, water availability had higher influence on seedling emergence. This highlights the importance of taking into account that the effect of microsite conditions in direct seeding can vary between species (Pérez et al. 2019). However, little research on this topic has been carried out for many native species of arid lands (Gornish et al. 2019; Pérez et al. 2019; Rodriguez Araujo et al. 2021), which emphasizes the need to evaluate different soil treatments on seedling emergence and establishment through direct seeding.

The *Monte* desert in Argentina, considered the most arid region in the country, has different degradation levels including severe degradation in areas affected by oil and gas exploitation, and moderate degradation in areas where cattle ranging has historically taken place (Mazzonia & Vazquez 2009). Oil-drilling platforms which produce highly compacted soils without vegetation cover are one of the worst impacts of the hydrocarbon activity (Gratzfeld 2004). Once the drilling platforms are abandoned soil is ripped to favor vegetation recovery, even though this process can take decades as it occurs in other arid land (Zuleta et al. 2003; Bainbridge 2007; Abella 2010). On the other hand, grazing leads to changes in species composition and soil properties due to animal trampling (Bisigato et al. 2005; Taboada et al. 2011). Therefore, it may be expected that seed-based restoration outcomes vary between environments with different degradation levels.

In this context, some questions arise about the application of direct seeding in different scenarios of arid lands degradation: are some shrub species suitable in order to achieve high emergence and establishment values from direct seeding? Can this technique be applied in sites with different degradation levels? Do soil treatments favor seedling emergence and establishment through direct seeding? In order to answer these questions, we evaluated the performance of five native shrub species from the arid *Monte* (Argentina) in direct seeding to assess the most suitable species to be used with this technique. We performed direct seeding in sites with different degradation levels and soil treatments in order to enhance microsite water availability.

Methods

Study Area

The study area is located in an area called "*Aguada Pichana*" (Neuquén Province, Argentina) (Fig. 1). The area was delimited for oil exploitation purposes, but traditional livestock has been implemented since the beginning of the twentieth century in

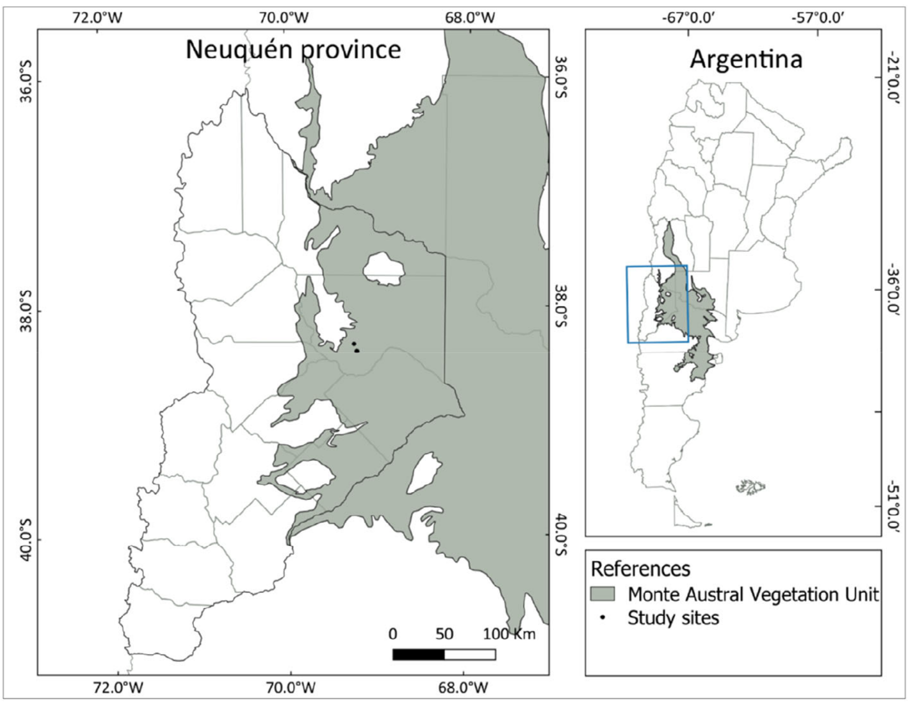

Figure 1. Location of the experimental sites and the *Monte Austral* vegetation unit of the *Monte* phytogeographical province, Argentina. Geographical coordinates system WGS-84.

Table 1. Species selected for direct seeding. Life form: PS, perennial shrub; PSS, perennial sub-shrub, . Dormancy alleviation treatments: CW7, cold-wet for 7 days; SR3 SO3, soaking and rubbing twice a day for 3 days; SO3; soaking for 3 days; CS5, chemical scarification for 5 minutes; CS45, chemical scarification for 45 minutes. [a]Beider (2012). [b]Rodriguez Araujo et al. (2019). [c]Peano (2016). [d]Rodriguez Araujo et al. (2017). [e]Paredes et al. (2018).

Species	*Family*	*Life form*	*Dormancy alleviation treatment*
Atriplex lampa (Moq.) D. Dietr.	Chenopodiaceae	PSS	SO3[a]
Ephedra ochreata Miers	Ephedraceae	PS	CW7[b]
Larrea divaricata Cav.	Zygophyllaceae	PS	SR3[c]
Neltuma flexuosa (DC.) C.E. Hughes & G.P. Lewis var. *depressa* (F.A. Roig) C.E. Hughes & G.P. Lewis	Fabaceae	PS	CS5[d]
Senna aphylla (Cav.) H.S. Irwin & Barneby var. *aphylla*	Fabaceae	PS	CS45[e]

the same place. The flora and fauna correspond to the most arid region of Argentina, called *Monte* phytogeographical province, subdivision *Austral* (Cabrera 1971; Oyarzabal et al. 2018).

