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Distribution and cycling of C, N, Ca, Mg, K and P in three pristine, old-growth forests in the Cordillera de Piuchué, Chile

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Abstract. We assessed a number of biomass and soil parameters in order to examine relationships among nutrient availability, forest productivity and vegetation patterns in two old-growth forested watersheds in a pristine montane landscape on Isla de Chiloé, Chile. We selected watersheds in both gymnosperm- and angiosperm-dominated forests and determined tree species, d.b.h. and health for all trees > 2 cm d.b.h. in plots established at 50 m intervals. Soils were sampled at two depths in each plot and analyzed for total C and N, and for exchangeable Ca, K, Mg and resin-extractable P. Allometric relationships and vegetation nutrient concentrations were used to determine above-ground pools from the vegetation survey data. Growth rates were derived from increment core measures. Soil pools of most elements measured appear adequate to support forest growth indefinitely. Mineralized nitrogen, which is similar in quantity to the annual demand for nitrogen from the soil is the exception, consistent with the possibility of N limitation in two of the forest types studied. A third type, an evergreen broadleaved forest, appears to require substantially more nitrogen than would appear to be available from net mineralization measurements. Productivity per unit of nitrogen required from the soil is quite high, largely as a consequence of the evergreen habit of the species in these forests. Compared to other temperate montane forests in the Northern Hemisphere, nutrient pools and cycling characteristics were found to be mostly similar across forest types, in spite of considerable variation in vegetation and soils.

Introduction

Human disturbances have important, long-term consequences for biogeochemical cycling in forests. Land uses such as logging and agriculture may affect nutrient availability for decades after cessation of these activities (Knops and Tilman 2000; Attiwill and Adams 1993). Atmospheric deposition of nitrogen and sulfur alters the ecosystem processing of those nutrient, and has been shown to affect leaching rates of base cations from soils (Johnson 1999; Fenn et al. 1998; Norby 1998; Goulding et al. 1998). Ultimately, understanding the consequences of these types of disturb-

ances necessitates understanding the underlying controls on nutrient cycling and how they shift in response to perturbation.

One useful approach is to carry out baseline studies in pristine forests followed by controlled experimentation to examine disturbance-related changes in processes governing nutrient cycling. Thus, in the first phase of the Cordillera de Piuchué study (*e.g.* Hedin et al. (1995); Armesto et al. (1995a)), we sought to quantify pools and fluxes of the major nutrients C, N, P, Ca, Mg and K in undisturbed broadleaf- and conifer-dominated watersheds on Isla de Chiloé, located off the coast of southern Chile. In this paper, we document the above- and below-ground pools of those nutrients, estimate annual nutrient uptake by vegetation, and compare the annual nutrient requirements to available nutrient pools in the soil. Additionally, we compare nutrient pools and productivity of these Chilean forests with analogous Northern Hemisphere montane temperature forests selected from published data summaries for the Integrated Forest Study [IFS] (Johnson and Lindberg 1992) and International Biological Program [IBP] (Cole and Rapp 1981; DeAngelis et al. 1981) to assess similarities and differences.

Study area

The experimental watersheds are contained within an area of some 30 km^2 of dissected ridgeline situated in the Cordillera de Piuchué (CP). This range attains approximately 800 m elevation, and is located on the western, uninhabited side of the Isla de Chiloé. At 42.5° S, 74° W, it is a southern extension of the Coastal Cordillera of Chile. Most of the CP is located within the Parque Nacional de Chiloé. The mountains contain a mixture of vegetation associations related to elevation, slope and exposure to the prevailing westerly winds. This paper focuses on two conifer-dominated watersheds of approximately 2.0 and 1.0 ha and an evergreen broadleaf-dominated watershed of about 2.1 ha. The elevations of the watersheds are 600–700 m. Many characteristics of the CP research site have been discussed by Huesser (1977) and Armesto et al. (1995a). There is no history of timber exploitation or agricultural clearing (Huesser 1977) and the precipitation is substantially free of anthropogenic chemicals (Levy and Moxim 1989). The only documented human impact in the study watersheds (other than the traffic of researchers) has been occasional removal of the outer bark of *Fitzroya cupressoides* for caulking boats (Armesto et al. 1994). This seems to have had no discernible effect on the vitality of the debarked individuals, but has altered the biomass of the epiphyte community to a small extent.

Climate

The climate of the CP is cool and rainy. Weather is dominated by west winds and the proximity to cool ocean waters about 12 km upwind. Rainfall measured at the site exceeded 6000 mm in 1996; typically, annual rainfall is in the range of 5000–6000 mm (C. Pérez, L. Hedin, K. Weathers, unpubl. data). Days are typically overcast, with low light levels; typical mean hourly maximum values for photosyntheti-

cally active radiation are in the range 350–400 μmol $m^{-2}s^{-1}$. Winter temperatures average 4.2 °C, and summer temperatures average 10.2 °C (Peréz et al. 1991).

Vegetation

A relatively even-aged (> 500 y), high-biomass ($\sim$ 700 $Mg \cdot ha^{-1}$) forest dominated by *Fitzroya cupressoides* (FC forest) covers the lower, sheltered slopes of the two conifer-dominated watersheds. This is a closed-canopy forest, with little understory. Catastrophic, stand-level disturbance appears to be infrequent given the relatively old age of the *Fitzroya*. The forest floor is covered with mosses and scattered individuals of the vine *Philesia magellanica*. This covering extends some 5 m up the trunks of the trees, where it grades into lichens. There are various other minor herbaceous species in the epiphytic layer, such as *Hymenophyllum* sp. and *Luzuriaga* sp. The subcanopy environment is shaded and moist. There is little reproduction of the major species. Locally, this type of vegetation is referred to as ''alerzale'' (Armesto et al. 1995a). Upslope, the FC forest type changes into one dominated by *Philgerodendron uviferum* and *Tepualia stipularis* on the upper slopes (PT forest). This forest is generally more open; canopy closure is irregular as there are more frequent gaps. Sapling trees are more frequent. Open areas may have reeds (*Juncus* sp.), *Desfontainea spinosa*, and occasional individuals of the tree fern *Blechnum chilense*. Most of the understory is similar to the alerzales, with a somewhat lesser development of the epiphytic layer. Wind-exposed hilltops and ridgelines are covered by Magellanic moorland (MM vegetation), typified by herbaceous and shrubby species, largely *Astelia pumila, Schoenus antarcticus, Sphagnum magellanicum, Donatia fascicularis, Drosera uniflora* and various *Baccharis* and *Juncus* species. Woody vegetation on the study watershed moorlands comprises clumps of *T. stipularis*, with scattered individuals of *F. cupressoides, P. uviferum*, and *Nothofagus* sp. The ages of cored trees in the conifer watershed range from over 200 to more than 550 y, with the trees on the lower slopes being oldest. The vegetative associations are described in more detail in Battles et al. (2001).

In contrast to the conifer-dominated watersheds, the angiosperm-dominated watershed (MS forest) is multi-aged with a fairly rapid turnover of canopy trees resulting in frequent small gaps and considerable structural heterogeneity (Armesto et al. 1995a). Sixteen different species were recorded for this forest, with the dominant species being the broad-leaved evergreens *Nothofagus dombeyi, Drimys winteri* and *Laureliopsis philippiana*. Together these account for 85% of the forest biomass. The conifer *Podocarpus nubigena* makes up an additional 5% of the biomass on the watershed. The largest trees are about 1 m dbh, and > 20 m tall. It is difficult to obtain accurate ages for the oldest trees due to the prevalence of heart rot, but the largest trees are > 300 y old.

