

INFLUENCE OF "EL NIÑO SOUTHERN OSCILLATION" PERIODS ON PLANT DENSITY OF *HOFFMANNSEGGIA APHYLLA* (FABACEAE), AN ENDANGERED SPECIES

INFLUENCIA DE LOS PERÍODOS DE "EL NIÑO OSCILACIÓN DEL SUR" EN LA DENSIDAD VEGETAL DE *HOFFMANNSEGGIA APHYLLA* (FABACEAE), UNA ESPECIE EN PELIGRO

Felipe S. Carevic^{1,3*} & Roberto Contreras^{2,3}

SUMMARY

- Background and aims: Studies on the natural regeneration of plant species under hyperaridity conditions have been scarce, mainly because of the low germination percentage of the species under these conditions. Presumably, sporadic phenomena such as the El Niño Southern Oscillation (ENSO) could have a positive effect on the natural germination of these species, although this effect has not yet been satisfactorily explored.
 - **M&M**: To test the crucial assumption of our statement, a hyperarid region (average rainfall below 5 mm/year) was used as a model to determine the effect of ENSO years on the natural regeneration rate of adult individuals of the endemic legume *Hoffmannseggia aphylla* (retama) in the Atacama Desert, northern Chile. Thus, the vegetation density of an endemic leguminous species in a sector of the Pampa del Tamarugal, Tarapacá Region, northern Chile, was analyzed for six years.
 - **Results**: The density of this species increased during ENSO years, mainly due to water flows from the highest sectors of the Tamarugal pampas, such as the town of Pica, in addition to the increase in humidity and summer rainfall.
 - **Conclusion**: Our results highlight the transcendence of the ENSO in the regeneration of leguminous plants.

KEY WORDS

Atacama desert, ENSO, Fabaceae, Hoffmannseggia, Hyperarid, legume.

RESUMEN

- Introducción y objetivos: Los estudios sobre la regeneración natural de especies vegetales en condiciones de hiperaridez han sido escasamente estudiados en terreno, principalmente por el bajo porcentaje de germinación de las especies en estas condiciones. Presumiblemente, fenómenos esporádicos como El Niño Oscilación del Sur (ENOS) podrían tener un efecto positivo en la germinación natural de estas especies, aunque este efecto aún no ha sido explorado satisfactoriamente.
- **M&M**: Para testear la suposición crucial de nuestra afirmación, se utilizó una región hiperárida (precipitación promedio inferior a 5 mm/año) como modelo para determinar el efecto de los años ENOS en la tasa de regeneración natural de individuos adultos de la leguminosa endémica *Hoffmannseggia aphylla* (retama) en el desierto de Atacama, norte de Chile. Así, se analizó durante seis años la densidad vegetal de esta especie en un sector de la Pampa del Tamarugal, Región de Tarapacá, norte de Chile.
- **Resultados**: La densidad de esta especie se incrementó durante los años ENOS, principalmente por los caudales de agua provenientes de los sectores más altos de la pampa del tamarugal, como el poblado de Pica, además del aumento de la humedad y las precipitaciones estivales.
- **Conclusión**: Nuestros resultados destacan la trascendencia del ENOS en la regeneración de plantas leguminosas.

PALABRAS CLAVES

Desierto de Atacama, ENSO, Fabaceae, hiperárido, Hoffmannseggia, leguminosa.

1. Laboratorio de Ecología Vegetal, Facultad de Recursos Naturales Renovables, Universidad Arturo Prat, Iquique, Chile

2. Centro Regional de Investigación y Desarrollo Sustentable de Atacama (CRIDESAT), Universidad de Atacama, Copiapó, Chile

3. Millennium Nucleus on Applied Historical Ecology for Arid Forests (Aforest). Santiago de Chile

*fcarevic@unap.cl

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INTRODUCTION

The natural regeneration processes of plant species are currently considered one of the main problems facing climate change because the real effects of this problem on the reproductive rates of the species are still unknown (Peters et al., 2012). In this sense, the Atacama Desert is no stranger to this type of process, mainly because of four determining factors: 1) the effect of the decrease in precipitation recorded at the beginning of this century in northern Chile (Soto & Ulloa, 1997); 2) the decrease in relative soil humidity in this area (Neilson et al., 2017); 3) the increase in salinity in high Andean limnetic bodies (Gajardo & Redón, 2019); and 4) the decrease in the groundwater table (Viguier et al., 2019). This type of groundwater has been described as one of the main sources of water supply for the maintenance of the vegetation present in this ecosystem, but the effect of precipitation pulses or the occurrence of climatic phenomena such as the El Niño Southern Oscillation (ENSO) could have some impact on vegetation density (Squeo et al., 2006). In the past decade Chile has experienced a mega drought, where the presence of a strong ENSO during most of 2015 stood out (Garreaud et al., 2019).

