The Influence of Tree Species on Nitrogen Mineralisation in the Forest Floor: Lessons From Three Retrospective Studies

Cindy E Prescott, Keith D Thomas and Gordon F Weetman
Faculty of Forestry
University of British Columbia
Vancouver, British Columbia
Canada

Abstract

Rates of net nitrogen mineralisation were measured during laboratory incubations of forest floor from adjacent plantations of different tree species at three locations: coastal British Columbia, interior British Columbia and Ireland. As expected, rates were generally high under broadleaves (oak and birch), and low under pine, cedar and *Calluna*. Rates were higher than expected under Douglas-fir and spruce, and lower than expected under larch. Neither pH nor rates of C mineralisation were good predictors of net N mineralisation.

Key words: *nitrogen mineralisation, laboratory incubation, forest floor, plantations*

Introduction

The influence of tree species on nitrogen (N) availability has been difficult to establish, because of interactions between the species and site factors that determine rates of N mineralisation. Studies in forests of different species have generally reported N availability to be high under broadleaves (Flanagan and Van Cleve 1983, Pastor *et al.* 1984, Harris and Riha 1991, Stump and Binkley 1993) and cedars (Turner and Franz 1985), and low under pines (Miller *et al.* 1979, Prescott *et al.* 1992) and spruces (Pastor *et al.* 1987, Mardulyn *et al.* 1993). Recent comparisons of N mineralisation rates in forest floors in adjacent plantations of different tree species on one site (ie common-garden experiments: Harmer and Alexander 1986, Binkley and Valentine 1991, Harris and Riha 1991, Gower and Son 1992) have demonstrated differences in N availability that have not always matched expectations. As Binkley (this volume) points out, classic expectations of high N availability under hardwoods have not been borne out in common-garden experiments, and some conifer species such as larch and white pine have had unexpectedly high rates of N mineralisation. More comparisons of rates of N mineralisation in forest floors in common-garden experiments are needed to isolate the influence of tree species on N availability.

In this study, we compare rates of net N mineralisation in forest floors under adjacent plantations of different tree species in two locations in British Columbia (BC), Canada, and one in Ireland. Relative rates of mineralisation under different species are compared at the 3 sites and with other studies, in order to look for consistent patterns among species. Some of the difficulties encountered in sampling old trials that were established for other purposes are discussed, and suggestions for more appropriate design of trials for testing the influence of tree species are offered.

Study sites

Complementary studies were conducted at: the University of British Columbia (UBC) Research Forest near Maple Ridge in coastal BC; the Skimikin Nursery near Salmon Arm in interior BC; and Trench 14 in Clonsast Bog, County Offaly, Ireland.

The UBC Research Forest is in coastal southwestern BC (49°17'N, 122°36'W) at 180 m elevation. Average daily temperature is 9°C; average annual precipitation is 2166 mm. The soil is an ortho-humo ferric podzol over glacial deposits. The original forest at this site was Douglas-fir (*Pseudotsuga menzesii* (Mirb.) Franco), western redcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), up to 800 years old. The forest was clearcut in 1955 and the slash was stockpiled and burned. Pictures taken at the time indicated that very little of the original forest floor remained after harvest. Seedlings of Douglas-fir, western redcedar and western hemlock were planted in 1957 on three 0.25 ha plots of each species. The original purpose of the trial was to test the effect of spacing on the growth of each species; spacings in each plot ranged from 1.8 to 4.5 m (Ruekema and Smith 1987). There were no buffer strips between the three plots, and brush was periodically removed from all plots. When the forest floor was sampled in 1993, the stands were 34 years old and the forest floors were about 5 cm thick.