Pollen studies indicate that the major vegetation types in the area have been stable for at least 7500 y (Villagran 1990). Therefore, these stands represent old-growth sites exhibiting patterns of species composition, structure and dynamics that appear to be free of human influence.

Soils

Montane soils of Chiloé have been discussed in general by (Holdgate 1961; Ruthsatz and Villagran 1991; Peréz et al. 1991). Bulk soil properties, exchangeable acids and bases, and C and N pools for the soils under the conifer watersheds have been discussed in detail by Zarin et al. (1998). The soils of the conifer-dominated watersheds are shallow and remarkably uniform in depth, typically 35–40 cm deep, with a few profiles > 40 cm restricted to the FC forest. Forested soils have a very high organic matter content, with a median value of 490 mg C g^{-1} in the 0–10 cm depth, and 93 C g^{-1} for the 10–40 cm depth increment. By USDA (1996) criteria, we provisionally classify the soils as Folists and Inceptisols based on the profile C contents and lack of well-defined mineral horizons (A. Joshi & D. Royer, unpubl. data). Median soil pH values reported by Zarin et al. (1998) fall in a narrow range, largely between 3.9 and 4.1 (n = 59) depending on vegetation type and depth. In the broadleaf-dominated watershed, the soils have less organic matter and are slightly less acid than soils of the conifer-dominated watershed.

Additionally, the following characteristics are relevant to the nutrient status of the CP forest soils: (1) The area was unglaciated during the last three glaciations (Huesser 1977; Villagran 1990); (2) The area has received minor inputs of volcanic ash from Andean volcanoes (Watters and Fleming 1962; Veit 1994; McElroy 1997); (3) Precipitation is essentially free of anthropogenic chemicals (Levy and Moxim 1989); (4) Atmospheric deposition of Ca (and probably Mg) has been shown via surrogate Sr isotopic composition to be a major source of exchangeable Ca in the soil and plant tissue Ca (M. Kennedy & L. Hedin, unpubl. data); (5) The soil shows moderate weathering intensity, as indicated by the clay fraction of the mineral soil. Mica-vermiculite dominates, with modest amounts of illite, chlorite and minor amounts of kaolinite present (McElroy 1997).

Materials and methods

Above-ground sampling

Thirty-one 10 × 10 m vegetation plots located on 50 × 50 m grids were established to sample the three watersheds. There were 18 plots in the conifer-dominated wathersheds, and 13 plots in the angiosperm-dominated watershed. All stems 2 cm d.b.h. and above were identified by species; diameter was determined using standard diameter measuring tapes. For trees with epiphytic cover on the trunk, the epiphytes were pulled a short distance away from the trunk, sufficient to allow determination of the trunk diameter. For trees 10 cm d.b.h. and up, canopy position and crown health were assessed. Crown position was assigned as understory, sub-canopy, canopy or emergent. Tree health was assessed visually as one of seven different states: healthy; healthy, partially debarked; healthy, fully debarked; unhealthy (some branches or foliage loss); decapitated (top missing, some to many branches

missing); leaning, and standing dead. The two 'debarked' states refer only to *F. cupressoides*; the fibrous bark of this species has long been used as caulking in boats. This activity does not appear to affect the tree greatly, although it disrupts the epiphytic community. Debarking does, however, have implications for the measured diameter of the tree and the biomass estimates derived from it. Dead stems were inventoried and identified where possible; they were further classified as recently dead (foliage and some branches missing), partly decomposed (branches missing, bark soft) or highly decomposed (parts of trunk missing). Growth rate was determined from cores obtained using either a 4.5 mm or 11 mm corer, or from bole slices. Growth rate was determined as the mean rate for the last ten years of annual ring increment.

Samples for nutrient analysis were obtained from each of the seven major species present in the forest. These samples were derived from material collected during harvests made in January of 1996 and 1998 to determine allometric relationships (Vann et al. 1998; Johnson 1999). This included 26 individuals of *F. cupressoides*, twelve of *P. uviferum*, nine of *N. nitidii*, six each of *D. winteri, L. phillipianna, P. nubigena* and *T. stipularis*. Four to six branches were removed from each tree; these were selected from different levels of the canopy. Samples of branch wood and foliage were obtained from each branch. In each case, foliage represented leaves combined with fine twigs (1–2 mm). Samples of trunk wood were obtained from each tree using an 11 mm tree corer (*F. cupressoides*) or wedges of wood cut using a chainsaw. All samples obtained were field weighed, placed into plastic bags and kept cool until they could be transported to the laboratory.

Soil Sampling

Collection and analysis of soils in the conifer-dominated watersheds is described in detail in Zarin et al. (1998). MS forest soils were collected and analyzed following the same procedures. In brief, after removal of loose, unincorporated litter material for analysis as the forest floor compartment, two 15 × 15 cm pits were quantitatively excavated to a depth of 10 cm adjacent to each vegetation plot. The remainder of the soil profile (10–40 cm deep) was sampled using a 5-cm diam AMS soil probe. Subsamples from these two depths were extracted with 2N NH_4CL using a 25:1 (V:W) ratio. Extracts were analyzed via ICP-AES (Plasma 400, Perkin-Elmer). Additional subsamples were ground to a powder using a mechanical mortar and pestle and analyzed for carbon and nitrogen content using an elemental analyzer (Fison/Carlo Erba Instruments).

Root sampling

Small roots (< 1 cm) were sampled via two pits excavated directly outside and at opposite corners of each plot. A 15 × 15 cm block was excavated to a depth of 10 cm. This block was split into two equal sections for (a) < 1 cm root mass determination and (b) soil chemical analysis. A 5 cm diameter AMS core sampler was used to sample bulk soil and < 1 cm roots from the 10–40 cm depth increment, and, if

present, the 40–70 cm depth. Each profile was sampled to the underlying lithic contact, or as close to it as the corer would penetrate. There were very few profiles deeper than 40 cm, consequently, for simplicity, we report only data for the 0–10 and 10–40 cm depths. These depths provide a representation of the root zone, as bedrock was encountered at most sites at about 40 cm. In the few deeper sites, rootless, gleyed soil was present at depths > 40 cm, and bedrock was encountered at 60–70 cm. The soil cores were bagged and kept cool until they could be transported to the laboratory. In the laboratory, small root samples were manually rinsed free of soil and organic material with de-ionized water. Rinse water was trapped on graded soil sieves. Fine roots and root fragments were isolated from the trapped material.

Coarse root biomass was estimated by excavating 1 × 1 m pits to bedrock, removing all roots greater than 1 cm in diameter. These pits were dug in adjacent, floristically similar watersheds to avoid disturbing the study watersheds. Eight pits were dug in each of the three forest types, for a total of 24 pits. Roots were removed from the pits using axes or saws, carried to a nearby stream and washed to remove soil. Washed roots were separated into live and dead roots and field weighed to determine pit totals. For laboratory anaysis, subsamples were obtained from each root in rough proportion to the total, such that the subsample would be representative of the whole. Roots were not identified as to species, but consisted exclusively of *F. cupressoides, P. uviferum* and *T. stipularis* in the FC and PT forests as a consequence of the pit location. In the MS forest, only roots from *D. winteri, Saxegothea conspicua* and *Pseudopanax latevirens* were readily identifiable, although the majority of roots excavated were most likely *Nothofagus* based on proximity of trees. Subsamples were field weighed, placed in plastic bags and kept cool until brought to the laboratory.