The natural regeneration of desert leguminous species under ENSO conditions has scarcely been evaluated under field conditions (Kraus et al., 2007). The occurrence of this phenomenon is a powerful tool for evaluating this type of ecological condition in plants, as precipitation and humidity tend to increase in arid areas of northern Chile when ENSO is present (Acosta et al., 2015). The genus Hoffmannseggia Cav. (Fabaceae) has a wide distribution, including the arid and semi-arid regions of Argentina, Chile, Peru, and Bolivia in South America, and Mexico and the southwestern United States in North America (Kraus et al., 2007). In the Atacama Desert, Hoffmannseggia aphylla (Phil.) G.P. Lewis & Sotuyo (Spanish "retama") is an endemic phreatophyte shrub legume that fixes atmospheric nitrogen, and its distribution is limited to the northern part of this desert, specifically the Pampa del Tamarugal in northern Chile (Lewis & Sotuyo, 2010). Recently, this species has been considered as "endangered"

(Ministerio de Medio Ambiente, 2022). The main threat to natural H. aphylla populations in northern Chile is associated with the current depletion of the water table, which may be a direct cause of the decline in legume populations (Chavez et al., 2013). Former studies denoted that the water flux into the aquifer of Pampa del Tamarugal, is calculated to be between 880 and 1000 l/s, while the water outflow is estimated to be as high as 4000 l/s (Dirección General de Aguas, 2011; Calderón et al., 2015; Viguier et al., 2019). In this ecosystem, groundwater aquifers are the only source of water, which are fed by the rainfall, glaciers and snowmelt from the Andes Mountain range. This shrub has conditions of successful natural adaptability in arid soils with high salinity (even with electrical conductivities of 182 Ds/m) and nitrogen impoverishment in the edaphic stratum (León et al., 2017). However, the natural regeneration of plant species in this area is almost null due to the almost nonexistent precipitation averaging 1 mm/year and the presence of a saline crust layer on the edaphic surface (León et al., 2017). In this sense, it fails to form a homogeneous shrub stratum, as the distribution of individuals on the ground is not very dense, with individuals that seem to form mosaics following the floods that usually occur in this ecosystem (Lewis & Sotuyo, 2010). Once established, adult individuals of Prosopis tamarugo Phil., for example, would depend on the flow of water present at the phreatic level, which is usually present in the first meters of soil depth owing to its ascent by capillarity (Calderón et al., 2015). Preliminary results have indicated a favorable increase in the regenerative rates of the species, although this trend should be further explored in detail, considering edaphic factors and flooding episodes during the summer (Carevic, 2020). Regarding this condition, natural seed germination could occasionally occur as a result of summer precipitation and water flooding during ENSO periods and to a lesser extent during Interdecadal Pacific Oscillation (IPO) periods. However, this effect has not yet been explored in this species.

Previous studies carried out in arid ecosystems have reported a positive effect of precipitation during ENSO events on the density of plant species growing at low altitudes above sea level; although the same precipitation was not significant for the increase in primary productivity of species established at high altitudes (2,500 m above sea level) (Squeo et al., 1999). However, the influence of seasonal environmental parameters and their effects on plant density and reproduction parameters in legume species growing under hyperarid conditions are poorly understood, considering that climate may play an important role in monitoring and predicting plant viability and reproduction. We hypothesized that the increased surface water flow resulting from precipitation during ENSO years would have an incremental effect on the germination rate and flower parameters (number of flowers, number of pods per plant and percentage of flower abortion) of H. aphylla seeds in northern Chile. Thus, our objective was to evaluate the long-term impact of environmental variables during ENSO events in northern Chile on the reproductive and ecological parameters of H. aphylla, an endangered endemic species of the Atacama Desert.

