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REGULAR ARTICLE

Availability of residual fertilizer ^{15}N from forest floor and mineral soil to Douglas-fir seedlings ten years after fertilization

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Abstract
Background and aims As low initial uptake and essentially zero later uptake limit efficacy of N fertilization for temperate conifers, we investigated factors limiting long-term tree uptake of residual ^{15}N-labeled fertilizer.
Methods We used a pot bioassay to assess availability of ^{15}N from soil sampled 10 years after fertilization of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand with ^{15}N-urea (200 kg N ha^{-1}). Douglas-fir seedlings were grown for 2 years in organic (designated LFH) and mineral soil (0–10 cm) layers reconstructed from control and fertilized plots; residual fertilizer N amounted to 10 % of LHF and 5 % of MIN N.
Results Percentage recovery of residual ^{15}N in seedlings was not affected by the original season of fertilization (spring vs. fall), but differed by the source of ^{15}N excess. LFH was a better source of residual ^{15}N; 12.4 % of residual LFH ^{15}N was taken up by seedlings and 7.6 % transferred to soil, whereas mineral soil yielded only 8.3 % of residual ^{15}N to seedling uptake and 2.4 % to LFH. Extractable inorganic N was 2–3 orders of magnitude higher in fallow pots.
Conclusions Ten-year residual fertilizer ^{15}N was clearly cycling between LFH and mineral soil and available to seedlings, indicating that other factors such as denitrification, leaching, and asynchrony of soil N mineralization and tree uptake limit long-term residual N fertilizer uptake in the field.

Keywords Douglas-fir · Forest fertilization · Seedling bioassay · ^{15}N · Nitrogen

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Introduction

Forest growth in coastal British Columbia (BC) is generally limited by nitrogen (N) availability, as repeatedly shown by response to fertilization trials in managed forests (Mitchell et al. 1996; Blevins et al. 2006; Jassal et al. 2010). In particular, much effort has been focused on developing N fertilization practices to increase growth and thereby shorten the time to harvest for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Weetman et al. 1997; Carter et al. 1998; Sucre et al. 2008; Littke et al. 2011; White et al. 2012), an important species in the forest products industry of the Pacific Northwest. Fertilizers are often applied to older stands (20–60 y), in which the growth response typically lasts 5–7 years, largely attributed to the greater photosynthetic capacity of the increased leaf area developed in the initial growth season (Mitchell et al. 1996; Balster et al. 2009). Studies using ^{15}N-labeled fertilizers indicate fertilizer N recoveries by crop trees of 2–20 %, with uptake essentially completed after 1 year (Preston and Mead 1994a; Chang and Preston 2000; Mead et al. 2008). As discussed in these studies, a high proportion of the ^{15}N-labeled fertilizer is usually retained in the soil in

organic N forms, with the remainder taken up by understory vegetation, or lost through leaching and denitrification, or volatilization of ammonia from urea fertilizer.

Forest fertilization since 1981 on Crown land in coastal BC has been highly variable, with the area fertilized annually ranging from zero to nearly 15,000 ha (British Columbia Ministry of Forests 2000; British Columbia Resources Practices 2011; Mel Scott pers. comm.). After low activity from 2002–6 for the whole province, fertilization activity has increased, with approximately 9,600 ha of Crown land in the coastal region treated in 2011/12. Increasing the growth-response and economic benefit of forest fertilization requires a better understanding of the factors that control uptake, loss and long-term availability of the applied nutrient. Although the bulk of fertilizer N is generally found as soil organic N, few studies have assessed the availability of residual fertilizer ^{15}N in forest soil. Soils sampled up to 31 months after fertilization in coastal and interior BC showed increasing stabilization of N in organic forms (Chang et al. 1999). However pot trials of mineral soils sampled up to 8 years after fertilization showed that ^{15}N was mineralized at a higher rate than native soil N (Preston and Mead 1994b).

Sampling of a coastal Douglas-fir site 10 years after fertilization with ^{15}N urea in fall and spring provided an opportunity to track the fate of N in the field (Mead et al. 2008), and to assess its availability in a greenhouse trial. Our previous pot studies examined residual ^{15}N availability from forest humus (Chang et al. 1999) or surface mineral soil (Preston and Mead 1994b). In this study we used reconstructed profiles with four combinations of non-fertilized and ^{15}N-fertilized organic and surface mineral soil to (1) determine the availability of N from these different layers to seedlings, (2) measure N transfer between layers, and (3) determine the effect of the original season of fertilization on biomass and ^{15}N availability.

Materials and methods

Site, ^{15}N-urea fertilization and 10-year sampling

The original plots and ^{15}N-urea fertilization were described in detail by Nason (1989) and Nason et al. (1988, 1990). Briefly, the plots were located on Vancouver Island (49° 15' N, 124° 10' W) at 300 m elevation, an area with cool wet winters and warm dry summers (annual precipitation 900–1,400 mm) that are often droughty from mid-July until October. The soil, a Typic Haplorthod, is well-drained, 75–125 cm thick gravelly loamy sand till overlying basaltic bedrock. The forest floor consisted of generally discrete Oi, Oe and Oa horizons, corresponding to L, F and H layers in the Canadian system (Soil Classification Working Group 1998), and designated LFH in this paper. At the 1982 fertilization, the stand was naturally-regenerated Douglas-fir (40 years old) with an understory dominated by salal (*Gaultheria shallon* Pursh), as described in greater detail by Mead et al. (2008). Urea granules enriched at 4.934 atom% ^{15}N excess (at% ^{15}Nex) were applied in spring (May 21, 1982) or fall (November 25, 1982) to 0.0121 ha plots at 200 kg N ha^{-1}, with three replicates of the spring application (Spring), three of the fall application (Fall), and two non-fertilized control treatments (Control).

10-year field sampling and greenhouse bioassay

As described by Mead et al. (2008), during the 10-year field sampling in October-November 1992, the combined LFH organic layer and 0–10 cm mineral soil were completely removed from 20 × 20 cm pits. Four LFH and two 0–10 cm mineral soil samples were taken from the ^{15}N-fertilized plots, and one LFH and one mineral soil sample from control plots. Samples were stored at 4 °C and sieved to <4 mm (Mesh #5) while in a field-moist state. For the pot trial, composite 0–10 cm mineral soil samples were made by combining material from two soil pits in each of three replicate plots of the Spring and Fall ^{15}N fertilizer treatments, and composite LFH material from the corresponding pits. Composite samples of 0–10 cm mineral soil and LFH for Controls were made by combining material from one pit from each of two Control plots. This resulted in three LFH (Control, Spring, Fall) and three mineral soil (Control, Spring, Fall) composites from which to construct soil profiles with the desired treatment combinations. The composites had the following values of total N and atom %^{15}Nex: Spring LFH, 8.2 g kg^{-1} and 0.4569 %; Spring MIN, 0.8 g kg^{-1} and 0.2336 %; Fall LFH, 9.2 g kg^{-1} and 0.4985 %; Fall MIN, 1.4 g kg^{-1} and 0.2558 %; Control LFH, 8.7 g kg^{-1}; Control, MIN 0.6 g kg^{-1}. We calculated the proportion of total N associated with the ^{15}Nex by dividing the amount of ^{15}Nex in a layer by the original atom ratio of fertilizer

^{15}N, and then normalizing that value by the total N in the layer.

