Aim To investigate the differential effects of position within gaps, coarse woody debris and understorey cover on tree seedling survival in canopy gaps in two old-growth *Nothofagus pumilio* (Poepp. & Endl.) Krasser forests and the response of this species to gaps in two forests located at opposite extremes of a steep rainfall gradient.

Location Nahuel Huapi National Park, at 41° S in north-western Patagonia, Argentina.

Methods In both study sites, seedlings were transplanted to experimental plots in gaps in three different positions, with two types of substrate (coarse woody debris or forest floor), and with and without removal of understorey vegetation. Survival of seedlings was monitored during two growing seasons. Soil moisture and direct solar radiation were measured once in mid-summer. Seedling aerial biomass was estimated at the end of the experiment.

Results Mid-summer soil water potential was lowest in the centre of gaps, in plots where the understorey had been removed, and highest at the northern edges of gaps. Direct incoming radiation was highest in gap centres and southern edges, and lowest at northern edges. Seedling mortality was highest in gap centres, in both sites. Coarse woody debris had a positive effect on seedling survival during summer in the mesic forest and during winter in the xeric forest. The removal of understorey cover had negative effects in gap centres during summer. Seedling final aerial biomass was positively affected by understorey removal and by soil substrate in both sites. In the dry forest gaps, seedling growth was highest in northern edges, whereas it was highest in gap centres in the mesic forest. Overall growth was positively related to survival in the xeric forest, and negatively related in the mesic forest.

Main conclusions Survival and growth were facilitated by the shade of gap-surrounding trees only in the xeric forest. Understorey vegetation of both forests facilitated seedling survival in exposed microsites but competed with seedling growth. Nurse logs were an important substrate for seedling establishment in both forests; however, causes of this pattern differed between forests. Water availability positively controls seedling survival and growth in the xeric forest while in the mesic forest, survival and growth are differentially controlled by water and light availability, respectively. These two contrasting old-growth forests, separated by a relatively short distance along a steep rainfall gradient, had different yet unexpected microenvironmental controls on *N. pumilio* seedling survival and growth. These results underscore the importance of defining microscale limiting factors of tree recruitment in the context of large-scale spatial variation in resources.
INTRODUCTION

Habitat microheterogeneity induced by gap size, orientation, gap-maker, understorey and coarse woody debris (CWD) are critical factors determining the regeneration response of trees in gaps (Sipe & Bazzaz, 1995). However, the potential role of each of this complex suite of microenvironmental factors on tree regeneration under contrasting environmental settings is not well known.

Availability of safe microsites for tree establishment in gaps is largely a function of the direct abiotic heterogeneity created by the gap-forming event in concert with biotic factors such as the subsequent filling of the gap by overstorey and understorey plants. Gap size and orientation will create heterogeneous microenvironments with respect to light, temperature and moisture (Poulson & Platt, 1989; Canham et al., 1990). Changes in light intensity and duration levels along a gradient from beneath the intact canopy to the gap centres will strongly influence the microclimate in gaps. Soil and air temperatures and moisture undergo changes due to differences in daily and seasonal radiation regimes at different locations within the gap (Bazzaz & Wayne, 1994). Direct insolation in the centre of gaps may favour abundant seedling establishment in forests where soil water availability is not limiting, but conversely, direct insolation may inhibit regeneration at xeric sites due to the desiccating effect on soil moisture.

The effect of understorey species in gaps on the survival of tree seedlings has been documented in several studies (Maguire & Forman, 1983; Berkowitz, 1995; Beckage et al., 2000), although there are few controlled, experimental studies of herb/shrub competition with tree seedlings in natural gaps at the microscale. Understorey vegetation as a biotic factor creates heterogeneity. It may inhibit regeneration (Veblen et al., 1981) by competing for light, growing space or other resources, or by allelopathic interactions. Alternately, understorey vegetation may facilitate seedling establishment (Callaway, 1995; Holmgren et al., 1997) by favourably altering the substrate or the microclimate. Results of an experiment where understorey vegetation was removed in treatment plots suggested that the cover of the understorey had a facilitative effect on the survival of Nothofagus pumilio seedlings on microsites with high levels of direct solar radiation (Heinemann et al., 2000). This positive shading effect, creating favourable microclimatic conditions for seedling survival, is expected to occur at xeric sites, whereas at moist sites the shading effect would probably have neutral or negative consequences for seedling survival.