MATERIALS AND METHODS

Study area

The study was carried out within the natural habitat of *H. aphylla* in Pampa del Tamarugal, northern Chile. The climate of this area is hyperarid. The site was dominated by *P. tamarugo*, *H. aphylla*, and *Atriplex atacamensis* Phil. The latter two species are small shrubs that are sparsely distributed on the grid. The study area is characterized by extreme hyperarid conditions, with annual precipitation not exceeding 0.6 mm/ year, which occurs mainly during the summer season (Carevic *et al.*, 2021). However, there are years with rainfall pulses that exceed 7 mm/ year, especially in sectors with an altitude above sea level higher than that present in Canchones (Arenas 2019; Lanino & Poblete, 2022).

Experimental design

During the period 2012-2018, an experimental grid of 3.1 ha was established in the Canchones sector in the Pampa del Tamarugal, northern Chile to evaluate *H. aphylla* density using the transect line method (Cox, 1981). Sampling was carried out during the fall (May) of each year and

spring (September). For this objective, 38 linear transects of 95 m were georeferenced within the grid, with points every 5 m. Flower sprouting was assessed semi-annually during the period of 2012-2016 by tagging the flowers which emerged using a thread of a particular color, with a distinctive color used for period so that at harvest, flower production as well as pods could be attributed to the respective period of sprouting (Leport et al., 2006). For this purpose, we selected 12 adult individuals of *H. aphylla*. This tagging was also used to record the total number of flowers produced per plant (total number of tags per plant), and the number of pods per plant (number of tags with a date of flower sprouting), and the proportion of aborted flowers. For environmental characterization, two meteorological stations were established near the study area to record daily environmental conditions (ambient temperature, precipitation, wind speed, and solar radiation), both located on slopes, to determine the effect of flooding on the study area. The first was located in Canchones (UTM: 7739099, 443867; 1005 m a.s.l.), located 1.5 km from the study area. Another meteorological station was in the town of Pica (UTM: 7734562, 465733; 1345 m a.s.l.), 15 km from the study area. Similarly, five digital soil humidity probes (ECHO) were established at 0.6 m depth distributed in the study area to record the seasonal evolution of this parameter. Each humidity sensor was separated by approximately 70 m from each other.

Statistical analysis

To evaluate interannual differences in H. aphylla density and flower parameters (number of flowers, number of pods per plant and percentage of flower abortion), we used a linear general model by means of repeated measures. The flower parameters data were log-transformed ln (x+1) to increase linearity and reduce the correlation between the mean and variance. Relationships between meteorological and edaphic data (temperature, precipitation, solar radiation, wind speed, and soil humidity) and H. aphylla density and flower production were evaluated using multiple matrix correlations (r). Data was analyzed by using SPSS Statistics for Windows, Version 23.0 (IBM SPSS Statistics for Windows, Version 23.0. Armonk, NY: IBM Corp).

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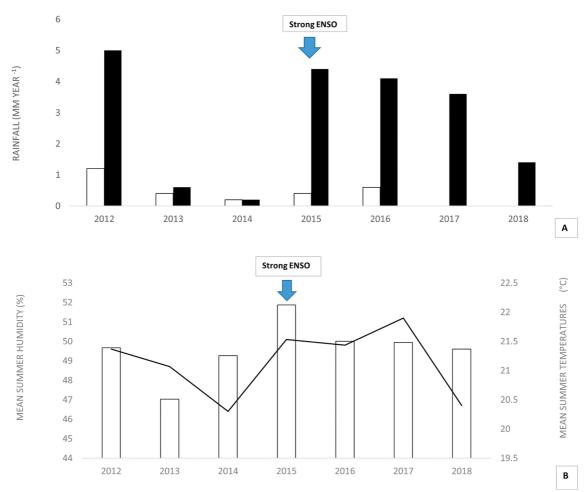