As shown in Table 1, for each of the original Spring and Fall fertilizer treatments, soil profiles were constructed with combinations of LFH and mineral soil from fertilized and control plots. This resulted in six profiles with one or both soil layers with ^{15}N-labeling, named according to the source of the fertilizer ^{15}N: LFH, MIN, and LFH + MIN, plus control pots taken from the original control plots with no fertilization. Soil profiles were reconstructed in pots to mimic the spatial arrangement of LFH and mineral soil at the field site. For each profile, 750 g (moist weight) of mineral soil was placed in a 130-mm diameter, 120-mm deep plastic pot and topped with 200 g (moist weight) of LFH. Subsamples of the composited mineral soil and LFH were dried at 105 °C and used to compute oven-dry weights of the profiles. The total N and ^{15}Nex per pot for each treatment are shown in Table 1. The six profile treatments and control were each replicated a total of eight times. Four replicates were planted with seedlings (Planted), and four replicates were left fallow (Fallow).

The 56 pots were placed in a greenhouse maintained at 20 °C during the day and 12 °C during the night (12 h each), under natural light. Humidity was not controlled, and varied within a range of 70–95 %. The pots were irrigated sufficiently to preclude drying. The profiles were allowed to equilibrate to these conditions for 3 weeks prior to planting.

Douglas-fir seed was obtained from collections made in close proximity to the fertilized plots. Seed was stratified and germinated in February, 1993. Four germinants were placed into the surface layer of the LFH. All pots were misted twice daily until the second leaf stage of development. From this point on, watering was on an ad hoc basis with care taken to not saturate soils. On a few occasions, flow-through of irrigant was captured by saucers and returned to the soil surface. Minor mortality occurred in the first growing period, so that some pots had only 3 seedlings. There was no indication that the initial minor mortality had an effect on overall biomass, as all pots grew to "closed canopy" and fewer stems appeared to be offset by higher biomass per stem, although we didn't conduct a formal analysis based on stem count.

The pots were destructively harvested in December 1994. Seedlings were cut off at the root collar and LFH removed from the pot with a spatula. The remaining mineral soil was poured into a porcelain tray, from which roots were removed with tweezers. Almost all roots originated in the mineral layer, although there was some invasion into the LFH. Separated roots were washed with water on a 1-mm sieve to remove any

Table 1 Descriptions of the constructed pot LFH + MIN profiles and amounts of total N and ^{15}Nex per pot

	Treatment[a]	Control	Spring LFH	Spring MIN	Spring LFH + MIN
	Layers	Control LFH	Spring[b] LFH	Control LFH	Spring LFH
		Control MIN	Control MIN	Spring MIN	Spring MIN
LFH Layer	mg N	552	581	552	581
	μg ^{15}Nex	0	2655	0	2655
MIN Layer	mg N	372	372	502	502
	μg ^{15}Nex	0	0	1173	1173
Pot total	mg N	924	953	1054	1083
	μg ^{15}Nex	0	2655	1173	3827
	Treatment		Fall LFH	Fall MIN	Fall LFH + MIN
	Layers		Fall LFH	Control LFH	Fall LFH
			Control MIN	Fall MIN	Fall MIN
LFH Layer	mg N		482	552	482
	μg ^{15}Nex		2401	0	2401
MIN Layer	mg N		372	840	840
	μg ^{15}Nex		0	2148	2148
Pot total	mg N		854	1391	1321
	μg ^{15}Nex		2401	2148	4549

[a]Each profile treatment was replicated four times in pots planted with seedlings (Planted) or left fallow (Fallow)

[b]Spring and Fall refer to LFH and mineral soil (MIN) from plots fertilized with urea-^{15}N (4.9 atom% ^{15}N) applied at a rate of 200 kg N ha^{-1} 10 years prior to sampling

adhered soil. Biomass values for whole seedlings were calculated by adding the values from roots and shoots.

Laboratory analyses

As described in Preston and Mead (1994a), field-moist samples of LFH (10 g) and mineral soil samples (30 g) were extracted with 100 mL of 0.1 M K_2SO_4, including 5 mg L^{-1} phenol mercuric acetate as a preservative. Samples were shaken for 30 min, centrifuged at 2,000 rpm for 7 min, and the resulting supernatants vacuum-filtered through Whatman #40 paper. Extracts were measured for NO_3^--N and NH_4^+-N concentrations (designated collectively as dissolved inorganic N, DIN) with Orion specific-ion electrodes (Preston and Mead 1994a), then frozen at 0 °C until measurement of atom% ^{15}N abundance.

Seedling biomass and K_2SO_4-extracted LFH residues were dried at 70 °C and ground to 30 mesh in a Wiley mill. Mineral soil residues were also dried at 70 °C, but were ground for 18 s in a Siebtechnik eccentric vibrating disc mill (Tema Siebtechnik, Mülheim an der Ruhr, Germany). Residues of LFH and soil extraction were analyzed using standard methods of Kjeldahl digestion and distillation followed by ^{15}N analysis with a Vacuum Generators SIRA 9 mass spectrometer (Preston et al. 1990). The ^{15}N abundance of NO_3^--N plus NH_4^+-N in extracts was determined using similar methods, after pretreatment with Devarda's alloy to reduce NO_3^- to NH_4^+ (Chang et al. 1999).

Residual fertilizer-N in pot profiles

Nason (1989) originally applied ^{15}Nex at 9.868 kg ha^{-1} to the Vancouver Island plots in 1982. Soil collection and mixing in our study was conducted primarily to facilitate the subsequent bioassay for residual ^{15}N availability, not to test the site for residual ^{15}N content. Although the measurements of the composited soil samples can be considered representative of the site, they are not suitable for use in statistical comparisons of soil recovery (as carried out in Mead et al. 2008) and should be considered with appropriate caution. In particular, the field study used 4 LFH samples per fertilizer-treated plot, but composite LFH samples for the pot trial were made using only the two LFH samples corresponding to the mineral soil pits. Analysis of the composited LFH plus 0–10 cm mineral soil from the Spring plots in 1992 indicated that 29 % (2.884 kg ha^{-1}) of the ^{15}Nex remained, while slightly more than 34 % (3.427 kg ha^{-1}) remained in the plots fertilized in the fall. Recoveries estimated from the composite LFH samples were similar for the two treatments, 20 % in Spring plots and 18 % in Fall plots. These are quite comparable to the results reported by Mead et al. (2008), with 17.8 % of applied ^{15}Nex recovered in Spring and 16.0 % recovered in Fall. For the mineral soil however, results were more disparate. The ^{15}Nex recoveries estimated from the 0–10 cm composite samples were about 9 % for Spring and 16 % for Fall compared to 18.3 and 12.3 % in the Mead et al. (2008) field study. Samples collected for the pot study (2 LFH samples and 2 mineral soil pits per 11 m × 11 m treatment plot) were composited prior to N and ^{15}N analysis, precluding statistical comparisons with the Mead et al. (2008) field study or between treatments at the initiation of the pot trial. As shown in Table 1, the initial N contained in the reconstructed profiles was highest in the Fall MIN and Fall LFH + MIN pots, followed by the Spring LFH + MIN and Spring MIN pots, and finally the Spring LFH, Control, and Fall LFH pots.

Data analysis

Atom% ^{15}N excess was calculated by subtracting the values of atom% ^{15}N abundance of control samples from those of ^{15}N-enriched samples. As in our previous studies, recovery of applied ^{15}N, or percentage derived from fertilizer, was estimated by dividing the mass of ^{15}N excess (^{15}Nex) of the layer by the ^{15}Nex of the fertilizer, then multiplying by 100. Similarly, the availability of residual fertilizer-^{15}N was calculated by dividing the ^{15}Nex of the layer or plant component at the termination of the bioassay by ^{15}Nex in the source-layer(s) at the beginning of the bioassay.

Measured variables were analyzed using analysis of variance (ANOVA) tests within a completely randomized design. The efficacy of seasonal fertilizer application was tested by comparing biomass grown in Control, Fall, and Spring treatments. Analyses of N and ^{15}N transfers and recovery used seedling and soil samples from season (Fall, Spring) and ^{15}N source (LFH, MIN, LFH + MIN) treatments in Planted and Fallow pots, such that season, source, and source x season were main effects. Before accepting the results of an ANOVA, residuals were examined for constant variance and normality. If necessary, the data were transformed and re-

analyzed. When the F-test indicated a significant difference (α=0.05), the Ryan-Einot-Gabriel-Welsch q test (REGWQ) was used for multiple comparisons. The REGWQ method was chosen because it controls the type I experiment-wise error rate, but is more powerful than conservative tests such as Tukey's HSD (Toothaker 1993). The alpha level for REGWQ was set at 0.05. All statistical analyses were conducted in SAS 8.1 (SAS Institute Inc 1999; 2000).

Results

Seedling biomass

The biomass of seedlings grown in Control and LFH + MIN profiles showed significant effects of the season of fertilizer application (root: $F_{2,11}$=6.03, P=0.02; shoot: $F_{2,11}$=5.66, P=0.03; whole: $F_{2,11}$=6.86, P=0.02). In general, Fall soils produced larger seedlings than Spring soils, which were not different from the Controls (Fig. 1a). In all treatments, biomass of whole seedlings tended to increase with the content of N in the profile (Fig. 1b, R^2=0.61, $F_{1,6}$=7.98, P=0.04). Total seedling N similarly increased with initial pot total N (not shown). As discussed later, this indicates minimal influence of residual ^{15}N fertilizer on the total N uptake of seedlings.

Availability of residual fertilizer^{15}N to seedlings

Comparisons of atom% ^{15}N abundance in seedlings grown in LFH + MIN vs. Control profiles revealed that the residual fertilizer ^{15}N continued to be available for plant uptake (roots: $F_{2,11}$=2,985, P<0.0001; shoots: $F_{2,11}$=216, P<0.0001, Table 2). The season of fertilization did not significantly affect the atom% ^{15}N abundance, but both fertilizer treatments yielded higher proportions of ^{15}N than the Control (Fig. 1c). The recovery of residual fertilizer-^{15}N in roots, shoots, and whole trees was not significantly influenced by the season of fertilization or by an interaction of the season and source of residual fertilizer-^{15}N. The source alone (LFH, MIN, or LFH + MIN profiles), however, significantly affected the availability of residual ^{15}N to seedlings (Table 3). The availability of total residual ^{15}N from LFH and LFH + MIN profiles did not differ, but was greater than the fraction available from the MIN profile (Fig.1d). At the termination of the bioassay, whole seedlings had assimilated approximately 12 % of the total initial ^{15}Nex in the LFH, and 8 % of the total ^{15}Nex in the MIN (Fig. 2).

Organic ^{15}N dynamics in profiles

Analysis of the recovery of ^{15}Nex in non-labeled layers in Planted profiles revealed that Spring fertilization resulted in higher transfer rates of ^{15}Nex than Fall fertilization ($F_{1,15}$=12.34, P=0.004, Fig. 2), and that a greater proportion of the ^{15}Nex in LFH was transferred to non-labeled mineral soil than was transferred from labeled mineral soil to non-labeled LFH ($F_{1,15}$=21.96, P=0.0005, Fig. 2). There was no interaction between the season of fertilization and profile treatment ($F_{1,15}$=0.32, P=0.58).

The behavior of ^{15}Nex in Fallow pots exhibited different patterns than in the Planted pots. These data were analyzed on the natural logarithm scale to stabilize residual variance. There was still no interaction between the source of ^{15}Nex (profile treatment) and the season of fertilization ($F_{1,15}$=0.06, P=0.24), but the season of fertilization did not significantly affect the movement of ^{15}Nex in the Fallow pots ($F_{1,15}$<0.01, P=0.98) as it did in the Planted pots. Additionally, in contrast to the Planted pots, in the Fallow pots a greater proportion of the ^{15}Nex in labeled mineral soil was transferred to non-labeled LFH than from labeled LFH to non-labeled mineral soil ($F_{1,15}$=141, P<0.0001). Averaged across seasons, only 4.3 % of LFH-^{15}Nex moved to the non-labeled mineral soil, while 14.4 % of MIN-^{15}Nex was transferred to the non-labeled LFH.