Litterfall

In the conifer watershed, litterfall was sampled via 0.5 m diameter circular traps placed at the four corners of four plots in the FC and PT forests, and randomly throughout the MS forest (16 per forest, total 48); in the moorland, 10 traps were placed adjacent to vegetation clumps. Litterfall was collected on a monthly basis for two years in the forests and for one year in the moorland site. Trap collections were analyzed as separate replicates and averaged to create per-plot estimates.

Chemical analysis

All tissue samples were rinsed in DI water and dried at 65 °C to constant weight. Samples were subsequently ground using a Wiley mill fitted with a 1 mm screen. Ca, Mg, K and P were determined by dry ashing 0.5 g ground material at 475 °C, followed by wet digestion in 5 ml 5N HC1; this was diluted to 30 ml with deionized water and analyzed via ICP-AES (Plasma 400, Perkin-Elmer). Carbon and nitrogen were determined by further grinding of the sample to pass through a 0.5 mm screen, then analyzed using an elemental analyzer (Carlo Erba). NIST pine needles

and citrus leaves were used as standard reference materials for tissue analyses. As further quality checks, 20% of the samples were run multiple times as between- and within-run replicates. Reproducibility was within 5% for samples run as separate digests.

Pool size and flux estimation

Standing nutrient pool sizes were estimated by multiplying the average tissue concentration by the biomass estimate for that tissue. This was done on a species-by-species basis for each individual in the 31 plots. The values for the individuals in each plot were summed; the average plot-based value was then used to estimate the per-hectare values. Biomass estimates for each compartment were calculated using allometric equations derived from the sampled trees (Vann et al. 1998; Johnson 1999) to determine the weight of foliage and/or twigs, branches, and boles.

Annual vegetation biomass increment was estimated from the annual radial increment growth obtained by coring 98 trees throughout the watersheds (Battles et al. 2001; Vann et al. 1998). The mean annual increment for the latest ten years was used as the individual's growth rate. The data set was separated by species into individuals with emergent, canopy-level and sub-canopy crowns; each of these was then averaged to obtain mean growth rates for each class. Annual diameter growth was assumed to be twice the annual radial increment; this value was added to each individual's d.b.h. value, and the watershed biomass recalculated as described above. The difference between the growth-incremented values and the measured values yielded the annual increase.

Since the allometric studies were based on healthy trees, foliage biomass was discounted based on the crown health and canopy position assessments. This was done as follows: foliage biomass values for trees assessed as having poor health were multiplied by 0.75 (25% reduction) and those assessed as ''leaning'' were decreased by 50%. Leaning trees are generally caused by neighboring snags or windthrow, and typically do not re-enter the canopy and subsequently die. Annual ring width data indicated that trees in the lower canopy were growing more slowly; foliage values were decreased by 20% for these individuals. The difference between foliar biomass calculated this way and calculated as consisting entirely of healthy trees was about 2%, reflecting the small number of trees in poor condition.

Allometric equations were available for *F. cupressoides, P. uviferum, P. nubigena, N. nitidii*, and *D. winterii*. The equation used for *T. stipularis* estimates total above-ground plant weight; this species has very small leaves which make up little of the total biomass. Consequently, *T. stipularis* was calculated only as bole. Based on morphological similarity, *S. conspicua* was calculated using the equations for *P. nubigena*. Other minor tree species (*Amomyrtus luma, Embothrium coccineum, Caldcluvia paniculata, Weinmannia trichospermum*) were calculated using the equations for *N. nitidii*. The shrub species *Pernettya mucronata* and *Myrceugenia chrysocarpa* were calculated using the *T. stipularis* equation. The robust shrub *D. spinosa* was calculated using the *N. nitidii* equation, with the exception that the

foliage biomass value was decreased by 25%, as understory individuals of this species tend to have less foliage than those in clearings (D. Vann, pers. obs.)

Coarse roots were assumed to be growing as fast as other woody tissues (Kozlowski et al. 1991), and the increment was calculated as total root weight per unit area multiplied by the average wood increment growth rate of all species in each forest. Fine roots were not segregated into live and dead at the time of separation for the conifer-dominated watersheds. In the MS forest we found that 30% of the small roots were dead, based on visual assessment. As an estimate of annual small root growth, 70% of the total small root weight was multiplied by the annual growth rate of the combined foliage and twigs (Kozlowski et al. 1991). The combined twig and foliage represents the above-ground < 1 cm portions of the plant, roughly analogous to the < 1 cm below-ground roots. Fine root turnover was estimated as the ratio of litterfall to total canopy foliage + twigs multiplied by the total live fine root estimate. A subset of the small root fractions was divided into < 2 mm fractions; this was found to be about 50% of the small root total (data not shown). There was some loss of very fine roots and root fragments in the washing process; this was also evaluated using a subset of the root samples, and was found to be about 4% of the total small root fraction.

Results and discussion

Nutrient pools

For the purposes of determining ecosystem pools and internal fluxes, we defined the following 12 compartments: Foliage, twig (woody tissue < 1 cm diam.), branches (non-bole woody tissue > 1 cm diam.), bole, stump, coarse root (> 1 cm diam.), small roots (< 1 cm diam.), litterfall, dead roots, forest floor, 0–10 cm deep soil horizon and 10–40 cm deep soil horizon. The first five compartments represent the above-ground portions of the trees; these were divided by species as well as tissue for nutrient content analysis. Roots, litterfall and forest floor were analyzed as unsorted samples. Soil concentrations in the FC and PT forests are based on data in Zarin et al. (1998). The nutrient concentration values obtained for these compartments are listed in Tables A1 & A2. Among the species studied, *L. phillipiana* stands out, having about twice the foliar concentrations of P and K, and nearly twice the concentration of N when compared with the other Chilean species. Woody tissues are also elevated, but to a considerably lesser degree. A similar result was reported for P in this species growing in coastal forests (Pérez 1995). This suggests that, in these environments, this species is a nutrient accumulator. Although present in only one-half of the plots, it accounts for about 13% of the above-ground biomass and 15% of the foliar mass, and represents about 25% of the above-ground pool of these elements. Depending on the foliar turnover and mortality rates for this species, the presence of *L. phillipiana* may affect the cycling of phosphorus to a greater degree than the other species present.

Overall, canopy foliar N content for the CP forest species are lower than the values for evergreen forests in the IFS/IBP datasets (range N:10–14, P:0.7–2.3 $mg \cdot g^{-1}$ dw) and for *Nothofagus* species measured at an Andean site (Hevia et al. 1999). Foliar concentrations for the other elements are mostly similar to reported values for IFS/IBP forests. Mg values are somewhat higher, possibly as a result of the relatively high soil values. Foliar Ca concentrations were about twice as high in the three conifer species measured than in the other Chilean species or the IFS/IBP forests (range 3.2–7.2 $mg \cdot g^{-1}$ dw).