Mean annual temperature in *Monte Austral* is 15°C with high seasonal variation (Morello et al. 2012). Data recorded at the study area over 4 years (October 2012 to May 2017) have shown a mean temperature during summer months of ca. 25°C, and ca. 9°C in winter. Over the last 20 years (January 1999 to December 2019), mean annual rainfall in the study area was 152 $\pm$ 60.3 mm, ranging from 52 to 250 mm annually. During the study period (July 2016 to June 2017), annual precipitation was 151 mm (data from “La Higuera” Meteorological Station, AIC, 2020, personal communication).

Vegetation in *Monte Austral* is distributed in shrub-dominated patches alternating with patches of very sparse plant cover (Busso & Bonvissuto 2009). The dominant shrub species include *Larrea divaricata* Cav., *L. cuneifolia* Cav., and *L. nitida* Cav. (Zygophyllaceae), *Monttea aphylla* (Miers) Benth. & Hook. var. *aphylla* (Scrophulariaceae), *Atriplex lampa* (Moq.) D. Dietr. (Chenopodiaceae), *Lycium chilense* Miers ex Bertero (Solanaceae), and *Neltuma flexuosa* (DC.) C.E. Hughes & G.P. Lewis var. *depressa* (F.A. Roig) C.E. Hughes & G.P. Lewis (Fabaceae). Among low-growing perennial life forms, three clump grasses are common, namely *Pappostipa speciosa* var. *speciosa* (Trin. & Rupr.) Romasch, *Panicum urvilleanum* Kunth., and *Poa ligularis* Nees ex Steud, as well as the subshrub *Hyalis argentea* D. Don ex Hook. & Arn. (Asteraceae) and the naturalized exotic species *Schismus barbatus* (Busso & Bonvissuto 2009).

Seed Source

We used seeds of five species that had been used in restoration of arid zones of the *Monte Austral* of Argentina, stored in the germplasm bank “Banco del Árido” (Rodríguez Araujo et al. 2015). They were collected following the standard protocols for ecological restoration work (i.e., harvesting seeds from at least 50 plants in a population without surpassing 20% of the available seeds per plant; Pedrini & Dixon 2020) in a 50 km radius from the experimental sites in Añelo Basin, Neuquén Province (Rodriguez Araujo et al. 2021). After collection, seeds were air dried at room temperature in a ventilated space, manually cleaned to remove impurities, and then stored at −18°C. Storage time was 2.5 years for *L. divaricata* and *N. flexuosa*, 3.5 years for *E. ochreata* and *S. aphylla* and 4.5 years for *A. lampa*. Seeds were treated to alleviate dormancy according previous studies developed in the *Monte Austral* (Table 1).

Ex Situ Reference Germination

We performed an ex situ germination test to determine the maximum germination potential (MPG) of the seeds used. The seeds were placed in Petri dishes on a moistened filter paper disk. Then they were taken to a germination chamber with a minimum temperature of 10°C ($\pm$1°C) during 12 hours of darkness, and a maximum temperature of 20°C ($\pm$1°C) during 12 hours of light. These characteristics represent the conditions to which the seeds would be exposed during natural germination during the fall in the *Monte Austral* region (Páez et al. 2005; Bonvissuto 2006). Germinated seeds, considering the emergence of the radicle, were counted every 2 days, until no more germination was observed and to a maximum period of 45 days. Five replicates of 25 seeds were used for each species in different Petri dishes from where germinated seeds were later removed.

Direct Seeding: Treatments and Variables Considered

We selected two experimental sites located in the *Monte* Region and separated 7.6 km from each other (Fig. 1). In each site, we defined three sectors for experimental trials: abandoned drilling-platform (DP), severely degraded by oil and gas exploitation; shrub patches (SP), and bare soil patches (BS) only affected by historical grazing. Direct seeding with native species was performed in the three sectors (DP, SP and BS).

The experimental design was completely randomized with five replicates per species, sector and treatment. Each replicate consisted of five 110 mm diameter polyvinyl chloride tubes, one for each species, sown with 25 seeds (seeding density of 2,500 seeds/m^2) and covered with soil at a depth equal to 1- or 2-fold the seed size. After sowing we irrigated with 500 mL of water per replicate in order to promote germination and then we covered the seeding pots with a small hexagonal wire mesh closure to keep mammalian herbivores away (Fig. 2A). We evaluated three soil treatments that have been cited as possible options to promote seed germination and seedling establishment due to their ability to improve water availability through water retention or water supply, increase microbiological activity, and increase the absorption of some nutrients (Vasudevan

Figure 2. (A) Replicate of control treatment in oil-drilling platform (DP) with enclosure details. (B) Well digging for hydrogel addition. (C) *Medicago sativa* seeding in native soil to produce arbuscular mycorrhizal fungi (AMF) enriched substrate. (D) AMF replicate in shrubs patches (SP) with protective enclosure. (E) Clay-pot irrigation replicate in bare soil patches (BS).

et al. 2011; Durović et al. 2007; Martínez de Azagra Paredes et al. 2022). The evaluated treatments were:

- Control (T0): seeds sown in unmodified soil.
- Hydrogel (T1): we dig wells of 60 × 20 cm and 20 cm deep. The extracted soil was mixed with 7.5 g of un-hydrated hydrogel and returned into the well. We added 5 L of water in order to promote gel hydration (Fig. 2B).
- Substrate enrichment with arbuscular mycorrhizal fungi (AMF) and hydrogel (T2): this treatment was prepared as T1 and we added 500 g of soil enriched with AMF. This substrate was produced in a greenhouse seeding a highly mycorrhizal host plant (*Medicago sativa* L.) in rhizosphere soil (Becerra & Cabello 2007) collected from below adult plants of *L. divaricata* (Fig. 2C & 2D). After 4 months of *M. sativa* growth, the aerial parts of the plants were cut and growing substrate with finely chopped roots was used to enrich the sowing substrate. Root colonization of *M. sativa* with AMF was confirmed by the Microbiology Laboratory of the Faculty of Environmental and Health Sciences of the National University of Comahue.
- Buried clay pot irrigation (T3): we dig a well, approximately 40 cm deep, to bury an unglazed 1.1 L clay pot (Fig. 2E). It was filled with water at the time of sowing and subsequently every 15 days.