Dissolved inorganic N and ^{15}N dynamics in profiles

All analyses of DIN and ^{15}N were conducted in the natural logarithm scale to stabilize residual variance. The most obvious and recurrent pattern of DIN and ^{15}N was that levels in Fallow pots were one to four orders of magnitude higher than those of Planted pots (Table 4). Nitrate in the LFH layer was the strongest example of this pattern, showing a three-way interaction between planting, season of fertilization, and profile treatments ($F_{2,47}$=3.89, P=0.03), in which the nitrate concentrations in Fallow pots were higher than those in Planted pots, and the Spring LFH produced the highest values in the Planted pots. Overall, nitrate values ranged from 0.04–1.5 μg N g^{-1} for LHF and mineral soil layers in Planted pots, compared to 1,006–1,970 μg N g^{-1} for

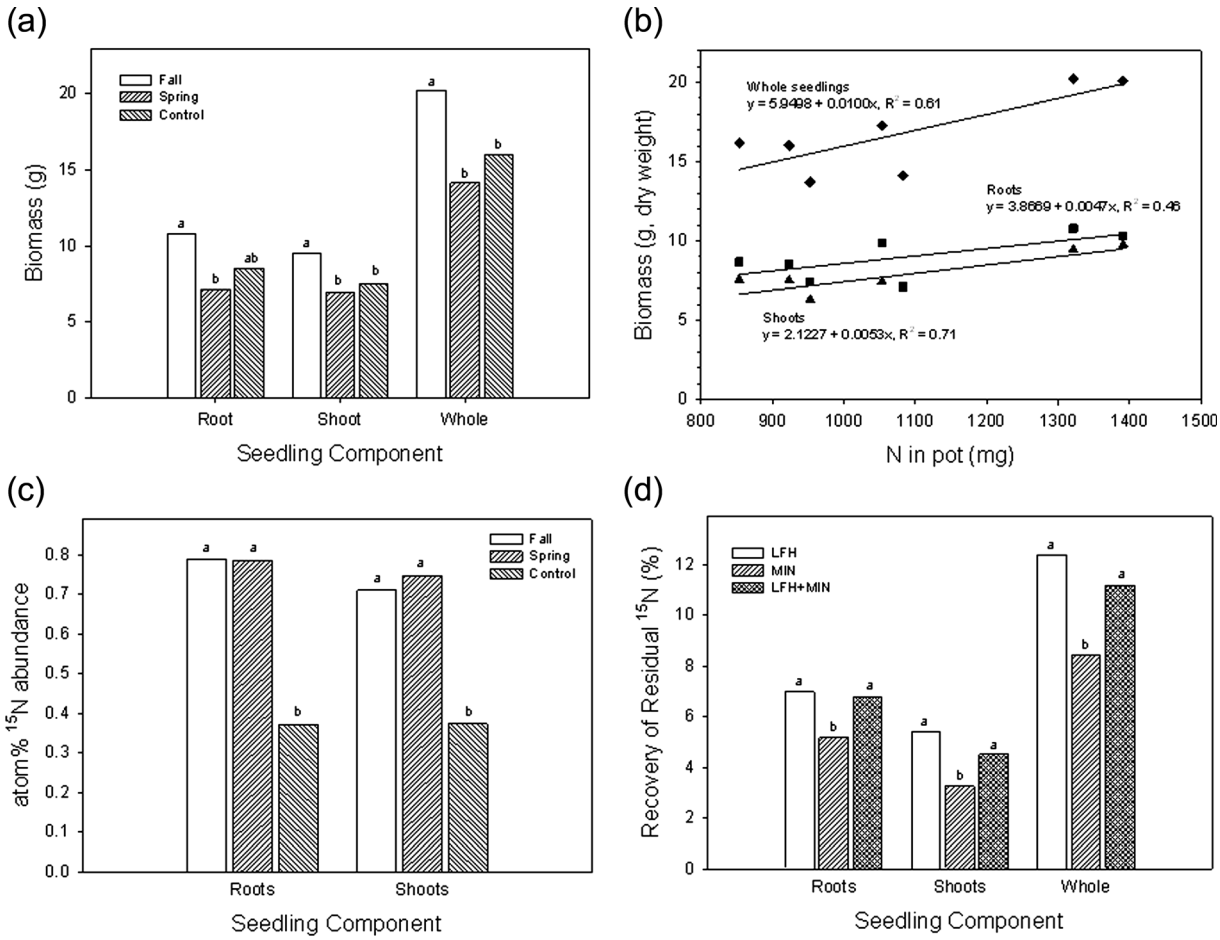

Fig. 1 Biomass and N recovery in roots, shoots and whole seedlings grown in pots with LFH and mineral soil from spring and fall ^{15}N fertilization, and in profiles from Control soil: (a) biomass in roots, shoots, and whole seedlings; (b) relationship between biomass in roots, shoots, and whole seedlings and pot N content; (c) atom% ^{15}Nex in seedling roots and shoots grown in pots with LFH and mineral soil from spring and fall ^{15}N fertilization (Spring LFH + MIN and Fall LFH + MIN), and in profiles from Control soil; (d) Percent recovery of residual fertilizer ^{15}N in roots, shoots and whole seedlings grown in LFH, MIN, and LFH + MIN treatments (Spring and Fall data, which were not significantly different, were combined)

LFH and 14.4–93.6 μg N g^{-1} for mineral soil layers in Fallow pots. Although there were no statistical differences between nitrate levels in the Fallow pots, nitrate levels of Spring MIN and Spring LFH in Planted pots were higher than the other Planted profiles, which were not different than each other. Ammonium concentrations in Fallow pots were lower than nitrate concentrations, and only exhibited an interaction between the planting and season of fertilization treatments ($F_{1,47}$= 4.55, P=0.04); the profile treatments did not significantly affect ammonium concentrations ($F_{2,47}$=0.59, P=0.56). Ammonium concentrations in Fall Fallow pots were higher than those in Spring Fallow pots. All Fallow pots showed higher ammonium concentrations than Planted pots, which were not different than each other.

Recovery of ^{15}Nex (μg) as DIN in the LFH layer was again characterized by a three-way interaction between planting, season of fertilization, and profile treatments ($F_{2,47}$=3.79, P=0.03). Fallow pots showed higher overall recovery than Planted pots. However, the only clear difference among Fallow pots was that recovery in Fall and Spring LFH + MIN profiles was higher than that in the Spring MIN profile treatment. Recovery of ^{15}N-DIN

Table 2 Recovery of ^{15}N in seedlings planted in pots from different ^{15}N treatments: LFH, fertilized LFH; MIN, fertilized mineral soil; and LFH + MIN, fertilized LFH and mineral soil. Standard error in brackets. ND is "not determined"

	Spring					Fall				
	Weight(g)	N (g kg^{-1})	atom % ^{15}N	^{15}Nex (μg)	recovery %	Weight (g)	N (g kg^{-1})	atom% ^{15}N	^{15}Nex (μg)	recovery %
Shoot										
LFH	6.31 (0.18)	7.58 (1.01)	0.6538 (0.0195)	134.7 (22.8)	5.1 (0.9)	7.51 (0.55)	5.83 (0.40)	0.6853 (0.0143)	138.5 (20.4)	5.8 (0.8)
MIN	7.42 (0.51)	7.42 (0.30)	0.4472 (0.0036)	40.6 (3.4)	3.5 (0.3)	9.76 (0.69)	6.43 (0.95)	0.4803 (0.0022)	65.3 (5.6)	3.0 (0.3)
LFH + MIN	6.97 (0.23)	7.28 (0.46)	0.7473 (0.0079)	189.9 (14.5)	5.0 (0.4)	9.46 (0.86)	5.96 (0.70)	0.7102 (0.0227)	183.9 (13.3)	4.0 (0.3)
Root										
LFH	7.40 (0.22)	7.27 (0.31)	0.7028 (0.0040)	177.9 (9.1)	6.7 (0.3)	8.68 (0.22)	6.51 (0.22)	0.6772 (0.0227)	173.9 (19.9)	7.2 (0.8)
MIN	9.88 (0.29)	7.11 (0.17)	0.4626 (0.0069)	63.6 (4.5)	5.4 (0.4)	10.32 (0.31)	7.59 (0.23)	0.5071 (0.0032)	105.8 (3.1)	4.9 (0.1)
LFH + MIN	7.16 (0.52)	8.27 (0.27)	0.7841 (0.0059)	243.8 (17.9)	6.4 (0.5)	10.78 (0.82)	7.13 (0.26)	0.7892 (0.0047)	317.8 (9.8)	7.0 (0.2)
Whole										
LFH	13.70 (0.27)	ND	ND	312.6 (27.8)	11.8 (1.0)	16.19 (0.70)	ND	ND	312.4 (33.0)	13.0 (1.4)
MIN	17.31 (0.51)	ND	ND	104.2 (4.6)	8.9 (0.4)	20.08 (0.97)	ND	ND	171.1 (8.0)	8.0 (0.4)
LFH + MIN	14.14 (0.68)	ND	ND	433.8 (29.9)	11.3 (0.8)	20.23 (1.66)	ND	ND	501.8 (13.5)	11.0 (0.3)

Table 3 Analysis of variance results for residual ^{15}N availability, with season (Fall, Spring) and source (LFH, MIN, LFH + MIN) treatments as main effects

	DF	F-ratio	P-value
Root			
season x source	2, 23	0.93	0.41
season	1, 23	0.36	0.55
source	2, 23	9.01	0.002
Shoots			
season x source	2, 23	1.11	0.33
season	1, 23	0.23	0.64
source	2, 23	7.70	0.004
Whole			
season x source	2, 23	0.93	0.41
season	1, 23	0.0003	0.99
source	2, 23	12.48	0.0004

from Planted pots ranged from 0.2 to 1.2 μg. Unlike the Fallow pots, the recovery of ^{15}Nex from Spring LFH + MIN profiles in Planted pots was more than three times higher than that from Fall LFH + MIN profiles. This difference was preserved when recovery was considered as a percentage of initial ^{15}Nex (Table 5), where there was also a three-way interaction between planting, fertilization, and profile treatments ($F_{2,47}=3.79$, $P=0.03$). Yet while mineral soil recovery (%) from the Fallow pots (9.3 to 12.4 % of ^{15}Nex) was still higher than that from the Planted pots (all <0.1 % of ^{15}Nex), there were no differences between profile treatments in the Fallow pots.

Experimental ^{15}N recoveries

Total mean recoveries of original ^{15}Nex for each treatment ranged from 87 to 105 % (Table 6), with recoveries

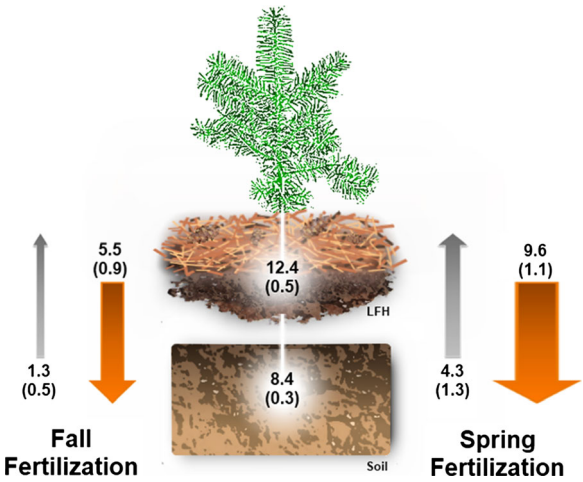

Fig. 2 Transfers of ^{15}Nex in pots between soil layers and to seedlings as a percent of initial ^{15}Nex for fall vs. spring fertilization. Orange arrows represent transfer of ^{15}Nex from LFH to mineral soil, and gray arrows represent the transfer from mineral soil to LFH. Season of fertilization had no effect on transfer of ^{15}Nex to seedlings, so spring and fall fertilization values are combined in estimating the transfer to seedlings (white arrow). Standard error in brackets

for 10 of the 12 treatments falling between 95-105 %. The two lowest recoveries were for Planted-Spring-MIN-^{15}N and Fallow-Fall-MIN-^{15}N. For the Planted pots, the ^{15}Nex was mainly found in the LFH and mineral soil (78–92 %), essentially all as organic N, with 8–13 % recovered in seedlings. For the Fallow pots, the bulk of the ^{15}Nex was similarly recovered in organic form (76–93 %), with ^{15}N-DIN recovery (9–12 %) essentially corresponding to that taken up by seedlings in the Planted pots.

Discussion

Experimental design considerations

Interpretation of our results requires consideration of the possible influence of some aspects of the experimental design. The original field site was established in a typical coastal Douglas-fir stand with high spatial heterogeneity, as reflected in the error analysis in Mead et al. (2008). Table 1 of that paper showed total N of 7.77 and 7.80 g kg^{-1} for LFH layers of spring- and fall-fertilized plots, respectively. The N concentration for LFH of control plots (not shown) was 6.45 g kg^{-1}. The corresponding values for 0–10 cm mineral soil for spring, fall and control plots were 0.82, 1.25 and 0.50 g kg^{-1}. This resulted in a range of total N concentrations for the

Table 4 Dissolved inorganic N (DIN) in LFH and mineral soil from pots with different ^{15}N treatments: LFH, fertilized LFH; MIN, fertilized mineral soil; and LFH + MIN, fertilized LFH and mineral soil (standard error in brackets)

	Spring					Fall				
	Nitrate		Ammonium		Total Pot	Nitrate		Ammonium		Total Pot
	LFH	Soil[a]	LFH	Soil	DIN	LFH	Soil	LFH	Soil	DIN
	μg g^{-1}				— mg—	μg g^{-1}				— mg—
Planted										
LFH	1.5 (0.4)	0.3 (0.09)	3.5 (1.2)	0.5 (0.07)	0.8 (0.1)	0.3 (0.1)	0.1 (0.02)	3.4 (0.3)	0.3 (0.06)	0.4 (0.03)
MIN	0.9 (0.3)	0.04 (0.001)	2.1 (0.5)	0.5 (0.2)	0.5 (0.1)	0.7 (0.1)	0.05 (0.003)	2.0 (0.4)	0.1 (0.05)	0.3 (0.05)
LFH + MIN	0.7 (0.2)	0.1 (0.01)	3.2 (1.2)	0.5 (0.07)	0.9 (0.09)	0.6 (0.1)	0.05 (0.02)	3.5 (1.6)	0.2 (0.02)	0.4 (0.09)
Fallow										
LFH	1006.2 (128.2)	18.9 (1.5)	9.8 (2.3)	0.1 (0.005)	73.9 (10.2)	1214.7 (130.0)	14.4 (2.5)	9.5 (1.2)	0.1 (0.01)	71.7 (7.5)
MIN	1761.1 (148.3)	39.2 (5.7)	10.9 (2.3)	0.1 (0.01)	134.1 (5.0)	1728.3 (141.1)	93.6 (22.5)	25.8 (16.9)	1.2 (0.01)	168.8 (24.2)
LFH + MIN	1668.6 (284.0)	29.6 (9.0)	7.1 (1.8)	0.3 (0.07)	117.0 (17.9)	1970.2 (506.8)	49.3 (7.4)	28.5 (11.6)	0.7 (0.09)	129.7 (31.3)

[a] Mineral soil abbreviated to soil in column headings

Table 5 Soil $^{15}N_{ex}$ belowground recovery, excluding plant biomass, in LFH and mineral soil from pots with different ^{15}N treatments: LFH, fertilized LFH; MIN, fertilized mineral soil; and LFH + MIN, fertilized LFH and mineral soil. DIN is "dissolved inorganic N". Standard error in brackets

	Spring					Fall				
	DIN		Organic N		Total	DIN		Organic N		Total
	LFH — % —	Soil[a]	LFH	Soil	recovery	LFH — % —	Soil	LFH	Soil	recovery
Planted										
LFH	<0.1	<0.1	78.1 (1.3)	9.6 (1.1)	87.7 (1.9)	<0.1	<0.1	86.5 (2.8)	5.5 (0.9)	91.9 (1.9)
MIN	<0.1	<0.1	4.3 (1.3)	73.8 (3.3)	78.1 (4.3)	<0.1	<0.1	1.3 (0.5)	85.2 (1.8)	86.6 (2.1)
LFH + MIN	<0.1	<0.1	56.1 (3.9)	31.2 (0.6)	87.4 (3.6)	<0.1	<0.1	43.3 (2.7)	37.6 (6.4)	80.9 (6.4)
Fallow										
LFH	8.1 (1.2)	1.2 (0.1)	83.0 (3.8)	2.9 (0.3)	95.2 (3.0)	9.7 (1.0)	1.1 (0.2)	89.3 (2.5)	3.6 (0.7)	103.7 (2.3)
MIN	10.0 (0.6)	2.4 (0.3)	5.6 (3.8)	79.8 (1.9)	97.8 (3.2)	7.7 (0.8)	4.5 (1.1)	5.9 (0.3)	70.5 (6.3)	88.6 (5.9)
LFH + MIN	9.9 (1.7)	1.9 (0.6)	63.4 (2.4)	26.1 (0.3)	101.2 (1.4)	9.6 (2.6)	2.6 (0.4)	44.5 (2.9)	38.6 (1.2)	95.4 (4.8)

[a] "Mineral soil" abbreviated to "soil" in column headings

composite samples and thus of total N and ^{15}Nex for the seven treatments. As discussed in the Methods, values for the composite samples do not correspond exactly to those from the field study, but there were comparable differences between the control, spring, and fall samples; namely, the composite Control MIN had lower N concentration than the Spring and Fall MIN composites (0.6 g kg^{-1}, compared to 0.8 g kg^{-1} for Spring MIN and 1.4 g kg^{-1} for Fall MIN). Unfortunately, total N concentrations for control and fertilized plots at establishment were not provided in the original studies (Nason 1989; Nason et al. 1988, 1990).

Table 6 Summary of percent$^{15}N_{ex}$ recoveries in seedlings and soil profiles from pots with different ^{15}N treatments: LFH, fertilized LFH; MIN, fertilized mineral soil; and LFH + MIN, fertilized LFH and mineral soil

^{15}Nex Source		Planted Spring	Planted Fall	Fallow Spring	Fallow Fall
LFH	Seedlings	11.8	13.0	0.0	0.0
	Soil N-DIN	0.0	0.0	9.3	10.8
	Soil N-Org	87.7	91.9	85.9	92.9
	Sum	99.5	104.9	95.2	103.7
MIN	Seedlings	8.9	8.0	0.0	0.0
	Soil N-DIN	0.0	0.0	12.4	12.2
	Soil N-Org	78.1	86.6	85.4	76.4
	Sum	87.0	94.6	97.8	88.6
LFH + MIN	Seedlings	11.3	11.0	0.0	0.0
	Soil N-DIN	0.0	0.0	11.8	12.2
	Soil N-Org	87.4	80.9	89.5	83.1
	Sum	98.7	91.9	101.3	95.3

How much could our results have been influenced simply by the higher total N in some treatments? Inclusion of LFH and MIN from plots originally fertilized with nonlabeled urea would be ideal, but these were not part of the original design, and there would be complications with two types of control treatments, including dealing with the fertilizer ^{15}N natural abundance. The question cannot be settled absolutely with the data available, but several arguments support our interpretation that native soil N behaved similarly in the control and fertilized composites. As discussed previously, first the spatial heterogeneity in the field and the way in which the pot composites were prepared could account sufficiently for the differences in N concentrations of the composites and second, total seedling biomass and N uptake were proportional to the total N in pots of each treatment. Third, the proportion of N

derived from fertilizer in the pots was 9.5 % for LFH and 5.0 % for MIN layers (very similar for Spring or Fall composites), supporting our interpretation that the original fertilization did not add enough N to substantially increase the N capital of the site, and hence the N concentrations in LFH and MIN layers. Finally, this is consistent with the results from the field study. Table 9 in Mead et al. (2008) shows LFH total N stocks for spring and fall fertilization as 361 and 320 kg ha^{-1}; the corresponding value for control LFH (not shown) is 240 g kg^{-1}. The 10-year ^{15}N recoveries in LFH corresponded to 36 kg N ha^{-1} for spring and 32 kg N ha^{-1} for fall fertilization, much smaller than the difference between Spring/Fall and Control site N stocks. Similarly, the N capital of 0–10 cm mineral soil in 1992 was 805 kg ha^{-1} for spring and 557 kg ha^{-1} for fall fertilization, of which the residual fertilizer N accounted for 37 kg ha^{-1} (spring) and 25 kg ha^{-1} (fall). The 0–10 cm N capital of the control plots was 431 kg ha^{-1}, so that the differences between control and fertilized plots are again much too large to be attributed to residual fertilizer N. Similar to the composites used in the pot trials, the fertilizer-derived N amounted to 4.5 % for LFH and 10 % for 0–10 cm MIN soil, with very little difference between spring and fall fertilization.

Experimental recovery of ^{15}N

The high ^{15}N total recoveries are similar to other pot trials that controlled leaching losses, both for seedling uptake of fertilizer ^{15}N (Marshall and McMullan 1976; Pang 1985; Amponsah et al. 2004) and for residual fertilizer N in ^{15}N-labelled litter (Setälä et al. 1996). These studies are in turn similar to some of the earliest reports of ^{15}N pot trials in agriculture (Jansson 1963; Legg and Allison 1967). Recoveries different from 100 % have generally been attributed to experimental error, including losses of plant and soil material during separation and processing and possible small amounts of denitrification.

Recovery of ^{15}N in seedling biomass

Although the bulk of applied ^{15}N in pot trials is usually found as soil organic N, seedling uptake can be substantially higher than in the field, as shown by the following three studies, all with prevention of leaching loss, and with varying addition of other nutrients. Pang (1985) grew 4-year-old Douglas-fir saplings for one growing season after application of ^{15}N-labeled urea, $^{15}NH_4NO_3$, or $NH_4{}^{15}NO_3$, and recovered 41 % of the applied ^{15}N-urea, 39 % of the $^{15}NH_4NO_3$, and 60 % of the $NH_4{}^{15}NO_3$. Increases after the second growing season were not significant. In a study to optimize timing of fertilization, seedlings of lodgepole pine similarly took up 43 % of $^{15}NH_4^+$-N in 30 days (Amponsah et al. 2004). Somewhat lower recovery (24 %) of applied ^{15}N-urea by Douglas-fir seedlings (Sept-June) was found by Marshall and McMullan (1976).

Although seedling uptake of residual fertilizer N in greenhouse trials is lower than that of directly applied fertilizer, our three studies show that residual fertilizer ^{15}N can still be accessed by seedlings. Preston and Mead (1994b) grew lodgepole pine seedlings in mineral soil (0–10 cm) sampled 8 years after fertilization with ^{15}N. Unfortunately total ^{15}N and N recoveries per pot were not determined, but after 9 months, seedlings took up an average of 8.5 % of ^{15}N recovered, compared to 4.6 % of native N. Assuming a typical overall ^{15}N recovery of 90 %, this would correspond to 7.7 % of residual soil ^{15}N. For pots without seedlings, mineralization (as percent of total recovered) corresponded to 2.3 % of residual fertilizer ^{15}N and 2.4 % of native soil N. Chang et al. (1999) established another pot trial using H horizon humus fertilized 7 or 31 months previously with $(^{15}NH_4)_2SO_4$ and showed 2-3 % uptake by seedlings of residual soil ^{15}N, corresponding to availability ratios (A-ratios) around 1.2. Mineral N was much higher in the Fallow pots, mostly as ammonium, and always had a higher enrichment (A-ratio >1) than the bulk soil N. Results in the present study showing 8–13 % seedling uptake of residual fertilizer ^{15}N, and a similar amount left as mineral N in plots without plants are thus consistent with the previous pot trials to assess mineralization and seedling uptake of residual fertilizer N. A pot trial using litter baskets with ^{15}N-labelled L layer (mostly Douglas-fir needles and twigs) taken during the same sampling as this study examined the role of soil fauna in decomposition (Setälä et al. 1996). While it was not focused on plant recovery, after 40 weeks, 3–6 % of the litter ^{15}N was found in poplar (*Populus trichocarpa* Torr. and Grey) seedlings, again showing availability of organic N to mineralization and plant uptake in a confined setting.

Consistent with results from conventional fertilizer N trials, however, three long-term field trials have failed to show significant additional long-term uptake of fertilizer ^{15}N (Preston and Mead 1994a; Chang and Preston

2000; Mead et al. 2008). Even those showing continued mineralization and loss of soil ^{15}N failed to demonstrate detectable long-term uptake by trees. An average of 7 % per year of soil ^{15}N was lost over 7 years for a lodgepole pine site (Preston and Mead 1994a), and annual losses from the Douglas-fir site of the present study averaged 3.0 % over 9 years from mineral soil and 3.7 % from LFH (Mead et al. 2008). Such losses are not always the case; for a site on northern Vancouver Island, with thick humus layers and dense understorey of ericaceous salal (*Gaultheria shallon* Pursh), there was essentially no change in soil or plant residual ^{15}N between sampling at 2 and 6 years (Chang and Preston 2000). Two-year humus from this site also showed the lowest ^{15}N availability to seedlings in a pot trial (Chang et al. 1999). Compared to a natural forest setting, N mineralization and plant uptake in pot trials is likely to be enhanced by soil disturbance during setup, favorable temperature and moisture conditions, and dense root mass where plants are present. In our study over 2 years, mineralization to DIN or seedling uptake in planted pots ranged from 4–6 % per year for all treatments, somewhat higher than the annual losses reported above during 9 years in the field site.

Uptake of ^{15}N from leaf litter has also been observed in the field, similar to the uptake of litter ^{15}N observed by Setälä et al. (1996). Approximately 3 % of ^{15}N in red alder (*Alnus rubra* Bong.) leaf litter placed in a clearcut site was found in vegetation after 21 months, with an overall recovery of 68.5 % (Swanston and Myrold 1997). Similarly, 2–4 % of ^{15}N from labeled beech (*Fagus sylvatica* L.) litter was found in trees after 3 years, with an overall recovery of 82–85 % (Zeller et al. 2001). Plant recovery of ^{15}N in these field studies is comparable to pot trials that showed uptake around 2–8 % of residual fertilizer N (Preston and Mead 1994b; Chang et al. 1999; Setälä et al. 1996). The importance of plant uptake can be seen by comparing Swanston and Myrold (1997) and Zeller et al. (2001) with a study of ^{15}N Douglas-fir litter placed on the surface and isolated from plant uptake (Preston and Mead 1995). After 1 year, only 54 % of ^{15}N was recovered, decreasing to 25 % at 3 years and 20 % at 7.5 years.

Uptake of residual fertilizer ^{15}N in agriculture

There has been much more study of this topic for agricultural crops. In a greenhouse study, 4 % of residual fertilizer ^{15}N was taken up by wheat in the first residual year; i.e., the first year following the original fertilizer application and harvest (Lam et al. 2013). A review for arable crops in England found about 6 % of residual fertilizer ^{15}N was taken up in the first residual year and 2 % in the second (Macdonald et al. 2002). Similar trends of declining ^{15}N availability were found in long-term pot trials (Jansson 1963; Legg and Allison 1967) and in a pot trial of ^{15}N uptake from soil sampled from a ^{15}N field trial (Preston 1982). Thus pot and field trials of residual ^{15}N from agricultural trials show similar availability or release of ^{15}N, in contrast with the lack of any convincing field demonstration of residual ^{15}N fertilizer uptake by temperate conifers.