Decaying logs in different stages of decomposition are an important source of within-gap heterogeneity. Large decaying logs provide safe sites for young tree seedlings in some old-growth forests, acting as elevated surfaces where dense understorey vegetation or a moss cover may inhibit establishment (Harmon & Franklin, 1989). On such logs where the danger of litter burial is reduced (Christy & Mack, 1984), soil moisture and nutrient availability may be more favourable than on the forest floor (June & Ogden, 1975).

In a xeric Nothofagus pumilio forest, 65% of seedlings were found growing on decaying logs under a closed canopy, although less than 7% of the ground was covered by CWD (Heinemann et al., 2000). The large surface area of the CWD and the capillary system formed by open xylem vessels create a strong water-retention capacity, which increases as decomposition progresses (Ponge et al., 1998). Indeed, Heinemann et al. (2000) documented higher water potential in CWD than in adjacent soil microsites during the critical late summer months of maximum water deficit. Thus, CWD is predicted to enhance seedling survival at xeric sites, while it may have no particular importance in moist sites.

Nothofagus pumilio (Poep. & Endl.) Krasser is a wide-ranging, economically important deciduous species that forms the highest altitudinal forest belt in the southern Andes. This species is found from 35°35′ S to 55° S, and covers more than 3 million ha. in Chile and in Argentina (Schmidt & Lara, 1985; Veblen et al., 1996). That the distribution of N pumilio spans a major precipitational gradient offers an opportunity to investigate its differential response to gap microheterogeneity. This is a complex gradient running east-west, where several factors vary simultaneously. The most important factor is precipitation, but other changing environmental conditions include soil age, growing season length, understorey species composition, and disturbance history.

Most studies addressing the issue of within-gap heterogeneity include monitoring or even experimental studies detecting spatial patterns (Wayne & Bazzaz, 1993; Sipe & Bazzaz, 1995). Fewer studies use an experimental approach including understorey removal and the manipulation of coarse woody debris. In this study we adopt a manipulative approach, contrasting a xeric and a mesic site of monospecific N. pumilio forests in north-western Patagonia. Specifically, we examine microenvironments and establishment success of N. pumilio, focusing on seedling survival patterns in tree-fall gaps, in relation to the combined effect of substrate (CWD or forest floor), understorey cover (with or without removal) and position in the gap (north edge, centre or south edge). Through this analysis we assess the relative importance of these factors on the regeneration of this species, and the role of gaps in regeneration. We make the following predictions. (1) The centre of gaps will have the highest rates of mortality due to higher radiation levels, and the northern edges will have the lowest mortality rates due to the shade of the canopy. (2) Seedlings growing on

Keywords

Argentina, coarse woody debris, forest dynamics, gaps, Nothofagus pumilio, Patagonia, precipitation gradient, seedlings, understorey removal.
coarse woody debris will have higher survival rates than those growing on the forest floor due to the higher moisture content of CWD, for the same within-gap position. (3) In brightly lit settings, the presence of understory cover will increase survival (centre of gaps) due to amelioration of otherwise desiccating conditions. (4) Where light may be the limiting factor (northern gap edges), the removal of the understory will have a positive effect on survival of seedlings. (5) The cumulative interaction of the three factors will result in highest mortality rates on forest floor with removal of the vegetation in the centre of gaps. (6) CWD will increase survival in the xeric forest, but will have no effect in the mesic one. (7) Growth will be negatively correlated with survival, being higher in more exposed microsites. (8) None of the three factors will affect winter survival.

**DATA AND METHODS**

**Study area**

The study was conducted at two sites located in Nahuel Huapi National Park, Argentina, representing extremes along the predominant west-to-east rainfall gradient within the widely distributed *N. pumilio* forest range at 41° S latitude. This gradient is caused by the Andes, which form an effective barrier to westerly air masses coming from the southern Pacific Ocean. The xeric site is located at Challhuaco Valley (hereafter Challhuaco; 41°12’ S, 71°19’ W), which is a disjunct outlier of forest located 15 km south of the city of Bariloche at the xeric boundary with the Patagonian steppe. The mesic site is located close to the Continental Divide at Paso Puyehue (hereafter Puyehue; 40°37’ S, 71°74’ W), approximately 100 km northwest from Bariloche city. At Challhuaco mean annual precipitation is 1200 mm of which only 10.5% falls during the growing season (Table 1). Mean annual precipitation increases sharply towards the west, so that Puyehue receives c. 3000 mm of annual precipitation, 17% of which falls during the growing season (Table 1; Barros et al., 1983). Although elevation is similar in both areas, the more easterly located Challhuaco has milder, slightly longer, growing seasons (Table 1) due to it having less cloud compared with the more Andean Puyehue, which has longer snowpack duration and hence higher cloud cover. Soils in the entire study area are derived from aeolian volcanic ash deposits with increasing ash depths towards Puyehue due to the proximity of Puyehue volcano. Accordingly, soil ages decrease towards the west due to more recent eruptive events. Information on the soil fertility of these study sites is scarce, although greater concentrations of N or P may indicate that Challhuaco has more fertile soil than Puyehue (Table 1).