The nutrient concentration values were used along with biomass data from Battles et al. (2001) or bulk density data from Zarin et al. (1998) to determine the nutrient pool values on an areal basis. These data are listed in Tables A3 & A4. The pool values are shown graphically in Figure 1 demonstrating the relationship of above to below ground pool sizes. An unusual aspect of the conifer forests is the high biomass:soil mass ratio, especially in the *Fitzroya* dominated plots. The soil weights for the FC and PT forest types are 482 and 698 $Mg \cdot ha^{-1}$ respectively; the average total biomass values are 656 and 350 $Mg \cdot ha^{-1}$ for the FC and PT forests respectively (Battles et al. 2001). This arises due to the shallow soils (about 40 cm deep) and low bulk density (0.07–0.17 $gm \cdot cm^3$, Zarin et al. (1998)). While this is not unique among montane forests, it does emphasize the fact that very thin organic soils can support large amounts of living tree biomass so long as the disturbance regime favors infrequent catastrophic disturbance. In comparison, the MS forests soil weighs about 3137 $Mg \cdot ha^{-1}$, with a total biomass value of 467 $Mg \cdot ha^{-1}$; the moorland soil weighs about 1878 $Mg \cdot ha^{-1}$ supporting perhaps 80 $Mg \cdot ha^{-1}$ (we did not measure roots in the moorland).

Figure 2 shows the CP watershed pool sizes in comparison with IFS/IBP montane forests. These include sites from both warm and cool temperate climate zones, as well as deciduous and evergreen forests. Overall, biomass and soil pool size and above vs. below-ground pools distribution are similar across this broad range of forest types. Most of the montane forests store more nutrients in the biomass than in the soil. The notable exception is nitrogen, where soil total N is 2.5 to > 20 times the biomass value.

Quantities of extractable soil Ca are similar in 8 of 13 forests, but Mg values are substantially higher in the CP watersheds; only the Andrews and Coweeta forests are similarly high in the northern hemisphere group. In CP forests, both Ca and Mg concentrations are highest in the 0–10 cm layer (Table A2). This is consistent with the suggestion that these minerals enter the ecosystem primarily through atmospheric deposition rather than mineral weathering, although the distribution may also reflect long-term accumulation and translocation of the nutrients from the mineral soil to the biomass, with subsequent return through litterfall. Canopy retention of Ca and Mg follow similar magnitudes and patterns for both elements in all three forests. Concentrations of these elements in the forest floor layer (Table A2) increase substantially relative to the litterfall values, possibly as a result of microbial mineralization of carbon. As the forest floor becomes incorporated into the soil, Ca concentrations drop dramatically, whereas Mg values change very little. The net loss of cycling Ca to woody biomass accumulation probably explains the low Ca

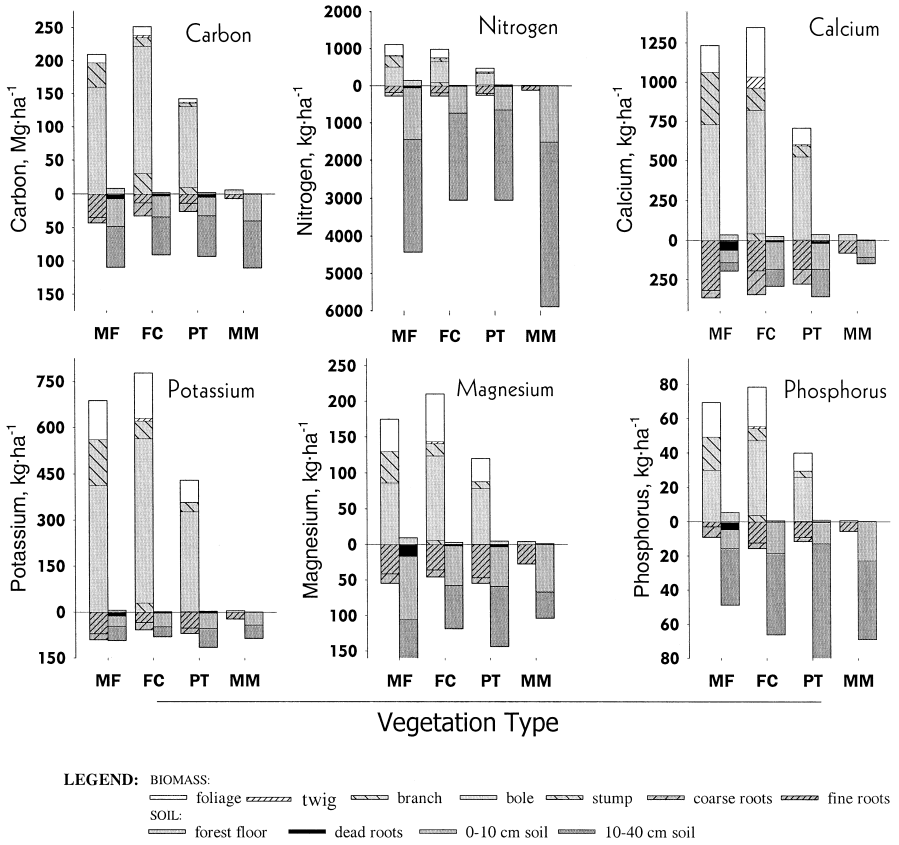

Figure 1. Distrubition of nutrients within various ecosystem compartments within three Chilean evergreen vegetation types. MS-Broadleaf species-dominated forest. FC-*Fitzroya cupressoides* forest. PT-*Pilgerodendron-Tepualia* forest. MM-Magellanic moorland. Bars on left represent biomass compartments; bars on right represent soil compartments

values, as the roots remove Ca from the soil. Additional data on Mg and Ca input rates are required before we can accurately evaluate the major source of these elements.

Of particular note is the forest floor compartment. In contrast to the other temperate montane forests, CP forests have little undecomposed litter at the soil surface. In the FC and PT forests, the lack of a forest floor is partly related to the low litterfall rate (see below) and partly due to the way we sampled the upper soil horizons. The soil surface is covered with a mossy layer consisting mostly of Sphagnum. These mosses grow over the loose litter, rapidly incorporating it. As the moss dies, the combined matter becomes a portion of what we sampled as the 0–10 cm soil layer.

Note that for phosphorus, a large part of the soil pool is stored in the forest floor in most forests. This pool is largely absent at the CP site as a result of the small