Transfers of ^{15}N

The 10-year field study (Mead et al. 2008) found no differences in Douglas-fir stand biomass, N content or fertilizer ^{15}N recovery between urea originally applied in spring vs. fall. This subsequent study found that seedling biomass and total N were greater in Fall treatment pots, but this was simply due to the higher total N values in Fall soils. Because of these differences in total N between the Spring and Fall mineral soils used in this study, we compared N transfers relative to amount of N per pot at the start of the pot study. Our study design uniquely revealed the net transfers between LFH and mineral soil and their separate contributions to seedling uptake. Although LFH pots began the study containing the least total N (along with the Control), both seedling uptake and transfers between layers showed the greater availability of LFH ^{15}N, with at least twice as much ^{15}N transferred from LFH to mineral, as vice versa. There was one effect of original season of fertilization, in that these transfers between layers were, for both directions, larger for spring- than for fall-applied fertilizer. These Spring effects occurred in spite of Fall MIN and Fall LFH + MIN pots beginning the study with more overall N. Our study used ^{15}N to show that fertilizer-N is still a sizeable portion of available N in both LFH and mineral soil 10 years after application. This continuing availability under controlled conditions without leaching loss is consistent with two previous pot studies of residual forest ^{15}N fertilization (Chang et al. 1999; Preston and Mead 1994b).

Long-term fertilizer-N dynamics

Studies of temperate conifers show recovery of ^{15}N-labeled fertilizers by crop trees of 2–20 %, with uptake

essentially completed after 1 year (Preston and Mead 1994a; Chang and Preston 2000; Mead et al. 2008), and the bulk of N found in organic layers. As discussed in these studies, in the absence of major losses due to leaching, denitrification or ammonia volatilization, initial low uptake is mainly attributed to immobilization of N in organic forms, especially in the forest floor, and in subsequent years to poor synchrony between N mineralization and plant N uptake. Our study showing greater availability of residual fertilizer N from the LFH than from the mineral soil suggests that the problem does not lie in lower release from the LFH per se. However, if the bulk of the fertilizer N is immobilized in forest floor, N mineralized from the LFH is then more likely to be taken up by understory roots or microflora, rather than the Douglas-fir roots concentrated in the mineral soil.

As discussed in Mead et al. (2008), factors limiting the ability of Douglas-fir roots to take up available N may include low temperature during the early flush of N mineralization, drought later in summer, competition by microbes and understorey vegetation, or limitation of another nutrient such as P. In a study of factors controlling nutrient uptake, Warren et al. (2003) demonstrated that Douglas-fir seedlings can benefit from a brief pulse of inorganic N, as might occur naturally; by contrast George et al. (1997) found a low ability of Douglas-fir to respond to heterogeneous soil nutrient distribution. However, these studies were limited to greenhouse seedlings, and there is very little information on temporal and spatial availability of N and other nutrients in Douglas-fir stands, or on the pattern of uptake by older trees. Douglas-fir is considered to be limited by low soil moisture in much of its range, especially on the drier east coast of Vancouver Island (Coops et al. 2007), but few studies have directly addressed the effect of soil moisture on fertilization. A 4-yr irrigation and fertilization trial showed no effect of increased soil moisture on N growth-response by 30-year old Douglas-fir in the Pack Forest of Washington (Gessel et al. 1990). However, much closer to our study site, Douglas-fir growth was enhanced by irrigation or N fertilization, with the combination producing twice the additive response of the individual treatments (Brix 1972). White et al. (2012) found that winter precipitation could help account for variable response to fertilization by Douglas-fir in the Inland Northwest USA, with growth-response limited by early dry winter periods. In our area, growth and N uptake could be limited both by summer drought, and then by intense rain events in other parts of the year, which combined with often thin and stoney soils, could contribute to leaching loss of mineralized N.

Phosphorus limitation has been observed for wetter coastal forests of Vancouver Island (Blevins et al. 2006), but is less likely for Douglas-fir in the drier east coast of Vancouver Island (Mitchell et al. 1996; Carter et al. 1998; Preston and Trofymow 2000), and sulfur was similarly found to be non-limiting (Weetman et al. 1997). The similarities between total N in seedlings and inorganic N in Fallow pots are particularly intriguing. Seedlings may profit from N-mineralization, but do not necessarily drive it. At least within the time span of the bioassay (almost 2 years), the amount of N mineralized may be independent of root growth. Over short time periods, N products of a non-leached Fallow system may in fact represent the probable uptake of a Planted system. To the extent that a planted system is unable to capitalize on the N release, this N may be lost.

Future directions

Despite the ongoing need to improve fertilizer N utilization and growth response in managed forest stands, there has been little process research into the factors that limit both initial and long-term uptake. Nitrogen isotope analysis is cheaper and requires less sample than a few decades ago, and is well-suited to single-tree plots. It may be possible to make more use of variations in natural abundance reported from large field trials (e.g., Balster et al. 2009) to quantify fertilizer N uptake, or even to use ^{15}N-depleted fertilizer. The ^{15}N root bioassay (Rosengren et al. 2003) could offer a rapid diagnosis of tree N demand, and complement improvements in site classification to predict nutrient supply from soil parent material and soil nutrient regime characteristics (Littke et al. 2011). More use could be made of soil remaining from ^{15}N experiments; rather than only for greenhouse trials, it should be possible to transplant ^{15}N-enriched LFH or mineral soil layers to new field sites to test release and uptake of residual ^{15}N. Hypotheses concerning the immobilization of N in forest floor could be tested by various approaches to deliver fertilizer N directly to the mineral soil, and the possible limiting role of other nutrients or moisture needs to be similarly addressed. These studies need to include older stands in the field, in order to optimize fertilization as a management option for shortening rotation length. The experimental design of a pot trial such as this one could

be improved by including application of non-labeled fertilizer in the initial field trial, along with selection of a more homogeneous site. Although it is unlikely that tree utilization of fertilizer N can rival levels achieved for agricultural crops, little progress can be made without research on the fundamentals, experiments designed without constraints of immediate operational suitability or economic viability.

Conclusions

Our three investigations of residual fertilizer ^{15}N in soil sampled 6, 8 and 10 years after application to coniferous species in British Columbia all demonstrate that it continues to be mineralized and can be taken up by seedlings in pots. Its availability is greater than that of native soil N, with little practical influence of the original chemical form or season of fertilization. The present study in particular demonstrated movement of ^{15}N between LFH and mineral soil layers, and greater availability from the LFH layer. Our results support previous studies indicating that in the field other factors such as denitrification, leaching and asynchrony of soil N mineralization and tree uptake may limit long-term uptake of residual ^{15}N. Further improvement of forest fertilizer N efficiency will require innovative departures from previous approaches.

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