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Intraespecific variation in drought resistance of *Nothofagus antarctica* (G. Forst.) Oerst. (Nothofagaceae)

Variación intraespecífica en resistencia a la sequía de *Nothofagus antarctica* (G. Forst.) Oerst. (Nothofagaceae)

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RESUMEN

Futuros escenarios climáticos limitarían el establecimiento de plántulas en bosques de los Andes del sur debido al estrés hídrico. Comparamos la resistencia a la sequía de plántulas de *Nothofagus antarctica* de dos límites arbóreos: Termas de Chillán (clima mediterráneo) y Antillanca (clima superhúmedo). También comparamos la resistencia a la sequía de plántulas de dos altitudes diferentes de Antillanca. No encontramos diferencias en resistencia a la sequía entre plántulas de los dos límites arbóreos. Las plántulas del límite arbóreo de Antillanca resultaron más resistentes que las de una menor elevación.

Alpine treelines are natural ecotones mainly controlled by low temperature and hence they are considered one of the most responsive systems to global warming (Körner 1998). Seedlings establishment is seriously impeded by low temperatures at treeline ecotones (Cavieres & Piper 2004, Körner 1998), and therefore warmer conditions could promote establishment (Holtmeier & Broll 2005, Taylor 1995). In regions like the southern Andes, where water availability already limits seedlings establishment (Daniels & Veblen 2004, Heinemann & Kitzberger 2006) and precipitation is predicted to decline (CONAMA 2006), to know the capacity of seedlings to overcome concomitant drought becomes important.

Widespread species frequently have high intraspecific variation which may entail different responses to climate change and eventually affect species distribution (Benito Garzón *et al.* 2011). In treeline species, traits improving the water economy (e.g., lower specific leaf area, smaller leaf and tree sizes) are generally observed at higher elevations and drier latitudes (Premoli *et al.* 2007, Fajardo & Piper 2011), although it is not clear whether drought resistance does vary accordingly.

At alpine treelines of the southern Andes seedlings establishment is co-limited by water availability and low temperatures (Daniels & Veblen 2004). Climatic models for the region predict 2-4°C temperature increment and 40% precipitation reduction for the growing season (CONAMA, 2006). In this study, we examined intraspecific variation in drought resistance of *Nothofagus antarctica* (G. Forst.) Oerst., related to altitude and latitude. *N. antarctica* is a deciduous broadleaf treeline species that extends across a wide latitudinal and altitudinal range in the southern Andes of Chile and Argentina (Rodríguez & Quezada 2003). We conducted a drought experiment using recently-emerged seedlings from three different provenances: Antillanca treeline (40°47'S, 72°11'W, 1350 m a.s.l., within the Puyehue National Park, hereafter Antillanca$_{treeline}$), Antillanca 1200 m a.s.l. (hereafter Antillanca$_{1200}$), and Termas de Chillán treeline (36°54′S and 71°24′W, 2080 m a.s.l., hereafter Termas de Chillán$_{treeline}$). Although *Nothofagus pumilio* is the most extensive treeline species in the Southern Andes, both *N. antarctica* and *N. pumilio* are treeline species in the two study sites. Mean annual precipitation is about 1900 mm in Termas de Chillán and 3660 in Antillanca, with a pronounced summer drought characterizing the former (Fajardo & Piper 2011). Given the wide distribution of *N. antarctica* across contrasting climates and its high level of intraspecific variation (Steinke *et al.* 2008) local adaptation can be expected. In particular, populations from Mediterranean provenances should account for a higher drought resistance than populations from more humid sites. Likewise, treeline species show a high intraspecific variation with altitude in physiological and structural traits related to drought resistance, suggesting an increasing drought resistance with elevation despite of higher precipitation (Li *et al.* 2004, Fajardo & Piper 2011). We hypothesized that seedlings from Termas de Chillán$_{treeline}$ are more drought resistant than seedlings from Antillanca$_{treeline}$. Between elevations, seedlings from Antillanca$_{treeline}$ are expected to be more resistant than seedlings from Antillanca$_{1200}$.