Direct seeding was performed in mid July 2016. We recorded the number of emerged seedlings (appearance of cotyledons) every 15 days until no more emergence was observed, and mortality every 15 days for 1 year. One year after sowing, we calculated seedling emergence percentage (%Em) (number of emerged seedlings/number of sown seeds, multiplied by 100) and seedling establishment percentage (%Es) (number of live seedlings/number of sown seeds, multiplied by 100) and we measured stem diameter (SD) and height to the last green leaf (H) in all established seedlings.

Soil and Environment Monitoring

We registered edaphic temperature, environmental temperature and humidity at each sector (DP, SP and BS). The edaphic temperature was recorded with I-button Termochrom data loggers buried 5 cm in the ground. Environmental humidity and temperature were recorded using HOBO Series U10 data loggers. To evaluate the effect of the treatments (T0, T1, T2 and T3) in soil moisture, edaphic moisture was recorded with Decagon Devices EC-5 sensors and EM-5B data loggers at a depth of 10 cm.

Statistical Analysis

Ex Situ Reference Germination Versus In Situ Emergence. The total number of germinated seeds for each species in the ex situ test was compared with the in situ emergence (in the field) by means of a Generalized Linear Model (GLM) with negative binomial distribution, *log* link function and sector (DP, BS, BS and ex situ) as fixed effect. Comparisons were made with the LSD Fisher method.

Direct Seeding Performance in the Three Sectors. In order to determine differences in seedling emergence and establishment among sectors with different degradation level (DP, SP, BS), the number of emerged and established seedlings after 1 year were analyzed using GLM with negative binomial distribution, *log* link function and site, sector and site*sector interaction as fixed effects. Comparisons were made with the LSD Fisher method.

Direct Seeding Performance in the Sector of Highest Seedling Establishment. To assess species and treatment performances in this specific case (oil-drilling platform), we resort to the variables %Em, %Es, SD, and H and carried out a principal components analysis (PCA) with the combination of species and treatment as classification criterion. Subsequently, we evaluated the effect of the treatments on seedling emergence and establishment for each species since there was a significant interaction between species and treatments on the studied variables. We performed a Generalized Lineal Mixed Model (GLMM) with negative binomial distribution, *log* link function treatment as fixed effect and site as random effect. Comparisons were made with the LSD Fisher method.

The SD and H for each species in the oil-drilling platform were analyzed using GLMM with Gamma distribution, *log* link function, treatment as fixed effect and site as random effect. Comparisons were made with the LSD Fisher method.

Additionally, we calculated seedling survival percentage (%S) for each species and treatment, as the ratio between the number of established and emerged seedlings, multiplied by 100. The %S between species and the effect of the treatment on species survival were compared with the non-parametric Kruskal-Wallis test, since the assumption of normality was not fulfilled and pairwise comparisons were made.

Edaphic and Environmental Context of the Experiment. Edaphic and environmental temperature and humidity were analyzed in annual and seasonal means between sectors using the non-parametric Kruskal-Wallis test because the assumptions of normality and homogeneity of variances were not met. In the cases in which significant differences were found, pairwise comparisons were made. Annual mean, maximum and minimum soil temperature and moisture were calculated from the daily mean, maximum and minimum values corresponding to 1 year of records. Annual mean, maximum and minimum environmental temperature and relative humidity were calculated on the daily mean, maximum and minimum values corresponding to 9 months of records. We considered 9 months of complete information for the three sectors due to data logging failure for the last 3 months in the environmental temperature and humidity sensor.

To evaluate the treatments effect on soil moisture, annual and seasonal mean, maximum and minimum soil moisture were calculated based on the daily mean, maximum and minimum values corresponding to 1 year of records. Comparisons by treatment for each sector were evaluated using the nonparametric Kruskal—Wallis test because the assumptions of normality and homogeneity of variance were not met. Subsequently, pairwise comparisons were made for cases in which there were significant differences.

We use InfoStat (2020, Di Rienzo et al. 2014) for nonparametric analyses and as an interphase with R (3.6.3) for GLMM. We set a uniform significance level at 0.05.

Results

Ex Situ Reference Germination Versus in Situ Emergence

Ex situ germination presented very high percentages (>90%) for *E. ochreata*, *N. flexuosa* and *S. aphylla*, while for *A. lampa* and *L. divaricata* the germination was 40–50%. When comparing these values with the emergence in the field (in situ), all species presented lower in situ emergence in the three sectors (*E. ochreata*: $x^2 = 10.83$, $df = 3$, $p < 0.0126$, *L. divaricata*: $x^2 = 12.04$, $df = 3$, $p < 0.0072$, *N. flexuosa*: $x^2 = 61.58$; $df = 3$, $p < 0.0001$ and *S. aphylla*: $x^2 = 59.71$, $df = 3$, $p < 0.0001$), except for *A. lampa* for which it was lower only in DP ($x^2 = 49.60$, $df = 3$, $p < 0.0001$). Among these species, *E. ochreata* presented the smallest difference between ex situ germination and in situ emergence. For this species and for *L. divaricata*, in situ emergence was uniform in the three sectors, while for the other three species it varied according to the sector (Fig. 3). Additionally, the standardization of in situ emergence by ex situ germination, understood as the proportion of germinable seeds that were able to emerge in the field, shows that *A. lampa* may have similar field emergence of germinable seeds to that of *E. ochreata* and that *N. flexuosa* yielded the lowest performance in in situ emergence (Fig. 4).

