Flora 214 (2015) 17–23

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Seed dormancy of *Nolana jaffuelii* I.M.Johnst. (Solanaceae) in the coastal Atacama Desert

Elisa Cabrera[a], Josefina Hepp[a,b], Miguel Gómez[a,b], Samuel Contreras[a,*]

[a] Departamento de Ciencias Vegetales, Facultad de Agronomía e Ingeniería Forestal, Pontificia Universidad Católica de Chile, Vicuña Mackenna 4860, Macul, Santiago, Chile
[b] Centro del Desierto de Atacama, Pontificia Universidad Católica de Chile, Vicuña Mackenna 4860, Macul, Santiago, Chile

ARTICLE INFO

Article history:
Received 12 January 2015
Received in revised form 4 May 2015
Accepted 18 May 2015
Edited by Hermann Heilmeier
Available online 21 May 2015

Keywords:
Lomas formations
Fog oasis
Arid zone
Physical dormancy
Physiological dormancy
Seed germination

ABSTRACT

Nolana (Solanaceae) is a genus composed of 88 species that inhabit arid and semi-arid environments throughout the Atacama Desert of Chile and Peru, and one from Galapagos Islands. Its greatest diversity is found in coastal localities, termed lomas formations, which are small isolated patches of vegetation sustained by the presence of low cloud layers. Alto Patache corresponds to one of these ecosystems, and *Nolana jaffuelii* I.M. Johnst., a summer annual herb, is the most abundant species in its persistent seed bank. Little is known about the seed germination requirements of this and other species present in Chilean lomas formations, despite the importance of that knowledge for taking appropriate conservation actions. The main objective of this study was to identify the germination requirements and possible dormancy mechanisms of *N. jaffuelii*'s dispersal units, which are mericarps. Mature mericarps of *N. jaffuelii* were collected at Alto Patache. Histological analyses of cross and longitudinal sections of the mericarps suggested the presence of physical dormancy imposed by an impermeable pericarp. Different germination treatments were also evaluated: (T1) control, i.e., intact mericarps imbibed in water; (T2) intact mericarps washed under running water; (T3) scarified mericarps (cut at the funicular scar) imbibed in water; (T4) scarified mericarps imbibed in gibberellic acid (500 mg l^{-1} GA_3); (T5) scarified mericarps imbibed in water with 2 weeks of stratification at 4 °C; and (T6) intact mericarps imbibed in GA_3. Only mericarps cut at the funicular scar were able to germinate, and the highest germination percentage was observed when the mericarps were imbibed in GA_3 (T4). The results of this investigation reveal the existence of physical and physiological dormancy in *N. jaffuelii* propagules, an adaptation that would allow this species to spend long periods waiting for favorable conditions for seedling establishment, which is characteristic of the coastal lomas formations of the Atacama Desert.

1. Introduction

The genus *Nolana* L. ex L. f. (Solanaceae-Nolaneae) comprises 88 species from arid and semi-arid environments in Chile and Peru, and one oceanic island endemic species from Galapagos Islands. Forty eight species are present in Chile, of which 44 are endemic (Dillon et al., 2009). They are generally herbaceous plants or small shrubs with succulent leaves and hermaphroditic tubular flowers (Dillon et al., 2007a). The most typical and unique feature of the genus within the Solanaceae is the fruit, a schizocarp separated into a variable number of hard mericarps due to a highly lignified endocarp (Johnston, 1936). The greatest diversity of the genus in Chile and Peru is found in the Chilean-Peruvian desert, also called the Atacama Desert, known for its extreme aridity. The coastal area of this desert receives moisture from the camanchaca, or coastal fog (Rundel et al., 1991), which is a low cloud layer that has a base usually located around 800–1000 m a.s.l., with a thickness of approximately 300–400 m (Cereceda et al., 2002). Its influence allows the development and maintenance of vegetation in discrete communities known as lomas formations or fog oasis, which have a rich and particular floristic composition that is characterized by high endemism and the dominance of herbaceous species (Muñoz-Schick et al., 2001). In Chile, 44 species of *Nolana* are distributed in these ecosystems (Dillon et al., 2009), and the genus stands out as one of the most conspicuous elements of the coastal Atacama flora (Dillon et al., 2007b).

Alto Patache (20° 49′33″S, 70° 9′15″W) is one of these lomas formations and is characterized by southwest oriented slopes that

Abbreviations: FAA, formol acetic acid; GA_3, gibberellic acid; m a.s.l., meters above sea level; MGT, mean germination time.

* Corresponding author. Tel.: +56 22354 4112.
E-mail address: scontree@uc.cl (S. Contreras).

http://dx.doi.org/10.1016/j.flora.2015.05.004
0367-2530/

are exposed to fog almost constantly throughout the year (Muñoz-Schick et al., 2001). There are 54 species of plants that have been described in Alto Patache belonging to 30 families and 42 genera (Pinto and Luebert, 2009), among them five species of *Nolana*. Thirty-five percent of these species are ephemeral herbs (Pinto and Luebert, 2009) that should survive unfavorable periods by forming persistent seed banks (Figueroa et al., 2004). In this area, an increase of vegetation development, blooming, and the replacement of the seed bank composition are associated with short periods of precipitations that occur every 5–7 years (Pinto and Luebert, 2009). After monitoring vegetation in Alto Patache between 1997 and 2000, Pinto et al. (2001) reported that in rainy years 45 species were identified, whereas only 24 species were found during dry years.