Seeds of *N. antarctica* were collected from five mature trees at each site in March 2009, sown in Petri dishes in August 2009, and maintained in a growth chamber (Universidad Austral de Chile) till the third week of September 2009 when germinant seedlings were transplanted to speedling trays containing a sand-organic (1:1) mix as substrate. These speedlings were then transported to a private greenhouse. Seed and seedling dry mass were similar between provenances. Two levels of watering (*control:* watering every other day; *drought*: no watering) were randomly assigned to even-sized seedlings of each seed-provenance. For Termas de Chillán$_{treeline}$, Antillanca$_{treeline}$, and Antillanca$_{1200}$, 15, 21, and 47 seedlings were subjected to drought, respectively, whereas 17, 22, and 59 seedlings were kept as control, respectively. The number of seedlings in each treatment varied due to different germination capacities among provenances, e.g. *N. antarctica* shows low germination capacity (Premoli 1991). In our study, very few seeds of Termas de Chillán$_{treeline}$ germinated, limiting the number of seedlings in the experiment for this provenance. Soil volumetric water content (VWC) was daily measured in each watering level by one probe (ECH2O S-SMA-M005) connected to a logger (HOBO® Micro Station, Onset Computer Corporation).

The experiment started by November 26th and finished on December 14th, 2009. Every 2-5 days, 3-11 seedlings per treatment –depending on the initial number– were randomly recorded for survival. Each seedling was recorded once. This procedure is similar to the one adopted by Piper *et al.* (2007). Time-courses of soil VWC (continuous variable) and survival (binary variable) were obtained for each provenance and the effect of VWC on survival was assessed by logistic regression. The VWC predicted for a given survival proportion was estimated by inverse prediction. Intraspecific differences between altitudes and latitudes in the effect of VWC on survival were tested by nominal logistic models. Significance effects were calculated using likelihood ratio Chi-square tests (JMP® 8.0 SAS Institute Inc.).

Treeline seed-provenances showed a similar decrease in seedling survival as VWC declined (provenance: χ^2=0.69, P=0.405; VWC: χ^2=46.46, P<0.0001; provenance x VWC: χ^2=0.09, P=0.766), indicating no intraspecific variation in drought resistance between seedlings of the two treeline provenances (Fig. 1A). In contrast, seedlings from Antillanca$_{treeline}$ were more drought resistant than seedlings from Antillanca$_{1200}$ (provenance: χ^2=9.745, P=0.002; VWC: χ^2=65.5, P<0.0001; provenance x VWC*:* χ^2=2.11, P=0.146; Fig. 1B).

The similar drought resistance between treeline provenances found in this study, along with the lower precipitation and soil humidity reported for Termas de Chillán$_{treeline}$ than for Antillanca$_{treeline}$, suggests that seedlings establishment at Termas de Chillan$_{treeline}$ is more impaired by drought than at Antillanca$_{treeline}$. This may explain the different abundance of *N. antarctica* seedlings between sites: in 60 sampling plots (1 m^2) along six transects, no single seedling was found in Termas de Chillan$_{treeline}$, whereas six seedlings (<10 cm height) were recorded at Antillanca$_{treeline}$ (F. Piper & A. Fajardo, unpublished). Although differences between the substrate used in the experiment and that of the treeline may limit more precise inferences on drought effects on seedling establishment, soil VWC measurements at the field sites are informative on the current impact of drought: average VWC corresponding to the upper 18 cm of ground for two growing seasons were 0.08 and 0.19 m^3m^{-3} for Termas de Chillan$_{treeline}$ and Antillanca$_{treeline}$, respectively (Fajardo *et al.* 2011), which according to the inverse prediction could reduce seedling survival to 62 and 95%, respectively (Fig. 1A). Climatic models for the region predict about 40% precipitation reduction for the two sites; we anticipate that seedling establishment could become reduced to ca. 32% in Termas de Chillan$_{treeline}$ and to 65% in Antillanca$_{treeline}$ (Fig. 1A). Nonetheless, this prediction must be interpreted as preliminary, in particular due to the reduced number of Termas de Chillán$_{treeline}$ seedlings used to construct the model.

