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Source: Arctic, Antarctic, and Alpine Research, 48(4):755-766.
Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado
DOI: http://dx.doi.org/10.1657/AAAR0016-015
URL: http://www.bioone.org/doi/full/10.1657/AAAR0016-015

Arctic, Antarctic, and Alpine Research, Vol. 48, No. 4, 2016, pp. 755–766
DOI: http://dx.doi.org/10.1657/AAAR0016-015

Establishment of *Nothofagus pumilio* at upper treelines across a precipitation gradient in the northern Patagonian Andes

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ABSTRACT

Trees at upper treelines are exposed to more extreme environmental conditions than those at lower elevations. Climate changes at the upper treeline facilitate the establishment or intensify the mortality of trees and, consequently, affect species distributions. The structure and density of individuals of *Nothofagus pumilio* above the upper treeline, together with their temporal patterns of establishment, were determined in three sites located along a west-east precipitation gradient across the Patagonian Andes. Patterns of tree establishment were compared to regional variations in temperature and precipitation, as well as to indexes of atmospheric circulation that modulate northern Patagonian climate. Mesic and dry sites along the moisture gradient have a lower density of newly established trees; however, individuals show larger basal diameters and greater annual growth rates, heights, and number of branches than those established in humid sites. In wet areas, the high density of individuals reflects the higher rates of *N. pumilio* establishment and survival. At drier treelines, low snow persistence, associated with longer growing seasons, appears to be related to the larger size of individuals. At all sites, patterns of tree establishment are characterized by an abrupt increase in recruitment starting in the mid-1970s and a marked decrease in the late 1990s. The onset of tree establishment above the treeline coincides with an increase in regional spring-summer temperature in the year 1977, concurrent with the negative-to-positive shift in the phase of the Pacific Decadal Oscillation (PDO). In contrast, the decrease in *N. pumilio* establishment since the late 1990s coincides with an opposite shift (positive to negative) in the PDO. This recent change in the PDO phase did not significantly modify the mean values but increased the interannual variability of the spring-summer temperatures in the region. Changes in the PDO, which encompasses complex variations in environmental conditions at the upper treeline, are more closely related to *N. pumilio* establishment than are variations in temperature or precipitation alone. In addition, the distinction between the effects of changes in mean values versus the effects of climate variability is crucial for properly predicting forest responses to climate changes.

INTRODUCTION

Trees at the upper treeline are particularly sensitive to environmental changes that modulate the rates of tree establishment and mortality. In a long-term context, these changes in tree dynamics cause the advance of forests into new areas or a reduction in the current distribution. Documenting treeline dynamics therefore provides excellent opportunities for predicting tree responses to future climate changes.

In mountain forests, the upper limit of tree distribution is generally determined by the mean temperature during the growing season. In most temperate and cold regions, mean temperatures during the growth period at the upper treeline oscillate between 5 and 7 °C (Tranquillini, 1979; Jobbágy and Jackson, 2000; Grace et al., 2002; Camarero and Gutiérrez, 2004; Körner and Paulsen, 2004; among others). However, predicting climate-driven changes at the upper treeline is challenging because tree establishment is not influenced by mean temperature fluctuations alone (Lindner et al., 2010). Variations in site conditions modulated by topography, soil properties, and species interactions introduce a high degree of heterogeneity in mountain habitats, and thus in the response of vegetation to climate (Lindner et al., 2010).

Temporal patterns of tree establishment at the upper treeline have been recorded over the past several decades to evaluate the response of vegetation to variations in environmental conditions. Woodward et al. (1995) demonstrated that spatial patterns of tree establishment along a steep precipitation gradient in the Olympic Mountains, Washington, U.S.A. are modulated by temporal changes in precipitation. At wet and cold Tsuga *mertensiana* sites, tree establishment occurred during drier than average summers. In contrast, at the dry end of the gradient, *Abies lasiocarpa* establishment occurred when site conditions were wetter than average. More recently, Elliott (2012) used regime shift analysis to establish the relationships between climate and tree recruitment at the upper treeline along a latitudinal gradient in the Rocky Mountains, U.S.A. Synchronous, sometimes abrupt changes in tree establishment on a regional scale occur when regional climate variability exceeds some bioclimatic thresholds. For example, reduced cool-season precipitation in the 1950s was associated with an abrupt increase in regional tree establishment, which was unprecedented in the past four centuries (Elliott, 2012).

Daniels and Veblen (2003, 2004) recorded the patterns of radial growth and tree establishment in the subalpine *N. pumilio* forests of northern Patagonia. They found that the increase in tree establishment during the 1980s was modulated by a rise in temperature concurrent with favorable moisture conditions (Daniels and Veblen, 2004). In southern Patagonia, a marked increase in *N. pumilio* establishment above the upper treeline has been associated with warmer summer temperatures since the mid-1970s (Srur et al., unpublished data). Other studies, however, relate tree establishment in the *N. pumilio* subalpine forests to biotic factors. For example, Cuevas (2000, 2002) reported peaks of seedling establishment in 1982, 1988, and 1996, concurrent with years of abundant seed production in subalpine *N. pumilio* forests at Cerro Balseiro, Tierra del Fuego.