Both sites are relatively pristine forests, with no sign of recent coarse-scale disturbances, e.g. grazing or logging. Trees are c. 20 m tall in these old-growth monospecific forests of *N. pumilio* undergoing gap-phase regeneration. While Challhuaco has a probable post-fire origin some 280 years ago (age of oldest trees, Heinemann et al., 2000), Puyehue underwent several episodes of volcanism caused by the Puyehue volcano.

<table>
<thead>
<tr>
<th>Site</th>
<th>Challhuaco</th>
<th>Puyehue</th>
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</tr>
</thead>
<tbody>
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<td>19 ± 4</td>
<td>e</td>
</tr>
<tr>
<td>d.b.h. (cm) ± SD</td>
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<td>36 ± 22</td>
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<td>1116</td>
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<td>Area of coarse woody debris (%)</td>
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<tr>
<td>Expanded gap area (m²) ± SD</td>
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<td>223 ± 108 (n = 21)</td>
<td>j</td>
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<td>Projected gap area (m²) ± SD</td>
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<tr>
<td>pH</td>
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<td>5.8</td>
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</tbody>
</table>

Data source: (a) Barros et al. (1983); (b) Meteorological data taken at INTA station (41°07’ S and 71°15’ W) for Challhuaco and a 4-year data set for Puyehue (National Parks Adm, unpubl. data); (c) Meteorological data taken at INTA station (41°07’ S and 71°15’ W) for Challhuaco and a data set from a data-logger for one growing season in Puyehue (J. Paritsis, unpubl. data); (d) this study, saplings are > 50 cm height, < 5 cm d.b.h.; (e) data taken from Satti et al. (2003) for Challhuaco, and from N. Mazia (unpubl. data) for Puyehue.
Climatic conditions during the first growing season (1999–2000) of this study were substantially drier and warmer than long-term mean values (0.89 SD below mean precipitation and 1.1 SD above mean temperature; Bariloche Airport meteorological data). Conditions during the second season were close to normal (0.27 SD below mean precipitation and 0.1 SD below mean temperature; Bariloche Airport meteorological data).

Stand characteristics

In each of both sites, four randomly placed plots of $25 \times 25$ m were delimited, and all saplings ($> 50$ cm tall and $< 5$ cm d.b.h.) were counted, and the d.b.h. and height of all trees ($> 5$ cm d.b.h.) was measured. The length and approximate d.b.h. of all fallen logs was measured to estimate the area occupied by CWD. The major and minor axes of 20 well-defined canopy gaps were measured in order to calculate the average gap size for each site.

The dominant understorey plant in Challhuaco is *Alstroemeria aurea*, a rhizomatous forb that forms dense thickets up to 1.20 m tall; it senesces in April, when *N. pumilio* seedlings are shedding their leaves. Other species present in the understorey include *Ribes magellanicum*, *Berberis serratodentata*, *Osmorhiza chilensis* and *Vicia nigricans*. In Paso Puyehue, *Drymis winteri*, an evergreen shrub up to 1 m tall, dominates the understorey. It has rather open branches, in contrast to the dense *Alstroemeria*. *Ribes magellanicum*, *Berberis darwinii*, *Myoschilos oblongum*, *Adenocaulon chilensis* and *Gunnera magellanica* occur at lower abundances.

CWD and understorey manipulations

At both sites, we selected five distinct gaps with similar slope, projected and expanded gap areas measured on the ground (Table 1), that were located on slopes with a northern aspect in a forest with an otherwise intact canopy of relatively uniform height. Experimental plots were established at the northern edge of the expanded gap, in the centre of the gap, and at the southern edge of the expanded gap (*sensu* Runkle, 1982). To justify the use of the three positions (north, centre and south) within gaps, we assessed differences in direct incoming radiation and mid-summer substrate water availability. In mid-summer 2001, hemispheric photographs of the canopy were taken 50 cm above the ground in one point along the mid-line at the north, centre and south positions in gaps, using a leveled north-oriented 7.5 mm fisheye lens. Spring–summer direct incoming solar radiation was manually estimated following Anderson (1964). Substrate water potential (0–10 cm depth) was measured with a Wescor dew point microvoltmeter (Wescor Inc., Logan, UT, USA) in each plot, in mid-summer 2001.