Direct Seeding Performance in the Three Sectors

The GLM analysis showed that site and sector effects and the interaction between them were not significant in seedling emergence (ca. 35%), considering all five species together ($x^2 = 0.94$, $df = 1$, $p = 0.3329$; $x^2 = 2.37$, $df = 2$, $p = 0.3055$; $x^2 = 0.90$, $df = 2$, $p = 0.6374$, respectively). On the other hand, there

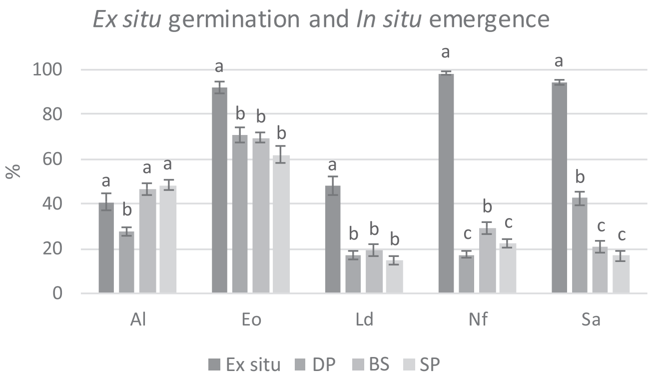

Figure 3. Ex situ germination and In situ seedling emergence for five native species of the *Monte* region (Al, *Atriplex lampa*; Eo: *Ephedra ochreata*; Ld, *Larrea divaricata*; Nf, *Neltuma flexuosa*; Sa, *Senna aphylla*) according to sectors (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches). The values represent the average (± SE) expressed as a percentage of the total seeds placed in the germination chamber and sown in situ. Means with a common letter for the same species are not statistically different ($p < 0.05$).

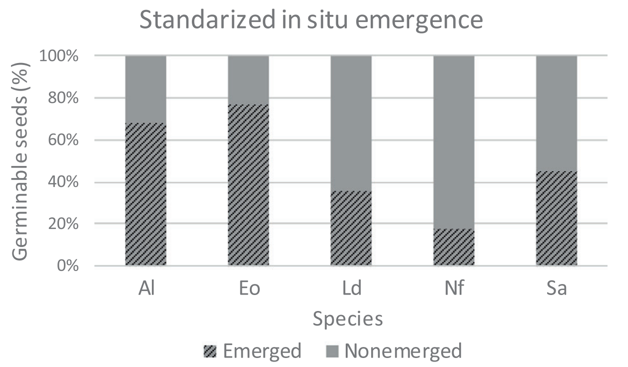

Figure 4. Seedling emergence standardized by ex situ germination for five native species of the *Monte* region (Al, *Atriplex lampa*; Eo, *Ephedra ochreata*; Ld, *Larrea divaricata*; Nf, *Neltuma flexuosa*; Sa: *Senna aphylla*).

was a significant effect of the sector in the number of established seedlings ($x^2 = 85.68$, $df = 2$, $p < 0.0001$), no effect of the site ($x^2 = 0.81$; $df = 1$, $p = 0.3329$, $p = 0.3691$) and no interaction between site and sector ($x^2 = 3.13$, $df = 2$, $p = 0.2091$). The number of established seedlings was higher in DP (15.2%), lower in SP (2.72%) and intermediate in BS (4.28%) (Fig. 5).

Direct Seeding Performance in the Sector of Highest Seedling Establishment

In DP, the sector with higher seedling establishment, PC 1 of the PCA performed with the %Em, %Es, SD and *H* explained 53.5% of the total variation. This allowed a differentiation between *E. ochreata*, in the positive side of the axis, and the other species due to its greater emergence, establishment and height at both sites. The second axis explained 28.8% of the variability of the data through stem diameter at both sites. In the upper part of the graph, we identified *N. flexuosa* as the species with the largest SD, particularly in T3 and *A. lampa* and *E. ochreata* with T2 (Fig. S1).

Without considering the treatments, the species that presented the greatest emergence and establishment was *E. ochreata* (70.7 ± SE 3.16 and 37.0 ± 3.75% respectively), followed by *S. aphylla* (42.4 ± 3.02 and 18.9 ± 2.37%), *A. lampa* (27.8 ± 1.85 and 7.9 ± 1.44%), *N. flexuosa* (17.3 ± 1.81 and 8.1 ± 1.36%) and *L. divaricata* (17.0 ± 1.83 and 4.5 ± 0.8%). The effect of the treatments in seedling emergence was significant for *L. divaricata* ($x^2 = 23.87$, $df = 3$, $p < 0.0001$) and *S. aphylla* ($x^2 = 24.11$, $df = 3$, $p < 0.0001$) while it was not significant of *A. lampa* ($x^2 = 0.65$, $df = 3$, $p = 0.8842$), *E. ochreata* ($x^2 = 4.92$, $df = 3$, $p = 0.1746$) and *N. flexuosa* ($x^2 = 3.32$, $df = 3$, $p = 0.3454$). For seedling establishment treatments effect was significant for *N. flexuosa* ($x^2 = 8.20$, $df = 3$, $p = 0.0419$) and *S. aphylla* ($x^2 = 9.08$, $df = 3$, $p = 0.0282$) and was not significant for *A. lampa* ($x^2 = 2.71$, $df = 3$, $p = 0.4391$), *E. ochreata* ($x^2 = 3.47$, $df = 3$, $p = 0.3252$) and *L. divaricata* ($x^2 = 4.26$, $df = 3$, $p = 0.2351$). However, none of the treatments improved seedling emergence or establishment compared to the control (Fig. 6). Regarding seedling growth, treatments effect on SD and H differed among species. The species *A. lampa* showed the higher values for both variables with T2 (SD: $x^2 = 35.61$, $df = 3$, $p < 0.0001$; *H*: $x^2 = 42.37$, $df = 3$, $p < 0.0001$). Similarly, *E. ochreata* presented taller plants with T2 ($x^2 = 10.54$, $df = 3$, $p = 0.0145$), but there was not significant effect of the treatments on SD ($x^2 = 7.21$, $df = 3$, $p = 0.0656$). Seedlings of *L. divaricata* had higher SD with T1 and T3, lower with T0 and intermediate with T2 ($x^2 = 10.41$, $df = 3$, $p = 0.0154$) but treatments effect on H was not significant ($x^2 = 1.90$, $df = 3$, $p = 0.5722$). In the case of *N. flexuosa* seedlings had higher SD ($x^2 = 10.30$, $df = 3$, $p = 0.0159$) and *H* ($x^2 = 19.42$, $df = 3$, $p = 0.0002$) with T3. Instead, treatments had no significant effect on SD ($x^2 = 4.24$, $df = 3$, $p = 0.2353$) or *H* ($x^2 = 4.24$, $df = 3$, $p = 0.2353$) for *S. aphylla* (Fig. 6).

We found significant differences in seedling survival (%S) depending on species ($H = 18.9$; $df = 4$; $p = 0.007$) but the effect of the treatments on %S was not significant for any of the evaluated species (*A. lampa*: $H = 3.47$; $df = 3$; $p = 0.2938$; *E. ochreata*: $H = 2.99$; $df = 3$; $p = 0.3922$; *L. divaricata*: $H = 1.51$; $df = 3$; $p = 0.6610$; *N. flexuosa*: $H = 6.78$; $df = 3$; $p = 0.0738$; *S. aphylla*: $H = 1.07$; $df = 3$; $p = 0.7826$). The species with higher survival were *E. ochreata* (53.32 ± 4.91%), *N. flexuosa* (47.09 ± 6.42%) and *S. aphylla* (44.45 ± 4.92%) while *L. divaricata* (28.55 ± 5.05%) and *A. lampa* (27.88 ± 4.56%) showed the lower values.

Edaphic and Environmental Variables of the Experiment

The annual averages of mean, maximum and minimum edaphic moisture were higher in DP (ca. 6–7%), lower in SP (ca. 2%) and intermediate in BS (ca. 2%) ($H = 404.37$, $df = 2$, $p < 0.0001$; $H = 417.55$, $df = 2$, $p < 0.001$ and $H = 403.25$, $df = 2$, $p < 0.0001$, respectively). The detailed analysis by season revealed that mean, maximum and minimum edaphic moisture

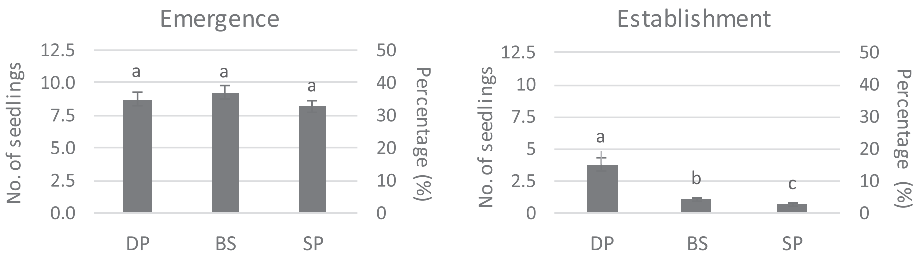

Figure 5. Seedling emergence and establishment, for the five species, by sector (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches). The values expressed as the number of seedlings on the main axis represent the average (± SE) for all species and treatments in each sector ($n = 5$ species × 4 treatments × 5 replicates = 100). On the secondary axis, they are expressed as a percentage of the total seeds sown (25 seeds per replicate). Means with the same letter are not significantly different ($p > 0.05$).

was higher in DP in the four seasons of the year (see Table S1 for statistical outputs, Fig. 7).

There were no significant differences in the annual averages of the mean, maximum and minimum edaphic temperature depending on the sector (Table 2). Absolute maximums and minimums recorded were 52.5°C in DP, 59.5°C in SP and 62.5°C in BS during the summer, and −1.5°C in DP and SP and −0.5°C in BS during winter. An analysis by season revealed that the mean and minimum temperatures did not differ between sectors in any season, while significant differences were observed between sectors in the maximum temperature of summer and autumn (see Table S2 for statistical outputs). In autumn, the maximum edaphic temperature was higher in DP and lower in SP and BS, while in summer it was lower in DP and higher in SP and BS.

Regarding the environmental variables, in the percentage of relative humidity of the environment (RH), there were no significant differences in the minimum RH (ca. 22%) depending on the sector ($H = 0.74$, $df = 2$, $p = 0.6051$). However, mean and maximum HR were higher in BS (41.26 and 65.29%), lower in SP (37.48 and 58.85%) and intermediate in DP (39.16 and 62.22%) ($H = 14.41$, $df = 2$, $p = 0.007$ and $H = 12.42$, $df = 2$, $p = 0.0020$, for mean and maximum HR respectively).

As regards environmental temperature, the mean annual temperature in the three sectors was ca. 18°C, the maximum between 27 and 28°C and the minimum between 9 and 10°C and there were no significant differences between sectors ($H = 0.06$, $df = 2$, $p = 0.9713$; $H = 0.96$, $df = 2$, $p = 0.6175$ and $H = 1.10$, $df = 2$, $p = 0.5757$ for mean, maximum and minimum environmental temperature respectively). The analysis carried out by season showed there were no significant differences in the mean, maximum and minimum environmental

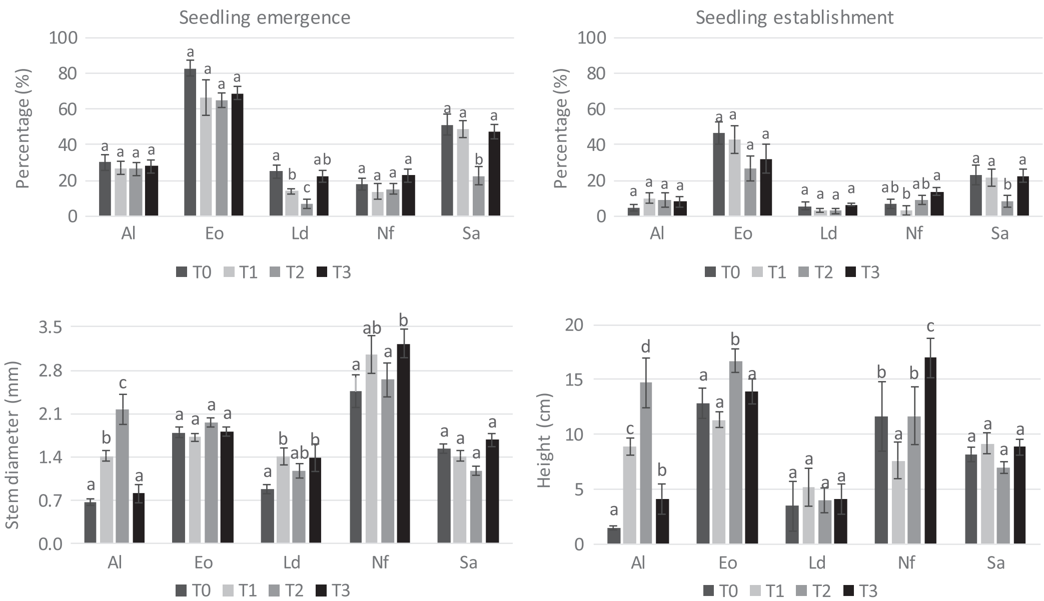

Figure 6. Seedling emergence, seedling establishment, stem diameter and height of established seedlings for five native species of the *Monte* region (Al, *Atriplex lampa*; Eo, *Ephedra ochreata*; Ld, *Larrea divaricata*; Nf, *Neltuma flexuosa*; Sa, *Senna aphylla*) according to treatment (T0, control; T1, hydrogel; T2, hydrogel + AMF enrichment; T3, clay pot irrigation) in the oil-drilling platform. Values represent mean (± SE) of the total live plants at both sites 1 year after sowing. Means with a common letter for the same species are not statistically different ($p > 0.05$).

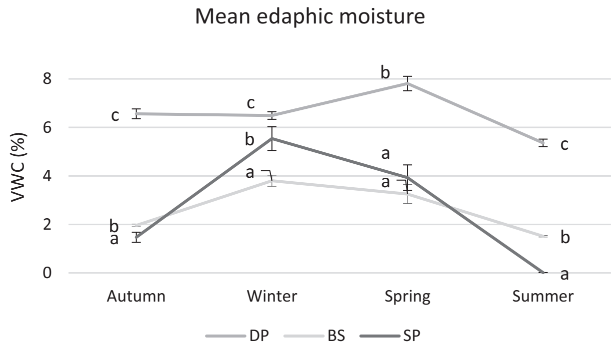

Figure 7. Mean edaphic moisture by season of the year and sector (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches). The values are expressed as volumetric water content (VWC%) and represent the average and ± SE calculated on the daily mean values recorded during 1 year (autumn $n = 92$; winter $n = 93$; spring $n = 91$; summer $n = 90$). Means with a common letter, for the same season, are not significantly different ($p > 0.05$).

Table 2. Annual mean, maximum and minimum edaphic temperatures according to sectors. The values represent the average and the standard error calculated based on the daily mean, maximum and minimum values recorded during 1 year ($n = 366$). Means with a common letter, in the same column, are not significantly different ($p > 0.05$).

	Edaphic temperature (°C)		
Sector	*Mean*	*Maximum*	*Minimum*
DP	19.25 ± 0.49a	28.94 ± 0.62a	11.77 ± 0.37a
SP	19.38 ± 0.50a	29.61 ± 0.80a	12.33 ± 0.35a
BS	19.60 ± 0.52a	30.05 ± 0.80a	11.78 ± 0.33a
	$H(2) = 0.17$, $p = 0.9190$	$H(2) = 0.54$, $p = 0.7625$	$H(2) = 1.52$, $p = 0.4674$

temperatures between sectors (DP, SP, and BS; see Table S3 for statistical outputs).

Treatments Effect on Edaphic Moisture

Annual mean, maximum and minimum soil moisture differed depending on the treatments for the three sectors (see Table 3 for statistical outputs). Higher edaphic moisture was observed for T2 in DP (between 8 and 9%), and BS (between 5 and 6%) while in SP it was higher with T3 (between 9 and 11%) (Table 3).

Discussion

Ex Situ Reference Germination Versus in Situ Emergence

Ex situ germination achieved by *A. lampa* (40.8 ± 3.88%), *E. ochreata* (92.0 ± 2.83%), *N. flexuosa* (98.4 ± 0.98%) and *S. aphylla* (94.4 ± 0.98%) are consistent with previous studies (Paredes et al. 2018; Rodriguez Araujo et al. 2021). For *L. divaricata*, germination percentage (40.8 ± 4.20%) exceeded reported values with the same seed batch, but with different dormancy alleviation treatment (Rodriguez Araujo et al. 2021).

When comparing the in situ and ex situ performances of the species, we observed that most of them had a lower emergence in the field (in situ), compared to the ex situ germination. Similar results were reported by Commander et al. (2019) with direct seeded species for mine rehabilitation, in which the five shrub species evaluated had lower in situ seedling emergence compared to ex situ germination. In the case of *A. lampa*, in situ emergence was lower than ex situ germination only in DP, this could be caused by soil physical–chemical properties that limited the emergence of cotyledons. On the other hand, the typical

Table 3. Mean, minimum and maximum edaphic moisture per treatment (T0: Control, T1: Hydrogel, T2: Hydrogel + AMF enrichment, T3: Clay pot irrigation) according to sector (DP: Oil-drilling platform, SP: Shrubs patches, BS: Bare soil patches). The values are expressed as volumetric water content (VWC%) and represent the average and the standard error calculated based on the daily mean, maximum and minimum values recorded during 1 year ($n = 360$). Means with a common letter, in the same column, are not significantly different ($p > 0.05$).

	Soil water content (%)		
Sector/treatment	*Mean*	*Maximum*	*Minimum*
DP			
T0	6.57 ± 0.12b	7.12 ± 0.14c	6.19 ± 0.11b
T1	5.48 ± 0.12a	5.47 ± 0.14a	5.32 ± 0.12a
T2	8.82 ± 0.17c	9.24 ± 0.21c	8.56 ± 0.17c
T3	5.33 ± 0.17a	5.94 ± 0.21b	4.98 ± 0.17a
	$H(2) = 270.36$, $p < 0.0001$	$H(2) = 257.14$, $p < 0.0001$	$H(2) = 270.96$, $p < 0.0001$
SP			
T0	2.80 ± 0.22a	3.03 ± 0.24a	2.59 ± 0.20a
T1	3.56 ± 0.17b	3.80 ± 0.19b	3.36 ± 0.16b
T2	3.10 ± 0.25a	3.42 ± 0.29a	2.86 ± 0.23a
T3	10.04 ± 0.27c	11.17 ± 0.33c	9.16 ± 0.27c
	$H(2) = 460.73$, $p < 0.0001$	$H(2) = 478.02$, $p < 0.0001$	$H(2) = 426.70$, $p < 0.0001$
BS			
T0	2.67 ± 0.13b	2.92 ± 0.15b	2.48 ± 0.11b
T1	2.73 ± 0.14b	2.99 ± 0.16b	2.53 ± 0.13b
T2	5.40 ± 0.16c	6.02 ± 0.16c	4.98 ± 0.15c
T3	1.78 ± 0.18a	1.98 ± 0.18a	1.66 ± 0.14a
	$H(2) = 403.22$, $p < 0.0001$	$H(2) = 436.15$, $p < 0.0001$	$H(2) = 366.67$, $p < 0.0001$

lower in situ emergence in relation to ex situ germination can be originated by the seeds or seedlings characteristics (Schütz et al. 2002), combined with environmental factors such as soil temperature and moisture, surface resistance of the soil, superficial crusts, and the presence of pathogens (James et al. 2011; Jiménez-Alfaro et al. 2016). In some arid areas of the world such as those of Patagonia, germination references come mostly from laboratory experiments. The results observed in this work alert us about the need to increase germination studies under field conditions, due to their fundamental importance for restoration practitioners.

Direct Seeding Performance in the Three Sectors

The absence of differences in seedling emergence, considering all five species together, regardless of the sectors (DP, SP, BS), can be attributed to the fact that we applied seed dormancy alleviation treatments and performed an initial irrigation in order to promote seed germination. These results are striking for future research and restoration practitioners, given that more degraded areas (totally devoid of vegetation and with highly altered soil) had similar seedling emergence to others whose environmental conditions could be considered more suitable due to the presence of native soil and vegetation.

Higher seedling establishment in abandoned oil-drilling platforms could be explained by the presence of higher edaphic moisture given that water availability is the main factor that controls biological processes in arid environments (Noy-Meir 1973; Golodets et al. 2013). Water retention capacity and thermal conductivity of the filling material in the oil-drilling platform could be the cause of the higher soil moisture, although additional studies are required to evaluate the causes that originate the values recorded. The low water content under the shrubs could be a consequence of an abundant growth of annual species (herbs and grasses, mainly of the exotic genus *Schismus*) with high water requirements (Sandquist et al. 1993; Housman et al. 2003; Rodríguez-Buriticá & Miriti 2009). In the BS, sand accumulation on the soil surface could favor water loss through infiltration. The low establishment percentages in areas degraded by cattle ranching (moderate degradation level in BS and SP), require new experimental evaluations (e.g., soil raking, litter or top-soil addition) in order to increase survival values. This is a complex area of intervention where many competition and facilitation interactions occur (Aguiar & Sala 1994; Bisigato & Bertiller 1999, 2004).

Direct Seeding Performance in the Sector of Highest Seedling Establishment

Seedling emergence in DP ranged from 6.78 to 82.8% depending on the species. *Ephedra ochreata* presented the highest values (64.8–82.8%) which are vastly higher than those achieved by direct seeding of shrubs species in arid or semiarid ecosystems (Abella et al. 2012; DeFalco et al. 2012; Commander et al. 2013). Even *E. ochreata* emergence doubles the highest emergence percentages achieved in arid ecosystems (~35–40% for a grass species, *Triodia pungens*), which required a specific combination of treatments to alleviate dormancy and enhancement technology (Erickson et al. 2017). The highest establishment was also observed for *E. ochreata* (26.8-46.4%), which exceeds the highest reported so far in arid ecosystems for *Hyalis argentea* (22.3%) after direct sowing in *Monte Austral* (Pérez et al. 2019). Although the survival of *E. ochreata* was similar to that of *N. flexuosa* and *S. aphylla* (>40%), its greater establishment is due to a higher in situ emergence. This shows that seedling emergence is the limiting stage for the recruitment for *N. flexuosa* and *S. aphylla* and that the three species have similar capacities to survive after field emergence has occurred. This coincides with what has been reported for shrub species of arid lands of Western Australia (Commander et al. 2019). Meanwhile, *A. lampa* presents a limitation in seedlings survival but not in seedling emergence, since its emergence was higher than *N. flexuosa* but it had a lower survival of the emerged seedlings. *Larrea divaricata* presented the lowest establishment percentage, due to a reduced in situ emergence and survival of seedlings. It is possible that its emergence and establishment require very particular soil conditions, as stated by Abella and Newton (2009) for *Larrea tridentata*, a similar species from the Sonoran Desert of the United States.

The large differences in seedling emergence and establishment according to species highlights the need to advance in the knowledge of species selection for direct seeding in arid land restoration. This can improve the ethical use of seeds by omitting unfavorable species in a given restoration substrate before seeding as proposed by Cross (2021).

We found no effect of the treatments for increasing seedling emergence or establishment. However, some species showed a higher growth depending on the treatment. There was a positive effect in seedling growth with hydrogel and mycorrhizae enrichment (T2) for *A. lampa* (SD and H) and *E ochreata* (H) and with clay pot irrigation (T3) for *N. flexuosa*. Root colonization with AMF has been described for *A. lampa* and for other *Ephedra* species from *Monte* but not specifically for *E. ochreata* (Fracchia et al. 2011; Soteras et al. 2013; Lugo et al. 2015). Further studies are required in order to determine if seedlings were effectively colonized by AMF and if these microorganisms are present in native soil without treatment. Also, the higher edaphic moisture content of the T2 treatment in DP could be related to the bigger size of *A. lampa* and *E. ochreata* seedlings. In the case of *N. flexuosa*, seedlings had larger stem diameter and greater height in the clay plot irrigation treatment. This may imply that this species is able to take advantage of the water supplied by clay pots. However, a substantial increase in costs and alternative irrigation methods should be considered.

Treatments Effects on Edaphic Moisture

In abandon oil-drilling platforms and bare soils, the treatment with hydrogel and mycorrhizae (T2) presented the highest edaphic moisture. The hydrogel treatment (T1) did not differ from the control (T0) in any of the three sectors. The complex relationship of hydrogel and soils, and the dose of hydrogel could explain why this treatment did not improve the water content of the soil (Al-Harbi et al. 1997; Mangold & Sheley 2007).

As regards clay pot irrigation (T3), the highest soil moisture with this treatment in shrub patches compared to oil- drilling platforms and bare soils could be due to the fact that vegetation cover prevented water evaporation through the mouth of the pot (Vasudevan et al. 2011).

Final Considerations

Even though our results were obtained from experimental scale and under some controlled field conditions (herbivory and granivory), direct seeding for restoring severely degraded sites in arid lands appears as a promising strategy. Nucleation seeding with high seeding densities and with different plant species could be a viable option to restore vegetation patches which are characteristic of these ecosystems, instead of seeding widespread areas. Climatic variability must be careful considered during planning and results evaluation in future research of direct seeding, since results could vary with different patterns of rainfall. Additionally, this study highlights the importance of prospecting species from the ecological reference, since previously unstudied species, such as *E. ochreata*, can provide promising results. More similar studies are needed in order to assess species performance and selection of framework species for restore degraded arid lands. In addition to species selection, seeding density and soil treatments, some issues as seed quality and herbivory protection pose challenges for scaling-up direct seeding. Therefore, international collaboration and knowledge sharing are essential to develop strategies that enable scaling-up restoration in several arid lands of the world.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Biplot showing the clustering of species and treatments (Al, *Atriplex lampa*; Eo, *Ephedra ochreata*; Ld, *Larrea divaricata*; Nf, *Neltuma flexuosa*; Sa, *Senna aphylla*; T0, control; T1, hydrogel; T2, hydrogel + AMF enrichment; T3, clay-pot irrigation) on PC 1 (circles with solid lines) and PC 2 (circles with dotted lines) according to the variables studied (%Em, percentage of emergence; %Es, percentage of establishment; SD, stem diameter; *H*, height; S1, site 1; S2, site 2).

Table S1. Annual mean, maximum and minimum edaphic moisture per season according to sectors (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches).

Table S2. Annual mean, maximum and minimum edaphic temperature per season according to sectors (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches).

Table S3. Annual mean, maximum and minimum environmental temperature per season according to sectors (BS, bare soil patches; DP, oil-drilling platforms; SP, shrubs patches).

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