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Soil–plant relationships and tree distribution in old growth *Nothofagus betuloides* and *Nothofagus pumilio* forests of Tierra del Fuego

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Abstract

The evergreen *Nothofagus betuloides* and deciduous *Nothofagus pumilio* live close together in Tierra del Fuego. The fact that these two species rarely form mixed forests suggests that the soil factor can contribute to the distribution of two species on a local scale. Most of these forests are undisturbed; therefore, soil characteristics may reflect both the influence of the species and of the dominant pedogenetic processes. In this paper, we aim to study how soil characteristics can affect nutrient cycling, the strategies of tree nutrition and the distribution of *Nothofagus* forests in Tierra del Fuego. Twenty-two soils in these two types of forests in contrasted topographic positions were sampled and analysed. The dominant soil processes were waterlogging in the evergreen forest and podzolisation in the deciduous one. Within each type of forest we observed large variability in soils. Nutrient-poor litter slowed down nitrogen cycling. However, phosphorus mobilisation was high in nutrient-poor environments because of low pH and waterlogging. Chemical and biological characteristics of the Oa horizon were able to discriminate between forest types while mineral soil characteristics were not. Biological activity of the organic horizons was limited by low pH and, in *N. betuloides* forests, also by waterlogging conditions. According to this pattern, *N. betuloides* grows in less fertile soils and thus has lower nutrient concentrations in leaves. In contrast, *N. pumilio* grows in soils with higher fertility and consequently has high nutrient content in leaves. Despite growing in low fertility sites, *N. betuloides* grows at a rate similar to that of *N. pumilio*. This suggests that the evergreen species is more efficient in using nutrients and better adapted to waterlogging conditions.
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Keywords: Forest floor; Soil nutrient availability; Nitrogen; Phosphorus; Leaf nutrient content

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1. Introduction

The southernmost forest ecosystems of our planet are in Tierra del Fuego (Argentina and Chile). These forests are mainly formed by three hardwood species of the genus *Nothofagus.* Evergreen *Nothofagus betuloides* (Mirb.) Oerst. and deciduous *Nothofagus pumilio* (Poepp. et Endl.) Krasser are the main tree species of the area. The third species, *N. antarctica* (Forst.f.) Oerst., is also deciduous, and normally forms scrubby vegetation at the upper limit of the forests, in less favourable habitats.

The altitudinal distribution of *N. pumilio* (*lenga*) forests at the latitudes of Tierra del Fuego is from 0 to 650–700 m a.s.l. (McQueen, 1976; Cuevas, 2000). However, *N. pumilio* generally occurs at cooler sites than *N. betuloides* (Frangi and Richter, 1994) and thus, *N. pumilio* is less abundant at lower elevations. The distribution area of *N. pumilio* in some areas adjoins the bounds of the semiarid grasslands. In contrast, the evergreen *N. betuloides* (*guindo*) in Tierra del Fuego grows along the coast, where temperatures are milder and rainfall higher (Gutiérrez et al., 1991). Although in general terms it appears that climate can account for the distribution of these species in Tierra del Fuego, the fact that these two species rarely form mixed forests suggests that the soil factor could contribute to their distribution at a finer scale. The soil control of the distribution of these species has already been pointed out by McQueen (1976), who has observed how the patches of these two species occasionally intermingle near sea level in freely drained morainic deposits (Pisano, 1981).

Many forests of the Isla Grande de Tierra del Fuego are undisturbed and forest soils in the area may highly express plant influence. By studying organic horizons, surface mineral soil characteristics, and tree nutrient use in an array of topographic situations of these two types of forests, we aim to study the soil characteristics resulting from the influence of plants and from some other site-specific dominant soil processes. Our intention is also to study how soil varies between these two forest types, and hence determine whether it may be influencing the distribution of the *Nothofagus* forests in Tierra del Fuego.

2. Area descriptions, methods and materials studied

2.1. Study area

This study was carried out in the southern part of La Isla Grande of Tierra del Fuego (54°49′S, 68°49′W), which is covered by *Nothofagus* forests. The climate of the forested area of Tierra del Fuego is cold–temperate with high humidity (DFk'c; Pisano, 1981). Mean annual temperature of the area is 4.5° and mean annual rainfall is 561 mm (Ushuaia climatic station; Holdgate, 1960). Mean annual variation of temperature is small for the latitude (less that 8 °C of thermic amplitude).

Deciduous forests of *N. pumilio* (*lenga*) in Tierra del Fuego form a single woody species forest; the evergreen *N. betuloides* (*guindo*) forests, when growing at lower elevations, form forests with *Drimys winteri* and *Maytenus magellanica* in the understory. The physiognomy of *N. betuloides* forests may reflect high precipitation (McQueen, 1976).

Prior to set the experimental design to characterise the typology of soils, we sampled and described several soil profiles in *N. pumilio* and *N. betuloides* forests in La Isla Grande of Tierra del Fuego. Here, we present one profile of each great group of soils observed in the area, except for the *aquents* suborder, which were described in the field but not analysed.

In order to study the soil–plant relationships, six sites were selected in La Isla Grande of Tierra del Fuego according to the forest type and the topographic position. In the *N. pumilio* area, we sampled three sites at different topographic positions covering from 260 to 555 m a.s.l. and three sites in *N. betuloides* area covering from 25 to 355 m a.s.l. (see Table 1). In each

Table 1
Soil types in the Tierra del Fuego *Nothofagus* forests as affected by slope position

Forest type	Slope position	Soil type
N. pumilio	Lower slope	Cryocrept
N. pumilio	Flat middle slope	Cryorthod
N. pumilio	Upper slope	Cryocrept
N. betuloides	Lower slope	Cryocrept
N. betuloides	Middle slope	Hydraquent and Cryaquent
N. betuloides	Upper slope	Borosaprist

site, we sampled four different plots except for the higher elevation *N. betuloides* site, where we sampled only two plots.

2.2. Soil sampling and analysis

In each site, we sampled four 13×13 m plots. For the organic layers, in each plot, we sampled four points per plot with a frame of 21 cm^2 of diameter. Organic layers were separated in the field into two horizons, Oi + Oe (Oie) and Oa. In the Oie horizon, we included the wood debris smaller than 20 cm in length. Undecomposed boles laying on the soil were not considered in this study. Samples were air-dried and weighed. Then, after sieving through a 2-mm mesh, a bulk sample was obtained per plot, horizon, and fraction for further analyses. At each sampling point, we measured the thickness of each organic horizon (Oie and Oa) and counted the number of earthworms that appeared in the sampled area. In each plot, a soil profile was described and the mineral soil was sampled from 0 to 15 cm.

Soil total C and N were determined with the elemental analyser CNHS Carlo Erba 1500. Soil total P was determined by wet digestion with HNO_3 and $HClO_4$ and by ICP spectrometry. Water-soluble P was extracted from the mineral and Oa horizon at 1:10 ratio (Humphreys and Pritchett, 1962). The total amount of P in the extract was determined by ICP spectrometry. For the cation exchange capacity and base saturation determination, we extracted soil samples with ammonium acetate at pH 7. Ca, Mg, K, and Na were analysed by atomic absorption. Fe and Al were extracted with pyrophosphate and with citrate-dithionite (Loeppert and Inskeep, 1996) and then analysed by atomic absorption.

2.3. Leaves sampling

In January (summer), leaves from 10 trees were sampled in each site following the methodology described in Ballard and Carter (1985). Leaves were separated according to their age and bulked to one sample per site. Foliar samples were analysed for total C, N, and P using the same methodology as the soil samples.

2.4. Experimental design and statistical analysis

The experimental design was set to study the differences between tree species. Different topographic conditions were selected in each case in order to include all soil types sampled in the area (see Table 1 and soil types in Appendices A–D). Thus, as the selected topographic positions were not exactly coincident in the two studied forest types topography was not introduced as a factor in a two-way ANOVA model with interaction. Significant differences between tree species and soil horizons were tested using a two-way ANOVA with interaction (SPSSX ver. 9.0). The topography effects were subsequently tested only within each species by one-way ANOVA and Duncan multiple range test. Within each horizon, the effects of forest type were also tested using one-way ANOVA. Foliar nutrients and specific leaf weight were analysed by one-way ANOVA and Duncan multiple range test. Proportions and percentages were previously transformed by using the arcsine of the square root. The Poisson distribution of earthworm abundance was transformed by the square root (Dickey and Kladivko, 1989). Principal component analysis was performed using SPSSX factorial analysis of 13 variables (see footnote of Fig. 3).

3. Results and discussion

3.1. Soil typology

In Appendix A, we show the general characteristics of well-drained soils of *N. pumilio*. In these soils, there are no stagnic features until 50 cm of depth. Under these conditions podzolisation processes are dominant. In steep positions, the E horizon is not well differentiated and stoniness is high (between 25 y 80%). In contrast in flat positions, the E horizon is well developed. These differences are reflected in the typology of soils. According to the Soil Taxonomy criteria (Soil Survey Staff, 1990), in high stability positions, soils were *Cryorthods* (Appendix A), while in unstable position soils were *Cryochrepts* (Appendix B).

The *N. betuloides* soils studied show waterlogging features. The water table often reaches the organic layers, a phenomenon that slows down organic

matter decomposition. On the upper plateau, the water table almost reaches the soil surface. The depth of the water table then increases as we go down the slope. Thus, the typology of soils in *N. betuloides* is very much related to the slope position. In soils of the lower slope, water table is subsuperficial at a depth of about 50 cm. Consequently, the profiles of lower slope soils are moderately well drained and have been described as *Cryochrepts* (Appendix C). The low degree of evolution may relate to the rejuvenation as a result of frequent treefell (Puigdefábregas et al., 1999). The shallow water table on the middle and upper slopes leads to the formation of highly organic soils with no E horizons. On the middle slope soils are *Hydraquents* and *Cryaquents*. They are waterlogged for a period of time each year and are characterised by an incipient development of soil horizons. On the higher part of the slope, soils are *Borosaprists* (Appendix D). These soils contain large amounts of poorly decomposed organic matter and are waterlogged during most of the year.

The evolution of Tierra del Fuego forest soils mainly depends on their stability and on water dynamics. Frequent and widespread landslides and fallen trees may alter the topography and microtopography of surfaces and thus soils may rejuvenate. On the other hand, water determines soil formation processes such as podzolization in well-drained soils and organic soil formation in waterlogging conditions.

3.2. Soil fertility

The concentrations of N and P in the Oie horizon were very much influenced by the quality of green leaves (Table 5), so that N and P concentrations in Oie horizon were always higher in *N. pumilio* soils (Table 2). C concentration in Oie layer was lower in *N. pumilio* forest floor, probably as a result of its higher content of mineral particles resulting from earthworm activity. Low C/N and C/P ratios were also observed under this species (Table 2).

The high C/N ratio observed in Oie horizons under *N. betuloides* will likely result in immobilisation of N in this horizon, slowing down the cycling of N. On the other hand, P mineralization is mostly controlled by P demand and it is more independent from C availability (Tate and Salcedo, 1988). However, some authors have stated that an optimum C/P ratio may exist that does not inhibit decomposition and leads to minimal loss (Chuyong et al., 2000). The high C/P ratio of the Oie horizon in *N. betuloides* forests (Table 2) may be a consequence of the high cell wall content of the evergreen leaves that may reduce P losses.

Table 3 summarises some characteristics of the Oa horizon across vegetation and soil types. While the quality of the Oie horizon was primarily dependent upon the type of vegetation (*N. pumilio*, *N. betuloides* forests), the quality of the Oa horizon was very much dependent upon the soil topography. In *N. pumilio* forests, the Oa horizon C/N, C/P, and N/P ratios

Table 2

Oie horizon C, N and P concentrations and ratios in *N. pumilio* and *N. betuloides* forests of Tierra del Fuego

Oie horizon	*N. pumilio*			*N. betuloides*			ANOVA species
	Lower slope	Middle slope	Upper slope	Lower slope	Middle slope	Upper slope	
C (mg g^{-1})	400.1 a	462.5 b	448.5 b	493.6 a	494.6 a	513.4 a	0.000
	(15.8)	(6.7)	(9.5)	(4.6)	(5.8)	(0.1)	
N (mg g^{-1})	10.2 a	11.2 a	10.0 a	7.7 a	7.3 a	8.5 a	0.000
	(0.5)	(0.5)	(0.3)	(0.5)	(0.4)	(0.5)	
P (mg g^{-1})	1.05 a	1.01 a	1.07 a	0.55 a	0.38 b	0.43 ab	0.000
	(0.11)	(0.04)	(0.05)	(0.04)	(0.03)	(0.08)	
C/N	39.52 a	41.47 a	44.83 a	65.19 a	68.62 a	60.61 a	0.000
	(2.51)	(2.13)	(1.45)	(4.33)	(3.79)	(3.57)	
C/P	395 a	462 a	421 a	916 a	1327 b	1230 b	0.000
	(42)	(24)	(18)	(75)	(94)	(226)	
N/P	8.3 a	7.3 a	11.5 b	14.1 a	19.33 b	20.2 b	0.000
	(0.74)	(0.29)	(0.17)	(0.60)	(0.90)	(2.54)	

Probability of ANOVA species comparison is shown. Different letters indicate significant differences within each species at a probability < 0.05 (Duncan's test). Standard errors are shown in parentheses.

Table 3
Oa horizon C, N, and P concentrations and ratios in *N. pumilio* and *N. betuloides* forests of Tierra del Fuego

Oa horizon	*N. pumilio*			*N. betuloides*			ANOVA species
	Lower slope	Middle slope	Upper slope	Lower slope	Middle slope	Upper slope	
C (mg g^{-1})	259.9 a (12.7)	357.8 b (5.9)	309.1 c (14.6)	225.9 a (26.4)	388.1 b (37.9)	495.0 b (6.4)	0.361
N (mg g^{-1})	12.0 a (0.6)	12.7 a (0.2)	11.9 a (0.5)	8.2 a (1.3)	11.6 a (0.5)	8.8 a (0.2)	0.002
P (mg g^{-1})	1.45 a (0.03)	1.11 b (0.08)	1.64 a (0.07)	1.04 a (0.10)	0.89 a (0.11)	0.46 b (0.05)	0.000
C/N	21.67 a (0.61)	28.3 b (0.28)	25.98 c (0.87)	28.30 a (2.21)	33.81 a (3.75)	56.26 b (0.56)	0.007
C/P	179.6 a (12.3)	327.2 b (22.9)	190.7 a (15.8)	219.2 a (19.3)	482.1 a (114.2)	1074.2 b (25.9)	0.021
N/P	8.31 a (0.64)	11.53 b (0.73)	7.32 a (0.50)	7.81 a (0.67)	13.81 b (2.07)	19.10 b (0.65)	0.052
pH	6.5 a (0.2)	4.6 b (0.2)	4.9 b (0.2)	5.6 a (0.3)	5.4 a (0.3)	3.5 b (0.2)	0.598
Sol. P (mg kg^{-1})	66.24 a (15.64)	341.19 b (26.52)	235.26 c (33.71)	20.71 a (5.75)	60.74 a (22.14)	169.95 b (25.56)	0.003
EW (Ind. m^{-2})	64.60 a (19.61)	16.96 b (6.14)	77.59 a (18.01)	34.28 a (12.97)	37.89 a (3.46)	0.0 b (0.0)	0.100
Ca (cmol$_q$ kg^{-1})	95.40 a (22.02)	62.20 a (4.60)	60.51 a (4.61)	23.19 a (6.18)	52.66 b (4.32)	13.32 a (1.82)	0.002
Mg (cmol$_q$ kg^{-1})	6.89 a (1.19)	7.74 a (0.82)	9.32 a (0.57)	9.87 a (1.35)	10.42 a (0.70)	8.88 a (0.86)	0.031
K (cmol$_q$ kg^{-1})	0.90 a (0.13)	1.35 a (0.21)	1.29 a (0.04)	0.51 a (0.09)	0.59 a (0.09)	0.72 a (0.12)	0.000
Na (cmol$_q$ kg^{-1})	0.32 a (0.07)	0.33 a (0.01)	0.24 a (0.01)	1.25 a (0.22)	0.85 a (0.06)	1.12 a (0.24)	0.000

Other soil characteristics such as pH in water, water soluble P (Sol. P), earthworm numbers (EW), and exchangeable cations are also shown. Probability of ANOVA species comparison is shown. Different letters indicate significant differences within each species at a probability < 0.05 (Duncan's test). Standard errors are shown in parentheses.

increased markedly with soil evolution (from *Cryo-chrepts* to *Cryorthods*). The increase in these parameters in *N. betuloides* soils was directly proportional to waterlogging conditions and to the slope position

(Table 1). In both types of forests, the N/P ratio increased with the carbon concentration in the Oa horizon (Fig. 1). The indication here is that P accumulates, with respect to N, in the more mineralized
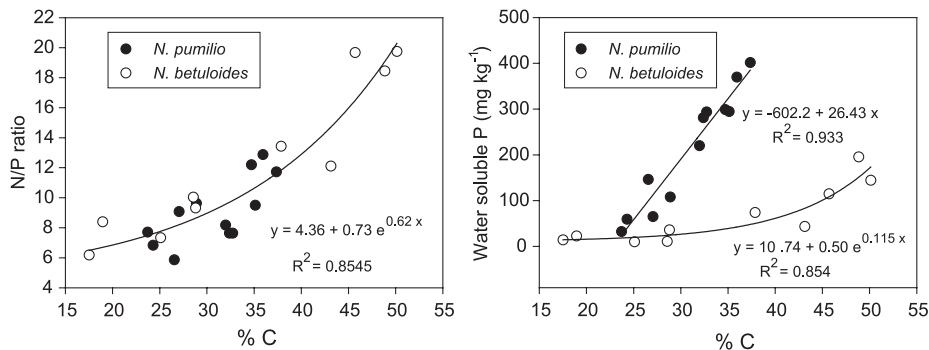

Fig. 1. Organic carbon vs. N/P ratio and water soluble P in Oa horizons of *N. pumilio* and *N. betuloides* forests, considering the individual horizons in each plot. All regression lines are significant at 5%.

organic horizons (Oa). Moreover, water-soluble P was strongly and positively related to the Oa horizon Carbon concentration (Fig. 1). These increases in water soluble P were especially relevant in *N. pumilio* forests. In *N. betuloides* soils, this increment was much less pronounced and occurred mainly in water-logged soils with high organic matter content in the Oa horizon (*Borosaprists*). While in both types of forests total N concentration was independent of water-soluble P, total P concentration decreased as water-soluble P increased (Fig. 2). This increase was highly significant ($p < 0.002$) under *N. betuloides*

species where the most waterlogged plots (upper slope plots of *N. betuloides*) showed the lowest total P concentrations while water soluble P was highest. On the upper slope, on *N. betuloides* soils, water soluble P represented as much as a 36% of the total P content, and the pools of total N and P were low. In these plots, carbon content, C/N, and C/P ratios were the highest observed in the study area. This indicates that the organic matter in these plots was poorly decomposed.

The increases of C/P and C/N ratios observed in both types of forest as water soluble P increases (Fig.
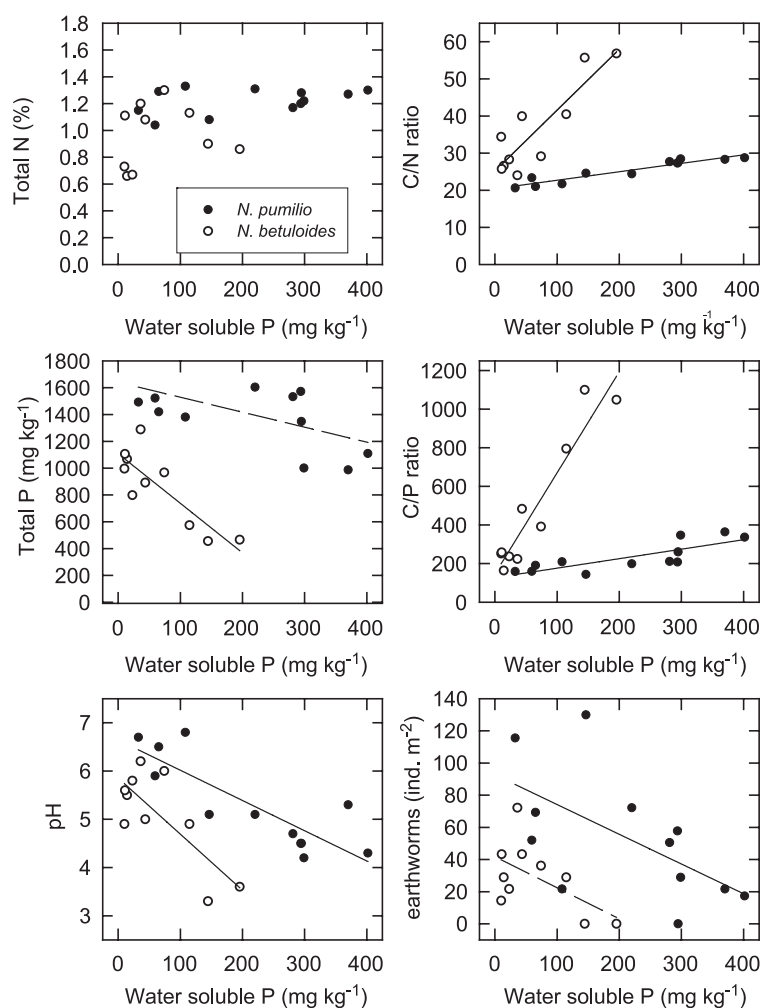

Fig. 2. Relationships between water soluble P and Oa horizon chemical characteristics (Total N, P, C/N ratio, C/P ratio and pH) and Oa horizon earthworm density of *N. pumilio* and *N. betuloides* in Tierra del Fuego. All regressions lines are significant at 5% except those indicated with a dashed line, which are significant at 10%.

2) suggest that water soluble P in the Oa horizon increases as the degree of decomposition of the organic matter decreases. This fact suggests a rapid mobilisation of P in soils with small pools of P and with poorly decomposed organic matter. Moreover, there were negative relationships between water-soluble P with both pH and earthworm density (Fig. 2). Using the C/N ratio as an indicator of the degree of decomposition of organic matter, less decomposed organic matter coincided with low earthworm density, low pH, and with high levels of water-soluble P. Paré and Bernier (1989a), working with sugar maple (*Acer sacharum* Marsh.) stands in the northern part of the Appalachians concluded that the humus forms may exert a major influence on the P nutrition of forests. These authors found that stands growing on soils with moderately acid mull humus exhibited low foliar P concentrations, while more acidic stands growing on soils with more humus had adequate P nutrition. The same authors observed that the dependence of P solubility on soil acidity is very different in the organic horizons (Oa) than in less organic horizons (Ah) where the availability of Fe and Al is much higher (Paré and Bernier, 1989b). They stated that concentrations of Fe and Al in Oa horizons were normally too low to induce P fixation under acidification. In organic horizons, acidification may lead to changes in organometal phosphate complexes and enhance the hydrolysis of organic P. Both processes may lead to abiotic P release. In anaerobic conditions, the reduction of iron may also enhance this abiotic release of P (Ennell et al., 1989; Willet, 1989; Wright et al., 2001). This large abiotic release of P in organic in Tierra del Fuego soils may represent up to a 37% of the total P in the Oa horizon. Because this mainly occurs in soils with low total N and P, it is not in agreement with the expected positive feedback of nutrient cycling and litter quality. Other authors studying Hawaiian montane forest also found a depletion of soil P in areas with low redox potential values (Miller et al., 2001).

In *N. pumilio* forests, earthworm density related negatively to the C concentration of the Oa horizon ($r = -0.719$; $p < 0.008$). Earthworm density in the Oa horizon in *N. pumilio* forests ranged from 17 to 78 ind. m^{-2} while in *N. betuloides* forest it ranged from 0 to 40 ind. m^{-2} (Table 3). If these figures are compared to those of other cold temperate forests of the Northern Hemisphere ranging from 65 to 175 ind. m^{-2} (Niepolomice Forest, Poland; Rozen, 1994), we find that our data are much lower. Our data only registered the earthworms in the organic horizons and thus probably show an underestimation of the total numbers, especially in soils with well-aerated mineral soils. Earthworm density is normally well related to the activity of soil microflora in bulk soil (Martin et al., 1992). Hence, we can presume that the activity of soil biota was high at high earthworm density and coincided with high pH. Under these conditions, high activity of soil biota could be responsible for keeping the levels of water-soluble P low and for transforming fresh organic matter to humus with low C/N and C/P ratios. The unexpected negative relationship between P solubility and earthworm density could be the result of the inhibition of biological activity at low pH. Moreover, in organic soils, poor substrate quality may limit microbial activity more than do low nutrient concentrations (Bridgham and Richardson, 1992). High C/N and C/P ratios (similar to ratios in Oie horizon; Table 2) observed in the most acid soils also indicate low biological activity. Thus, in highly organic soils of Tierra del Fuego forests, biological activity appeared to be regulated first by pH and secondly by carbon quality.

Waterlogging conditions also appeared to have large effects on the cycling of N. In such conditions (middle and upper slope of *N. betuloides* sites), the Oa horizon C/N ratio was often twice as high as in more aerated sites (Table 3), so that N mineralization was unlikely to occur. Nevertheless, Verhoeven et al. (1990) found net N mineralization in mires with Sphagnum carpets having C/N ratios well above 40.

Exchangeable Ca and K in the Oa horizon were higher in *N. pumilio* forests while Na was higher in *N. betuloides* (Table 3), probably as a result of its proximity to the sea. Mg was slightly higher in *N. betuloides* forests. Ca was the uppermost cation, especially in *N. pumilio* forests. In *N. betuloides* sites, Ca was especially high in middle slope soils (*Cryaquents* and *Hydraquents*); and in extremely acid soils (upper slope, *Borosaprists*), Ca dropped to the levels of Mg. Oa horizon pH was higher at lower slope position and did not show any species effect, although the highest pH values were observed

under *N. pumilio* and the lowest under *N. betuloides* forests.

Carbon and N content in mineral soils were higher in *N. betuloides* forests, especially on those growing on *Hydraquents* (middle slope position; Table 4). In *N. pumilio* sites, the mineral soil C/N ratio showed a similar behaviour to C/N in the Oa horizon (Table 4). In *Cryortods* of the flat middle slope of *N. pumilio* forests and in *N. betuloides* soils, C/N in mineral soil was unchanged in relation to the overlying Oa horizon. Such unchanged C/N ratios can be interpreted as partial organic matter decomposition due to low pH and/or anaerobic conditions. High variability of C/N among plots could be the result of large amounts of decaying wood scattered over the sites (Frangi et al., 1997).

Except in waterlogged areas (see *N. betuloides* middle slope, Tables 3 and 4) the concentration of total P was higher in the Oa horizon than in the mineral soil. The high P content in Oa horizons was specially relevant in *N. pumilio* forests in which, in some cases, more than twofold that of the mineral

soil (upper slope). Increases of water-soluble P in Oa horizon compared to the mineral soil occurred in both types of forest although they were much higher in *N. pumilio* forests. In these forests water-soluble P was from 17 to 130 times greater than that of the mineral soil. In *N. betuloides* forest this increment was from 6 to 28 times that of the mineral soil (Tables 3 and 4). Mineral soil soluble P did not differ between the two types of forests while it did organic horizons water-soluble P. Exchangeable Ca, Mg and K were much lower in mineral soil than in organic layers, while Na did not show any change. In *N. betuloides* soils, Mg and Na in mineral soil were higher than in *N. pumilio*, while K did not show any difference. Exchangeable Ca showed a positional effect. Coinciding with the Oa horizons, mineral soil pH was high at lower slope position and did not show any difference between forest types. The large difference in exchangeable cations in Oa horizons indicates that organic horizons in these soils are able to hold large amounts of exchangeable sites.

Table 4

Mineral soil (0–15 cm) total C, N, and P concentrations and ratios in *N. pumilio* and *N. betuloides* forests of Tierra del Fuego

Mineral soil (0–15 cm)	*N. pumilio*			*N. betuloides*			ANOVA species
	Lower slope	Middle slope	Upper slope	Lower slope	Middle slope	Upper slope	
C (mg g^{-1})	29.5 a (1.93)	63.9 b (1.99)	45.9 c (1.75)	84.0 a (13.6)	147.5 a (46.7)	*n.s.*	0.001
N (mg g^{-1})	1.6 a (0.1)	2.2 a (0.2)	2.2 a (0.3)	2.9 a (0.8)	5.5 a (1.8)	*n.s.*	0.012
P (mg g^{-1})	0.83 a (0.04)	0.78 a (0.07)	0.74 a (0.03)	0.61 a (0.22)	1.02 a (0.19)	*n.s.*	0.787
C/N	18.71 a (0.84)	29.63 b (2.35)	22.10 a (2.29)	32.08 a (4.19)	26.92 a (0.23)	*n.s.*	0.044
pH	5.5 a (0.35)	4.0 b (0.07)	4.5 b (0.12)	4.9 a (0.27)	5.7 a (0.45)	*n.s.*	0.205
Sol. P (mg kg^{-1})	3.74 a (0.42)	2.56 a (0.41)	2.39 a (0.61)	3.37 a (1.01)	2.17 a (0.18)	*n.s.*	0.911
Ca (cmol$_q$ kg^{-1})	14.87 a (3.64)	7.93 ab (0.78)	4.20 b (0.99)	11.03 a (1.05)	27.76 b (3.09)	*n.s.*	0.049
Mg (cmol$_q$ kg^{-1})	1.23 a (0.27)	0.96 a (0.25)	0.76 a (0.21)	1.80 a (0.25)	1.32 a (0.10)	*n.s.*	0.015
K (cmol$_q$ kg^{-1})	0.25 a (0.07)	0.23 a (0.05)	0.17 a (0.02)	0.25 a (0.03)	0.36 a (0.09)	*n.s.*	0.184
Na (cmol$_q$ kg^{-1})	0.13 a (0.02)	0.14 a (0.02)	0.10 a (0.01)	1.06 a (0.19)	0.75 a (0.27)	*n.s.*	0.000

Other soil characteristics such as pH in water, water soluble P (Sol. P), and exchangeable cations are also shown. Probability of ANOVA species comparison is shown. Different letters indicate significant differences within each species at a probability <0.05 (Duncan's test). *n.s.* refers to no available sample. In *N. betuloides*, middle slope only in hydraquent mineral soil was sampled (two replicates). Standard errors are shown in parentheses.

Nutrient concentration in Tierra del Fuego forests was in general much higher in the Oa horizon than in the surface mineral soil. Rooting density in such holorganic horizon was also high. In some water-logged areas in *N. betuloides* forests, rooting depth was exclusively confined to this horizon. Consequently, it is reasonably to think that in such forests, as in boreal forests (e.g., Tamm, 1991; Van Cleve et al., 1993), nutrient cycling mostly occurs in organic layers.

Principal component analysis, performed using 13 variables describing the chemical characteristics of the Oa horizon and its earthworm density (Fig. 3), was able to discriminate between the two types of forests and between the different soil types described in the studied area. The first axis of principal components analysis accounted for 42% of variability and its high values indicated high N, P, and Ca content, a high number of earthworms and a high pH. Low values of this axis coincided with high C/N and C/P ratios. Thus, this axis discriminated between high and low organic matter turnover rates. The second axis accounted for 25% of variability and represented in its high values high water-soluble P, exchangeable K, and total N, while in its low values it represented high exchangeable Na and pH. This axis discriminated between sites with high amounts of available P and K and sites with low available P and K and higher pH. In general, principal components analysis based on Oa horizon chemical and biological attributes was able to discriminate among vegetation and topography, suggesting that Oa horizon characteristics were good indicators of the interaction between vegetation and soil.

3.3. Tree nutrition and productivity

Both specific leaf weight and nutrient content of the two studied species showed large differences (Table 5). The leaves of *N. betuloides* are more sclerophyllous and quite persistent on the trees, and some leaves may last up to 7 years. These leaves showed low N and P concentrations. In contrast, deciduous leaves of *N. pumilio* were thinner and showed high N and P content, suggesting higher fertility in these forests. Hevia et al. (1999), studying *N. pumilio* at lower latitudes (∼ 37°S), found lower
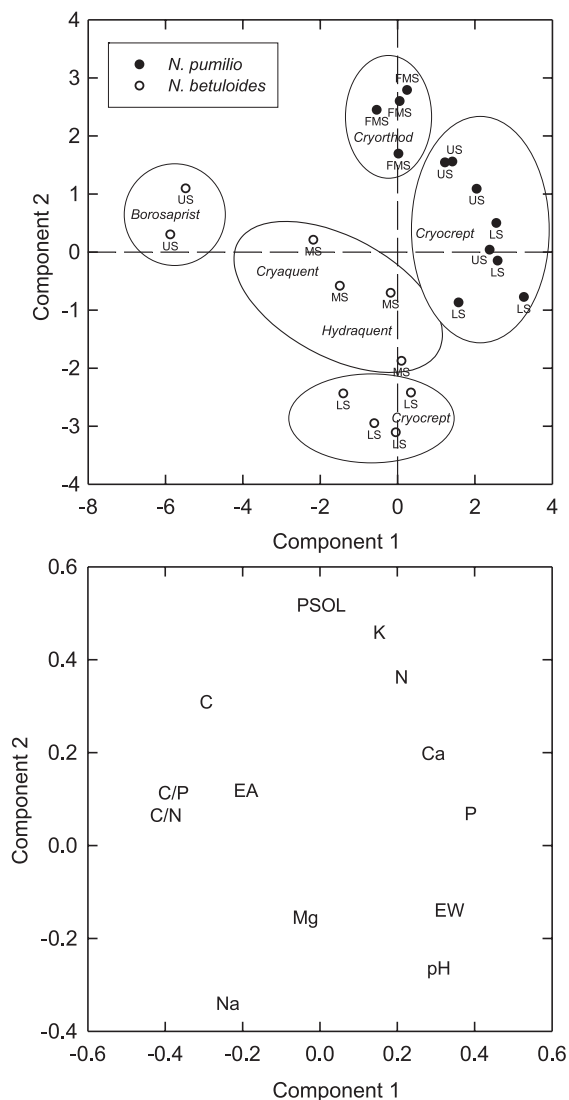

Fig. 3. Principal components analysis of 13 variables of the Oa horizon of the 22 studied plots. The variables are also represented. C refers to total C concentration; N to total N concentration; P to total P concentration; PSOL to water soluble P; Ca, Mg, K and Na to exchangeable cations; EA to pH in water-pH in KCl and EW to earthworm density. LS refers to lower slope, MS to middle slope, US to upper slope, and FMS to flat middle slope.

specific leaf weight and N and P content than we did in Tierra del Fuego. They also found that the evergreen *N. dombeyi* had thicker leaves and lower nutrient content than the deciduous *Nothofagus* of their study (*N. pumilio* and *N. obliqua*). When compared to our data, *N. dombeyi* showed lower specific

Table 5
Specific leaf weight and foliar N and P concentrations of *N. pumilio* and *N. betuloides* foliage of Tierra del Fuego

	N. pumilio	*N. betuloides* leaf cohorts						
		1	2	3	4	5	6	7
Specific leaf weight (mg cm^{-2})	8.68 a	12.60 b	17.97 c	18.59 c	17.86 c	18.56 c	19.06 c	19.83 c
	(0.25)	(1.00)	(0.67)	(0.61)	(0.94)	(0.03)	(0.145)	(0.215)
Foliar N (mg g^{-1})	22.9 a	14.2 b	10.2 b					
	(1.0)	(1.3)	(0.6)					
Foliar P (mg g^{-1})	2.70 a	0.89 b	1.03 b					
	(0.15)	(0.04)	(0.00)					

Figures are means of three samples. Different letters show significant differences (Duncan's test). Standard errors are shown in parentheses.

leaf mass than *N. betuloides* and similar N and P content.

The large differences in leaf structure and nutrient concentrations observed between *N. pumilio* and *N. betuloides* could have resulted from adaptations of tree species to the different soil characteristics. In waterlogged boreal environments, the evergreen and sclerophyllous characters can be associated with low nutrient content in plant tissues that can result from low O$_2$ in the soil and low organic matter turnover (Larsen, 1982). Large leaf N variation in *N. betuloides* and high leaf N/P ratio (see Table 5) suggest that this species growing in waterlogged soils faces N shortages in comparison to *N. pumilio*. However, as reported by Gutiérrez et al. (1991) productivity of *N. betuloides* forest was similar to that of *N. pumilio* suggesting that *N. betuloides*, by increasing leaf life span and by reducing nutrient concentration, can grow well in waterlogged soils.

4. Conclusions

Soil formation processes in forests of Tierra del Fuego are highly influenced by the water regime in the soil profile. *N. pumilio* grows in areas of well-drained soils where the dominant soil formation process is podzolisation while *N. betuloides* grows in areas that range from moderately to highly water-logged conditions in which the dominant process is organic soil formation. The contrasted quality of litter from the two studied forests can also contribute to differentiate their soils. In Tierra del Fuego, especially in *N. betuloides* forests, soil fertility is very much

concentrated in the ectorganic Oa horizon; thus, it is mainly related to organic matter cycling. The cycling of N is principally determined by litter quality and thus largely controlled by tree species. However, the cycling of P in the organic layers occurs in association with abiotic processes mainly controlled by soil characteristics such as pH and waterlogging. Hence, somewhat surprisingly, P is readily mobilised in P-poor substrates. Organic matter characteristics and biological activity in the ectorganic Oa horizon are sensitive to the vegetation (litter quality) and soil type (pH and waterlogging conditions). Therefore, a characterisation of the organic layers could be useful for predicting site fertility in Tierra del Fuego forests. *N. betuloides* grows in waterlogged sites with low fertility while *N. pumilio* grows in soils with higher soluble P and decomposition rates and thus with higher fertility. Despite the differences in soil fertility reported in this study, forest productivity was similar in both studied cases. This fact could be attributed to small climatic differences between the studied areas and/or to different nutrient use efficiencies of the studied species. However, it appears that the distribution of *N. pumilio* and *N. betuloides* in Tierra del Fuego is very much associated with the soil variation of the area.

Appendix A

Lithic cryorthod from a *N. pumilio* forest at the upper slope (525 m a.s.l.). CEC refers to cation exchange capacity at pH 7 as measured with ammonium acetate, S to the sum of basic cations and n.d. to nondetermined data.

Horizon	Depth (cm)	pH	Total N	Total C	CEC	S	S/CEC	Fe	Al	Fe	Al	Gravel and stones	Clay
			(mg g^{-1})		(cmol$_q$ kg^{-1})			Pyrophosphate (%)		Dithionite-citrate (%)		(%)	
Oa	− 5	3.7	7.5	234.5	18.86	11.05	58.55	0.16	0.14	0.80	0.20	0	n.d.
A	0–2.5	3.7	3.1	90.3	n.d.	n.d.	n.d.	0.27	0.31	0.83	0.10	11.8	1.4
E	2.5–8	4.2	1.3	18.5	4.53	0.65	14.39	0.28	0.19	0.85	0.11	41.3	13.7
Bs1	8–27.5	5.1	2.3	43.1	12.95	0.54	4.18	3.44	1.49	6.41	2.02	26.74	10.5
Bs2	27.5–30	5.3	1.9	35.1	n.d.	n.d.	n.d.	1.85	0.82	6.02	1.66	49.63	26.9
IIB	30–43	5.4	1.3	19.2	7.95	0.28	3.52	1.22	0.77	5.83	1.18	39.41	9.1
IIC	43	5.3	1.3	20.3	11.34	0.23	2.08	1.03	0.69	4.22	1.05	86.8	n.d.

Appendix B

Dystric cryocrept from a *N. pumilio* forest at the middle slope (490 m a.s.l.). CEC refers to cation exchange capacity at pH 7 as measured with ammonium acetate, S to the sum of basic cations and n.d. to nondetermined data.

Horizon	Depth (cm)	pH	Total N	Total C	CEC	S	S/CEC	Fe	Al	Fe	Al	Gravel and stones	Clay
			(mg g^{-1})		(cmol$_q$ kg^{-1})			Pyrophosphate (%)		Dithionite-citrate (%)		(%)	
A	0–2.5	4.2	7.3	204.5	n.d.	n.d.	n.d.	0.09	0.03	0.5	0.06	52.3	3.7
E	2.5–8	4.5	2.2	23.2	5.68	2.37	41.18	0.23	0.07	0.95	0.08	55.0	1.2
Bs	8–13	4.3	1.1	22.7	2.99	0.63	21.09	2.20	1.09	5.33	0.54	67.8	18.4
B	13–23.5	4.3	1.7	30.3	14.75	1.05	7.12	1.62	0.91	7.63	1.36	44.1	11.7
C1	23.5–40	5.2	1.2	13.0	7.42	0.84	11.40	0.30	0.44	5.64	1.07	35.1	8.7
C2	40	5.1	1.6	17.8	6.97	0.94	13.53	0.48	0.62	6.47	1.32	26.2	1.1

Appendix C

Aquic cryocrept from a *N. betuloides* forest at the low slope (10 m a.s.l.). CEC refers to cation exchange capacity at pH 7 as measured with ammonium acetate, S to the sum of basic cations and n.d. to nondetermined data.

Horizon	Depth (cm)	pH	Total N	Total C	CEC	S	S/CEC	Fe	Al	Fe	Al	Gravel and stones	Clay
			(mg g^{-1})		(cmol$_q$ kg^{-1})			Pyrophosphate (%)		Dithionite-citrate (%)		(%)	
Oa	− 10–(− 5)	4.6	11.5	419.8	21.2	21.2	100	0.11	0.43	0.11	0.07		
Oa2	− 5–0	4.7	10.2	342.6	24.0	19.12	80	0.01	n.d.	0.06	0.06		
E	0–4	4.7	1.3	40.5	7.25	5.95	82	0.05	0.10	0.19	0.11	19.75	14.7
IIB	4	4.7	1.3	27.8	7.47	6.54	88	0.75	0.28	1.07	0.05	60.01	19.5

Appendix D

Borosaprist from a *N. betuloides* forest at the high slope (350 m a.s.l.). n.d. refers to nondetermined data.

Horizon	Depth (cm)	pH	Total N	Total C	CEC	S	S/CEC	Fe	Al	Fe	Al	Gravel and stones	Clay
			$(mg\ g^{-1})$		$(cmol_q\ kg^{-1})$			Pyrophosphate (%)		Dithionite-citrate (%)		(%)	
Oa	0–10	3.4	11.5	484.3				0.17	0.81	0.41	n.d.		
Oa2	10–25	3.5	15.2	492.2				1.73	5.54	1.76	4.18		

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