The seed banks of lomas formations in northern Chile have not been studied extensively. When the Alto Patache seed bank was studied, densities varied from six to 1200 seeds per square meter among sectors, and seeds from only seven species were found (Gómez et al., 2012). *Nolana jaffuelii* I.M. Johnst. was the most abundant species observed in that study, with approximately 700 mericarps (dispersal unit of the species) per square meter. *N. jaffuelii* is an annual herb distributed throughout the coastal hills of Atacama Desert (22° 04′ S to 16° 23′ S) and is believed to be a species of Chilean origin with a small extension range in southern Peru (Muñoz-Schick et al., 2001; Tago-Nakazawa and Dillon, 1999). The relict and vulnerable characteristics of the vegetation present in lomas formations (Schultz et al., 2011), due to current and predicted climate changes, warrant study of the flowering and germination of seeds and bulbs (Schultz et al., 2011). Our research in the Alto Patache fog oasis has allowed for the partial determination of the seed bank composition, but the germination strategies used by species present in this ecosystem are still poorly understood. There is no information available of the germination requirements of *Nolana* species present in alto Patache; therefore, the overall objective of this study was to identify and characterize the seed dormancy mechanisms of *N. jaffuelii* as a first step to understanding the biology of species in these ecosystems and to take appropriate conservation actions. The specific objectives were to determine the conditions necessary for the germination of *N. jaffuelii* mericarps and to identify the type(s) of dormancy (if any) present in them. The proposed hypothesis is that the dispersal units of *N. jaffuelii* have at least one type of dormancy that ensures its persistence in the soil until suitable environmental conditions for germination are present.

2. Materials and methods

2.1. Plant material

N. jaffuelii mericarps were collected in the Alto Patache lomas formation at two opportunities: April and October 2013. Mature mericarps were collected from the soil surface under plant individuals and were stored in paper bags at room temperature until evaluation. Under a binocular magnifier, the visually intact mericarps (i.e., those with a black pericarp and sealed funicular scar) were selected.

2.2. Histological analysis

Mericarps from the first collection were selected and fixed in formol acetic alcohol (FAA) and then dehydrated and preserved in paraffin to be sectioned. Cross- and longitudinal histological sections were made through the mericarp using a microtome (to a thickness of 15 μm), and the sections were stained with safranin-fast green. Sections were observed under a light microscope and photographed.

2.3. Evaluation of germination

An evaluation of the germination for *N. jaffuelii* mericarps was performed in two experiments. In both cases, 25 mericarps were placed in 9 cm diameter Petri dishes over three layers of filter paper saturated with distilled water or a solution of 500 mg l^{-1} gibberellic acid (GA_3). The plates were sealed with parafilm to prevent drying. Physiological germination (i.e., radicle emergence) was evaluated daily, and water was added as needed.

2.3.1. Experiment 1

Germination testing began in May 2013 using fruits collected one month earlier. Propagules were randomly assigned to one of the following treatments (T): (T1) control, i.e., intact mericarps imbibed in water; (T2) intact mericarps washed under running water for 5 min and then imbibed in water; (T3) scarified mericarps, i.e., cut at the funicular scar, imbibed in water; (T4) scarified mericarps imbibed in GA_3 (T5) scarified mericarps imbibed in water with 2 weeks stratification at 4 °C; and (T6) intact mericarps imbibed in GA_3. The plates were placed in a chamber with alternating temperatures of 20 °C (12 h, light) and 10 °C (12 h, dark). Each treatment was replicated three times (25 seeds each) in a completely randomized design.

Scarification of T3, T4 and T5 consisted of cutting the pericarp at the funicular scar with a scalpel, avoiding radicle damage. To check the importance of the placement of the cut in the scarification, a variation of T3, T4 and T5 was carried out by cutting the pericarp in an area distant to the funicular scar. This was performed in 25 mericarps that were imbibed in water (variation of T3), 25 mericarps that were imbibed in GA_3 (variation of T4), and 25 mericarps that were stratified (variation of T5). Germination was evaluated under the same conditions as described above.

2.3.2. Experiment 2

Germination testing began in December 2013 using mericarps collected two months earlier. There were three treatments, equivalent to T1 (control), T3 (scarification) and T4 (scarification + GA_3) in Section 2.3.1. The experimental unit consisted of a plate with 25 mericarps, and there were four replicates arranged in a completely randomized design. The plates were placed in a chamber at 20 °C with constant light, and germination was evaluated daily for 30 days. The results are reported as the germination percentage and mean germination time (MGT). The MGT was calculated using the formula cited by Ellis and Roberts (1980):

$$\mathrm{MGT} = \frac{\Sigma n \times d}{\Sigma n}$$

where n is the number of seeds newly germinated at time d, d is the number of days from the beginning of the germination test, and Σn is the total number of seeds germinated during the test.

2.4. Statistical analysis

Data from Section 2.3.1 were analyzed using confidence intervals (95%) obtained according to an analysis of proportions (Mead et al., 1993). For the data from Section 2.3.2, analysis of variance (ANOVA) was used to determine the existence of significant differences between treatments. When differences were detected ($p < 0.05$), the least significant difference (LSD; $\alpha = 0.05$) test was used. Before the analysis, germination percentages were transformed to the arcsin of the square root of the fraction value, but untransformed data are presented and used for the discussion below.

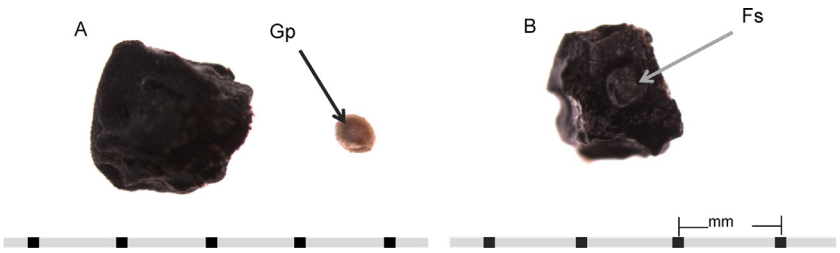

Fig. 1. A nucule of *Nolana jaffuelii* photographed with a binocular magnifier, mm scale. (A) The side view of a nucule and germination plug. (B) The area of the cut nucule showing the operculum of the funicular scar where the germination plug covers the funicular scar. Abbreviations: Gp, germination plug; Fs, funicular scar.

3. Results and discussion

3.1. Fruit histology

The fruit of the genus *Nolana* is a schizocarp that separates into mericarps (Tago-Nakazawa and Dillon, 1999). Each mericarp is a nucule (Johnston, 1936) that, such as some Malvaceae species, consists of ½ I ½ carpels, i.e., the walls of the fruit are constituted of two halves of neighboring carpels (Saunders, 1936). The mericarps of *Nolana* are multiseminate and variable in size and degree of fusion, presenting a cover with very hard tissues (Dillon et al., 2007a) that become detached from the funiculus when ripe (Lindley, 1824, quoted in Saunders, 1936).

At the base of the mericarp is the areola, an area of the pericarp in which the funicular scar is located that is covered by a germination plug or cap (described by Bondeson (1986); for *Nolana humifusa* and *Nolana paradoxa,* and confirmed by Douglas and Freyre (2006)). The germination plug was easily detached when performing tangential cuts in the pericarp, which suggests that the mechanical impediment to germination in this operculum area is lower than in the rest of the fruit wall (Fig. 1).

A histological analysis of transverse and longitudinal sections performed in mature mericarps of *N. jaffuelii* showed the presence of a pericarp with three distinct layers (Fig. 2): the outer or exocarp corresponds to a monolayered epidermis that has cells that contain vacuoles with tannins and a thin protective cuticle (Fig. 2D). The middle layer or mesocarp occupies the bulk of the pericarp and is formed by radially elongated cells that have walls that are suberized (Fig. 2A). The innermost layer or endocarp possesses irregular lobes toward the mesocarp. It is constituted by sclereids, which give strength and rigidity to the fruit (Fig. 2A, B and E).

Inside the endocarp, one or two embryonic chambers are found, each of which generally contains an embryo, but which are sometimes empty. The embryo is curved linear and morphologically well differentiated (Fig. 3), such as those of the Solanaceae family described by Martin (1946). It is surrounded by a thin oily endosperm, as described by Watson and Dallwitz (1992) for the genus *Nolana* (Figs. 2C and 3A).

The Baskin and Baskin (1998, 2004),) dormancy classification considers five classes of seed dormancy: (i) physiological, (ii) morphological, (iii) morpho-physiological, (iv) physical, and (v) combinational (physical and physiological). Physical dormancy implies the presence of one or more water-impermeable layers covering the embryo and preventing its imbibition (Baskin and Baskin, 1998). These layers may be composed of sclereids and contain hydrophobic substances, such as cutin, quinones, suberin, waxes, callose and phenolics. Each component contributes a different magnitude of waterproofing (Bewley et al., 2013). In the case of *N. jaffuelii*, there are several layers that the water must move through to reach the embryo, which suggests the presence of physical dormancy. First, water must move through the cutin and tannins of the epidermis, as in cotton seeds (Halloin, 1982); then, the mesocarp with suberized cells; and lastly, the woody endocarp, the thickness of which, in addition to providing rigidity, isolates the embryo from the external environment surrounding the fruit due to its lignified walls.

3.2. Evaluation of germination

The results of germination from Section 2.3.1 are summarized in Fig. 4. Results are expressed as percentage of germinated mericarps, which means that even if two embryos germinated from a mericarp, it was counted as one germinated mericarp. The absence of germination in intact mericarps (control, T1) was understood to indicate the presence of dormancy in propagules of *N. jaffuelii*. Washing the mericarps (T2) did not have an effect on promoting germination; thus, dormancy would not be explained by presence of inhibitory compounds in the fruit walls. Bansal and Sen (1981) studied several species of the Indian arid zone and found that, for some of them, seeds started germinating after washing.

Only scarified mericarps were able to germinate. The treatment with the highest germination percentage (32%) was the method involving cutting the funicular scar and imbibing the mericarps in the GA_3 solution (T4), which would indicate the presence of physical and physiological dormancy, i.e., combinational dormancy (Baskin and Baskin, 2004). If physical dormancy was the only dormancy type present in *N. jaffuelii*, a similar germination rate should be obtained with any treatment that involves cutting the funicular scar (i.e., T3, T4 and T5). On the other hand, if mericarps have only physiological dormancy, the imbibition of intact fruits in GA_3 (T6) should present similar results to T4; however, there was no germination for T6, revealing that gibberellic acid could not reach the embryo, probably because of the barrier imposed by the surrounding endocarp.

Stratification at 4 °C for 2 weeks in mericarps cut at the funicular scar (T5) had an effect that was similar to the addition of GA_3, but weaker in magnitude. According to Baskin and Baskin (1998), cold stratification is often used as a treatment to break intermediate to deep physiological dormancy, the same as GA_3 imbibition; therefore, the results from T4 and T5 suggest the existence of physiological dormancy. The variations in the effectiveness of treatment might be associated with the short stratification and suggest that a longer period of stratification should be used. The present study evaluated only this short stratification period due to the restricted number of mericarps available.

Bondeson (1986) described the presence of a germination plug in the pericarp of *N. humifusa* and *N. paradoxa*. This structure was identified in the present study (Fig. 3) and was chosen for scarification treatments. The importance of the pericarp location in which the cut is performed was confirmed by the results obtained from the experiments involving variations in T3, T4 and T5 (Table 1); when the cut was performed in a different area of the fruit, lower germination percentages were observed compared with the same treatment with the cut made at the funicular scar. By cutting the fruit at the funicular area, the adjacent endosperm may have been partially eliminated. This tissue has been described as a limiting

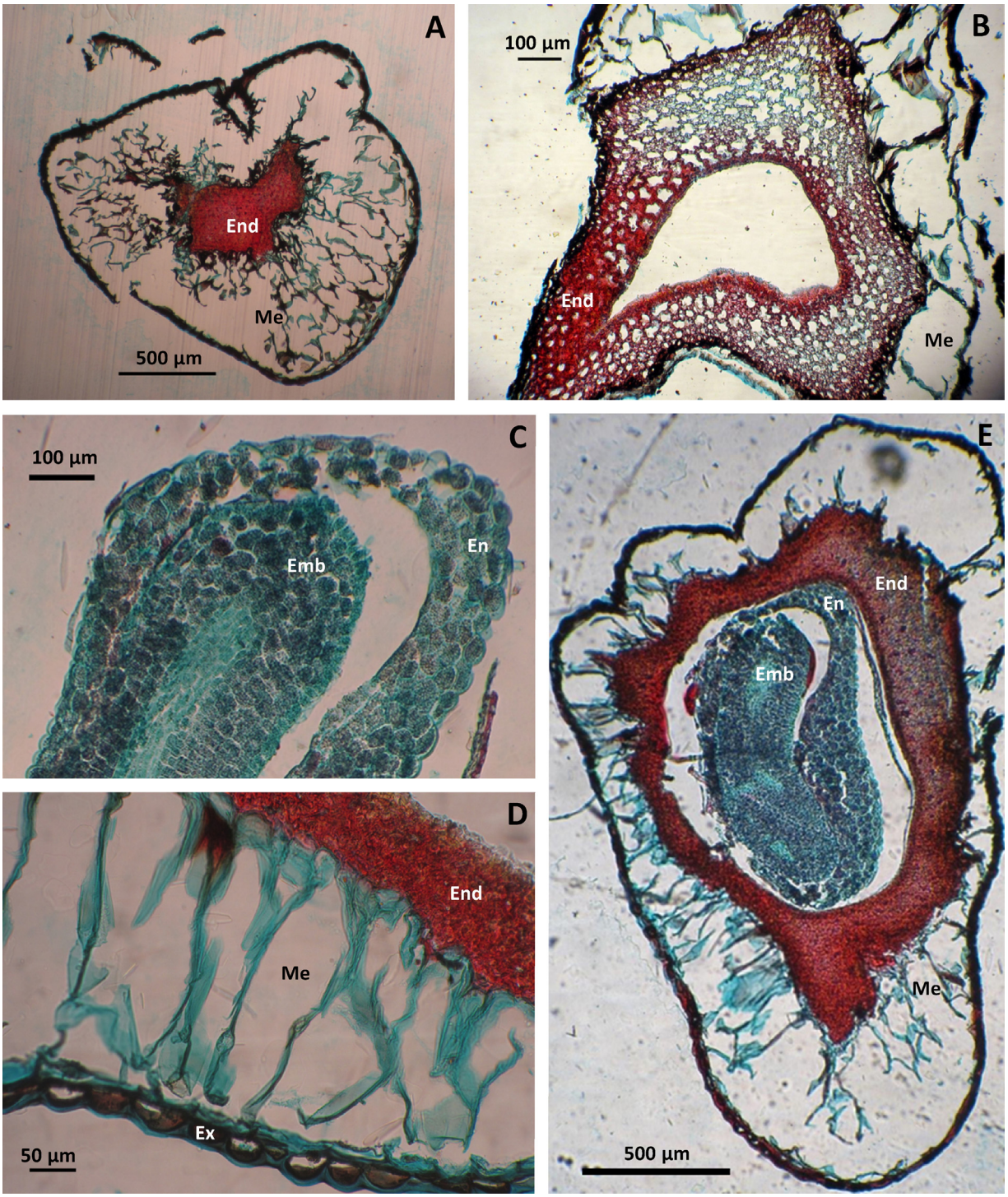

Fig. 2. Histological sections of the fruit of *Nolana jaffuelii* photographed with a light microscope. (A) A tangential section of the pericarp, 40×. (B) A cross-section of a nucule with an empty embryonic cavity, 100×. (C) A longitudinal section of embryo covered by the endosperm, 100×. (D) A cross-section through the mericarp and exocarp, 200×. (E) A cross-section of nucule through the pericarp, embryonic camera and embryo, 40×. Abbreviations: End endocarp; Me, mesocarp; Em, embryo; En, endosperm; Ex, exocarp.

factor for the germination of Solanaceae species, particularly tomatoes (*Solanum lycopersicum*) and peppers (*Capsicum annuum*) of the Solanoideae subgroup, to which *Solanum* and *Nolana* also belong (Finch-Savage and Leubner-Metzger, 2006); therefore, by eliminating or weakening the endosperm in this area, the physiological dormancy may be reduced.

A second experiment (Section 2.3.2) was conducted to verify the existence of physical and physiological dormancy. The results of this experiment (Table 2) confirm the results obtained in Section

Table 1
The germination percentage of *Nolana jaffuelii* seeds scarified with a cut in the funicle scar or in a different area of the pericarp, with and without the application of gibberellic acid (500 mg l^{-1} GA_3) or stratification (14 days at 4 °C). For each value, the 95% confidence interval is presented between brackets.

Type of scarification	Additional treatment		
	None	Gibberellic acid	Stratification
Cut in funicular scar	1.3[0–3.9]	32.0[21.4–42.6]	9.3[2.7–15.9]
Cut in a different area	0	8.0 [0–18.6]	4.0 [0–11.7]

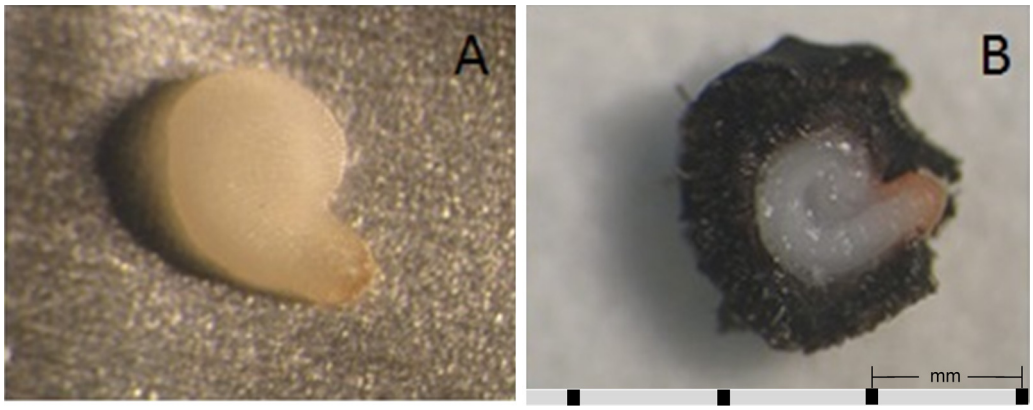

Fig. 3. An embryo of *Nolana jaffuelii* photographed with a stereomicroscope (120×), mm scale. (A) An embryo covered by the endosperm. (B) A longitudinal section of a nucule, showing the curved embryo.

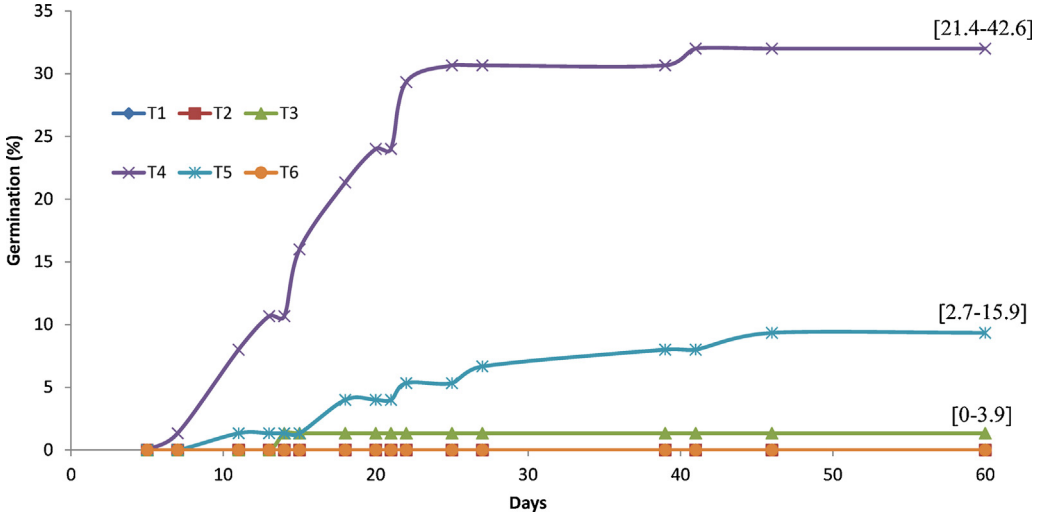

Fig. 4. Cumulative germination of *Nolana jaffuelii* seeds after six treatments (T): (T1) control, i.e., intact fruits imbibed in water; (T2) intact fruits washed for 5 min under running water and imbibed in water; (T3) scarified fruits, i.e., cut at the funicular scar, imbibed in water; (T4) scarified fruits imbibed in gibberellic acid (500 mg l^{-1} GA_3); (T5) scarified fruits imbibed in water with 2 weeks stratification at 4 °C; and (T6) intact fruits imbibed in GA_3. The 95% confidence interval for the germination percentage after 60 days is shown between square brackets for T3, T4 and T5.

2.3.1 regarding the absence of germination when intact mericarps where imbibed, occurrence of germination when mericarps were scarified, and improvement of the germination percentage when scarification was combined with GA_3 imbibition, supporting the existence of combinational dormancy (i.e., physical and physiological; Baskin and Baskin, 2004) in *N. jaffuelii*. However, in Section 2.3.2, scarified mericarps imbibed in water reached 38% germination, higher than the 1% germination observed in mericarps treated the same way in Section 2.3.1. A possible explanation for this change is that the physiological dormancy present in these mericarps was partially broken due to after-ripening, which is defined as a progressive loss of dormancy in mature dry seeds (Black et al., 2006). The mericarps used in Section 2.3.1 were collected in April 2013 and stored for one month, while the mericarps used in Section 2.3.2 were collected in October 2013 and stored for two months. Although the exact moment of maturation and shedding for these mericarps is unknown, it probably occurred around November or December 2012. Because the mericarps were dry and have physical dormancy, embryo after-ripening may have occurred before seed collection and during storage. According to Baskin and Baskin (1998, 2004),), after-ripening reduces the length of cold stratification needed to break intermediate physiological dormancy and promotes germination in seeds with non-deep physiological dormancy. Douglas and Freyre (2006) also mentioned after-ripening as an effective treatment for other *Nolana* species. The MGT, which is a measure of the germination speed, was shorter (i.e., there was faster germination) when scarified mericarps were imbibed in GA_3 (Table 2), although this difference was not statistically significant. The improvement of germination by GA_3 and the possible after-ripening effect support the presence of intermediate to non-deep physiological dormancy in *N. jaffuelii* mericarps.

Table 2
The germination percentage and mean germination time of *Nolana jaffuelii* seeds after different treatments. Control: intact fruits imbibed in water; scarification: fruits cut at the funicular scar imbibed in water; scarification + GA_3: fruits cut at the funicular scar imbibed in a solution of gibberellic acid (500 mg l^{-1} GA_3). Germination was evaluated at 20 °C for 30 days.

Treatment	Germination(%)	Mean germination time (days)
Control	0 c[b]	–
Scarification	38[b]	4.8
Scarification + GA_3	50[a]	3.4
P value[a]	<0.001	0.167

[a] *P* value from an analysis of variance.
[b] In each column, values with different letters are significantly different according to a LSD test ($\alpha = 0.05$)

The physical and physiological dormancies found in *N. jaffuelii* propagules would be related to the climatic conditions under which this species grows and are characteristic of the coastal lomas formations of the Atacama Desert. In this area, as occurs in other deserts of the world, periods where environmental conditions are favorable for the development of the entire life cycle of an annual plant are spaced between long and variable periods of time with adverse conditions (Baskin and Baskin, 1998; Gutterman, 2002). For this reason, dormancy mechanisms to prevent the mericarps from germinating at inappropriate times were expected.

Baskin and Baskin (1998) found that the percentage of species with seeds that have some type of dormancy increased from 39% in rainforests to 84% in hot deserts and was up to 90% in cold deserts. According to Gutterman (2000), the most common type of seed dormancy occurring in desert environments is physiological, followed by physical. Bansal and Sen (1981) reported that a water impermeable seed coat was the most common mechanism responsible for dormancy for the Indian arid zone species they studied.

The presence of a waterproof coat may contribute to the formation of a persistent seed bank for *N. jaffuelii* because it would protect the embryo from moisture fluctuations and delay the breaking of physiological dormancy by preventing the imbibition of the embryo. Furthermore, the presence of an impermeable seed coat would decrease the deterioration of the propagule (Halloin, 1983). Persistent seed banks have been described as one of the main adaptations of species in arid climates (Baskin and Baskin, 1998). In these environments, which are unpredictable in terms of the moment and duration of rainfall, seeds possess dormancy mechanisms that allow them to remain viable for long periods of time (Figueroa et al., 2004) until environmental conditions are favorable for germination and seedling establishment. Rainy years would therefore correspond to an opportunity for the regeneration, replacement and maintenance of the seed bank (Gutiérrez et al., 2000).

The ecological goal of dormancy is to allow seed germination at a time when the environmental conditions are favorable for the establishment and reproduction of the species (Walck et al., 2005); however, the question regarding how this dormancy is broken for *N. jaffuelii* in its natural habitat remains unanswered. Gutterman (1994) suggested that mechanical scarification could happen to a seed by rolling and rubbing against sand grains and stones whenever rains fall, but this has not been proven either in the laboratory or in the field (Baskin and Baskin, 1998). The presence of the germination plug in *N. jaffuelli* mericarps suggests that another mechanism related to the release of the plug probably takes place to break dormancy, rather than a scarification by friction, particularly because scarification in other areas of the pericarp was not shown to be as effective as removing the germination plug (Table 1).

Little is known about the survival and germination strategies used by *N. jaffuelii* and other species present in Chileans fog oases. The information provided in this study will improve our understanding of the reproductive biology and adaptation strategies of the species in these ecosystems and in turn, will allow us to develop better propagation and conservation programs, which is very important given the current crisis in terms of the loss of biodiversity (Chapin et al., 2000). Future studies should attempt to evaluate if dormancy mechanisms observed in *N. jaffuelii* mericarps are present in other species of the lomas formations, in particular other *Nolana* such as *N. sedifolia*, *N. intonsa* and *N. aplocaryoides*. Another aspect that deserves investigation is the mechanism by which this dormancy is broken under natural conditions.

4. Conclusions

Propagules of *N. jaffuelii* exhibit a low percentage of germination. For the best results, it was necessary to perform mechanical scarification on the funicular zone and to imbibe the mericarps in a solution of gibberellic acid (500 mg l^{-1} GA_3). The results of this investigation revealed the existence of physical and physiological dormancies (combinational dormancy) in the propagules, an adaptation that would allow the species to survive in seed banks until the occurrence of favorable conditions.

Acknowledgements

We thank the Centro del Desierto de Atacama (Atacama Desert Center) for facilitating the visit to the study site and funding the travel and thank Gloria Montenegro for assistance and for providing access to the laboratory. We also thank Luis González for making the histological sections used in this investigation. Economic support that helps performance of this study was provided by a Conicyt Scholarship to Josefina Hepp.

References

Bansal, P., Sen, D.N., 1981. Differential germination behavior in seeds of the Indian arid zone. R Folia Geobot. Phytotax. 16, 317–330.
Baskin, C.C., Baskin, J.M., 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego, California.
Baskin, J.M., Baskin, C.C., 2004. A classification system for seed dormancy. Seed Sci. Res. 14, 1–16.
Bewley, J.D., Bradford, K.J., Hilhorst, H.W.M., Nonogaki, H., 2013. Seeds: Physiology of Development, Germination and Dormancy, 3rd Edition. Springer Science+Business Media, LLC, New York, http://dx.doi.org/10.1007/978-1-4614-4693-4
Black, M., Bewley, D., Halmer, P., 2006. The Encyclopedia of Seeds: Science, Technology and Uses. CAB International, Wallingford, UK.
Bondeson, W.E., 1986. Gynoecial morphology and funicular germination plugs in the Nolanaceae. Nordic J. Bot. 6, 183–198.
Cereceda, P., Osses, P., Larrain, H., Farias, M., Lagos, M., Pinto, R., Schemenauer, R.S., 2002. Advective, orographic and radiation fog in the Tarapacá region, Chile. Atmos. Res. 64, 261–271.
Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242.
Dillon, M.O., Tu, T., Soejima, A., Yi, T., Nie, Z., Tye, A., 2007a. Phylogeny of *Nolana* (*Nolaneae, Solanoideae, Solanaceae*) as inferred from granule-bound starch synthase I (GBSSI) sequences. Taxon 56, 1000–1011.
Dillon, M.O., Arancio, G., Luebert, F., 2007b. Five new species of *Nolana* (*Solanaceae-Nolaneae*) from Chile. Arnaldoa 14, 191–212.
Dillon, M.O., Tu, T., Xie, L., Quipuscoa, V., Wen, J., 2009. Biogeographic diversification in *Nolana* (Solanaceae), a ubiquitous member of the Atacama and Peruvian Deserts along the western coast of South America. J. Syst. Evol. 47, 457–476.
Douglas, A., Freyre, R., 2006. Determination of seed germination requirements in *Nolana* sp. HortScience 41, 1002 (abstr.).
Ellis, R.H., Roberts, E.H., 1980. Toward a rational basis for testing seed quality. In: Hebblethwaite, P.D. (Ed.), Seed Production. Butterworths, London, pp. 605–635.
Figueroa, J.A., León-Lobos, P., Cavieres, L.A., Pritchard, H., 2004. Ecofisiología de semillas en ambientes contrastantes de Chile: un gradiente desde ecosistemas desérticos a templado-húmedos. In: Marino, H. (Ed.), Fisiología Ecológica en Plantas: Mecanismos y Respuestas a Estrés en los Ecosistemas. Ediciones Universidad Católica de Valparaíso, Valparaíso, pp. 81–98.
Finch-Savage, W.E., Leubner-Metzger, G., 2006. Seed dormancy and the control of germination. New Phytol. 171, 501–523.
Gómez, M., Munita, K., Guerrero, B., 2012. El banco de semillas del oasis de niebla de Alto Patache. In: Alonso, P. (Ed.), Deserta. ARQ ediciones, Santiago, pp. 69–75.
Gutiérrez, J.R., Arancio, Jaksic, G., F, 2000. Variation in vegetation and seed bank in a Chilean semi-arid community affected by ENSO 1997. J. Veg. Sci. 11, 641–648.
Gutterman, Y., 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. Bot. Rev. 60, 373–425.
Gutterman, Y., 2000. Seed dormancy as one of the survival strategies in annual plant species occuring in deserts. In: Viemont C, J.D., Crabbé, J. (Eds.), Dormancy in Plants: from Whole Plant Behavior to Cellular Control. CABI, Wallingford, pp. 139–159.
Gutterman, Y., 2002. Survival adaptations and strategies of annuals occurring in the Judean and Negev Deserts of Israel. Isr. J. Plant Sci. 50, 165–175.
Halloin, J.M., 1982. Localization and changes in catechin and tannins during development and ripening of cottonseed. New Phytol. 90, 651–657.
Halloin, J.M., 1983. Deterioration resistance mechanisms in seeds. Res. Plant Physiol. 73, 335–339.
Johnston, I.M., 1936. A study of the *Nolanaceae*. Proc. Am. Acad. Arts Sci. 71 (1–83), 85–87.
Martin, A.C., 1946. The comparative internal morphology of seeds. Am. Midl. Nat. 36, 513–660.

Mead, R., Curnow, R.N., Hasted, A.M., 1993. Statistical Methods in Agriculture and Experimental Biology, 2nd Edition. Chapman & Hall/CRC Press LLC, New York and Boca Raton, FL.
Muñoz-Schick, M., Pinto, R., Mesa, A., Moreira-Muñoz, A., 2001. Oasis de neblina en los cerros costeros del sur de Iquique, región de Tarapaca, Chile, durante el evento El Niño 1997–1998. Rev. Chil. Hist. Nat. 74, 389–405.
Pinto, R., Luebert, F., 2009. Datos sobre la flora vascular del desierto costero de Arica y Tarapaca, Chile, y sus relaciones fitogeográficas con el sur de Peru. Gayana Bot. 66, 28–49.
Pinto, R., Larraín, H., Cereceda, P., Lázaro, P., Osses, P., Schemenauer, R.S., 2001. Proceedings of the 2nd International Conference on Fog and Fog Collection. Saint Johnís Canada, pp. 293–296.
Rundel, P.R., Dillon, M.O., Palma, B., Mooney, H.A., Gulmon, S.L., Ehleringer, J.R., 1991. The phytogeography and ecology of the coastal Atacama and Peruvian deserts. Aliso 13, 1–50.
Saunders, E.R., 1936. On certain unique features of the gynoecium in *Nolanaceae*. New Phytol. 35, 423–431.
Schultz, N., Aceituno, P., Richter, M., 2011. Phytogeographic divisions, climate change and plant dieback along the coastal desert of Northern Chile. Erdkunde 65, 169–187.
Tago-Nakazawa, M., Dillon, M.O., 1999. Biogeografía y evolución del Clado *Nolana* (*Nolaneae-Solanaceae*). Arnaldoa 6, 81–166.
Walck, J.L., Baskin, J.M., Baskin, C.C., Hidayati, S.N., 2005. Defining transient and persistent seed banks in species with pronounced seasonal dormancy and germination patterns. Seed Sci. Res. 15, 189–196.
Watson, L., Dallwitz, M.J., 1992 onwards. The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version: 19th August 2013. http://delta-intkey.com