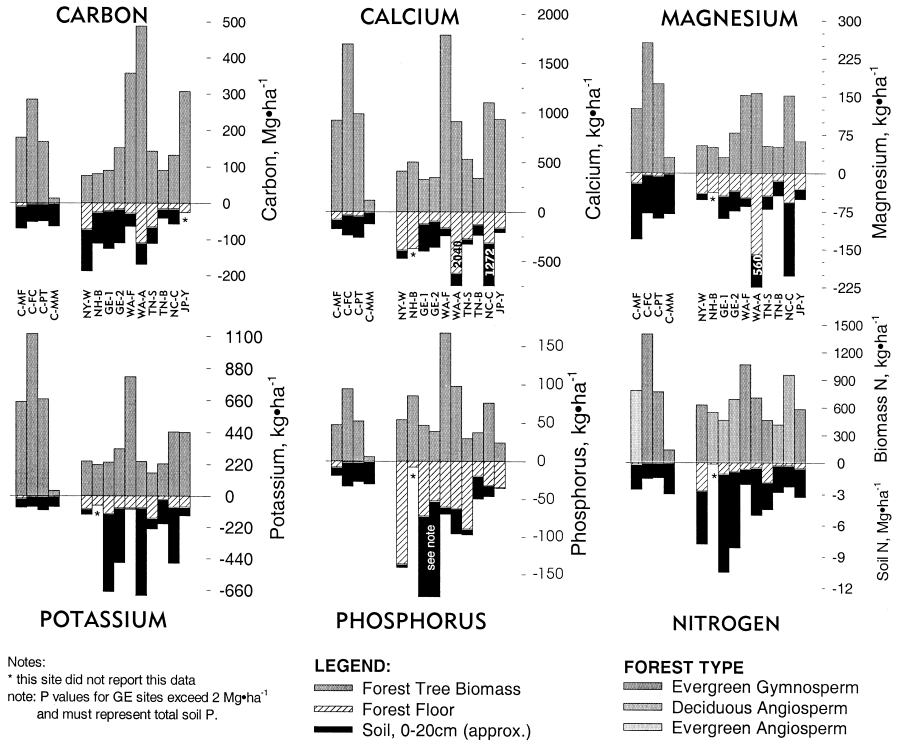

Figure 2. Biomass and soil nutrient pool comparison between CP conifer and other montane forests. Positive values represent total biomass pool; negative values are soil pools. See text for details. Site Codes: C-, Cordillera de Piuchué (this study), MS, FC, PT, MM are mixed forest, *Fitzroya* forest, *Pilgerodendron-Tepualia* forest and Magellanic moorland values respectively; NY-W, spruce-fir forest, Whiteface mt., New York; NH-B, Hubbard Brook, New Hampshire; GE-1, GE-2, beech forest, Solling, Germany; WA-F, fir-hemlock forest, Findly Lakes, WA; WA-A, Douglas-fir forest, Andrews forest, WA; TH-S, spruce forest, Smokey Mts, TN; TN-B, beech forest, Smokey Mts, TN; NC-C, hardwood forest, Coweeta, NC; JP-Y, hemlock forest, Yusuhara Takatoriyama, Japan. CP, NY-W, NH-B, GE, WA-F and WA-A are cool-temperature forests; TN-S, TH-B, NC-C and JP-Y are warm-temperate forests. Data compiled from sources in: (Johnson and Lindberg 1992; Cole and Rapp 1981). Values printed in bars are reported values when they exceed the scale.

amount of forest floor. The remainder of the soil P pool at the various sites was determined using varying chemical methods, consequently, the pools are not strictly comparable. The CP forest values were obtained using the resin-extractable inorganic P fraction (Thomas et al. 1999). Other forests were evaluated using the HC1/ NH_4F extractable inorganic P (Johnson and Lindberg 1992) or other methods (Cole and Rapp 1981).

Nutrient requirement

Table 1 shows the balance sheet for the estimated annual vegetation nutrient requirements for these watersheds. Growth increment is the sum of the annual incre-

Table 1. Annual nutrient requirements for three Chilean forest types. FC refers to conifer forest dominated by *Fitzroya cupressoides*; PT is forest dominated by *Pilgerodendron uviferum* and *Tepulia stipularis*. MF forest consists largely of evergreen angiosperms, dominated by *Nothofagus nitidii*. Growth increment is the total biomass increment estimate, including above- and below-ground compartments. Fine root turnover is estimated as the ratio of litterfall to total canopy foliage + twigs multiplied by the total live fine root estimate. Annual uptake is the total of the first three columns. Annual requirement (amount of nutrient not cycling annually) is equal to the growth increment. All values in kg·ha^{-1}.

Element	Forest	Growth increment	Litterfall	Fine root turnover	Annual uptake	Available soil pool
	MF	5628	3334	1845	12029	
BIOMASS	FC	5114	1751	1257	8122	
	PT	5894	1554	3265	10713	
	MF	2760	1679	745	5675	
CARBON	FC	2385	869	329	3583	
	PT	2743	780	862	4385	
	MF	15.3	25.2	8.9	49.4	34.[a]
NITROGEN	FC	9.3	8.0	3.4	20.7	22.[a]
	PT	9.2	7.7	9.0	25.9	~22.[a]
	MF	1.03	1.36	0.58	2.97	21.
PHOSPHORUS	FC	0.57	0.36	0.31	1.24	67.
	PT	0.50	0.41	0.58	1.49	54.
	MF	11.06	7.96	2.67	21.69	103.
POTASSIUM	FC	7.29	1.39	1.15	9.83	106.
	PT	5.83	1.52	4.30	11.65	155.
	MF	18.6	15.9	4.5	39.0	133.
CALCIUM	FC	13.9	21.9	4.9	40.7	309.
	PT	12.6	15.7	11.5	39.8	376.
	MF	2.64	8.93	1.24	12.81	154.
MAGNESIUM	FC	1.69	4.35	0.91	6.95	120.
	PT	1.48	3.47	2.91	7.86	145.

[a] Soil Pool value is annual net N mineralization rate from (Peréz et al. 1991). Values for MF and FC forest only. Soil total N is ca. 3 Mg·ha^{-1}. (see text)

ment for all biomass compartments. Annual uptake reflects the total amount of the nutrient required for both the accreting pools and the cycling components. From the data in (Table 1) it appears that the soil pools of exchangeable Ca, Mg and K are more than adequate to sustain forest growth. With regard to P, it is generally accepted that resin-extractable P is available to plants in the short term (Cross and Schlesinger 1995; Tiessen et al. 1984). In the CP forests, available P pools exceed by many fold the annual requirement.

In contrast to the other nutrient measured, nitrogen demand is quantitatively similar to net annual N mineralization measured by Peréz et al. (1991) in the conifer dominated watersheds and substantially lower than the calculated annual requirement in the MS forest (Table 1). Although field measurements of N mineralization do not necessarily represent actual rates of *in situ* mineralization, nitrogen

Table 2. Above-ground Productivity for three Chilean forests compared with IFS/IBP forests.

Forest	Above-ground Productivity ($Mgha^{-1}y^{-1}$)
Chile Mixed (MF)	8.7
Chile Fitzroya (FC)	8.2
Chile PT (PT)	8.5
Andrews Experimental Forst, WA (WA-A)	10.5
Yusuhara Takatoriyama, Japan (JP-Y)	8.5
Hubbard Brook Forest, NH (NH-B)	11.3
Solling B3 (GE-2)	12.9
Beech forest, Solling, Germany (GE-1)	13.3
Mixed hardwoods, Coweeta, NC (NC-C)	13.8
Whiteface Mtn., NY (NY-W)	7.9
Findley Lake, WA (WA-F)	5.1
Clingman's Dome, TN Beech (TN-B)	10.5
Clingman's Dome, TN Spruce (TN-S)	6.1

seems to be the logical candidate for a limiting nutrient. This is supported in general by the findings of Hedin et al. (1995) that there is virtually no leakage of mineral N from the forested watersheds of this region. The nitrogen returned in the litterfall for the three forests is low- 25 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ in the mixed forest, and 7.7–8 $kg{\cdot}ha^{-1}y^{-1}$ (Tables A3 & A4); these values are below the measured mineralization rates (Table 1, Peréz et al. (1991)). This implies that (1) atmospheric sources (precipitation input or N fixation) contribute to the N supply and/or (2) the microbial community may be mineralizing nitrogen from soil organic matter and/or (3) additional N is mineralized in the deeper soil horizons and/or (4) a portion of the mineralization substrate may come from sources other than measured litterfall, such as plant material from the epiphyte/moss layer and/or (5) mycorrhizal associations access organic N pools (*e.g.* Goulding et al. (1998)).