Traditionally, studies documenting the responses of vegetation to climate variability have been based largely on comparisons with temperature or precipitation changes at local or regional scales (Briffa et al., 1998; Camarero and Gutiérrez, 2004; Büntgen et al., 2007; Aune et al., 2011; Camarero et al., 2015; among others). However, Stenseth et al. (2003) postulated that atmospheric circulation indexes, such as El Niño Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO), are more strongly related to biological changes than to temperature or precipitation records. The circulation indexes act as "climate packages" that combine a set of variations in climate, simultaneously encompassing changes in temperature, precipitation, wind, and solar radiation, among others. According to Stenseth et al. (2003), these climate indexes reduce the spatial complexity and temporal variability of climate to simpler and more robust measures.

General circulation models estimate an increase in mean temperatures between 1 °C and 3 °C by the end of the 21st century for the Patagonian Andes (IPCC, 2014). They also predict a reduction in summer precipitation, which, depending on the geographical location, will oscillate between 10% and 30% over the same period (IPCC, 2014). However, recent studies show that these trends in climate are nonlinear and largely affected by natural climate variability. For example, a deceleration in the rise of global temperatures since 1999 has been attributed to a change from positive to negative in the PDO phase (Trenberth and Fasullo, 2013; Trenberth et al., 2014). This PDO phase change has been associated with drier conditions and lower temperatures in northern Patagonia (Trenberth et al., 2014; Vuille et al., 2015).

The present study examines the relationship between variations in *Nothofagus pumilio* establishment and regional climate along a west-to-east precipitation gradient in the northern Patagonian Andes. To this end, we documented the structure and density of trees at three sites above the upper treeline along the precipitation gradient. Temporal patterns of tree establishment were reconstructed using dendrochronological methods and compared with interannual variations in precipitation and temperature, as well as with indexes of atmospheric circulation such as ENSO and PDO. Finally, we explored differences in forest structure along the precipitation gradient and discussed how climate fluctuations induced by changes in circulation indexes modulate tree establishment at upper treelines in the Andes of northern Patagonia.

MATERIALS AND METHODS

Study Area

The mountainous relief of the Patagonian Andes includes major chains cut transversally by extended valleys with lakes of glacial origin. The climate is temperate-cold with rainfall concentrated during the winter. The interannual and long-term climatic variability in the region is modulated by a combination of tropical and high-latitude forcings, the ENSO-PDO and SAM (Southern Annular Mode), respectively. ENSO is the main source of interannual variability in precipitation and temperature across South America, whereas decadal to multidecadal variability in climate is associated with PDO (Garreaud et al., 2009). SAM influences precipitation patterns across the southern Andes mainly during spring and summer, and temperature regimes all year round in southern South America (Garreaud et al., 2009).

The presence of the Andes, which intercept dominant moist air masses from the Pacific Ocean, imposes a marked west-to-east precipitation gradient (Villalba et al., 2003; Garreaud et al., 2009). At 40 °S, precipitation decreases from 4000 mm per year in the highest peaks of the Cordillera to less than 800 mm in the forest-steppe ecotone to the east (De Fina, 1972; Cordon et al., 1993; Villalba et al., 2003). Snow cover duration varies along the precipitation gradient, ranging from 90 to more than 140 days at the dry and wet ends of the east-to-west transect, respectively (meteorological data for 2013–2014 from IANIGLA).

Across the Patagonian Andes, the upper limit of the subalpine forest is dominated mostly by *N. pumilio*. In our study areas, the limit of tree vegetation is marked by stunted individuals, which have assumed a krummholz form in response to the large and persistent snow cover during winter and early spring. Erect *N. pumilio* trees, up to 25 m in height, grow at lower elevations, demonstrating the large morphological plasticity of this species. The upper limit of the forest is abrupt, without small patches or isolated trees as recorded in treelines elsewhere (Fig. 1). The three study sites are located in Parque Nacional Nahuel Huapi, Provincia de Río Negro, Argentina (Table 1 and Fig. 2).

Fieldwork and Laboratory Methods

Sampling was conducted during the austral summers of 2008–2009 and 2009–2010. Two rectangular plots (~600 m^2) were established at each of the three sites, extending from the local treeline up to the alpine grasses (Fig. 1). Tree height, number of stems per tree, and diameter at the base of the stem for all *N. pumilio* individuals were recorded at each plot to determine tree density and structural characteristics. In order to determine the year of establishment, increment cores were taken as close to the base as possible using an increment borer. Individuals with a basal diameter of < 3 cm were cut at the root collar, and their cross-sections sliced in the laboratory using a sliding microtome. At the Challhuaco and Diego de León sites, 19 and 22 individuals were sampled, respectively, in order to determine the year of establishment. In La Almohadilla, the site with the highest tree density, we sampled, at random, 1 in every 4 individuals for a total of 61 samples. Increment borer samples were mounted on wooden mounts and subsequently polished. For samples not reaching the pith, the number of missing rings was estimated following Villalba and Veblen (1997). Cross sections and increment borer samples were dated under a microscope following the technique proposed by Stokes and Smiley (1968). Tree-ring widths were measured