Precipitation in Antillanca$_{treeline}$ is not significantly different from Antillanca$_{1200}$ (Almeyda & Sáez 1958) and therefore we could assume that both elevations have similar VWC (0.19 m^3m^{-3}, see above). According to our model, this value reduces seedlings survival in Antillanca$_{1200}$ to 68%, indicating thus that current soil humidity impacts more negatively at this elevation than at the treeline (where survival is reduced to 95%, see above). Likewise, predicted 40% decrease in annual precipitation could imply more important reductions in seedlings survival of Antillanca$_{1200}$ than Antillanca$_{treeline}$ (Fig. 1B).

Our results suggest genetic differences in drought resistance between the two populations of Antillanca, in spite of the reduced difference in elevation. Similarly, genetic differences in ecophysiological traits between populations separated by a few hundred meters along altitude have been reported for the congeneric *N. pumilio* (Premoli & Brewer 2007). Different morphotypes likely adapted to their habitats have been described in *Nothofagus antarctica* across different elevations, in particular, a high-elevation morphotype is indicated as genetically distinctive (Steinke *et al.* 2008). According to our study, elevation may have selected for drought resistance within this morphotype.

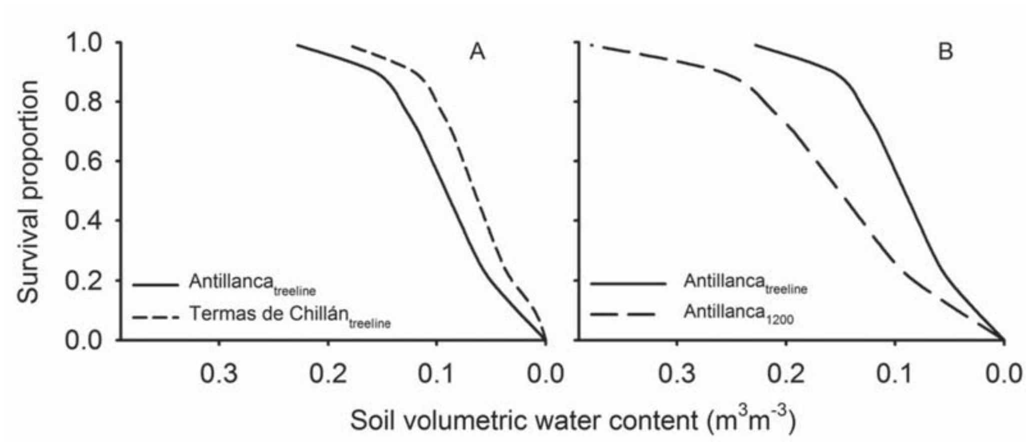

Figure 1. Effect of soil volumetric water content on survival of seedlings coming from different seed-provenances, modeled by logistic regression. A: Treeline comparison; B: Altitudinal comparison in Antillanca. Termas de $Chillan_{treeline}$: $R^2 = 0.52$, P=0.001; $Antillanca_{treeline}$: $R^2 = 0.51$, P < 0.0001; $Antillanca_{1200}$: $R^2 = 0.40$, P < 0.0001.

Figura 1. Efecto del contenido volumétrico de agua en el suelo sobre la sobrevivencia de plántulas de diferentes procedencias, modelado por regresión logística. A: Comparación de límites arbóreos de diferente latitud; B: Comparación de dos elevaciones en Antillanca. Termas de $Chillán_{treeline}$: $R^2 = 0.52$, P=0.001; $Antillanca_{treeline}$: $R^2 = 0.51$, P < 0.0001; $Antillanca_{1200}$: $R^2 = 0.40$, P < 0.0001.

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