In each of the five gaps, twelve $40 \times 40$ cm plots were established (four per position, 1 m apart from each other). In each of these groups of four plots, one of the following treatments was randomly assigned: (1) decaying wood substrate added, understorey vegetation removed (DR); (2) decaying wood substrate added, understorey vegetation intact (DU); (3) forest floor, understorey vegetation intact (SU); or (4) forest floor, understorey vegetation intact (SR). For decaying wood substrate treatments (D) soil was removed to a depth of approximately 30 cm, and carefully replaced by a section of a decaying log (decay class III – no bark, with partly decomposed wood (Graham & Cromack, 1982)), which remained exposed at the soil level. The log sections were buried to isolate the effect of increased water holding capacity, from that of growth on an elevated surface. For understorey vegetation removal treatments (R), all aerial parts of understorey plants were removed from an area of 1 m² centred in the plot. This removal was repeated once a month during both summers. Substrate (CWD vs. forest floor) and cover (removal vs. intact understorey) treatments were considered as nested within the gap position (north, centre and south).

In spring (October–November) of 1999, 20–25 *N. pumilio* seedlings were randomly selected and transplanted to each of the 60 plots per site. All seedlings belonged to the same cohort that germinated c. 3–4 weeks earlier in the forest floor after a mast year in Challhuaco. Only seedlings that survived transplanting and were still alive in December 1999 were considered in the analyses (92% and 100% survived in Challhuaco and Puyehue, respectively). Seedling survival was monitored monthly during three growing seasons (1999–00, 2000–01 and 2001–02) but only data for the two first seasons are included as so few seedlings survived the third season. In Challhuaco, in 35 plots with high mortality during the first year (< 10 surviving seedlings) new seedlings of the 1999 cohort were transplanted in November 2000 to maintain a minimum of 10 seedlings per plot. First and second year transplants were distinguished by red wire tags.

At the end of the third growing season (2001–02), the remaining seedlings in each experimental plot were removed and dried for 24 h at 70 °C. Before weighting, roots were clipped and discarded because excavation and extraction (although done as carefully as possible) damaged fine roots and thus we were not confident that roots were recovered consistently. Therefore, seedling dry weight was used only as an indication of above-ground growth with the potential confounding effects of changes in biomass allocation.

Monitoring of naturally established seedlings

While the manipulative experiment in gaps progressed, we established 128 plots beneath the closed canopy to monitor survival of naturally established seedlings. This monitoring was conducted following a masting event in 1999 at Challhuaco valley. Initial germinant densities in December 1999 were 416 and 368 seedlings m⁻² on decaying logs and on the forest floor, respectively. As mast-seeding did not occur at Puyehue, this monitoring was performed at Challhuaco only. Four 45 m-long transects were randomly established within a 3 ha area of *N. pumilio* forest. Along each transect, four pairs of $25 \times 25$ cm plots were systematically positioned around...
central points 15 m apart from each other. Each pair of plots consisted of one plot on top of the nearest decaying log and one plot on the forest floor, separated by no more than 2 m. Seedlings of the 1999 cohort were monitored monthly, during the 1999–00 and 2000–01 growing seasons. Direct radiation was estimated with hemispherical photographs over each plot, and water potential was measured in the mid-summer of 2001 as described for the manipulative experiment.

Data analyses

We used nested ANOVA to test main effects of the factors: position in the gap (north, centre or south; hereafter POS), understory (intact or removed; hereafter UND) and substrate type (forest floor or CWD; hereafter SUB) on seedling survival (arc-sine-transformed) at the end of each growing season (March 2000 and March 2001). Substrate type and understory treatments were nested within position in gaps. The same test was used to evaluate differences in survivorship during winter (from March to December), for years 2000 and 2001, and to evaluate the effects of the treatments on seedling mean shoot biomass. A correlation between shoot biomass and survival was also performed. Because an extra number of seedlings were transplanted at the beginning of the second growing season, an ANOVA was performed with each group separately (seedlings transplanted in 1999 and those transplanted in 2000) to assess their survival at the end of that season. Preliminary analyses indicate that the effect of seedling group (1999 vs. 2000 cohorts) was not significant (P < 0.05); thus, seedlings were pooled for the analysis of survival in the second growing season. To control for potential effects of the initial number of seedlings transplanted to each plot, analyses of covariance (with initial density as the co-variable) were performed for both seasons separately at Challhuaco, where a variable number of seedlings was transplanted to each plot. This test was not necessary for Puyehue, where each plot had exactly the same number of seedlings at the beginning of the experiment.

The effect of substrate on survival of naturally established seedlings was tested by one-way repeated measures ANOVA (Gurevitch & Chester, 1986). Statistical differences in direct solar radiation and water potential between substrates were analysed with Mann–Whitney U-tests.

RESULTS

Forest structure and micro environmental abiotic factors

Due to the long-term limited regeneration observed in xeric forests, the Challhuaco forest includes large trees with few intermediate to small sized individuals. In contrast, wet forests such as Puyehue are denser with a more even distribution of tree sizes and lower mean trunk diameters (Table 1). The density of trees and particularly of saplings is several times higher in the Puyehue forest, indicating more favourable conditions for regeneration. Due to lower densities and larger crowns, gaps in the xeric forest tend to be larger than those in the mesic forest. To overcome differences caused by gap size in this experimental study we actively selected gaps of similar size (Table 1).

In the experimental plots of the xeric forest at Challhuaco, mid-summer soil water potential varied significantly depending on position within the gap (POS, P < 0.05) and was affected by understory removal (UND, P < 0.05). The driest topsoils were found in the centres of gaps ($\Psi_{\text{centre}} = -3.2$ MPa vs. $\Psi_{\text{north}} = -1.6$ MPa, $\Psi_{\text{south}} = -1.8$ MPa) and where understory was removed ($\Psi_{\text{removed}} = -2.6$ MPa vs. $\Psi_{\text{intact}} = -1.7$ MPa). CWD and forest floor substrates in gaps did not differ in their water potential (SUB, P > 0.5). In contrast, plots beneath the canopy in which natural establishment was monitored, had significantly higher mid-summer water availability on CWD substrates than on the forest floor ($\Psi_{\text{CWD}} = -1.3$ MPa vs. $\Psi_{\text{f. floor}} = -1.8$ MPa, SUB, P < 0.005). In the mesic forest of Puyehue, soil water potential (P > 0.05) was not significantly influenced by the measured factors.

Direct incoming spring–summer radiation was affected by position within the gap in both forests (Kruskal–Wallis median test, POS, P < 0.05). Northern peripheries of gaps at Challhuaco had significantly higher blocking (c. 70%) than gap centres or southern edges (c. 59% and 58%, respectively). In the smaller gaps of Puyehue, blocking was highest at northern gap edges (c. 67%), intermediate at gap centres (c. 60%) and lowest at southern edges (c. 49%). Blocking of direct incoming spring–summer radiation in monitoring plots of natural establishment under canopy was similar to those of northern gap edges (c. 68%).

Summer seedling survival

Average seedling survival over two seasons was 27% and 69% at Challhuaco and Puyehue, respectively (Figs 1 & 2). Mortality was higher in the first growing season than in the second growing season, particularly in plots with the highest mortality at Challhuaco (Fig. 1).

In the dry forest, position within the gap was the factor that best explained seedling survival (POS, P < 0.001; Tables 2a and 3) during both first and second seasons. Clearly, the position most susceptible to mortality was the centre of the gap, whereas the position with least mortality was the north (shaded) edge of gaps (Fig. 1). Understorey removal reduced seedling survival (UND, P < 0.001; Tables 2a and 3), in the second season, particularly in gap centres. At the northern edges of gaps, understory removal enhanced seedling survival in both growing seasons, although the effect was not statistically significant (Fig. 1). Substrate type was not important in determining summer survival rates in the dry forest.

In the wet forest at Puyehue experimental factors were much less important in determining summer seedling survival than in the xeric forest. The most important factor for seedling survival was substrate during the first growing season (SUB, P < 0.03). Seedling survival was c. 30% higher on CWD compared to forest floor (Fig. 2). Seedling survival during the
second summer season was significantly decreased in plots where understorey had been removed (UND, \( P < 0.04 \); Table 2b), particularly in central and southern positions compared to northern positions (Fig. 2).

**Winter seedling survival**

Winter seedling mortality was substantial (15% in Puyehue for both winter seasons, 20% and 35% in Challhuaco for the first and second winter seasons, respectively). In Challhuaco, survival of seedlings growing on CWD was significantly higher than that of seedlings growing on the forest floor during the first winter (SUB, \( P < 0.002 \)). Winter survival also tended to be higher in shaded northerly gap positions (POS, \( P < 0.001 \), first winter). There was a weak tendency for greater survival on logs relative to forest floor at the more exposed gap positions (south or centre). The presence of understorey was not significant in determining winter survival rates at Challhuaco. In contrast, no significant effects of treatments were found in Puyehue for either winter season.

**Naturally established seedlings**

At the end of the second growing season densities of seedlings were 224 m\(^{-2}\) on decaying logs and 158 m\(^{-2}\) on the forest floor, 53% and 43%, respectively, of the initial density. Summer seedling survival of naturally established seedlings was not related to substrates during either growing season (SUB, \( P > 0.3 \)) (Fig. 3). In contrast, winter survival on logs during 2000 was significantly higher than on the forest floor (87% and 70%, respectively) (SUB, \( P < 0.005 \)). This effect was not significant during the second winter (2001).

**Seedling above-ground growth**

Three years after initiation of the experiment, mean seedling shoot height averaged 7 cm for both sites, but mean shoot biomass was two-fold higher in Challhuaco than in Puyehue (0.103 ± 0.08 g and 0.057 ± 0.007 g, respectively). At Challhuaco, final seedling shoot biomass could not be assessed in the centre of the gaps due to high seedling mortality. For surviving seedlings in plots without understorey vegetation, above-ground biomass was twice that of plots with intact understorey vegetation (0.125 g vs. 0.06 g; UND, \( P < 0.015 \)). These biomass differences were amplified on forest floor treatment plots (0.162 g with removal vs. 0.05 g in intact plots). Understorey removal had a similar significant effect in the wet forest of Puyehue (UND, \( P < 0.03 \)). Position in the gap significantly affected seedling shoot biomass (POS, \( P < 0.03 \)).
Above-ground biomass in the centre of gaps was twice the biomass of seedlings along the gap periphery. The effect of understorey removal was amplified at gap centres so that removal in gaps increased mean final seedling shoot biomass by a factor of 250% compared to 25% increases along the gap periphery. This pattern contrasts with patterns of seedling growth in the dry forest gaps where shoot biomass was minimal in gap centres and increased toward peripheries, particularly the shady north edges and where biomass increases induced by understorey removal were greatest along north gap edges (Fig. 4).

Survival and seedling shoot biomass (log-transformed) were positively correlated in the Challhuaco plots \( (r = 0.617, P < 0.05) \), whereas this correlation was not significant in the mesic Puyehue plots \( (r = 0.03, P > 0.05; \text{Fig. 4}) \).

**DISCUSSION**

Factors that affected *N. pumilio* seedling survival within gaps were different at the two study sites, which were separated by a distance of c. 50 km along the trans-Andean gradient. Gap position was the most important factor determining *N. pumilio* recruitment in the xeric forest but not in the mesic forest. In the latter, position within the gap altered radiation levels and seedling growth rates, while seedling survival and water status were unaffected. Seedling shoot growth showed opposite patterns in xeric and mesic gaps. In the mesic forest, shoot growth was maximized toward centres of gaps but in the xeric forest seedling above-ground biomass was highest in northern edges of gaps. These results may indicate that moisture and light availability are limiting factors to seedling growth in Challhuaco and Puyehue, respectively. Alternatively, seedlings may have allocated a large fraction of biomass to

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**Table 2** Nested ANOVA for seedling survival during both growing seasons

<table>
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</table>

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**Figure 2** Mean seedling survival rates of *Nothofagus pumilio* per plot in Puyehue in relation to position in gaps, removal of the understorey plants and substrate. The numbers present at the beginning of each season is referred to as 100%. In (a), centre and north removal plots had 100% survivorship throughout the growing season, as did the centre plots in (d). Seedlings had high survival rates in all treatment combinations, with the exception of log substrate plots at the southern edge of gaps and soil substrate plots in the centre of gaps that had their understorey cover removed.
shoots according to moisture and light availability gradients, respectively.

Seedling survival responses are due to both genotype and environment. By transplanting seedlings germinated in Challhuaco to experimental gaps at both sites, we isolated the environmental effects.

Direct solar radiation patterns in gaps of both sites were slightly different: in Challhuaco, the highest radiation was received in the centre of gaps, whereas in Puyehue southern edges of gaps received more direct radiation. This pattern is probably due to the smaller gap size in Puyehue and consequently a higher ratio between surrounding tree height and gap diameter. Clearly, treefall gaps induced strong radiation gradients in both forests but only in the xeric forests were important soil moisture gradients established — where seedling shoot growth and survival were greatest in shady, moist microsites. This effect explains the seedling and sapling spatial distribution patterns detected in gaps. Xeric forests tend to have numerous seedling/saplings concentrated in the northern edges of gaps (Heinemann et al., 2000) whereas distribution of recruits in mesic forests is uniform.

### Table 3: Effects of treatments on seedlings in the experimental plots and for monitored seedlings

<table>
<thead>
<tr>
<th>Location</th>
<th>Puyehue</th>
<th>Chall-huaco</th>
<th>Chall-huaco</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approach</td>
<td>Experiment</td>
<td>Experiment</td>
<td>Monitoring</td>
</tr>
<tr>
<td>Treatment</td>
<td>POS</td>
<td>UND</td>
<td>SUB</td>
</tr>
<tr>
<td>Variable</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water potential</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Direct incoming radiation</td>
<td>S (\uparrow)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer survival</td>
<td>n.s.</td>
<td>Rem C(S)(\downarrow)N(\uparrow)*</td>
<td>CWD (\uparrow)*</td>
</tr>
<tr>
<td>Winter survival</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Seedling biomass</td>
<td>C(\uparrow)*</td>
<td>Rem(\uparrow)*</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

*\(P < 0.05;\) treatments are: POS, position in gaps (N, north; C, centre; S, south); UND, understorey removed (Rem) or intact; SUB, substrate type (CWD or forest floor). Arrows show trends, not necessarily statistically significant effects.

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**Figure 3** Mean survival rates of monitored *Nothofagus pumilio* seedlings beneath a closed canopy in Challhuaco forest for both growing seasons, on the forest floor and on coarse woody debris (SD values oscillated between 19% and 23%). Seedlings suffered a differential mortality during winter, but survival rates during the summer seasons were similar on both substrates.

**Figure 4** Mean above-ground biomass of *Nothofagus pumilio* ± 1SD plotted against mean survival rates ± 1SD for each treatment. ( ■ = plots in southern edges of gaps, ○ = plots in centre positions, and ▲ = plots in northern edges of gaps). Variability in survival rates per treatment was in general much higher than for seedling biomass.
with respect to aspect within the gap (Heinemann et al., unpubl. data).

Contrary to our predictions, the presence or absence of understorey vegetation played a similar role in the two forests. In general, understorey removal decreased summer seedling survival at the microsites with highest water demand (centres and southern edges) and increased seedling growth (or shoot allocation) at microsites with highest potential growth. Such locations were gap centres in mesic forests, and forest soil substrate in northern edges of gaps in xeric forests, where soil moisture was high enough for the corresponding light environment in each site. This outcome suggests that understorey vegetation has a facilitative effect on seedling establishment but a competitive or inhibiting effect on seedling shoot growth. This dual role has been found in other systems such as shrub–conifer interactions in the Patagonian steppe (Kitzberger et al., 2000), and herbaceous cover–tree seedling interactions in old-field succession in northern hardwood forests (De Steven, 1991a,b).

Intensity of effects of the understorey did however change from east to west. Positive effects of understorey vegetation on seedling survival at Puyehue were weak and appeared only in the second growing season, possibly due to the influence of interannual climatic variability (Kitzberger et al., 2000). Facilitation was more consistent in the xeric forest, with evidence of facilitation during both summer seasons. Surprisingly, competitive effects of understorey on seedling growth were stronger in the xeric forest than at the mesic Puyehue site. This observation may be explained by a higher overall potential growth in Challhuaco compared to Puyehue, possibly due to nutrient limitations caused by young, less developed volcanic soils (N. Mazia, pers. comm.) and/or shorter growing season at Puyehue.

Substrate type played a different role on seedling survival and growth in the two forests. In contrast to our predictions, summer seedling survival was increased on CWD in the mesic forest gaps but not in xeric forest. In the xeric forest, logs increased seedling survival during the winter season at microsites protected from direct radiation, i.e. the northern edges of gaps and under a closed canopy. These results suggest that CWD does not provide safe sites in gaps through the mechanism of increased water holding capacity as previously suggested (Heinemann et al., 2000). In Challhuaco, CWD had higher water potential than soil under a closed canopy but not in gaps. Apparently, CWD dries rapidly when exposed to high amounts of radiation. This effect was not apparent in the mesic forest during the first growing season when summer survival of seedlings was higher on logs than on the forest soil. It is likely that increased water holding capacity of decaying logs at the wetter site or in years of high rainfall has a lasting effect in the maintenance of high water availability over the dry summer season.

Variation in climate and substrates also affected seedling mortality. High summer seedling mortality during the first growing season in Challhuaco, in gaps as well as in plots under a closed canopy, were likely to have been influenced by regional climatic conditions, because the summer of 1999–2000 was drier than the long term average. We measured unexpectedly high seedling mortality (c. 21%) during the winter seasons. However, log surfaces provided safe sites for seedlings during the cool season at both the gaps and the closed forest in Challhuaco. This variation in survival and mortality associated with substrates cannot be explained by a differential exposure to herbivores, as the manipulated CWD was buried to soil level in the gap experiment. Therefore, the differences must be due to some intrinsic quality of decaying wood as a substrate. We have no direct mechanistic explanation for this observation, but a combination of factors such as pathogens or uprooting caused by frost heaving may have been the cause: there are probably more pathogens and a higher risk of frost heaving on the forest floor relative to CWD substrates. As seedling roots are very small and not well-anchored during their first year, it is possible that soft decaying wood offers a better anchoring substrate than forest soil, thus limiting the risk of uprooting.

Notophagus pumilio seedlings remained very small after three growing seasons and they have a relatively high persistence in the understorey as shown by the monitoring of naturally established seedlings. These observations suggest this species may be considered shade-tolerant with a seedling bank strategy, in the north-eastern part of its distribution, although it has been described as a ‘gap-strategy’ species by Donoso (1993) for more mesic forests. According to other research on N. pumilio at a similar latitude, this species can germinate and persist in the understorey with little growth for years before it has the opportunity to grow into the canopy (Puntieri et al., 1999; Daniels & Véblen, 2004). Sudden increases in light levels caused by canopy openings may severely damage or even kill seedlings in the understorey by photoinhibition (Bazzaz, 1996) if the increase in light occurs when water is limiting, as is the case in the xeric N. pumilio stand we considered. Acer saccharum and Fagus grandifolia, late-successional species in many temperate deciduous forests in North America, are small gap specialists (Canham, 1988). From our observations we infer N. pumilio to be a small gap specialist. Rusch (1992) found that the amount of radiation received in small gaps (10 m diameter) was enough for N. pumilio saplings to survive in a stand receiving intermediate rainfall (1400 mm).

The average gap size in Challhuaco (c. 390 m²), determined mainly by the size of old trees, was too large, offering few adequate microsites for regeneration. Even in the moist forest, where gaps are smaller and soil moisture does not seem to be a limiting factor, seedling mortality was high in gap centres. This mortality pattern suggests that the effect of direct solar radiation was negative for survival, although it turned out to be favourable for the shoot growth of a small number of seedlings. Apparently, there is a trade-off between seedling shoot growth and survival. At shaded microsites, survival is great but growth is slow and the probability of recruitment to the canopy is low. At microsites with high exposure to insolation, probabilities of survival are low but shoot growth rates are high. Therefore, the possibilities of perpetuating the forest system in time are different for the two sites considered.
in this study. Our results suggest fewer regeneration opportunities at Challhuaco than in Puyehue, which is directly supported by the scarcity of established saplings at Challhuaco and the abundance of saplings at Puyehue (Table 1).

Within the framework of the original predictions, a brief summary of the outcomes of this study is as follows. (1) The centres of gaps had definitively higher rates of mortality, and northern edges the lowest rates of mortality. (2) CWD did not favour survival compared to the forest floor for the same position within a gap. (3) Intact understory cover increased seedling survival in centres of gaps during the second growing season. (4) The removal of the understory in shaded northern edges favoured survival of seedlings for the same period. (5) The highest mortality rates were found in the centre of gaps with removal of understory vegetation on forest floor substrate. (6) CWD did not increase survival in the xeric forest in general, as expected. Rather, survival on CWD was greatest in shaded microsites during the growing season and, unexpectedly, during the first winter. In the mesic forest, CWD increased seedling survival during the first growing season. (7) As predicted, seedling shoot growth was negatively related to survival rates in the mesic forest. However, seedling survival and shoot growth were positively related at the xeric site. Removal of the understory was positively related to seedling shoot growth at both sites. (8) Contrary to our prediction, winter survival was affected by CWD substrate in the xeric forest.

Geographical variation in species responses to gaps is a common pattern documented along major environmental gradients (Spies & Franklin, 1989; Veblen, 1989). Causes of this variation are generally attributed to geographic variation in disturbance regimes, forest and understory composition and structure, and abiotic factors along the species range. In our case, differences between sites was because the responses of _N. pumilio_ to gaps are due to the combined effects of the within-gap microheterogeneity on early survival and growth of seedlings in the context of a macroenvironmental gradient.

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