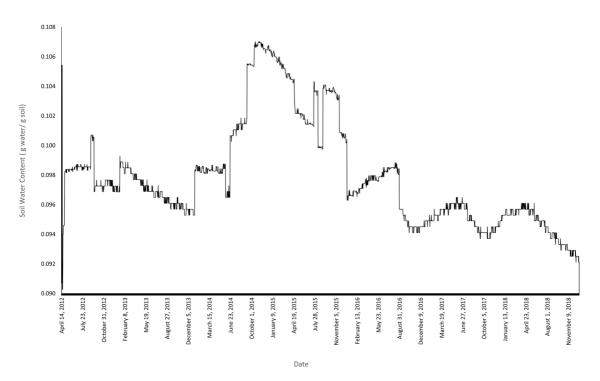
Fig. 1. Precipitation, temperature and humity in the study area. **A**: Annual precipitation detected in Pica (black columns) and Canchones (white columns) (left, above). **B**: Mean annual summer temperatures (black line) and mean humidity (white bars) in Canchones.

RESULTS

During the present study, the presence of two flooding events during the summers of 2015 and 2016 was observed, reflected in the increase in soil humidity during those periods and the presence of summer rainfall that exceeded 4 mm/year in Pica (Figs. 1; 2).

The most important variation associated with *H. aphylla* density parameters was related to an increase in the number of individuals per area after the 2015 event (Table 1), when new individuals of low size were recorded, typical of regeneration phenomena, which subsequently decreased (2017 and 2018).

The environmental humidity and temperatures detected during summer had different fluctuations, with the highest environmental humidity values recorded in 2015 and the highest summer temperature averages in 2017. Likewise, the density determined during 2015 and 2016 was strongly correlated with the environmental humidity detected during summer 2015 in Canchones (December 21st to March 21st); r=0.56, p<0.01, and with the annual precipitation recorded in Pica the same year (r=0.51, p=0.02). Furthermore, we observed a significant relationship between soil humidity and plant density during the same period (r=0.39, p=0.03). Regarding flower parameters, we did not find significant differences between numbers of



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Fig. 2. Seasonal evolution of average soil humidity by season of the year.

Table 1. Area density of *H. aphylla* individualsduring the study. Differences between years are
denoted by different letters.

Plant density H. aphylla								
Year	p value	Individuals/m ²	F value					
2012	0.12 ^{ab}	0.001	24.55					
2013	0.21 ^b	0.001	29.09					
2014	0.22 ^b	0.001	30.87					
2015	0.04ª	0.001	41.76					
2016	0.04ª	0.001	41.08					
2017	0.08 ^{ab}	0.001	21.22					
2018	0.09 ^{ab}	0.001	21.97					

flower sprouts at population level. Furthermore, flower parameters did not show any relationship with climatic parameters (Table 2).

DISCUSSION

Our findings constitute the first large-scale study of the natural regeneration processes generated under hyperarid conditions in the Atacama Desert. Thus, precipitation generated during ENSO events seems to be an essential factor for the germination of H. aphylla in northern Chile, consistent with previous studies indicating that the increase in sporadic water pulses present during this phenomenon plays an essential role in the regeneration of arid zone plant species (Gutiérrez et al., 2000; Squeo et al., 2006; León et al., 2011). In the present study, rainfall recorded in Pica, that is, in a sector with a higher altitude above sea level, had the greatest relationship with the increase in vegetation density of this legume (Fig. 3). This record is not surprising, as, in "wet" periods, precipitation tends to carry water to lower

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Table 2. Summarized data on flower sprout at intrapopulation level.									
	Periods measured								
Parameter	December 2012	August 2013	April 2014	November 2014	March 2015	November 2015	May 2016		
Number of flowers (mean±SE)	12±2	13±4	10±3	11±2	13±2	13±3	10±2		
Number of pods per plant (mean±SE)	0	0	3±2	3±2	4±2	3±3	2±2		
Percentage of flower abortion (%)	0	0	76.9	76.9	69.2	76.9	84.6		

areas such as Canchones, where this water forms real lagoons that tend to dry up or infiltrate as the summer progresses (Houston, 2001). However, the increase in water availability must necessarily be accompanied by an increase in humidity during the summer in the same study site for this germination phenomenon to take place, in which values above 50% seem to break the physiological dormancy of this species. Previous investigations, carried out at the laboratory level, agree that water availability, temperature and increased environmental humidity are limiting factors for breaking dormancy in species of this genus (Alves *et al.*, 2018; Moreno *et al.*, 2018).