Aboveground productivity

A number of studies, summarized by Reich et al. (1997), have examined relationships between N-mineralization rates and above ground productivity. Reich found a positive but insensitive relationship where a six-fold increase in mineralized N was associated with only about a two-fold increase in annual above-ground growth. Table 2 summarizes annual aboveground productivity (wood + foliage) for CP and the IFS/IBP forests of similar elevations. The latter forests are, by and large, growing on mineral soils which are considerably deeper than the CP soils. Mean annual temperatures and growing season temperatures are not available for all of the sites compiled for this study, so we cannot determine how much of the differences in productivity are due to those variables.

Compared to northern temperate forests, the CP forests have low N mineralization rates and a substantially higher rate of wood production and above-ground

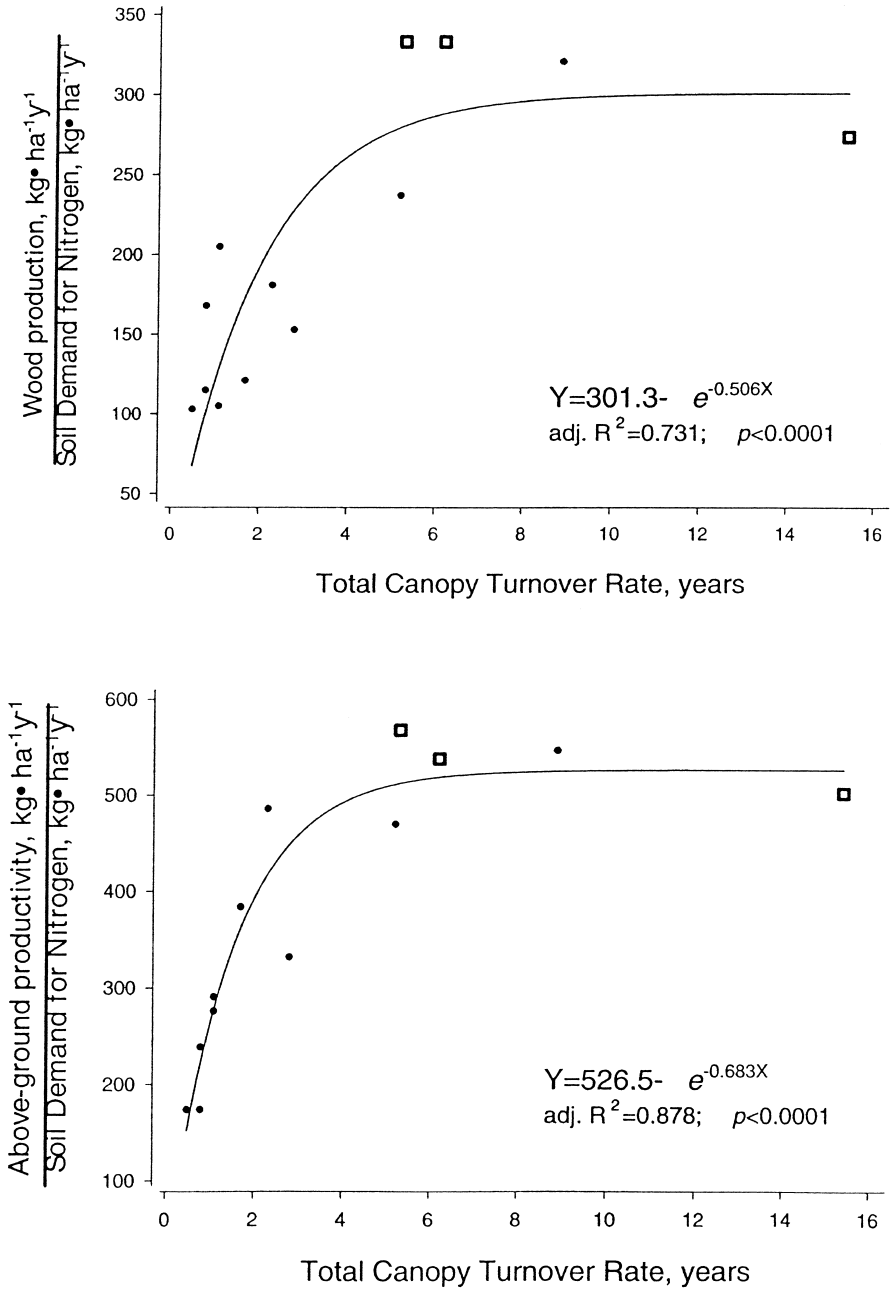

Figure 3. Relation between productivity and canopy turnover rate. Open squares are the Chilean forests; circles are IFS/IBP montane forests

productivity per unit of N mineralized ($\sim$ 200 kg·ha^{-1}·y^{-1} wood per kg N mineralized for the CP forests, *cf.* Reich et al. (1997); *ca.* 100 kg wood per kg N mineralized). The Chilean species all have high foliar C:N ratios, low annual growth rates and evergreen canopies. These all contribute to a low demand for nitrogen from the soil. The relation between canopy turnover rate and productivity per unit nitrogen required from the soil is illustrated in Figure 3. A decreasing canopy turnover rate results in an increase in production per unit N required from the soil due both to a lower demand as less N is returned to the soil and to a lower loss of carbon through litterfall. This pattern continues for canopy retention times up to about five years; after this, added foliar retention does not affect production rates, probably due to a decrease in the metabolic activity of the older leaves (Kozlowski et al. 1991). This strategy of retaining N-rich foliage likely limits the size of the mineralizable litter-N pool, and contributes to rather low N mineralization rates in the CP soils.

Whether production in these forests is limited by total nitrogen availability cannot be resolved without examination of the amount of available N contributed by atmospheric deposition, N-fixation or mycorrhizal uptake from SOM. The production rates are similar to other forests having a wide range of N availability as measured in mineralization studies. It is possible that N in the CP forests is tightly cycled through the biological components of the system, moving along pathways not assessable by N-mineralization studies. The low ecosystem temperature, low litter input rates and quality, and high rainfall would all appear to limit N available through mineralization, possibly shifting the system to one where the dominant pathway is through mycorrhizal transfers of organic N. The large deficit of N mineralized compared with N required in the MS forest indicates that buried-bag mineralization studies do not adequately measure plant-available forms of N in this forest.

Finally, as we complete other aspects of the CP study, we will be able to provide a more complete picture of the nutrient cycles in this ecosystem. The data in this paper serves to illustrate that the cycling of nutrients within the vegetation is not particularly different from that seen in other ecosystems having some impact from anthropogenic emissions. In this respect, we believe that this system may be able to provide useful baseline data for comparison. The apparent imbalance in demand and mineral nitrogen supply deserves further study, especially as regards interpretations related to both this system's sensitivity to external nitrogen input, and to comparisons with other forests.

Acknowledgements

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Table A1. Tissue nutrient concentrations of above-ground components of the CPES forests. All values in $mg \cdot g^{-1}$.

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Foliage													
Fitzroya cupressoides		107	460	±14	6.8	±0.2	0.51	±0.01	3.94	±0.93	12.01	±0.30	1.21	±0.37
Pilgerodendron uviferum		52	490	±10	10.0	±0.2	0.62	±0.01	5.53	±0.15	11.08	±0.34	1.45	±0.08
Podocarpus nubigena		13	483	±2	9.0	±0.3	0.60	±0.03	5.38	±0.31	10.64	±0.11	1.30	±0.11
Nothofagus nitidii		13	508	±2	11.3	±0.4	0.70	±0.03	5.22	±0.22	5.02	±0.04	1.30	±0.04
Drimys winterii		6	508	±2	9.8	±0.9	0.67	±0.08	6.56	±0.68	3.02	±0.24	2.67	±0.24
Laureliopsis phillipiana		5	474	±2	15.7	±0.9	1.34	±0.05	11.61	±0.78	8.15	±0.08	2.25	±0.08
Tepualia stipularis		15	501	±2	7.7	±0.1	0.43	±0.02	4.25	±0.12	6.73	±0.42	1.62	±0.07
	Twig													
F. cupressoides		105	480	±1	3.9	±0.1	0.23	±0.00	1.96	±0.04	12.07	±0.47	0.49	±0.12
P. uviferum		52	486	±1	4.7	±0.1	0.25	±0.01	1.61	±0.04	3.47	±0.15	0.51	±0.02
	Branch													
F. cupressoides		98	471	±7	2.5	±0.1	0.13	±0.01	1.36	±0.45	4.25	±0.19	0.24	±0.14
P. uviferum		39	482	±1	3.1	±0.1	0.13	±0.01	1.16	±0.05	1.66	±0.05	0.24	±0.01
P. nubigena		11	483	±4	3.4	±0.2	0.19	±0.01	1.76	±0.11	8.21	±0.02	0.43	±0.02
N. nitidii		13	477	±1	3.3	±0.3	0.22	±0.02	2.25	±0.19	5.41	±0.05	0.51	±0.05
D. winterii		8	498	±4	4.6	±0.5	0.26	±0.03	3.17	±0.44	1.09	±0.07	0.77	±0.07
L. phillipiana		5	475	±2	4.8	±0.4	0.33	±0.03	3.29	±0.14	2.64	±0.02	0.53	±0.02
	Bole													
F. cupressoides		6	475	±3	1.5	±0.2	0.07	±0.01	0.75	±0.21	0.82	±0.13	0.11	±0.02
P. uviferum		16	450	±31	1.2	±0.1	0.06	±0.01	0.46	±0.09	0.96	±0.11	0.12	±0.01
P. nubigena		8	488	±2	1.4	±0.0	0.07	±0.00	1.18	±0.09	2.11	±0.02	0.21	±0.02
N. nitidii		11	470	±2	1.0	±0.1	0.07	±0.01	0.77	±0.07	2.73	±0.01	0.16	±0.01
D. winterii		5	482	±1	1.4	±0.2	0.07	±0.01	1.79	±0.18	0.46	±0.03	0.34	±0.06
T. stipularis		5	462	±4	1.1	±0.1	0.06	±0.01	0.56	±0.12	3.46	±0.61	0.36	±0.04
L. phillipiana		3	482	±2	1.9	±0.1	0.18	±0.05	2.62	±0.33	1.66	±0.05	0.35	±0.05
	Bark													
F. cupressoides		6	499	±14	3.2	±0.2	0.13	±0.00	1.57	±0.30	7.35	±1.60	0.75	±0.07
P. uviferum		9	487	±12	2.9	±0.5	0.16	±0.01	1.35	±0.17	15.24	±2.44	0.81	±0.06

Table A2. Tissue nutrient concentrations of below-ground components of the CPES forests. All values in $mg \cdot g^{-1}$.

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Large Roots													
Mixed forest (MF)		8	495	±7.49	2.6	±0.16	0.23	±0.02	1.17	±0.27	4.83	±1.41	0.80	±0.17
Fitzroya forest (FC)		8	478	±2	2.1	±0.1	0.10	±0.01	1.05	±0.10	3.79	±0.38	0.32	±0.03
P-T forest (PT)		8	484	±2	2.8	±0.4	0.11	±0.01	1.23	±0.16	3.75	±0.44	0.34	±0.03
	Small Roots, 0–10 cm													
Mixed forest		24	497	±3	5.8	±0.2	0.34	±0.03	1.17	±0.14	2.58	±0.32	0.64	±0.05
Fitzroya forest		29	488	±7	5.8	±0.2	0.23	±0.01	1.09	±0.13	5.07	±0.41	0.79	±0.03
P-T forest		24	466	±11	4.7	±0.3	0.20	±0.01	1.72	±0.10	5.10	±0.41	0.95	±0.04
Moorland		20	441	±15	6.4	±0.2	0.15	±0.01	1.18	±0.19	3.13	±0.47	1.09	±0.10
	Small Roots, 10–40 cm													
Mixed forest		24	436	±24.1	5.8	±0.2	0.35	±0.08	1.27	±0.28	1.80	±0.40	0.62	±0.14
Fitzroya forest		18	135	±57	3.9	±0.9	0.39	±0.16	0.88	±0.05	2.68	±0.46	0.80	±0.09
P-T forest		23	148	±39	3.8	±0.5	0.17	±0.01	1.10	±0.17	2.69	±0.42	0.82	±0.09
Moorland		18	170	±63	3.8	±0.6	0.18	±0.02	1.04	±0.10	3.00	±0.37	0.89	±0.04
	Litterfall													
Mixed forest		120	502	±1	8.2	±0.2	2.64	±0.12	1.80	±0.06	2.73	±0.19	2.64	±0.12
Fitzroya forest		120	493	±5	5.3	±0.1	0.99	±0.06	1.80	±0.05	2.03	±0.13	0.99	±0.06
P-T forest		45	500	±4	5.2	±0.1	0.98	±0.06	1.80	±0.05	2.07	±0.13	0.98	±0.06
Moorland		120	508	±3	5.0	±0.2	0.65	±0.05	1.82	±0.09	2.22	±0.25	0.65	±0.05
	Forest Floor													
Mixed forest		26	481	±6	8.4	±0.22	0.43	±0.02	0.97	±0.05	4.51	±0.26	1.16	±0.05
Fitzroya forest		28	479	±2	4.2	±0.2	0.14	±0.01	0.65	±0.05	7.08	±0.53	0.80	±0.05
P-T forest		23	477	±2	4.7	±0.2	0.15	±0.01	0.95	±0.17	7.02	±0.49	0.89	±0.04
Moorland		9	449	±9	4.2	±0.4	0.09	±0.01	0.48	±0.07	2.34	±0.80	0.67	±0.11

Table A2. Continued.