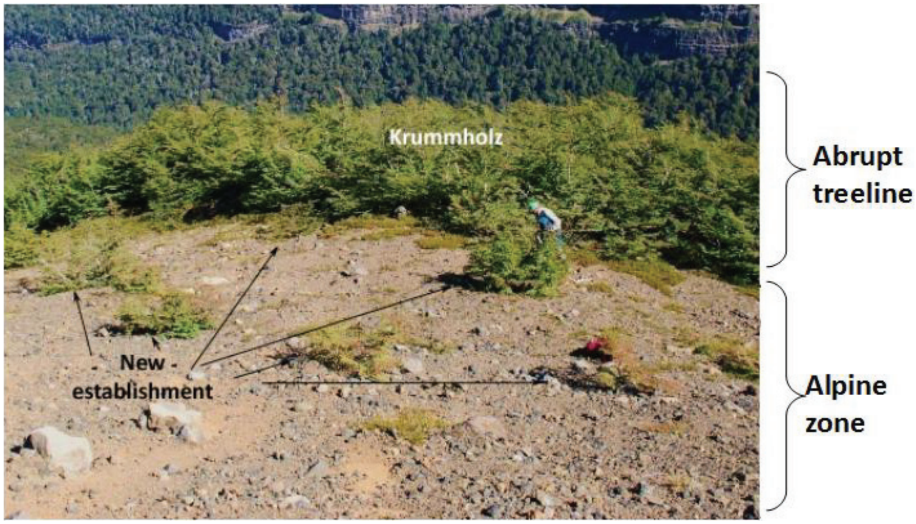

FIGURE 1. Establishment of new Nothofagus pumilio individuals above the upper altitudinal limit of the forest in the area of Cerro Tronador, Río Negro, Argentina.

TABLE 1

Geographic location and characteristics of sample sites. Precipitation data are indicated using the isohyet nearest to the study site. Snowpack duration in days and mean growing season temperature (November–March) from data loggers placed at the sites by the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-CONICET).

	Challhuaco	Diego de León	La Almohadilla
Code	CHA	DDL	ALM
Latitude S	41.27°	41.28°	41.18°
Longitude W	71.30°	71.65°	71.80°
Elevation (m)	1709	1389	1515
Slope (°)	22.83	32.71	23.58
Aspect	SE	NW	SW
Soil type	Inceptisols	Inceptisols	Inceptisols
Precipitation (mm)	1000	1500	2500
Temperature (°C)	9.1	8.9	8.8
Snowpack duration (days)	ND	95	130
Characteristic	Dry treeline	Mesic treeline	Wet treeline

ND = no data.

with a Velmex measuring system with a precision of 0.001 mm. The program COFECHA was used to detect measurement and dating errors (Holmes, 1983).

Climate Data

The meteorological stations used to develop regional temperature and precipitation records are listed in Table 2. Following Masiokas et al. (2008), the meteorological records available for the area were compared; those showing correlation coefficients of $r > 0.8$ with neighboring stations were selected. Monthly standard deviations were calculated for each selected record. A regional temperature record was produced by averaging the monthly standard deviations from the selected records (Masiokas et al., 2008). Temperature deviations were estimated over the interval 1969–1988, the period common to all temperature records. The regional precipitation record was developed by averaging the standard deviations of total monthly precipitation and expressed as percentages over the common interval 1961–1990 (Masiokas et al., 2008).

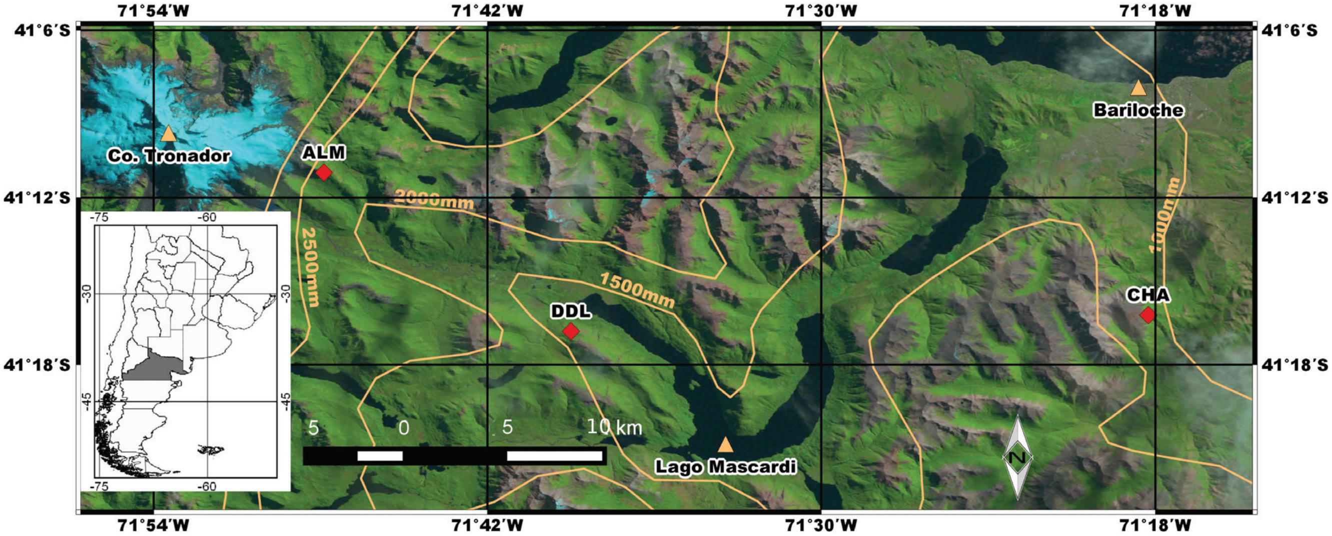

FIGURE 2. Location of the sample sites along the precipitation gradient. Isohyets from Cordon et al. (1993). For more details regarding the sampling sites, refer to Table 1. Orange triangles = Tronador mountain, Mascardi lake, and Bariloche town; red diamonds = sample sites.

TABLE 2

Temperature and precipitation records used in this study.

Station	Latitude S	Longitude W	Period	Source	Variable
Lumaco	38.15°	72.90°	1948–2001	DGA	Precipitation
Temuco	38.80°	72.80°	1912–2010	GHCN	Precipitation
Los Laureles	38.98°	72.23°	1947–2001	DGA	Precipitation
Flor del Lago	39.15°	72.12°	1961–2001	DMC	Precipitation
Purulón	39.47°	72.60°	1936–2000	DMC	Precipitation
Ea. Campo Grande	39.50°	70.63°	1947–1998	AIC	Precipitation
Valdivia	40.00°	73.10°	1912–2011	GHCN	Precipitation
Ea. Collún Co	40.07°	71.17°	1911–1998	AIC	Precipitation
Ea. Quechuquina	40.15°	71.58°	1957–1998	AIC	Precipitation
Río Bueno	40.30°	72.93°	1940–2000	DMC	Precipitation
Osorno	40.60°	70.07°	1951–2011	DMC	Precipitation
Bariloche	41.13°	71.30°	1956–2012	SMN	Temperature
Punta Huano	41.13°	72.28°	1961–2000	DMC	Precipitation
Mascardi	41.25°	71.66°	1969–1994	SMN	Temperature
Puerto Montt	41.40°	73.10°	1909–2011	CHGN	Precipitation
Esquel	42.90°	71.35°	1956–2009	SMN	Temperature

Sources: DGA—Dirección General de Agua (Chile); GHCN—Global Historical Climatology Network; DMC—Dirección Meteorológica de Chile; AIC—Autoridad Interjurisdiccional de Cuencas de los Ríos Neuquén, Limay y Negro (Argentina); SMN—Servicio Meteorológico Nacional (Argentina).

Because seasonal rather than monthly temperature or precipitation comparisons are better estimates of plant growth (Fritts, 1976), comparisons between climate and tree establishment were conducted on a seasonal basis. Soil temperature and moisture at the Almohadilla and Diego de León sites have been recorded since March 2013. Based on soil temperature, we estimated the number of days with snow cover at each site. When the ground is covered by snow, soil temperature remains constant and close to zero without any manifestation of a daily temperature cycle. Although this is not a direct measurement of snow cover, this information provides a reasonable estimate of snowpack duration. El Niño 3.4 and the PDO indexes were obtained, respectively, from:

- http://www.cgd.ucar.edu/cas/catalog/climind/TNI_N34/index.html (access date 8 September 2015)
- http://research.jisao.washington.edu/pdo/PDO.latest (access date 20 June 2015)

Statistical Analysis

Differences between means were estimated to compare density and morphometric parameters of *N. pumilio* individuals between sampling sites. Differences in density and annual growth of individuals between sites were assessed using an ANOVA test. The density and the annual growth data were transformed to square root and natural logarithm, respectively, to meet the statistical assumptions required for this analysis. The Mann-Whitney U test was used to establish differences in height, diameter, number of stems, and age among individuals growing in the different sites. This nonparametric test was applied because structure variables do not comply with the assumption of normality (Zar, 1999).

In order to analyze the temporal variations in *N. pumilio* establishment, the technique of robust regime shift detection (Rodionov, 2004, 2006) was applied to the records of (1) regional temperature and precipitation and (2) ENSO and PDO atmospheric circulation indexes. This technique detects changes in the mean value of the temporal series and assesses the magnitude of the changes (Rodionov, 2004). An ANOVA test was performed to determine changes in *N. pumilio* establishment between periods with statistically significant differences in climate, as determined by the robust regime-shift-detection technique.