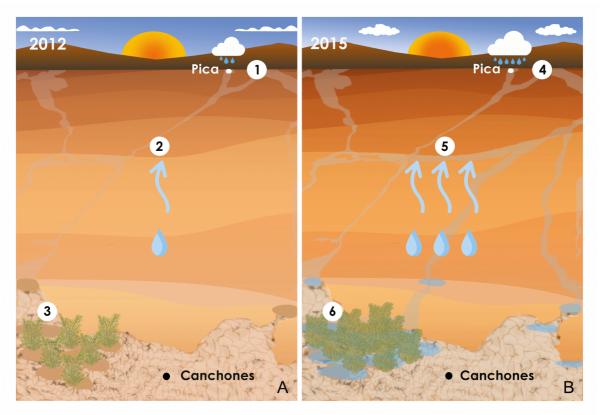


Fig. 3. Schematic illustration of comparative situation ENSO observed in the study area. **A**: In 2012. Normal periods of rainfall in Pica (1) and environmental humidity in Canchones (2) do not generate an incremental variation in the density of *H. aphylla* population (3). **B**: In 2015. Increasing rainfall at Pica (4) and environmental humidity in Canchones (5), the plant density of *H. aphylla* increasing notably (6).

There has been some controversy regarding the effects of environmental variables on germination. Formerly, some authors have claimed that temperature and sunlight are the limiting factors for germination processes in plants in the arid zones of Asia (El-Keblawy & Al-Rawai, 2005). Such studies on the regeneration of native species have been limited to a few years of evaluation and are usually restricted to semiarid ecosystems with the highest availability of precipitation. In our study, we found no direct evidence of the effect of sunlight and temperature on H. aphylla density, presumably because these parameters remained homogeneous during much of the summer, the time when increased density was detected (Arenas, 2019). Nevertheless, this natural regeneration decreased during 2017 and 2018, probably because of predation by goat cattle, which is usually abundant in this area and is associated with the consumption of native legumes (Carevic et al., 2015; Contreras et al., 2020). At reproduction level, we did not find any relationship between climatic traits and flower production. The highest values of flower abortion and the reduced number of flowers per plant are not surprising, because it has a slow growth with few production of leaves and flowers, consistent with the hyperarid habitat of Atacama Desert (Lewis & Sotuyo, 2010). In conclusion, the presence of ENSO has a transcendental influence on the regeneration of leguminous plants, especially due to the increase in precipitation in Pica (which only falls within a few hours) and, to a lesser extent, Canchones, which cause water flooding to lower sectors of the Tamarugal pampas, a fact that was detected by an increase in soil humidity. In addition, this effect must be combined because it must be accompanied by an increase in the average environmental humidity during the summer (January-March).

CONCLUSIONS

We demonstrate at the field study level, the positive influence of the ENSO phenomenon on the natural regeneration rate of *H. aphylla* in the Atacama Desert. The presence of this climatic phenomenon generates water floodings that allow the germination of seeds, although this aspect must be accompanied by an increase in environmental

humidity. It should be noted the positive effect that the flooding registered as a result of the precipitation in the Pica sector, contributed to a greater extent to the increase in the density of H. aphylla plants, which has an explanation due to the higher altitude above the ground sea level that Pica presents in relation to the study area (300 m higher), since when precipitation falls on that area, the effect of gravity probably allows the displacement of these masses of water to the flatter areas of the Tamarugal pampa, where it was carried out the study. Our research was developed over a long period of time, with the aim of evaluating the effect of climatic phenomena on the population of an endangered plant species. It is essential that monitoring is embedded in a long management program by the accountable agency or research institutions that is working towards the recovery and monitoring of a given threatened species or threatened ecosystem. We highlight that these benefits of monitoring will be far more likely to be achieved if the monitoring program is well designed with clearly articulated objectives, with due attention to long term biological traits and its dynamics based on future climatic effects.

AUTHOR CONTRIBUTIONS

FC did all experimental work and prepared first draft of the paper; RC participated on field sampling and prepared final version of the paper.

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SUPPLEMENTARY DATA

Supplementary data to this article can be found at: https://github.com/carevicunap/haphylla.

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