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Dead Roots													
Mixed forest		8	453	±10.7	2.1	±0.32	0.19	±0.07	0.82	±0.29	5.77	±2.04	1.06	±0.38
Fitzroya forest		8	486	±7	2.5	±0.2	0.06	±0.01	0.50	±0.10	1.59	±0.28	0.36	±0.03
P-T forest		8	477	±3	1.7	±0.2	0.05	±0.01	0.32	±0.06	1.49	±0.40	0.40	±0.05
	Soil, 0–10 cm													
Mixed forest		26	260	±20.8	8.4	±0.6	0.07	±0.01	0.33	±0.05	0.53	±0.13	0.62	±0.11
Fitzroya forest		24	412	±29	9.2	±0.5	0.10	±0.02	0.84	±0.14	2.58	±0.29	0.77	±0.07
P.T forest		24	442	±26	10	±0.5	0.14	±0.03	1.33	±0.16	2.80	±0.31	0.91	±0.07
Moorland		24	316	±30	9.0	±0.5	0.08	±0.02	0.71	±0.17	1.33	±0.25	0.72	±0.11
	Soil, 0–40 cm													
Mixed forest		26	64	±14.5	2.7	±0.41	0.02	±0.01	0.07	±0.02	0.09	±0.03	0.10	±0.04
Fitzroya forest		24	119	±15	4.2	±0.4	0.03	±0.02	0.09	±0.02	0.39	±0.09	0.18	±0.04
P-T forest		24	116	±20	4.2	±0.5	0.04	±0.02	0.22	±0.08	0.46	±0.16	0.26	±0.10
Moorland		24	58	±8	3.1	±0.3	0.01	±0.00	0.05	±0.01	0.06	±0.02	0.04	±0.01

Table A3. Nutrient pools in above-ground components of the CPES forests. All values in kg·ha^{-1}, eceept Carbon (Mg·ha^{-1}). *n* refers to number of plots. Moorland pools were determined only for total plant values; these are listed under bole.

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Foliage													
Mixed forest (MF)		13	17	± 8.8	199	±45	14	±3	115	±25	103	±23	31	±6
Fitzroya forest (FC)		7	13	±1.6	217	±25	23	± 4	196	±33	314	±52	67	±12
P-T forest (PT)		5	5	±0.6	90	±11	10	±4	93	±42	103	±21	32	±17
	Twig													
Fitzroya forest		7	4	±0.7	31	±6	1.4	±0.3	12	±2.2	71	±14	2.9	±0.6
P-T forest		5	1	±0.2	13	±2	0.2	±0.1	1.4	±0.6	9	±4	0.3	±0.2
	Branch													
Mixed forest		13	26	±7	206	±57	13	±4	139	±39	218	±60	30	±8
Fitzroya forest		7	13	±1.4	79	±9	7	±0.8	76	±9	144	±14	17	±2
P-T forest		5	5	±0.8	35	±5	4	±1.5	40	±18	69	±14	9	±4
	Bole													
Mixed forest		13	136	±38	376	±104	21	±6	394	±109	599	±166	65	±18
Fitzroya forest		7	222	±31	656	±101	47	±8	753	±138	819	±97	124	±20
P-T forest		5	131	±23	335	±59	26	±7	438	±186	526	±83	78	±24
Moorland		5	62	±12	15	±3	0.7	±0.1	7	±1.3	39	±7	4	±0.8
	Bark													
Fitzroya forest		7	16	±3	133	±27	6	±1.2	56	±11	156	±30	14	±3
P-T forest		5	4	±1.0	36	±8	4	±1.0	29	±8	56	±15	8	±2

Table A4. Nutrient pools in below-ground components of the CPES forests. All values in kg·ha^{-1}, except Carbon (Mg·ha^{-1}). Soil values calculated from data in (Zarin et al. 1998).

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Large Roots													
Mixed forest (MF)		8	35	±8	187	±45	16	±4	95	±25	317	±142	42	±17
Fitzroya forest (FC)		8	19	±4	88	±25	3.3	±0.7	32	±5	150	±33	10	±2
P-T forest (PT)		8	12	±4	53	±10	2.3	±0.5	24	±5	92	±33	8	±2
	Small Roots, 0–10 cm													
Mixed forest		26	5	±0.3	51	±4	3.0	±0.2	11	±2	6	±1	29	±6
Fitzroya forest		27	11	±0.9	130	±10	5.0	±0.4	22	±2	117	±20	17	±1
P-T forest		20	9	±0.8	87	±8	3.3	±0.3	30	±3	93	±11	17	±2
Moorland		15	3	±0.4	49	±6	1.1	±0.2	7	±1	23	±5	7	±1
	Small Roots, 10–40 cm													
Mixed forest		20	3	±1	44	±7	3.2	±0.4	14	±4	7	±2	19	±5
Fitzroya forest		5	2	±0.6	61	±15	12.3	±1.7	24	±3	77	±16	19	±4
P-T forest		15	5	±1.5	119	±16	6.0	±0.6	40	±8	93	±18	30	±5
Moorland		6	3	±1.2	74	±27	4.5	±0.9	22	±6	57	±9	20	±4
	Litterfall													
Mixed forest		16	3.3	±0.01	25.2	±0.1	1.4	±0.21	8.0	±1.2	15.9	±3.0	8.9	±1.9
Fitzroya forest		16	0.9	±0.01	8.0	±0.08	0.4	±0.00	1.4	±0.02	21.9	±0.3	4.3	±0.1
P-T forest		16	0.8	±0.01	7.7	±0.05	0.4	±0.01	1.5	±0.01	15.7	±0.1	3.5	±0.04
Moorland		10	0.3	±0.01	2.9	±0.03	0.1	±0.05	0.4	±0.2	4.4	±1.4	1.1	±0.4
	Forest Floor													
Mixed forest		26	8.3	±0.9	147	±17	8	±1.1	16	±1.6	19	±2	75	±7
Fitzroya forest		28	2.0	±0.4	16	±3	0.5	±0.1	2	±0.4	27	±5	3	±0.5
P-T forest		23	2.3	±0.3	25	±4	0.9	±0.2	5	±1.1	38	±6	5	±1.1
Moorland		9	0.6	±0.3	6	±3	0.2	±0.1	1	±0.6	4	±2	1	±0.4

Table A4. Continued.

Species	Tissue	*n*	C	±se	N	±se	P	±se	K	±se	Ca	±se	Mg	±se
	Dead Roots													
Mixed forest, small, 0–10		20	0.8	±0.1	9	±1	0.5	±0.1	2	±0.3	2	±0.3	4	±1
Mixed forest, small, 10–40		17	2.4	±0.6	31	±6	2.6	±0.6	9	±1.9	7	±2.3	13	±4
Mixed forest, coarse		8	3.5	±0.5	16	±3	1.3	±0.3	6	±1.4	45	±17	8	±1.5
Fitzroya forest		8	2.6	±0.4	13	±2	0.4	±0.1	4	±1.1	11	±3	2	±0.3
P-T forest		8	4.5	±1.3	18	±8	0.5	±0.2	4	±1.7	18	±8	4	±1.2
	Soil, 0–10 cm													
Mixed forest		26	42	±1.6	1385	±70	66	±9	46	±5	89	±13	80	±16
Fitzroya forest		24	412	±29	916	±53	8	±1	84	±14	258	±29	77	±7
P-T forest		24	442	±26	1001	±51	9	±2	133	±16	280	±31	91	±7
Moorland		24	316	±30	897	±49	8	±1	71	±17	133	±25	72	±11
	Soil, 0–40 cm													
Mixed forest		26	61	±6	2983	±258	21	±10	62	±28	65	±10	53	±9
Fitzroya forest		24	119	±15	421	±42	13	±4	9	±2	39	±9	18	±4
P-T forest		24	116	±20	417	±48	16	±6	22	±8	46	±16	26	±10
Moorland		24	58	±8	310	±34	10	±4	5	±1	6	±2	4	±1

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