The Skimikin trial was in south-central interior BC (50°48'N, 199°26'W) at 750 m. The average daily temperature is 8°C; average annual precipitation is 521 mm. The soil is eutric brunisol of glaciofluvial origin. The original forest at this site was primarily Douglas-fir and lodgepole pine (*Pinus contorta* Dougl.), up to 80 years old. The forest was whole-tree harvested in 1968, and the soil was root-raked to a depth of 45 cm. The original purpose of the trial was to test the effectiveness of root-raking to reduce root diseases (Morrison *et al.* 1988). A 1.28 ha area was divided into 32 plots, each 20 x 20 m, and seedlings were planted the same year. There were three plots each of Douglas-fir, lodgepole pine and paper birch (*Betula payrifera* Marsh.), and three plots each of mixtures of fir/birch, fir/cedar, fir/pine, pine/birch, cedar/birch and pine/cedar. The remaining two plots were planted with either Engelmann spruce (*Picea engelmannii* Parry) or western larch (*Larix occidentalis* Nutt.). Trees were planted at 1.5 m spacing, and there were no buffer strips between plots. When sampled in 1993, the stands were 25 years old, and the forest floors were about 2–3 cm deep. The forest floors under spruce and cedar were shallow and discontinuous and were not sampled. The mixed plots had not been maintained due to superior growth of one of the species and were also not sampled. The plots that were sampled were Douglas-fir, lodgepole pine and paper birch.

The Clonsast Bog trial was a cutaway raised peat bog in County Offaly, Ireland, at 73 m. Average daily temperature is 8.4°C; average annual precipitation is 849 mm. The original bog had a layer of obligotrophic peat with *Sphagnum* and *Calluna* over a layer of woody fen peat, underlain by till over carbonaceous limestone. The average peat depth was 4–8 m. Part of the bog was drained in 1936, by digging trenches about 1.5 m deep. Sod peat was machine-harvested from 1940 through 1955, by which time the peat depth had been reduced to about 1–3 m. The upper layer was a mixture of young peat, dried sod debris and mixed peat. The site was levelled in 1955 and divided into 18 plots, each 0.2 ha, along Trench 14, 1.6 km. Different tree species were planted in each plot, to test the suitability of several species for reforesting cutaway bogs (Carey and Barry 1975, Carey *et al.* 1985). When sampled in 1993, the stands were 38 years old and the forest floors were 2–5 cm deep. One plot of each of the following species was sampled: sessile oak (*Quercus petraea* (Matt.) Lieb.), Sitka spruce (*Picea sitchensis* (Bong.) Carr), Norway spruce (*Picea abies* (L.) Karst.), Grand fir (*Abies grandis* Lindl.), Douglas-fir, lodgepole pine, Scots pine (*Pinus sylvestris* L.), Monterey pine (*Pinus radiata* Don.), western hemlock, western red cedar, Japanese larch (*Larix leptolepis* Sieb.), Sitka spruce + Japanese larch, and *Calluna vulgaris* (control). None of the plots used in this study had been thinned or fertilised.

Methods

The forest floors were sampled in February 1993 at the UBC Forest, in June 1993 at Clonsast Bog, and in July 1993 at the Skimikin trial. Samples were taken at least 5 m from plot boundaries to minimise contamination of the forest floor with litter from adjacent plots of different species. In the plots at the UBC Forest, half of the samples were taken from the more densely stocked areas and half from the widely spaced portions of each plot, and there were no differences in rates of N mineralisation in samples from the two areas. At each point, the surface litter from the previous autumn was brushed away and the remaining forest floor material down to mineral soil or peat was collected. Each sample of FH material was placed in a polyethylene bag and transported to the laboratory at UBC The time required for transport and processing samples prior to the first extraction in the laboratory was 4 days for the samples from the UBC Forest and Skimikin, and 8 days from Ireland. The number of samples collected from each plot was 14 at the UBC Forest (one plot per species), 8 from Skimikin (three plots per species), and 10 from Clonsast Bog (one plot per species).

In the laboratory, a portion of each forest floor sample was dried at 70°C to determine moisture content. A 10-g dry weight equivalent portion of each fresh sample was shaken in 100 mL of 2N KCl (Page *et al.* 1982), and concentrations of NH4-N and NO3-N in the initial samples were measured with a Lachat autoanalyser. A second 10-g portion of each fresh sample was remoistened with distilled water to 75% water (wet weight basis) and put into a 1 pint glass jar. Each jar was sealed with a lid equipped with a septum and incubated at about 20°C for about 30 days. At weekly intervals, a 0.1 mL sample of the headspace gas in each jar was extracted with a syringe, and the concentration of CO_2 was estimated with an infrared gas analyser (Clegg *et al.* 1978). After each measurement, the jars were opened to outside air for 10 minutes and resealed. The forest floor samples were incubated for about 30 days, after which the concentrations of NH_4-N and NO_3-N in each sample was estimated after extraction in KCl as described earlier. The difference between the concentrations of N in the initial and final extractions was used to estimate the rate of net N mineralisation in each sample during the incubation. The amount of CO_2 that accumulated in each jar was summed for the entire incubation period and converted to mg C, to estimate the rate of C mineralisation in each sample. The pH of 5-g moist forest floor samples mixed with 20 mL of distilled water was measured with a Fisher Accumet model 750 pH meter.

Within each trial, differences between species in rates of C and N mineralisation and pH were tested for significance using one way analysis of variance and Bonferroni's multiple range test. In the Skimikin trial, the three plots of each species served as replicates. In the other two trials, there was no true replication, and each sample was used as a replicate in the analysis. Relationships between pH, C mineralisation and N mineralisation in the Clonsast trial were explored by linear regression analysis. SPSS for Windows was used for all statistical analyses.

Results and discussion

Rates of N and C mineralisation are summarised in table 1. There were some consistent patterns in relative rates of net N mineralisation of tree species in the three trials. The relative rates of the three species in the UBC trial (Douglas-fir > western hemlock > western redcedar) were the same in the Clonsast Bog trial. Douglas-fir also had the highest rate of N mineralisation of the 3 species in the Skimikin trial. We might expect, therefore, to find relatively high rates of N mineralisation in forest floors under Douglas-fir, and relatively low rates under western redcedar. There have been few studies of the relative rates of N mineralisation in forest floor under Douglas-fir. Slow mineralisation of N from cedar litter was suggested as contributing to low N availability in forest floors in old-growth forests of western redcedar and western hemlock (Prescott *et al.* 1993, Keenan *et al.* 1995). However, Harmer and Alexander (1986) found rates of N mineralisation and nitrification in forest floors under western redcedar to be among the highest of the 16 species of conifers examined.

The highest rate of net N mineralisation in the Clonsast trial was under sissile oak, which is in keeping with the classic expectation of higher N availability under broadleaved species. However, net N mineralisation under paper birch in the Skimikin trial was intermediate to that of the two conifers. Net N mineralisation under Japanese larch in the Clonsast trial was less than that under oak and several conifers. This finding is contrary to reports of high N mineralisation rates under Japanese larch (Gower and Son 1992) and *Larix kaempferi* (Harmer and Alexander 1986).

Rates of N mineralisation in spruce forest floors in the Clonsast trial were surprisingly high, and do not support the suggestion of Pastor *et al.* (1987) that spruce trees create conditions of low N availability. Harmer and Alexander (1986) also found relatively high rates of N mineralisation in forest floors under some species of spruce. Significantly more N was mineralised in Sitka spruce forest floors than in Japanese larch in the Clonsast trial. The rate of net N mineralisation in the mixed plot of Sitka spruce and Japanese larch was similar to that in the pure larch plot and less than that in the Sitka spruce plot. These observations do not support reports (Carey *et al.* 1988, Carlyle and Malcolm 1986) that N availability is greater in mixtures of larch and spruce than in pure spruce forests.

The slow mineralisation in pine plots in the Skimikin and Clonsast trials is in keeping with low availability of N reported in other pine forests (Miller *et al.* 1979, Fahey *et al.* 1985, Prescott *et al.* 1992). This applies only to two-needle pines; white pine, which has relatively high rates of N mineralisation (Binkley, this volume), was not included in these trials. The

Table 1: Rates of N and C mineralisation during laboratory incubations and pH of forest floors from adjacent plantations of different tree species in three trials

Species and Trial	N Mineralisation µg⁻¹ d⁻¹	C mineralisation µg⁻¹ d⁻¹	pH
UBC Forest			
Douglas-fir	5.5 *a*	191.4 *a*	5.2 *a*
Western hemlock	3.2 *ab*	202.1 *a*	4.2 *a*
Western red cedar	1.6 *b*	144.5 *b*	5.1 *a*
Skimikin			
Douglas-fir	4.6*a*	415.2 *b*	5.8 *b*
Paper birch	2.1 *ab*	406.5 *b*	6.4 *a*
Lodgepole pine	1.6 *b*	820.3 *a*	4.9 *c*
Clonsast Bog			
Sissile oak	22.3 *a*	355.2 *abc*	4.7 *bc*
Sitka spruce	15.1*b*	313.8 *bcd*	4.8 *bc*
Grand fir	15.1 *bc*	234.9 *def*	5.0 *b*
Douglas-fir	13.9 *bc*	282.6 *cde*	4.4 *cde*
Norway spruce	12.7 *bc*	239.0 *def*	4.9 *b*
Lodgepole pine	12.6 *bcd*	195.3 *ef*	3.9 *e*
Japanese larch	12.4 *cde*	279.0 *cde*	5.7 *a*
Sitka spruce +Japanese larch	9.8 *cde*	216.1 *def*	4.3 *cde*
Western hemlock	8.9 *cdef*	204.0 *ef*	3.9 *e*
Scots pine	7.4 *def*	385.4 *abc*	4.7 *bc*
Monterey pine	5.3 *efg*	138.1 *f*	4.1 *de*
Calluna	4.1*fg*	446.5 *a*	4.6 *bcd*
Western red cedar	1.2*g*	409.4 *ab*	6.1 *a*

Note: Each value is the mean of 14 (UBC), 24 (Skimikin), or 10 (Clonsast) samples. Within each trial, values for different species followed by the same letter are not significantly different ($p > 0.05$), based on one way ANOVA and Bonferroni's multiple range tests

very low rate of net N mineralisation in the *Calluna* plot at Clonsast Bog is consistent with very low N availability in heathlands (Van Vuuren *et al.* 1992).

The correlation was poor between the pH of the forest floor and the rate of net N mineralisation during the laboratory incubations (figure 1). Western red cedar had the highest pH and the lowest rate of mineralisation in the UBC and Clonsast trials. High pH of cedar forest floors was also reported by Harmer and Alexander (1986) and Turner and Franz (1985), and was attributed to the high pH and base cation content of cedar foliar litter. There was also poor correlation between the pH of the forest floor and the rate of C mineralisation, measured as cumulative CO_2 evolution during the incubations (figure 2). These observations indicate that pH is not a good predictor of mineralisation rates in the forest floor, and that

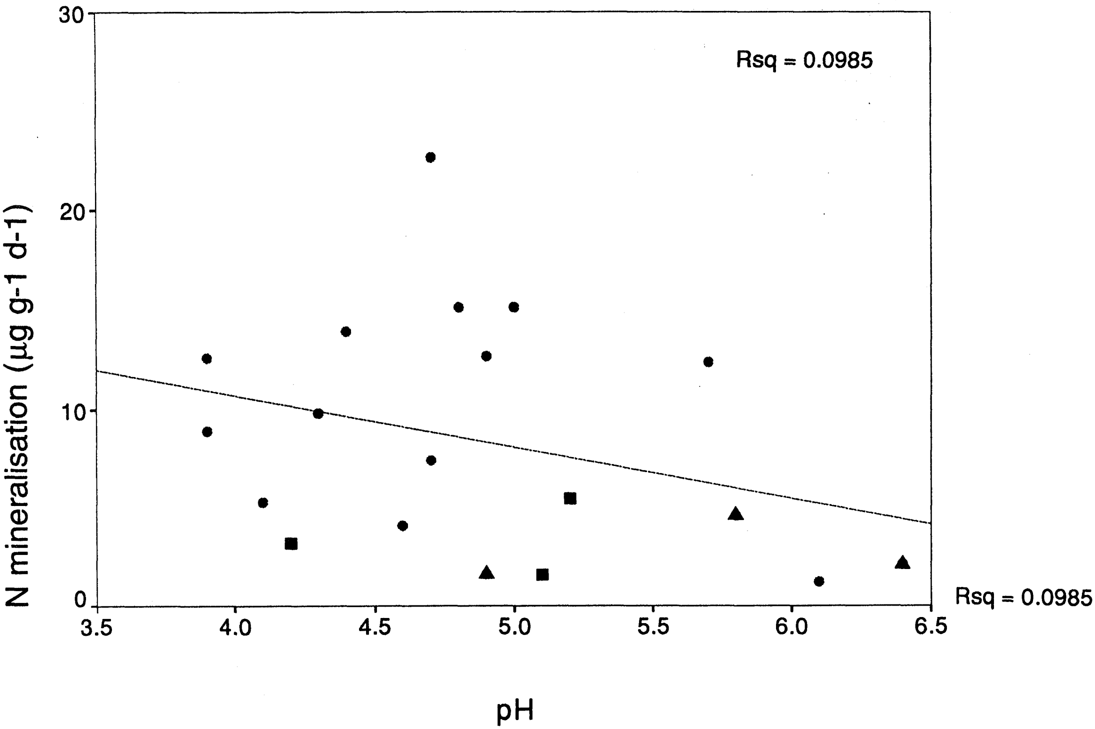

Figure 1: Relationship between pH and rate of N mineralisation in forest floors under different tree species in the three trials. Each value is the mean of 14 (UBC ■), 24 (Skimikin ▲), or 10 (Clonsast ●) samples. The best-fit regression line and corresponding coefficients of determination apply to the Clonsast trial only

species which alter the pH of the forest floor do not necessarily improve or degrade the site with respect to N availability.

The poor relationship between rates of C mineralisation and net N mineralisation (figure 3) during the incubations suggests that measurements of microbial activity are not useful for predicting N availability in forest floors. Furthermore, since rates of C mineralisation are an index of gross N mineralisation, this discrepancy indicates that immobilisation of N may be important in determining N availability in these forest floors. Recent studies with ^{15}N in the species trial used by Gower and Son (1992) demonstrated that most of the mineralised N was subsequently re-immobilised by the micro-organisms, so that measurements of net N mineralisation did not correspond to rates of gross N mineralisation (Binkley, this volume). Harris and Riha (1991) reported poor relationships between rates of net N mineralisation and CO_2 evolution in forest floors under four different tree species, and suggested that factors other than the rate of decomposition of organic matter determine N availability. Additional investigations with ^{15}N in the three trials in this study are needed to determine relative rates of gross and net N mineralisation

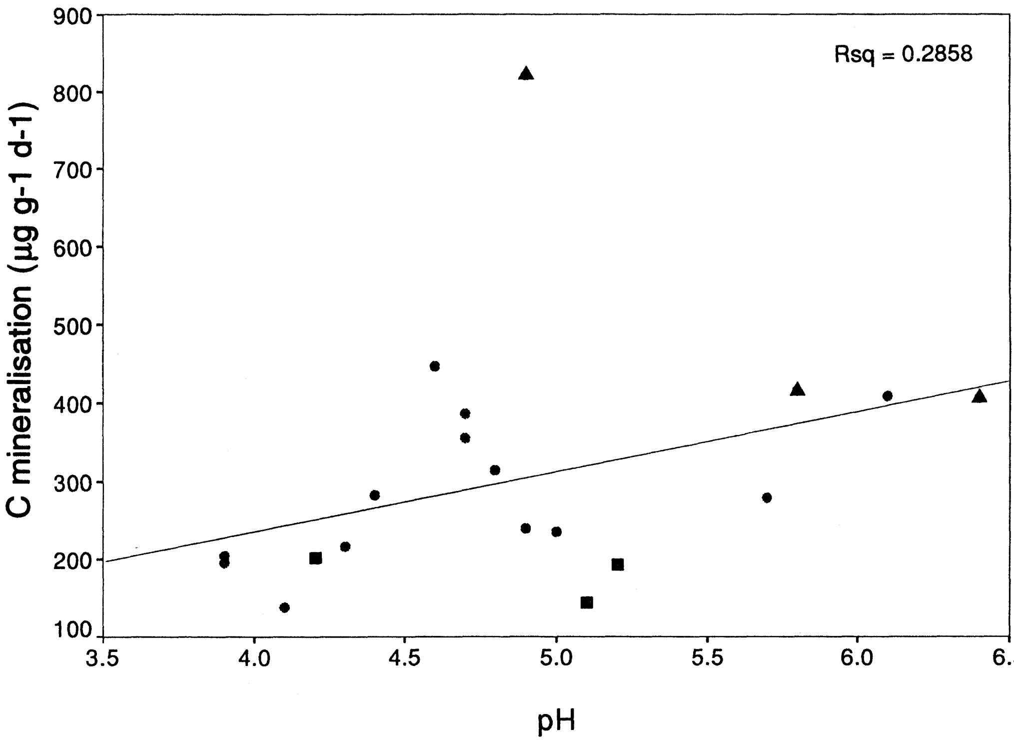

Figure 2: Relationship between pH and rate of net C mineralisation in forest floors under different tree species in the three trials. Each value is the mean of 14 (UBC ■), 24 (Skimikin ▲), or 10 (Clonsast ●) samples. The best-fit regression line and corresponding coefficients of determination apply to the Clonsast trial only

in forest floors under different tree species.

Gower and Son (1992) found a significant relationship between the lignin:N of litter and the rate of net N mineralisation in the forest floor in their experiment. Litter lignin:N has also been used for simulating the effects of tree species on soil N availability (Pastor *et al.* 1987). Litter is being collected in the three trials used in our investigations, and will be used to assess the utility of litter lignin:N for predicting rates of net N mineralisation in the forest floors under different tree species.

None of the trials that we investigated was originally designed to determine the influence of tree species on N mineralisation in the forest floor, but they nevertheless provided an opportunity to identify patterns that could be tested in more rigorously designed experiments. Our experiences in these plantations also provided some useful lessons for the design of long-term trials to investigate the influence of species on soils. The lack of replication of plots of each species in two of the trials was the major drawback, precluding conclusions about the influence of each species. As suggested by Madgwick (this volume), five plots of each species would be preferable, although the resources required for such replication must

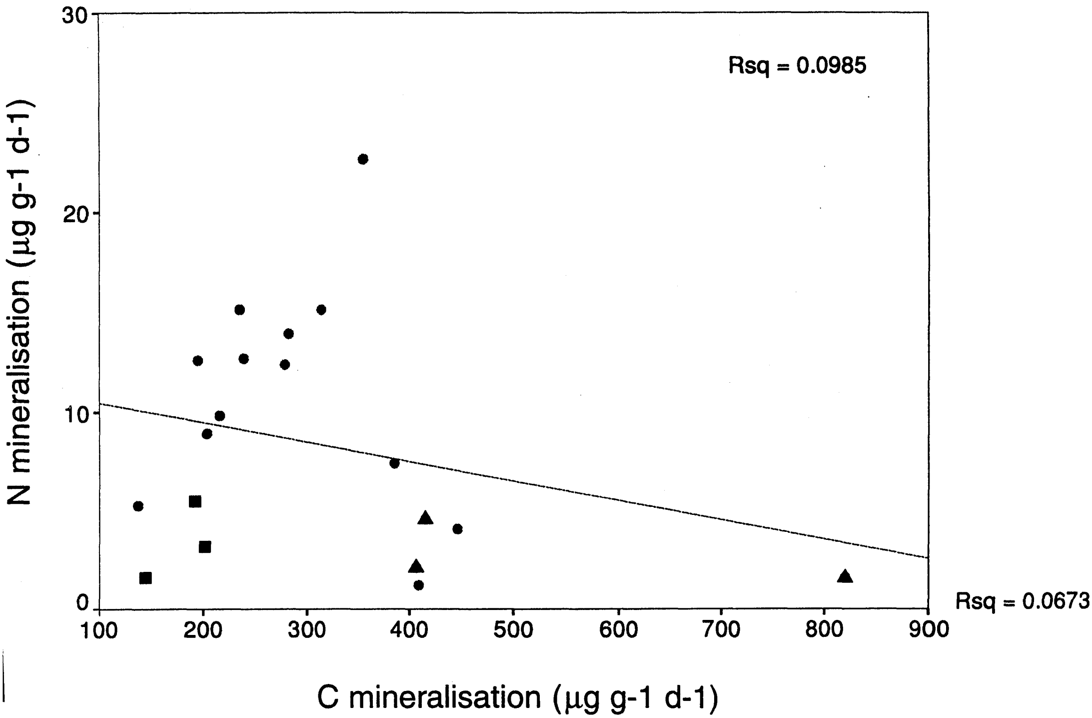

Figure 3: Relationship between rate of C mineralisation and rate of net N mineralisation in forest floors under different tree species in the three trials. Each value is the mean of 14 (UBC ■), 24 (Skimikin ▲), or 10 (Clonsast ●) samples. The best-fit regression line and corresponding coefficients of determination apply to the Clonsast trial only

be considered. There were no buffer strips between plots in any of the trials, so the litter on the forest floors near the perimeters was mixed. To keep the forest floor samples relatively pure, we did not use the outer 5 m of each lot, but this reduced the area available for sampling. It was not possible in these retrospective studies to ensure that the site was uniform across all plots at the time of planting. This was especially problematic at the Clonsast trial, where the natural variation in peat depth and varying intensities of peat-harvesting led to uneven peat depths along the trench of 1.6 km.

Differences in the rates of survival, growth and litter production among tree species made it difficult to compare the forest floors under all species in each trial. In the Skimikin trial, the forest floor under cedar and spruce was not sufficiently developed by 25 years to permit comparison with the other species. Species mixtures were also problematic, because of the tendency for one species to outgrow the other. Most of the mixed plots in the Skimikin trial were single-species at 25 years. Intensive monitoring and culling are necessary to maintain mixed plots. Another result of different growth rates was that plots of some species had been thinned and others had not by the time we sampled the trials at Skimikin and Clonsast Bog. We could not use thinned plots in these trials because the forest floors would have received substantial inputs of N in foliage from the thinned trees.

There were not enough species available in the UBC Forest and Skimikin trials to allow us to use correlation analyses properly to explore factors such as litter quality that may cause differences among species in rates of N mineralisation in the forest floors. A minimum of five species would make such analyses possible. More overlap among the species in the three trials would have been useful for determining if the relative rates of N mineralisation among the species are constant across the sites, or if they are strongly influenced by site factors. Establishment of trials with the same suite of species on a range of sites is needed to determine the ubiquity of species influences.

There were considerable differences in the amount and composition of understorey vegetation in plots of different tree species in each of these trials. Overstorey-understorey relationships were also evident in the Gisburn trial (Brown 1981). The extent to which the understorey vegetation contributes to differences in N mineralisation in forest floors under different tree species is difficult to establish in these trials. We are attempting to elucidate this in the Skimikin trial by measuring the understorey biomass in each plot and rates of N mineralisation in small plots from which the understorey has been removed. The influence of understorey vegetation could be determined by establishing plots of each species with and without understorey vegetation.

In conclusion, our investigations supported some earlier suggestions about the influence of different tree species on N mineralisation in the forest floor, but contradicted others. Rates were generally high under broadleaves and low under *Calluna*, pine and cedar. Rates were higher than expected under Douglas-fir and spruce, and lower than expected under larch. Neither pH nor rates of CO_2 evolution were good predictors of rates of net N mineralisation in the forest floors. Suggestions for more appropriate design of trials to test the influence of tree species on N availability include: replicated plots of each species, buffer strips of at least 5 m between plots, uniform site conditions in all plots, planting the same suite of species on a range of sites, and including at least five species so that the causes of differences among species can be explored.

Acknowledgments

Our thanks are extended to C Staley for assistance in the laboratory, and to R McCarthy (Coillte Teoranta), H Merler (BC Ministry of Forests) and C Power (UBC) for cooperation and access to the trials. Chemical analyses were done by A Gammell at MacMillan Bloedel Laboratory in Nanaimo, BC. The research was supported by a Strategic grant from the Natural Sciences and Engineering Research Council of Canada.

References

Binkley, D and Valentine D. 1991. Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. *Forest Ecology and Management* ***40***, 13–25.

Brown, A H F. 1981. The effects of tree species, planted pure and in mixtures, on vegetation and soil at Gisburn. *Annual Report of the Institute of Terrestrial Ecology* pp. 74–75.

Carey, M L and Barry, T A. 1975. Coniferous growth and rooting patterns on machine sod-peat bog (cutover) and Trench 14, Clonsast. *Irish Forestry* ***32***, 18–29.

Carey, M L, Hammond, R F and McCarthy, R G. 1985. Plantation forestry on cutaway raised bogs and fen peats in the Republic of Ireland. *Irish Forestry* ***42***, 106–122.

Carey, M L, McCarthy, R G and Miller, H G. 1988. More on nursing mixtures. *Irish Forestry* ***45***, 7–20.

Carlyle, J C and Malcolm, D C. 1986. Nitrogen availability beneath pure spruce and mixed larch + spruce stands growing on deep peat. 1. Net N mineralisation measured by field and laboratory incubations. *Plant and Soil* ***93***, 95–113.

Clegg, M D, Sullivan, C Y and Eastin, J D. 1978. A sensitive technique for the rapid measurement of carbon dioxide concentrations. *Plant Physiology* ***62***, 924–926.

Fahey, T J, Yavitt, J B, Pearson, J A and Knight, D H. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. *Biogeochemistry* ***1***, 257–275.

Flanagan, P W and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. *Canadian Journal of Forest Research* ***13***, 795–817.

Gower, S T and Son, Y. 1992. Differences in soil and leaf litterfall nitrogen dynamics for five forest plantations. *Soil Science Society of America Journal* ***56***, 1959–1966.

Harmer, R and Alexander, I. 1986. The effect of starch amendment on nitrogen mineralisation from the forest floor beneath a range of conifers. *Forestry* ***59***, 36–45.

Harris, M M and Riha, S J. 1991. Carbon and nitrogen dynamics in forest floor during short-term laboratory incubations. *Soil Biology and Biochemistry* ***23***, 1035–1041.

Keenan, R J, Kimmins, J P and Pastor, J. 1995. Modeling carbon and nitrogen dynamics in western red cedar and western hemlock forests. In *Carbon Forms and Functions* (eds W W McFee and J M Kelly) pp 547–568. Soil Science Society of America, Madison.

Mardulyn, P, Godden, B, Amiano Echezarrets, P, Penninckx, M, Gruber, W and Herbauts, J. 1993. Changes in humus microbiological activity induced by the substitution of the natural beech forest by Norway spruce in the Belgian Ardennes. *Forest Ecology and Management* ***59***, 15–27.

Miller, H G, Cooper, J M, Miller, J D and Pauline, O J L. 1979. Nutrient cycles in pine and their adaptation to poor soils. *Canadian Journal of Forest Research* ***9***, 19–26.

Morrison, D J, Wallis, G W and Weir, L C. 1988. Control of *Armillaria* and *Phellinus* root disease: 20-year results from the Skimikin stump removal experiment. Canadian Forest Service, Pacific Forestry Centre, Inf. Report BC–X–302.

Page, A L, Miller, R H and Keeney, D R. 1982. *Methods of soil analysis. Part 2. Chemical and microbiological properties.* Soil Science Society of America Inc., Madison, Wis.

Pastor, J, Aber, J D, McClaugherty, C A and Melillo, J M. 1984. Aboveground production and N and P cycling along a nitrogen mineralisation gradient on Blackhawk Island, Wisconsin. *Ecology* ***65***, 256–268.

Pastor, J, Gardner, R H, Dale, V H and Post, W M. 1987. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. *Canadian Journal of Forest Research* ***17***, 1394–1400.

Prescott, C E, Corbin, J P and Parkinson, D. 1992. Availability of nitrogen and phosphorus in the forest floors of Rocky Mountain coniferous forests. *Canadian Journal of Forest Research* ***22***, 593–600.

Prescott, C E, McDonald, M A and Weetman, G F. 1993. Availability of N and P in the forest floors of adjacent stands of western red cedar-western hemlock and western hemlock-amabilis fir on northern Vancouver Island. *Canadian Journal of Forest Research* ***23***, 605–610.

Ruekema, D L and Smith, J H G. 1987. Development over 25 years of Douglas-fir, western hemlock and western redcedar planted at various spacings on a very good site in British Columbia. USDA Forest Service Pacific Northwest Forest and Range Experimental Station, Olympia, WA Report PNW–RP–381.

Stump, L M and Binkley, D. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Canadian Journal of Forest Research* ***23***, 492–502.

Turner, D P and Franz, E H. 1985. The influence of western hemlock and western redcedar on microbial numbers, nitrogen mineralisation, and nitrification. *Plant Soil* ***88***, 259–267.

Van Vuuren, M M I, