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A new approach for restoring tropical dry forests: Using local shrubs as nurse plants to improve the recruitment of *Tara spinosa* in Lomas de Atiquipa (Andean Region, Perú)

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ABSTRACT

Tropical dry forests are among the most threatened ecosystems worldwide, with severe deforestation and regeneration problems compounded by an increasing climate change threat. Lomas de Atiquipa in the Peruvian–Chilean Coastal Desert (Atacama Desert) comprises one of these formations, mainly dominated by the Tara tree (*Tara spinosa*), which is a Neotropical legume tree with high ecological and commercial value. However, approximately 80% of the original area has been reduced mainly by deforestation. An ecological restoration experience was demonstrated in this study by investigating the use of thorny shrubs as nurse plants to promote forest regeneration. This approach is based on the idea of facilitation between plants and can be a suitable “nature-based solution” to decrease reforestation costs. Accordingly, 170 seedlings and 128 seeds of Tara were installed in two contrasting environments: 1) under the cover of the nurse plant and 2) outside the vegetation cover. Survival rates of the seedlings and germinated seeds were periodically monitored from August to December. We also measured microclimatic conditions outside and under the canopy of the nurse plant, including temperature (°C), relative humidity (%), soil moisture (v:v), and illumination (lux), to assess the recruitment niche. Our results showed the highest seedling survival rates at the end of the experiment under the canopy of the nurse plant (22.4%) vs. outside (8.2%). This could be linked to the better performance of juvenile plants owing to the nursing effect of shrubs, as we detected a significant reduction in the extreme environmental conditions under the canopy of the nurse plant, with the lowest temperatures and highest humidity, as well as a significant reduction in light incidence. Our findings suggest that using local shrubs as nurse plants is a promising method for restoring Tara in the Lomas ecosystem because it reduces the stress of direct insolation and high temperatures and reduces the cost and effort of hand watering the seedlings after planting.

1. Introduction

Dry tropical forests are among the most threatened ecosystems worldwide (Cordero et al., 2016; Miles et al., 2006; Siyum, 2020).

Abbreviations: PCA, principal component analysis; GLM, generalised linear model.

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This ecosystem structure is a mosaic of disturbed open canopies and relatively undisturbed closed canopy patches at several spatial scales (Khurana and Singh, 2001). Most dry tropical forests are typically influenced by severe deforestation and regeneration problems (Portillo-Quintero and Sánchez-Azofeifa, 2010). This forest degradation in tropical dry forests is because of unsustainable management regimes (Quesada et al., 2009), over-exploitation of species with commercial value (Lopez-Toledo et al., 2011), and the loss of suitable areas due to climatic constraints (Suresh et al., 2010). Approximately 54.2% of the tropical dry forested area is located in South America (Miles et al., 2006). In Latin America, 66% of this ecosystem type has already been converted to other land uses, whereas 95% has been lost in Peru (Portillo-Quintero and Sánchez-Azofeifa, 2010), additional problem, the rising temperature and increased droughts decrease the survival of trees and seedlings in tropical dry forests (Meir and Pennington, 2011; Young et al., 2011). Therefore, understanding both forest management and climatic constraints (present and future) is particularly important to recover the functionality of this ecosystem (Manchego et al., 2017) and reduce failure in restoration projects.

On the Pacific Coast adjacent to the Peruvian–Chilean Coastal Desert (Atacama Desert) there is a typical tropical dry forest, a seasonal fog forest, locally called "fog oasis" or "Lomas" (Balaguer et al., 2011). "Lomas" vegetation develops on hill slopes facing the sea and is maintained by fog from wet oceanic winds (Péfaur, 1982; Tovar et al., 2018). When intercepted by the canopy of trees, this fog produces the main water contribution to the ecosystem (Jiménez et al., 1999).

The ecosystem of "Lomas de Atiquipa" is dominated by herbaceous communities of plants but includes fragmented forest, primarily characterised by the presence of *Tara spinosa* trees, a neotropical legume that ranges from Venezuela to northern Chile (de la Cruz, 2004; Martel et al., 2014). This forest has undergone an intense deforestation process, as a result only one-tenth of the original forest area remains (Balaguer et al., 2011; Manrique, 2011).

In Peru, this species is present across a broad altitudinal range (0–3000 m), extending from coastal areas to the Andean region (Aronson, 1990; Brako and Zarucchi, 1993). Since pre-Columbian times, Tara has been highly valued for its multiple non-timber uses, such as dyes, tannins, gums, and oils obtained from its seeds (Villanueva, 2007). From an ecological perspective, the value of Tara trees in "Lomas" ecosystems lies in their ability to intercept fog droplets, increase the water input into the soil (Balaguer et al., 2011), and fix nitrogen (Cordero et al., 2017). High soil water content and fertility facilitate vegetation cover and prevent runoff and soil erosion and thus provides valuable ecosystem services for the local communities.

Local stakeholders have recently initiated various forest management projects to conserve ecosystem services and expand the forested areas on these hills (PER/01/G35, TNC-UNSA-Finland Government; Sotomayor and Jiménez, 2008). In dry ecosystems, water shortages negatively affect many physiological and morphological parameters, hindering plant survival, growth, and/or fitness (McDowell et al., 2008). Therefore, common reforestation techniques require periodic watering during the early stages of development to ensure the success of forest plantations. Furthermore, in a previous study, we found that the water supply for Tara seedlings resulted in better performance in the field (Balaguer et al., 2011) and under controlled conditions (Cordero et al., 2021). Nevertheless, in "Lomas," the only human-assisted water source for planted seedlings originates from fog collectors (Tognetti, 2015), where water is directed to irrigation reservoirs, and the local communities are responsible for watering by hand (Fig. S1). Therefore, as both labour and maintenance costs are high, it seems appropriate to propose new techniques derived from ecological restoration (SER, 2004), which are based on facilitating the ecosystem to recover with minimal human intervention and emulating natural patterns and processes (Balaguer et al., 2014), according to the "nature-based solutions" approach (Seddon et al., 2020).

The use of shrubs as nurse plants is based on the concept of facilitation between plants. Facilitation refers to the positive influence of an adult plant on the recruitment of other species (Gómez-Aparicio et al., 2004). Several mechanisms can be implicated in this positive relationship, including the amelioration of extreme environmental conditions, reduction of herbivory (Gómez-Aparicio, 2009), and improvement of soil quality (Mihoč et al., 2016). This approach has provided good results for Mediterranean and arid environments (Castro et al., 2002; Gómez-Aparicio et al., 2004; Gómez-Aparicio, 2009), as well as in high Andean forests (Gómez-Ruiz et al., 2013) and high elevation montane coniferous forest (Carbajal-Navarro et al., 2019).

In a previous study at the same location, we detected an aggregated pattern between young individuals of Tara and both conspecific adults and adult thorny shrubs (*Citharexylum flexuosum* and *Randia rotundifolia*), which we interpreted as potential nurse plant effect (Cordero et al., 2016). Moreover, for Tara seedlings, we observed that photoprotection under drought stress is a functional mechanism to prevent photooxidative damage by excess light and, consequently, improve carbon assimilation and growth (Cordero et al., 2021). Based on these findings, in this study, we present the results of an experiment conducted under field conditions for the improvement of Tara recruitment through ecological restoration.

This study aimed to explore the possible effects of native shrubs present in the study area on the survival of Tara seeds and seedlings. We hypothesised increased successful recruitment under shrubs due to the microclimatic conditions under their canopy. Specifically, a reduction of the extreme conditions of high temperature and radiation can benefit Tara seedlings because they diminish the evaporative demand and avoids photodamage (Cordero et al., 2021). Therefore, we expected to observe a positive effect on the early establishment of plants. Finally, we provide some recommendations for restoration practices.

2. Materials and methods

2.1. Study area

The study site was at "Lomas de Atiquipa" (15°47'43.66" S, 74°21'48.20" W; 300–1200 m a.s.l.), Department of Arequipa, southwest Peru, on the western slopes of the Peruvian Andes. The entire "Lomas" ecosystem has an area of approximately 28,000 ha, and it is probably the greatest extension of this type of ecosystem on the Peruvian coast (Canziani and Mujica, 1997). Vegetation is dominated by annual plants (*Alternanthera ferreyrae, Grindelia tarapacana, Nicotiana paniculata*) and shrubs (*Cytharexylum flexuosum,* *Duranta armata, Randia rotundifolia*). However, the current extension of forested Lomas is 2190 ha, dominated by the Tara tree (*Tara spinosa*).

Soils are acidic (pH 4.88–5.09) and poor in nutrients (% C = 0.97 ± 0.39; % N = 0.11 ± 0.05), according to data reported by Balaguer et al. (2011).

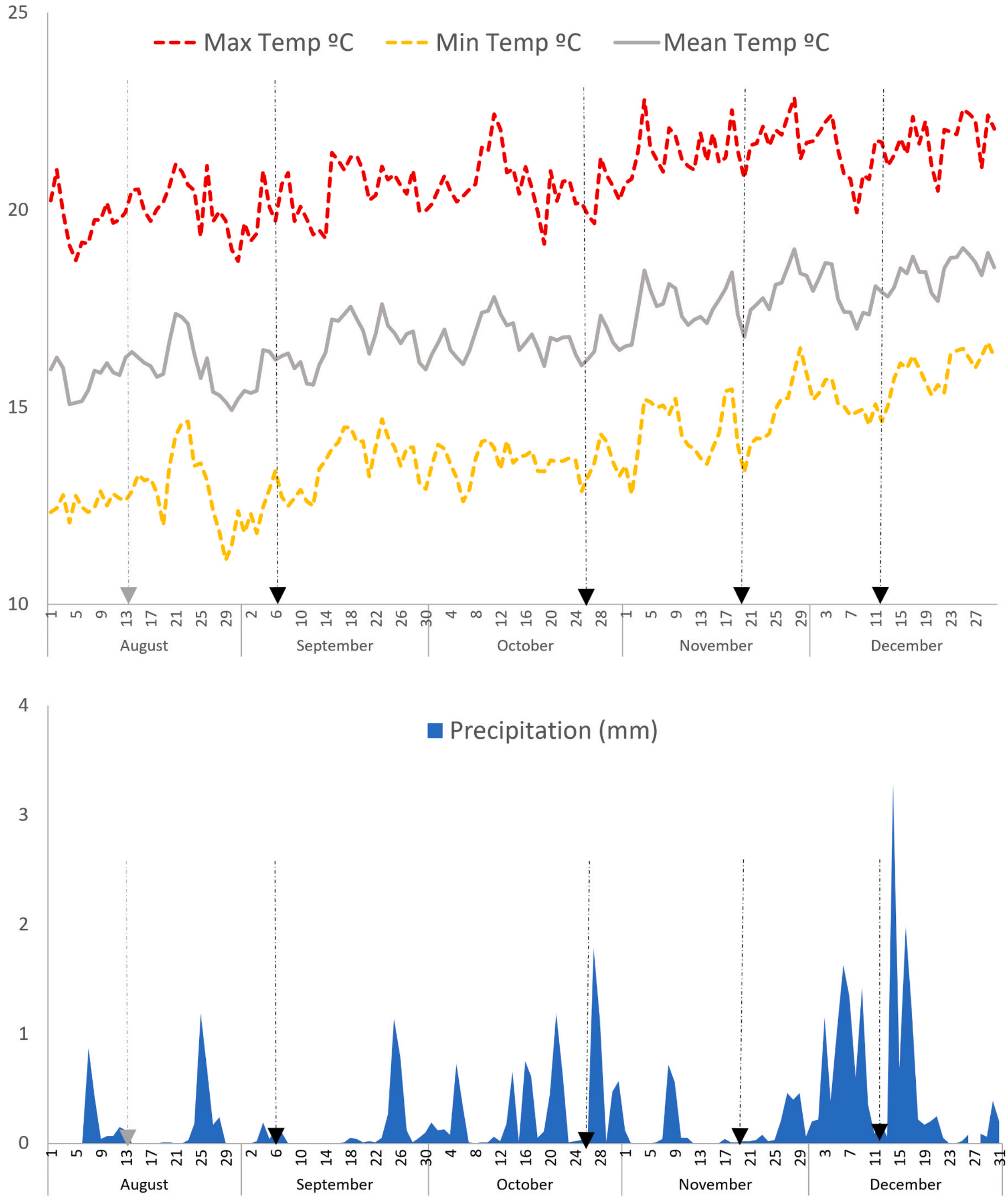

Fig. 1. Local climatic conditions from August to December 2016. Planting and sowing were on 13 Aug (grey arrow). Black arrows (from September onwards) show the four dates (6 Sep; 26 Oct, 20 Nov, 13 Dec) of the survival evaluation for seeds and seedlings of Tara. The top figure represents the temperature measured at 2 m above the Earth's surface in Celsius (°C): Maximum temperature (red dotted line), mean temperature (solid grey line), and minimum temperature (yellow dotted line). The figure below is the accumulated precipitation in millimetres (mm). Data were obtained from the application POWER Data Access Viewer (DAV), which provides geospatial information and meteorology parameters (https://power.larc.nasa.gov/data-access-viewer/).

The climatic conditions are extremely harsh, and according to Sotomayor and Jiménez (2008), there are two well-marked seasons: 1) The dry season (January–June), without precipitation, but having a water influx by fog of 8.35 $l\ m^{-2}\ day^{-1}$ and temperature values of 16.85 °C, and 2) the wet season (July–December), with peaks of precipitation in September (24.9 mm), mean temperature of 12.8 °C and an average water contribution by fogs of 40.9 $l\ m^{-2}\ day^{-1}$. In this type of ecosystem, fog trapped by vegetation is the main source of water influx.

Tara seeds germinate during the wet season under natural conditions; therefore, we performed the experiment according to their natural phenology. The local climatic conditions during the study period are shown in Fig. 1 and were obtained from the NASA Langley Research Center (LaRC) POWER Project funded by the NASA Earth Science/Applied Science Program (NASA, 2020).

2.2. Species description

Tara spinosa is a valuable neotropical legume belonging to the Caesalpinia group, a large clade of 205 species in the subfamily Caesalpinioideae, comprising 26 genera (Gagnon et al., 2016). The cpDNA haplotypes along the entire distribution rank inside Peru shows reduced genetic variability, probably because of human activities from pre-Columbian times (Balaguer et al., 2011). At "Lomas," it is the only dominant tree in the ecosystem despite showing poor natural seedling recruitment (Cordero et al., 2016). The stand structure in the forest remnant has a very low density of saplings (1–10 cm diameter; 20.1 individuals ha^{-1}) and a density of adults of 172.22 individuals ha^{-1} in the study area (Cordero et al., 2016).

The selected nurse plants were as follows: 1) *Citharexylum flexuosum* (Ruiz & Pav.), and 2) *Randia rotundifolia* (Ruiz & Pav.). Both species are tropical perennial thorny shrubs. These species are abundant and naturally occur alongside *T. spinosa* in the "Lomas de Atiquipa" (Talavera et al., 2017), and have a wide distribution throughout the coastal "Lomas" ecosystems in Peru (Galán de Mera et al., 2009). In the "Loma de Atiquipa," both shrubs do not reach a substantial height (0.5–1.20 m), and the coverage of its crown is variable, depending on the stage of development of the plant (0.5–2 m crown diameter). *Citharexylum flexuosum* (Ruiz & Pav.) D. Don belongs to the Verbenaceae family, and the taxonomy of the *Citharexylum* genus was recently revised by Frost et al. (2021). *Randia rotundifolia* (Ruiz & Pav.) belongs to the Rubiaceae family, and its phylogenetic and morphological traits are detailed in Gustafsson and Persson (2002).

2.3. Experimental design

2.3.1. Seedlings and seeds

The selected seeds for planting in the field were chemically scarified (96% H_2SO_4, 45 min) and soaked in distilled water for 48 h (Cordero et al., 2021), and the pre-germinated seeds (showing an incipient radicle) were sown in 250 mL containers filled with substrate composed of black peat moss (PRO MIX®) and vermiculite 3:1 (v:v) supplemented with Osmocote (NPK 11:11:18) and microelements. All seedlings were grown for two months in a greenhouse at Universidad Nacional de San Agustín de Arequipa (UNSA, Perú) and maintained under semi-controlled conditions (well-watered by drip-irrigation, mean temperature of 15 ± 5 °C, and relative humidity 50 ± 10%). Seedlings were grown until they acquired an adequate size for planting (7–10 cm, according to prior experience), the leaves were fully expanded, and the root system was well-formed for transplanting in the field. Only 170 seedlings were selected for planting in the field experiment because we selected seedlings of similar size, number of leaves, and well-formed root systems.

Seeds selected for direct sowing in the field were stored in darkness under constant temperature conditions in a cold chamber at 5 °C. They remained in this environment for 10 days before being scarified, as described above. Only stored seeds of similar size and showing an incipient radicle (of similar size) were planted. Therefore, only 128 seeds were considered for sowing in the field experiment.

2.3.2. Field experiment

During August 2016 (day 13, Fig. 1), an experiment was conducted in the Huayahuani area, in the Tara forest of "Lomas de Atiquipa". We selected an experimental plot of 1.35 ha (450 × 30 m) located on the windward side of the hills where the selected nurse plant species were present (*C. flexuosum* and *R. rotundifolia*). We considered two transects separated by 20 m to conduct the plantation and direct seeding of Tara. A total of 170 seedlings of similar size and 128 seeds were sowed according to the following design: on the plots with nurse plant treatment, seedlings and seeds were planted and sowed, respectively, under the canopy protection of the shrubs (at a point equidistant between the stems and the outer boundary of the crown, always on the windward side). On the plots outside the nurse plant, seedlings and seeds were placed in the centre of areas without shrub cover (with an extension of approximately 5 m^2) ensuring they were at a minimum distance of 1 m from the canopy of nearby bushes. Regardless of their treatment, distances between successive seeds or seedlings in the transect were between 4 and 6 m. Each seed was buried (2 cm depth) inside a 5 ×5 cm plastic mesh bag (mesh size 2.5 mm) to prevent predation (James and Rahman, 2000). Seeds and seedlings were assigned to the treatment site (outside or under the canopy of the nurse plant), and their spatial arrangement in the field was randomly distributed.

Both the seeds and seedlings were irrigated with 100 mL of water once at the onset of the experiment, as recommended for arid environment. Planted tree seedlings, in arid environment, are very sensitive to drought stress and mortality until roots are established in ambient soil (Dalton, 1992). Each seed and seedling was marked for its subsequent location, and its geographical location was recorded using a GPS device (Garmin GPSMAP 60 Series). The survival of all individuals was monitored four times during the early stages, from September to December (dates are shown in Fig. 1). To determine the vital status of the planted seedlings, we considered an individual dead if all leaves and buds were dry, the stem was broken, or the individual was absent. Seeds were considered alive if they had emerged from the ground and dead if they never emerged or if they met any of the conditions for dead seedlings.

2.3.3. Microclimatic conditions

At the time of sowing and planting and for subsequent visits for survival, microclimatic conditions were characterised by the proximity of seeds and seedlings. Air temperature (°C), relative humidity (% RH), soil moisture (TDR 100 Spectrum Technologies), and illumination (lux) were measured.

2.4. Statistical analyses

All statistical analyses were carried out using IBM SPSS Statistics v.27. To model the effect of nurse plants over all four months, survival analyses were performed using the non-parametric Kaplan–Meier method. We compared the survivorship curves across the different treatments (seeds under the canopy, seeds outside, seedlings under the canopy, and seedlings outside). In addition, we analysed survival outside and under the canopy of the nurses for each month (from September to December) using generalised linear models (GLM) with a binomial response variable (alive = 1; dead = 0) and a logit link function. We considered a saturated model with two factors: site (outside vs. under the canopy of the nurse plant), type of propagule (seeds vs. seedlings), and their interactions. Supplementary analyses were conducted by separating the seed and seedling data.

To characterise the microclimatic conditions (air temperature, relative humidity, soil moisture, and radiation) outside and under the canopy of the nurse plant, a repeated measures ANOVA was carried out (site as a fixed factor and date as a repeated factor) after checking the ANOVA assumptions. Additionally, the post hoc Fisher's PLSD test was conducted to assess the differences between sites on each date.

Finally, we aimed to incorporate the possible effect of the microclimate linked to the effects of nurses on the early survival of seeds or seedlings. Accordingly, principal component analysis (PCA) (Table S3) with all microclimatic variables (temperature and relative humidity of the air, illumination, and soil moisture) was conducted. The principal component (microclimatic component; MC factor) was incorporated as a covariate into the GLM models for each date. Total survival was used as the dependent variable, and site was used as a factor, also considering the interaction between site and the MC factor.

3. Results

The Kaplan–Meier analysis results showed differences in survival among treatments ($\chi^2 = 31.6, p < 0.001$). For example, at 25 days, 50% of seedlings were still alive, whereas < 25% of seeds were alive at that time. Eventually, survival was higher for seedlings planted under the canopy of the nurse plant, with 25% survival after 4 months. When analysed in each recorded period, the survival of seeds and seedlings differed (Fig. 2; GLM results in Table S1). We detected high seedling survival; in most cases, seedling survival was double the seed survival rate. For example, we observed that in September, 50% of the seedlings were alive, compared to 16% of the seeds. The GLM model also detected a "site" effect on the last seedling survival in December ($p = 0.012$) and marginally significant values ($p = 0.07$) in October and November (Table S1), showing higher survival under the canopy of the nurse plant than outside, from October onwards. In terms of the survival of planted seedlings, the positive effect on survival was significant in both October ($p = 0.044$) and December ($p = 0.014$) and marginally significant in November (Table S2).

The microclimatic conditions measured in the field during the study are shown in Fig. 3. The average temperature was 25 °C (minimum of 19 °C, maximum of 39 °C), the relative humidity throughout the experiment was, on average, 54% (ranging from 23% to 99%), and the soil water content fluctuated between 10% and 58%. In November, we measured the highest values for temperatures (29.94 ± 4 °C) and radiation (51,251 ± 46,164 lx) and the lowest for relative humidity (38.8 ± 8%) and soil water content (21.36 ± 5%). These values are consistent with the regional climatic conditions reported in November because in the days prior to field survival in November, temperatures were high, and rainfall was very scarce (Fig. 1).

Finally, when considering the combined effect of microclimatic conditions (MC factor as a covariate, Table 1) on total survival in

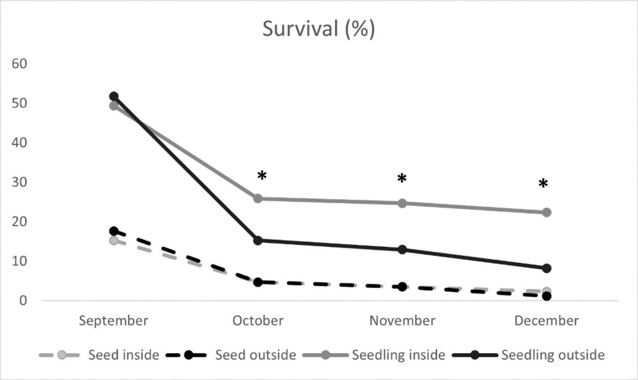

Fig. 2. Tara seedlings and seeds survival percentage across the months outside (black lines) and under the canopy of the nurse plants (grey lines). The GLM whole model results show significant differences between seeds and seedlings ($p_{type\ effect} < 0.005$; Table S1). Survival differences outside *vs.* under the canopy of the nurse plant for planted seedlings are marked by an asterisk ($p_{site\ effect} < 0.05$; Table S2).

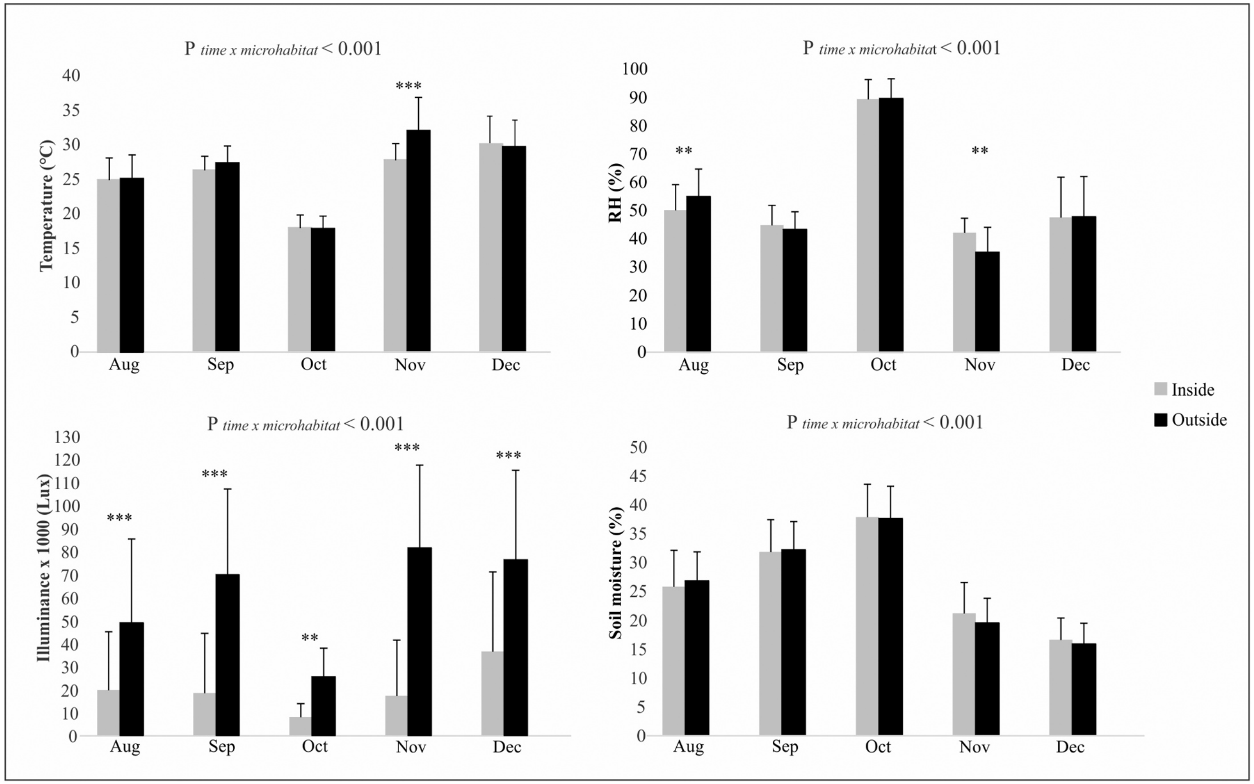

Fig. 3. Microclimatic conditions (means ± S.D.) outside (black) and under the canopy of the nurse plants (grey) during the experiment ($p_{date \times site} < 0.001$). Significant differences between sites are marked by an asterisk (post-hoc Fisher's PLSD test $p < 0.05$).

each recording period, we observed that differences due to site ($p_{site\ effect} < 0.05$; Fig. 2) could be partially explained by the covariable (MC factor) in November (Table 1). The rest of the selected models by AIC values reflects that the interaction between microclimatic conditions and site effects should be considered.

4. Discussion

This study ascertained that using local shrubs as nurse plants can improve the early establishment and survival of Tara seedlings. However, the causes have not been clearly determined. We hypothesised that higher seedling survival rates under the shrub canopies could be due to mitigation of environmental stressors such as radiation and temperature. Nevertheless, support for this hypothesis is limited since significant microclimatic differences (soil moisture, temperature, and radiation) were only found in November. For the rest of the dates, survival is explained by the combined effect of microclimate and site. Therefore, other facilitation processes such as herbivory protection should also be considered. Despite these challenges, findings suggest that plant facilitation could play a crucial role in the regeneration of the Tara forest, particularly in the singular ecosystem of Lomas within tropical dry forests. Our results are consistent with those of previous studies that reported facilitation effects in other ecosystem types, such as semiarid and tropical systems (Gómez-Aparicio, 2009; Gómez-Ruiz et al., 2013; Lu et al., 2016).

In the present study, we detected a positive effect of nurse plants on the percentage of seedling survival and partial support for the modulation by the microclimatic component This effect may be due to the alleviation of radiation, temperature and relative humidity in November, the month when we detected higher radiation and temperature values and lower relative air humidity as shown in Figs. 1 and 3. Accordingly, during this month, the shading effect of the canopy on seedlings may turned into a net benefit for their survival, as shading reduced the evaporative demand (Franco and Nobel, 1988, 1989) and prevented photodamage during the early stages of plant recruitment. Previous studies have suggested that the amelioration of microclimatic conditions by thorny bush canopies is relevant for explaining the increased survival of seedlings beneath nurse plants in Mediterranean ecosystems (Castro et al., 2002; Marañón et al., 2004) as well as the Andean region of Chile (Cavieres et al., 2007). Furthermore, in this ecosystem type, where the main water input into the soil occurs by the interception of fog by leaves and branches of trees and bushes during wet seasons, living under shrubs can be an additional factor favouring the microclimatic conditions for seedling survival by drop interception, even if it occurs only during short periods during fog events, which can be decisive for seedling recruitment (Khurana and Singh, 2001).

The mechanisms underlying this improved survival under the canopy of the nurse plants may be related to the capacity to withstand prolonged water stress by physiological adjustments at the leaf level (Kozlowski and Pallardy, 2002). For example, osmotic adjustment ensures leaf turgor and, consequently, leaf functionality through better stomatal control (Binks et al., 2016; Jiménez et al., 2009). Different acclimation responses to drought have been described in Tara seedlings (Balaguer et al., 2011; Cordero et al., 2021). However, prolonged, and severe water stress can compromise physiological adjustments and hinder plant survival and growth (Binks et al., 2016; Hessini et al., 2009; McDowell et al., 2008). Therefore, irrigation is a common afforestation practice that ensures seedling survival and growth in the early stages after planting. In a previous study on a reforested Tara stand where local communities periodically hand-watered Tara seedlings, we observed that irrigated seedlings exhibited better field performance (an increment of 126% height, 121% crown width and 200% number of leaves, Balaguer et al., 2011). However, the only human-assisted water source was the fog collectors, which were previously installed. Harvested water is conducted towards and accumulates in reservoirs, forming a complex irrigation system that requires continuous maintenance (Tognetti, 2015; Fig. S1). Although irrigation enhances seedling survival in the field, it significantly increases the cost of reforestation (Benayas, 1998). Therefore, the use of nurse plants can decrease both radiation stress and evaporative demand, thereby reducing the costs of installing artificial irrigation and shading.

On the other hand, our results showed that planted Tara seedlings had a higher survival rate than those germinated from seeds, with seedling survival doubling in most cases. The transition from the seed to the seedling stage can have critical effects on recruitment

Table 1

Results of the three GLM models considered to elucidate seedling survival across each sampling date are presented. The entire microclimatic effect was summarised in a new component extracted by PCA (MC factor, Table S3) and incorporated into the models. In Model I, Site, MC component, and their interaction are considered as fixed factors. The interaction was removed for Model II, while only the MC component was maintained for Model III. Models with lower Akaike information criterion calculated (AICc) values were selected and marked in bold.

		September			October			November			December		
		Wald Stat.	***p***	***AICc***	***Wald Stat.***	***p***	***AICc***	***Wald Stat.***	***p***	***AICc***	***Wald Stat.***	***p***	***AICc***
Model I	Site	**1.436**	**0.231**	**229.885**	**4.200**	**0.040**	**179.077**	0.725	0.395	161.056	**5.457**	**0.019**	**135.279**
	MC factor	**5.412**	**0.020**		**0.373**	**0.541**		2.947	0.086		**6.286**	**0.012**	
	Site × MC factor	**6.979**	**0.008**		**2.726**	**0.099**		1.106	0.293		**1.757**	**0.185**	
Model II	Site	1.450	0.229	235.339	3.725	0.054	179.935	0.091	0.763	160.040	8.013	0.005	135.582
	MC factor	6.013	0.014		0.108	0.742		6.230	0.013		7.640	0.006	
Model III	MC factor	4.771	0.029	234.735	0.472	0.492	181.719	**8.515**	**0.004**	**158.059**	5.835	0.016	142.59

success (Postma and Ågren, 2016; Rother et al., 2013). The seedlings used in this study were cultivated under semi-controlled conditions in a greenhouse at the UNSA University facilities and then transplanted into a field with fully expanded leaves and developed primary root systems. The ontogenetic state of seedlings, their size, and the presence of fully developed leaves are traits that enhance field performance (Andivia et al., 2021; Ostertag et al., 2015), especially in degraded areas with microclimatic stress, such as low availability of soil nutrients and water content (Gallo et al., 2017), which are common in tropical dry forest ecosystems (Ceccon et al., 2006) and which were predominant in our study area. Plants exhibit a coordinated leaf-level response to cope with light and water stress (Reddy et al., 2004). For example, in a previous study, we described how Tara seedlings exhibited a rapid response to drought stress by reducing stomatal conductance and evapotranspiration and to light stress by increasing structural (leaflet angle) and chemical photoprotection (pigments related to thermal dissipation; Cordero et al., 2021). Therefore, our results support the use of seedling planting for Tara rather than the direct sowing of seeds in the field, as it ensures leaf-level adjustments to cope with stress.

5. Conclusions and management implications

In the present study, we found partial evidence for a net positive effect on overall survival at the early stages of Tara seedlings through a facilitating effect of shrubs on Tara, which overcame both biotic and abiotic filters (Hobbs and Norton, 2004). These findings agree with those of previous studies that recommended the use of shrubs as nursing plants to improve the early establishment of woody seedlings under stress conditions (Gómez-Aparicio et al., 2004, 2005; Khurana and Singh, 2001; Marañón et al., 2004; Miller, 1995). Furthermore, considering the predicted scenarios under global warming for South America by the IPCC, where the mean daily temperature and consecutive numbers of dry days (precipitation < 1 mm) will increase (Pörtner et al., 2022), the ability of these forests to regenerate naturally could be compromised. Therefore, we propose using shrubs as nurse plants to restore Tara trees in tropical dry forests by improving the microclimatic conditions in their recruitment niche, thereby promoting ecosystem recovery (Aronson et al., 2006) through "nature-based solutions" (Seddon et al., 2020). Restoration methods based on natural processes, such as the use of shrubs as nurse plants, have the potential to reduce operational costs and minimise the risk of plant failure (Marañón et al., 2004).

CRediT authorship contribution statement

María_Dolores Jiménez: Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luis N Villegas-Paredes:** Resources, Methodology, Investigation, Funding acquisition. **Juan Antonio Delgado:** Writing – original draft, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **G. Anthony Pauca-Tanco:** Methodology, Data curation. **Cesar R. Luque-Fernández:** Software, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03004.

References

Andivia, E., Villar-Salvador, P., Oliet, J.A., Puértolas, J., Dumroese, R.K., Ivetić, V., Molina-Venegas, R., Arellano, E.C., Li, G., Ovalle, J.F., 2021. Climate and species stress resistance modulate the higher survival of large seedlings in forest restorations worldwide. Ecol. Appl. 31, e02394 https://doi.org/10.1002/eap.2394.

Aronson, J., 1990. Desert plants of use and charm from northern Chile. Desert Plants 10, 65–86.

Aronson, J., Clewell, A.F., Blignaut, J.N., Milton, S.J., 2006. Ecological restoration: A new frontier for nature conservation and economics. J. Nat. Conserv. 14, 135–139. https://doi.org/10.1016/j.jnc.2006.05.005.

Balaguer, L., Arroyo-García, R., Jiménez, P., Jiménez, M.D., Villegas, L., Cordero, I., Rubio de Casas, R., Fernández-Delgado, R., Ron, M.E., Manrique, E., Vargas, P., Cano, E., Pueyo, J.J., Aronson, J., 2011. Forest restoration in a fog oasis: evidence indicates need for cultural awareness in constructing the reference. PLoS ONE 6, e23004. https://doi.org/10.1371/journal.pone.0023004.

Balaguer, L., Escudero, A., Martín-Duque, J.F., Mola, I., Aronson, J., 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. Biol. Conserv. 176, 12–20. https://doi.org/10.1016/j.biocon.2014.05.007.

Benayas, J.M.R., 1998. Growth and survival in *Quercus ilex* L. seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural land. Ann. . Sci. 55, 801–807. https://doi.org/10.1051/forest:19980704.

Binks, O., Meir, P., Rowland, L., da Costa, A.C.L., Vasconcelos, S.S., de Oliveira, A.A.R., Ferreira, L., Mencuccini, M., 2016. Limited acclimation in leaf anatomy to experimental drought in tropical rainforest trees. Tree Physiol. 36, 1550–1561. https://doi.org/10.1093/treephys/tpw078.

Brako, L., Zarucchi, J., 1993. Catálogo de las Angiospermas y Gimnospermas del Perú. Monogr. Syst. Bot. Mo. Bot. Gard. Vol 45.

Canziani, J., Mujica, E., 1997. Atiquipa: un caso prehispánico de manejo sustentable en ecología de Lomas. En: E. In: González, E., Revesz, B., Tapia, A. (Eds.), Perú: El problema agrario en debate. Seminario Permanente e Investigación Agraria VI. Lima-Perú, Páginas, pp. 503–526.

Carbajal-Navarro, A., Navarro-Miranda, E., Blanco-García, A., Cruzado-Vargas, A.L., Gómez-Pineda, E., Zamora-Sánchez, C., et al., 2019. Ecological restoration of Abies religiosa forests using nurse plants and assisted migration in the Monarch Butterfly Biosphere Reserve, Mexico. Front. Ecol. Evol. 7, 421. https://doi.org/10.3389/fevo.2019.00421.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2002. Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. Restor. Ecol. 10, 297–305. https://doi.org/10.1046/j.1526-100X.2002.01022.x.

Cavieres, L.A., Badano, E.I., Sierra-Almeida, A., Molina Montenegro, M., 2007. Microclimatic modifications of cushion plants and their consequences for seedlings survival of native and non-native plants in the high-Andes of central Chile. Arct. Antarct. Alp. Res. 39, 229–236. https://doi.org/10.1657/1523-0430(2007)39[229:MMOCPA]2.0.CO;2.

Ceccon, E., Huante, P., Rincón, E., 2006. Abiotic factors influencing tropical dry forests regeneration. Braz. Arch. Biol. Technol. 49, 305–312. https://doi.org/10.1590/S1516-89132006000300016.

Cordero, I., Jiménez, M.D., Delgado, J.A., Balaguer, L., Pueyo, J.J., Rincón, A., 2021. Local adaptation optimizes photoprotection strategies in a Neotropical legume tree under drought stress. Tree Physiol. 41, 1641–1657. https://doi.org/10.1093/treephys/tpab034.

Cordero, I., Jiménez, M.D., Delgado, J.A., Villegas, L., Balaguer, L., 2016. Spatial and demographic structure of Tara stands (*Caesalpinia spinosa*) in Peru: Influence of present and past forest management. . Ecol. Manag. 377, 71–82. https://doi.org/10.1016/j.foreco.2016.06.034.

Cordero, I., Ruiz-Diez, B., Balaguer, L., Richter, A., Pueyo, J.J., Rincón, A., 2017. Rhizospheric microbial community of *Caesalpinia spinosa* (Mol.) Kuntze in conserved and deforested zones of the Atiquipa fog forest in Peru. Appl. Soil Ecol. 114, 132–141. https://doi.org/10.1016/j.apsoil.2017.02.015.

Dalton, G.S., 1992. Establishing native plants in the arid zone. J. Adel. Bot. Gard. 15, 65–70.

de la Cruz Lapa, P., 2004. Aprovechamiento integral y racional de la tara *Caesalpinia spinosa – Caesalpinia tinctoria*. Rev. Inst. Invest. FIGMMG 7, 64–73. https://doi.org/10.15381/iigeo.v7i14.733.

Franco, A.C., Nobel, P.S., 1989. Effect of nurse plants on the microhabitat growth of cacti. J. Ecol. 77, 870–886. https://doi.org/10.2307/2260991.

Franco, A.C., Nobel, P.S., 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. Ecology 69, 1731–1740. https://doi.org/10.2307/1941151.

Frost, L.A., O'Leary, N., Lagomarsino, L.P., Tank, D.C., Olmstead, R.G., 2021. Phylogeny, classification, and character evolution of tribe Citharexyleae (Verbenaceae). Am. J. Bot. 108, 1982–2001. https://doi.org/10.1002/ajb2.1750.

Gagnon, E., Bruneau, A., Hughes, C.E., de Queiroz, L.P., Lewis, G.P., 2016. A new generic system for the pantropical Caesalpinia group (Leguminosae). PhytoKeys 71, 1–160. https://doi.org/10.3897/phytokeys.71.9203.

Galán de Mera, A., Linares Perea, E., Campos de la Cruz, J., Vicente Orellana, J.A., 2009. Nuevas observaciones sobre la vegetación del sur del Perú. Del Desierto Pacífico al Altiplano. Acta Bot. Malacit. 34, 107–144. https://doi.org/10.24310/abm.v34i0.6904.

Gallo, J., Baláš, M., Linda, R., Kuneš, I., 2017. Growth performance and resistance to ground late frosts of *Fagus sylvatica* L. plantation treated with a brassinosteroid compound. J. . Sci. 63, 117–125. https://doi.org/10.17221/67/2016-JFS.

Gómez-Aparicio, L., 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. J. Ecol. 97, 1202–1214. https://doi.org/10.1111/j.1365-2745.2009.01573.x.

Gómez-Aparicio, L., Gómez, J.M., Zamora, R., 2005. Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. J. Ecol. 93 (6), 1194–1202. https://doi.org/10.1111/j.1365-2745.2005.01047.x.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14, 1128–1138. https://doi.org/10.1890/03-5084.

Gómez-Ruiz, P.A., Lindig-Cisneros, R., Vargas-Ríos, O., 2013. Facilitation among plants: a strategy for the ecological restoration of the high-andean forest (Bogotá, DC—Colombia). Ecol. Eng. 57, 267–275. https://doi.org/10.1016/j.ecoleng.2013.04.049.

Gustafsson, C., Persson, C., 2002. Phylogenetic relationships among species of the neotropical genus *Randia* (Rubiaceae, Gardenieae) inferred from molecular and morphological data. Taxon 51, 661–674. https://doi.org/10.2307/3647328.

Hessini, K., Martínez, J.P., Gandour, M., Albouchi, A., Soltani, A., Abdelly, C., 2009. Effect of water stress on growth, osmotic adjustment, cell wall elasticity and water-use efficiency in *Spartina alterniflora*. Environ. Exp. Bot. 67, 312–319. https://doi.org/10.1016/j.envexpbot.2009.06.010.

Hobbs, R.J., Norton, D.A., 2004. Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. In: Temperton, V.M., Hobbs, R.J., Nuttle, T., Halle, S. (Eds.), Assembly rules and restoration ecology: bridging the gap between theory and practice, pp. 72–95.

James, T.K., Rahman, A., 2000. Longevity of buried ragwort seed in four soils. N. Z. Plant Prot. 53, 253–257.

Jiménez, M.D., Pardos, M., Puertolas, J., Kleczkowski, L.A., Pardos, J.A., 2009. Deep shade alters the acclimation response to moderate water stress in *Quercus suber* L. Forestry 82, 285–298. https://doi.org/10.1093/forestry/cpp008.

Jiménez, P., Talavera, C., Villegas, L., Huamán, E., Ortega, A., 1999. Condiciones meteorológicas en las Lomas de Mejía en "El Niño 1997–98" y su influencia en la vegetación. Rev. Peru. Biol. 6, 133–136. https://doi.org/10.15381/rpb.v6i3.8439.

Khurana, E.K.T.A., Singh, J.S., 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ. Conserv. 28, 39–52. https://doi.org/10.1017/S0376892901000042.

Kozlowski, T.T., Pallardy, S.G., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68, 270–334. https://doi.org/10.1663/0006-8101(2002)068[0270:AAAROW]2.0.CO;2.

Lopez-Toledo, L., Horn, C., Endress, B.A., 2011. Distribution and population patterns of the threatened palm *Brahea aculeata* in a tropical dry forest in Sonora, Mexico. . Ecol. Manag. 261, 1901–1910. https://doi.org/10.1016/j.foreco.2011.02.013.

Lu, Y., Ranjitkar, S., Xu, J.-C., Ou, X.-K., Zhou, Y.-Z., Ye, J.-F., Wu, X.-F., Weyerhaeuser, H., He, J., 2016. Propagation of native tree species to restore subtropical evergreen broad-leaved forests in SW China. Forests 7 (12). https://doi.org/10.3390/f7010012.

Manchego, C.E., Hildebrandt, P., Cueva, J., Espinosa, C.I., Stimm, B., Günter, S., 2017. Climate change versus deforestation: Implications for tree species distribution in the dry forests of southern Ecuador. PLoS ONE 12, e0190092. https://doi.org/10.1371/journal.pone.0190092.

Manrique P.R., 2011. El Niño southern oscillation and its effect on fog oases along the Peruvian and Chilean coastal deserts. PhD Thesis. Università di Bologna. https:// doi.org/10.6092/unibo/amsdottorato/3436.

Marañón, T., Zamora Rodríguez, R., Villar Montero, R., Zavala, M.A., Quero Pérez, J.L., Pérez-Ramos, I.M., Mendoza Sagrera, I., Castro Gutiérrez, J., 2004. Regeneration of tree species and restoration under contrasted Mediterranean habitats: field and glasshouse experiments. Int. J. Environ. Sci. 30, 187–196.

Martel, C., Rojas, N., Marín, M., Avilés, R., Neira, E., Santiago, J., 2014. *Caesalpinia spinosa* (Caesalpiniaceae) leaves: anatomy, histochemistry, and secondary metabolites. Braz. J. Bot. 37, 167–174. https://doi.org/10.1007/s40415-014-0059-0.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? N. Phytol. 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.

Meir, P., Pennington, R.T., 2011. Climatic change and seasonally dry tropical forests. In: Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G. (Eds.), Seasonally Dry Tropical Forests. Island Press, Washington, DC, pp. 279–299. https://doi.org/10.5822/978-1-61091-021-7_16.

Mihoč, M.A.K., Giménez-Benavides, L., Pescador, D.S., Sanchez, A.M., Cavieres, L.A., Escudero, A., 2016. Soil under nurse plants is always better than outside: a survey on soil amelioration by a complete guild of nurse plants across a long environmental gradient. Plant Soil 408, 31–41. https://doi.org/10.1007/s11104-016-2908-z.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, J.E., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. J. Biogeogr. 33, 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x.

Miller, H.G., 1995. The influence of stand development on nutrient demand, growth and allocation. In: Nilsson, L.O., Hüttl, R.F., Johansson, U.T. (Eds.), Nutrient Uptake and Cycling in Forest Ecosystems. Developments in Plant and Soil Sciences, vol 62. Springer, Dordrecht. https://doi.org/10.1007/978-94-011-0455-5_25.

National Aeronautics and Space Administration (NASA) Langley Research Center (LaRC), (2020) C.K. POWER data access viewer. Online resource accessed on January 2020. URL https://power.larc.nasa.gov/data-access-viewer/.

Ostertag, R., Warman, L., Cordell, S., Vitousek, P.M., 2015. Using plant functional traits to restore Hawaiian rainforest. J. Appl. Ecol. 52, 805–809. https://doi.org/10.1111/1365-2664.12413.

Péfaur, J., 1982. Dynamics of plant communities in the Lomas of southern Perú. Vegetatio 49, 163–171. https://doi.org/10.1007/BF00123840.

Portillo-Quintero, C.A., Sánchez-Azofeifa, G.A., 2010. Extent and conservation of tropical dry forests in the Americas. Biol. Conserv. 143, 144–155. https://doi.org/10.1016/j.biocon.2009.09.020.

Pörtner, H.O., Roberts, D.C., Adams, H., Adler, C., Aldunce, P., Ali, E., Ibrahim, Z.Z., 2022. Climate change 2022: Impacts, adaptation and vulnerability. IPCC, Geneva, Switzerland, p. 3056.

Postma, F.M., Ågren, J., 2016. Early life stages contribute strongly to local adaptation in *Arabidopsis thaliana*. Proc. Natl. Acad. Sci. 113, 7590–7595. https://doi.org/10.1073/pnas.1606303113.

Quesada, M., Sanchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.S., Rosas-Guerrero, V., Sayago, R., Sanchez-Montoya, G., 2009. Succession and management of tropical dry forests in the Americas: review and new perspectives. . Ecol. Manag. 258, 1014–1024. https://doi.org/10.1016/j.foreco.2009.06.023.

Reddy, A.R., Chaitanya, K.V., Vivekanandan, M., 2004. Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. J. Plant Physiol. 161, 1189–1202. https://doi.org/10.1016/j.jplph.2004.01.013.

Rother, D.C., Jordano, P., Rodrigues, R.R., Pizo, M.A., 2013. Demographic bottlenecks in tropical plant regeneration: a comparative analysis of causal influences. Perspect. Plant Ecol. Evol. Syst. 15, 86–96. https://doi.org/10.1016/j.ppees.2012.12.004.

Seddon, N., Chausson, A., Berry, P., Girardin, C.A.J., Smith, A., Turner, B., 2020. Understanding the value and limits of nature-based solutions to climate change and other global challenges. Philos. Trans. R. Soc. B 375, 20190120. https://doi.org/10.1098/rstb.2019.0120.

SER, 2004. The SER International Primer on Ecological Restoration. Tucson: Society for Ecological Restoration International Science & Policy Working Group. Available: http://www.ser.org/pdf/primer3.pdf. Accessed 22 July 2010.

Siyum, Z.G., 2020. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecol. Process. 9, 25. https://doi.org/10.1186/s13717-020-00229-6.

Sotomayor, D.A., Jiménez, P., 2008. Meteorological conditions and vegetal dynamics of the Atiquipa Lomas (Caravelí-Arequipa) coastal ecosystem in the South of Peru. Ecol. Apl. 7, 1–8.

Suresh, H.S., Dattaraja, H.S., Sukumar, R., 2010. Relationship between annual rainfall and tree mortality in a tropical dry forest: results of a 19-year study at Mudumalai, southern India. . Ecol. Manag. 259, 762–769. https://doi.org/10.1016/j.foreco.2009.09.025.

Talavera, C., Pauca, A., Fernández, C., Villasante, F., Villegas, L., Delgado, A., 2017. Flora de Lomas de Atiquipa. Editorial UNSA. Arequipa.

Tognetti, R., 2015. Trees harvesting the clouds: fog nets threatened by climate change. Tree Physiol. 35, 921–924. https://doi.org/10.1093/treephys/tpv086.

Tovar, C., Sanchez Infantas, E., Teixeira Roth, V., 2018. Plant community dynamics of lomas fog oasis of Central Peru after the extreme precipitation caused by the 1997-98 El Niño event. PLoS ONE 13, e0190572. https://doi.org/10.1371/journal.pone.0190572.

Villanueva, C., 2007. La Tara, el oro verde de los incas. Lima. Ed. AGRUM 1, 163–167.

Young, B., Young, K.R., Josse, C., 2011. Vulnerability of tropical Andean ecosystems to climate change. In: Herzog, S.K., Martinez, R., Jorgenson, P.M., Tiessen, H. (Eds.), Climate Change and Biodiversity in the Tropical Andes. SCOPE, IAI, pp. 170–181.