RESULTS

Structure

The mean density of individuals at the dry and mesic sites are 84.4 and 240 trees per hectare at CHA (Challhuaco) and DDL (Diego de León), respectively. In contrast, significantly lower mean density was found at the wet site (4975 trees per hectare; $p = 0.017$; Fig. 3). Individuals with larger basal diameters were also taller, with a greater number of stems and a higher rate of radial growth (Fig. 3). Mean base diameter for the dry and mesic sites (39 mm and 46 mm, respectively) was comparatively greater than that of trees at the wet site (15 mm; $p < 0.001$; Fig. 3). Signifi-

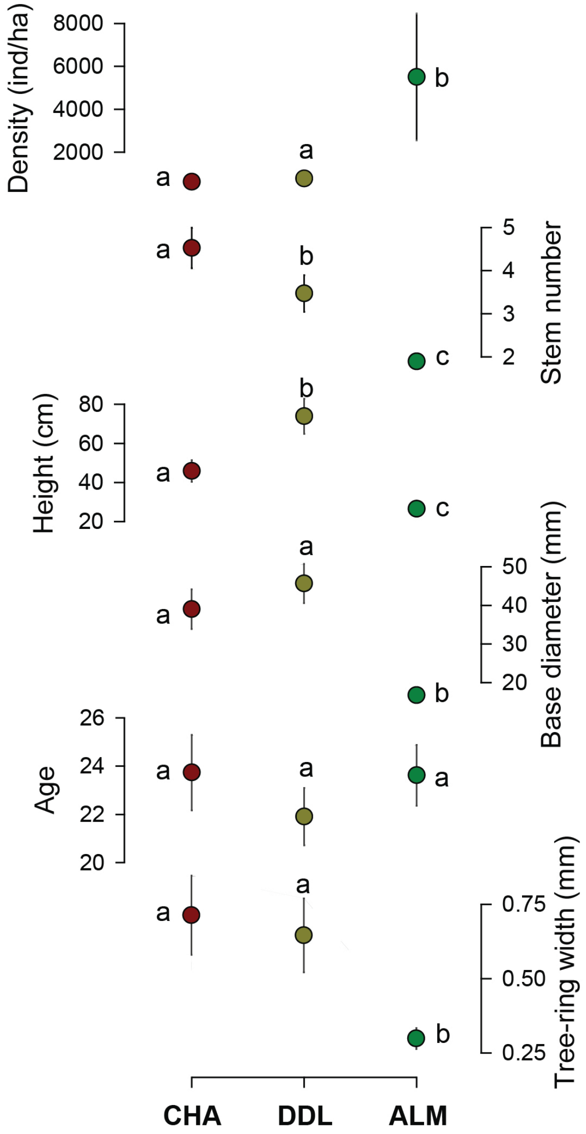

FIGURE 3. Differences in tree structural variables in the upper treeline area for the three study sites along the precipitation gradient. Challhuaco = CHA, Diego de León = DDL, and La Almohadilla = ALM. Mean value and standard error of each variable measured at the upper treeline for each site: *N. pumilio* density, stem number (number of stems per individual), height, base diameter, age, and mean tree ring width. Different letters show statistically significant differences at p ≤ 0.05.

cantly taller individuals were recorded at DDL (73 cm; $p < 0.001$; Fig. 3), whereas those with the highest number of branches were found at CHA (4.5 stems; $p < 0.001$; Fig. 3). At the most humid site (ALM), individuals were smaller and had fewer stems. Variability in diameter, height, and number of stems was higher at the dry and mesic sites (Fig. 3). In contrast to the recorded differences in structure, the mean age of individuals was not significantly different between the three sites ($p = 0.73$; Fig. 3).

Temporal Patterns of Establishment and Their Relationships to Climate

The establishment of *N. pumilio* individuals above the upper treeline was concentrated over a period of about two decades (Fig. 4). There was an abrupt increase in establishment at the three sites starting in the mid-1970s and extending to the mid-1990s. However, whereas a significant reduction in establishment at CHA and DDL was recorded after 1995, sporadic establishment continued at ALM until the late 1990s. At the driest CHA site, recruitment in the year 1988 was two to four times greater than in other years with establishment records. The mesic site also exhibited abundant establishments during 1988, but the establishments were similar in magnitude to those registered in 1982. At ALM, the establishment events with the greatest number of trees occurred in the years 1980, 1984, 1985, and 1987.

The robust regime shift detection technique shows an increase in spring-summer temperatures around 1976, which coincides with the abrupt increase in individual establishments at the three treelines (Fig. 5). Shifts in the annual PDO phases also coincide with changes in *N. pumilio* establishment at the upper treelines. The shift from the negative to the positive phase of the PDO in 1976–1977 was concurrent with the increase in establishment, whereas the positive to negative shift in PDO around 1998–1999 coincided with the end of the tree recruitment period (Fig. 5).

Jumps in regional temperature and PDO clearly accompanied the recorded changes in establishment at the upper treelines (Fig. 6). Our data showed significant differences between the number of individuals established before and after the increase in temperature in 1976 ($p = 0.01$; Fig. 6). A significant relationship between phase changes in the PDO and establishment was observed. The negative phases of PDO were concurrent with low rates of *N. pumilio* establishment, whereas the recruitment of new individuals was significantly higher during the positive PDO phase from 1977 to 1998 ($p = 0.013$, Fig. 6).

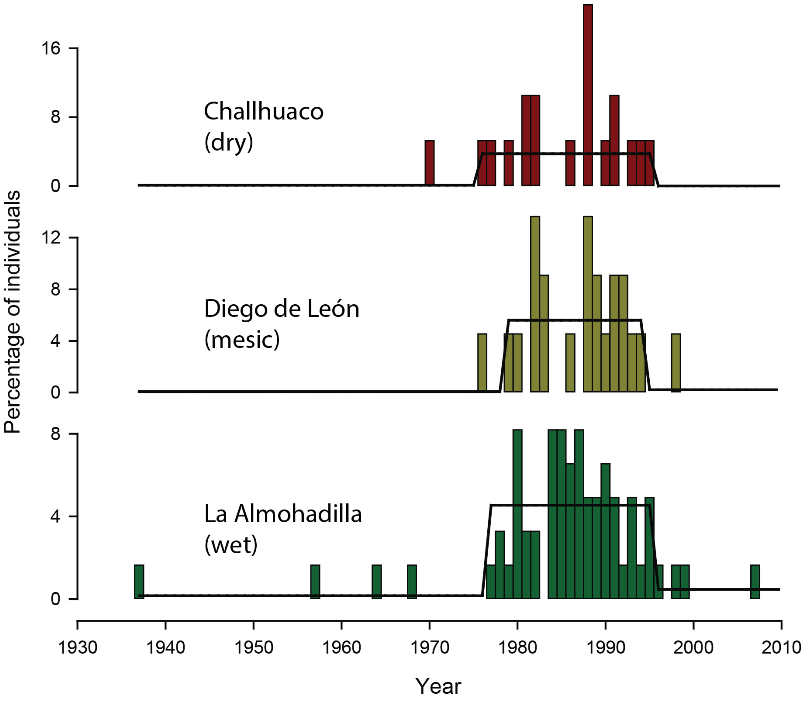

FIGURE 4. Frequency distribution of individuals established at the treeline. Sampling sites ordered from the driest (top) to the most humid (bottom) along the precipitation gradient. The black line displays shifts in mean establishment levels identified in the series using Rodionov's technique.

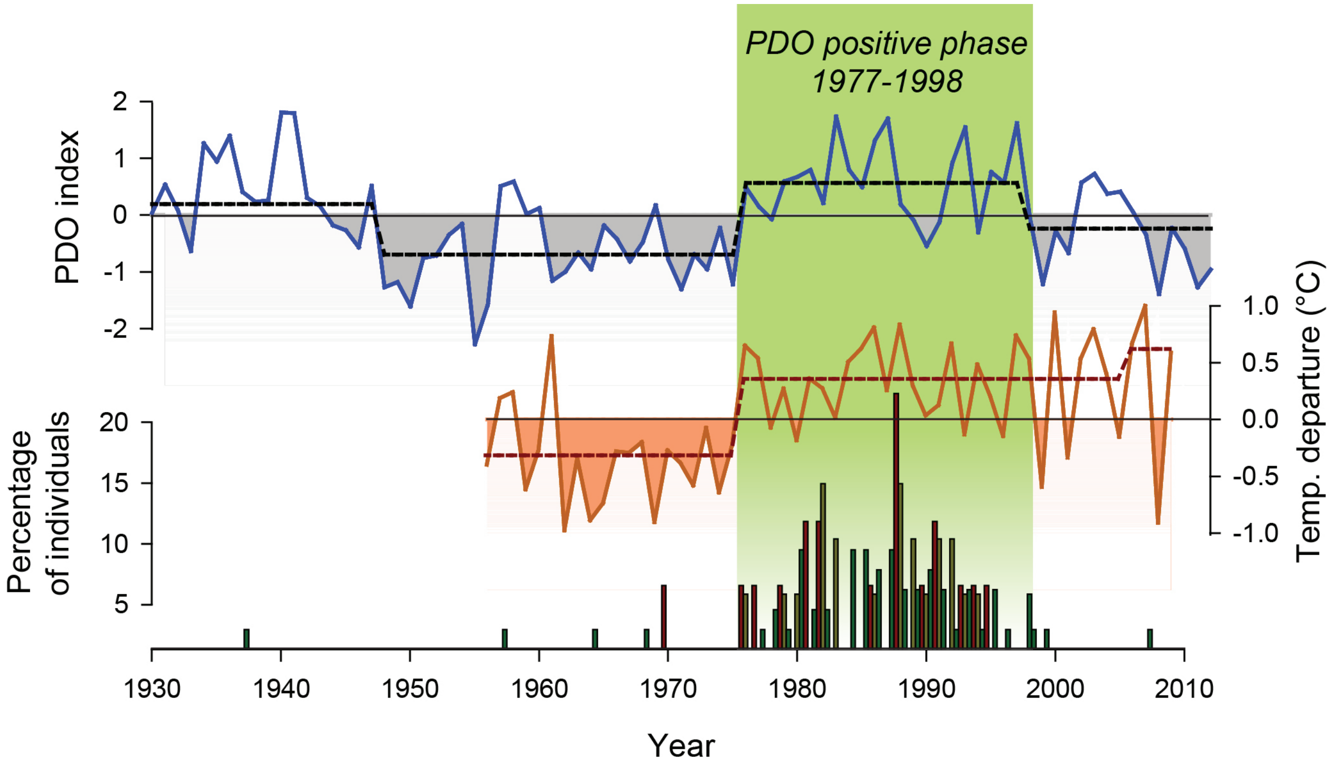

FIGURE 5. Frequency of seedling establishment at the upper treelines and variations in regional spring-summer temperature and the annual Pacific Decadal Oscillation (PDO) index. Shifts in mean regime levels for PDO (dashed black line) and regional temperature (dashed brown line) were identified in these series using Rodionov's technique.

DISCUSSION AND CONCLUSIONS

Morphological characteristics and regeneration dynamics of *Nothofagus pumilio* individuals at the upper treelines in northern Patagonia are largely modulated by climate. Trees recently established at dry and mesic treelines (CHA and DDL) show greater rates of apical and radial growth than those at wetter treelines (ALM; Fig. 3). In addition, individuals at dry and mesic treelines are mostly multistem trees. In relatively dry areas in the northern Patagonian Andes, warm summer temperatures damage the terminal apex of *N. pumilio* and induce the production of new stems (Magnin et al., 2014).

In contrast, individuals at relatively dry treelines are taller than those at wet sites. The higher rates of growth at relatively dry sites at the upper treeline reflect the occurrence of longer and warmer growing seasons in combination with shorter snowpack duration (Table 1). Previous studies have suggested that tree growth at the upper treeline is largely influenced by the length of the growing season (Woodward et al., 1995; Wieser and Tausz, 2007; Körner, 2012). Several aspects of plant growth, such as the opening of buds, require temperatures above 6 °C (Grace et al., 2002), which are recorded earlier in the growing season in the

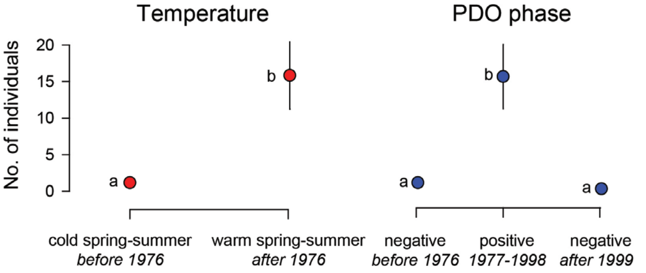

FIGURE 6. Differences in *N. pumilio* establishment during different regimes in temperature and Pacific Decadal Oscillation (PDO) identified using the robust shift detection technique: (1) establishment before and after the change in spring-summer temperature in 1976/1977 (left), and (2) establishment during different phases of the annual PDO (right). Different letters in each panel indicate significant differences at $p \leq 0.05$.

dry eastern sector of the precipitation gradient than in the wet western sector. Soil temperature sensors near our sampling sites show differences in snow cover duration of up to 35 days between drier and wetter environments across the upper treeline in the northern Patagonian Andes. At the wet treelines, the annual period of snow cover is about 130 days, whereas snow cover lasts only 95 days in the mesic sector (Table 1). Differences in the length of the growing season may explain the lower rates of growth recorded in the humid sectors (ALM). In addition, the lower soil temperatures at wetter treelines reduce nutrient supply and negatively affect the rates of growth (Coomes and Allen, 2007; Körner, 2007).

Given the high sensitivity of *N. pumilio* seedlings to water deficits, the high density of individuals at humid treelines (ALM) reflects a large number of microsites with soil water content adequate for tree establishment and survival. Higher mortality rates in response to more extreme summer conditions (higher temperatures and lower soil water content) may be responsible for the lower rate of establishment at drier sites. Lloyd and Graumlich (1997) listed several environmental factors that drive mortality at dry treelines. They noted that while drought severity may not change with elevation, transpiration rates increase with altitude, making trees more vulnerable to drought at the upper treeline (Smith and Geller, 1979; Baig and Tranquillini, 1980). In addition, reduced snowpack during drought years may lead to an increase in desiccation injuries during winter (Lloyd and Graumlich, 1997; Klasner and Fagre, 2002).

Starting in the mid-1970s, *N. pumilio* establishment rates increased across the entire west-to-east precipitation gradient. Thereafter, the rate of establishment remained relatively stable for more than two decades, only decreasing in the late 1990s. Although we registered single years with more abundant establishment (Fig. 4), there is no clear evidence of cyclical patterns in *N. pumilio* recruitment that could be associated with seed production. Peaks in *N. pumilio* seed rain have been documented every 7–8 years in Tierra del Fuego (Cuevas, 2002); however, these observations are too short to validate persistent cycles in seed production.

Similarities in the temporal evolution of *N. pumilio* establishment in the three areas suggest the presence of a regional, decadal-scale climatic forcing that modulates tree recruitment across the precipitation gradient in northern Patagonia. The abrupt increase in the regional spring-summer temperature (>0.5 °C) in 1977 was followed by persistently higher temperatures over the next two decades. Subsequently, temperature variability increased significantly with low temperatures in the spring-summers of 2000 and 2009 comparable to those recorded prior to 1977 (Fig. 5).

Consistent with previous studies at upper treeline in northern Patagonia, we did not find a significant relationship between interannual variations in *N. pumilio* tree establishment and growing season temperatures. Daniels and Veblen (2004) compared *N. pumilio* establishment patterns with interannual variations in temperature and ENSO and concluded that establishment at treeline is not associated with interannual variations in either regional temperature or ENSO. Our results are also consistent with those of Elliott (2012), who observed that decadal rather than annual-scale climate variability is a better predictor of tree establishment at the upper treeline in the Rocky Mountains, U.S.A.

We show that variations in the rate of establishment clearly coincide with decadal-scale shifts in the phases of the Pacific Decadal Oscillation (PDO; Fig. 5). The shift from the negative to the positive phase of the PDO in 1976–1977 was consistent with well-documented climate and ecosystem changes all along the Pacific domain (Ebbesmeyer et al., 1991; Mantua et al., 1997; Mantua and Hare, 2002). In northern Patagonia, previous studies have documented the influence of the PDO on decadal-scale variability in temperature and precipitation (Villalba et al., 2003; Garreaud et al., 2009; Vuille et al., 2015). At our study treelines, *N. pumilio* establishment was abundant during the positive phase of the PDO from 1977 to 1998 (Fig. 6). After that, a reduction in establishment during the first decade of the 21st century was concurrent with the onset of the recent negative phase of the PDO (Trenberth et al., 2014; Vuille et al., 2015).

Above-average temperatures from 1977 to 1998 induced a reduction in the snow cover period at the upper forest limit and, consequently, an extension of the growing season. In addition, the higher temperatures during the positive phase of the PDO likely facilitated the survival of recently established trees by increasing their photosynthetic rates and inducing the release of nutrients from the soil. However, because the *Nothofagus* seedlings are very sensitive to water stress, tree establishment was more successful in the wettest limits of the precipitation gradient in northern Patagonia. Seedling density at the wet ALM site is significantly higher than at the mesic (DDL) and dry (CHA) limits (Fig. 3). The persistence of relatively warm spring-summer conditions for more than 20 years not only facilitated the establishment but also the survival of newly established seedlings. With the onset of the negative phase of the PDO in 1999–2000, temperature variability during the growing season increased, reaching in some years low temperature levels similar to those recorded during the period prior to 1977. Although not significant, an increase in spring-summer precipitation was also observed in the Bariloche record after the year 1999. The return to growing seasons with lower temperatures and abundant precipitation appeared to be detrimental to the establishment and survival of new seedlings. As Elliott (2012) has previously reported for upper treelines, the successful establishment of trees is regulated by the occurrence of long-term periods, rather than single years, with adequate climate conditions. Long-term periods with climate favorable for tree growth allows newly established individuals to develop extensive root and stem systems that can withstand adverse weather events occurring in the following years. In contrast to the stable climatic conditions prevailing during the positive phase of the PDO from 1977 to 1998, years with favorable climatic conditions for tree establishment during the first decade of the 21st century alternated with relatively cold and snowy growing seasons (years 2000, 2002, 2009; Fig. 6) that limited the establishment of new trees. Our observations suggest that models of tree expansion above upper treelines in relation to global warming should consider not only changes in mean climate but also in climate variability.

Our study suggests that in addition to mean spring-summer temperatures, changes in climate variability induced by the PDO also modulate tree establishment at the upper treeline. Changes in the PDO, which likely encompass variations in several environmental conditions in addition to mean growing season temperatures, appear to more closely affect the establishment of *N. pumilio* at the upper treeline than variations in temperature or precipitation alone. As indicated by Stenseth et al. (2003), variations in atmospheric circulation indexes, which incorporate simultaneous changes in temperature, precipitation, wind, and solar radiation, among others, are more strongly related to biological processes than to changes in a single climate variable. Overall, our results emphasize the complexity of climate-tree dynamics along environmental gradients and the need for long-term monitoring approaches to determine consistent relationships between tree establishment and climate at upper treelines.

ACKNOWLEDGMENTS

This study was partially supported by CONICET, Argentina, the Inter-American Institute for Global Change Research (CRN II # 2047), and the Australian Research Council (ARC DP120104320). The authors would like to thank Alberto Ripalta, Andrea Medina, Daniel Falaschi, Silvia Delgado, and Jorge Puga for field work assistance. Valeria Aschero and Lidia Ferri provided useful comments on the manuscript. Mariano Masiokas, the Subsecretaría de Recursos Hídricos and the Servicio Meteorológico Nacional provided the climate data. Anabela Bonada and Erin Gleeson helped with the preparation of the English version.

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MS submitted 1 March 2016
MS accepted 25 September 2016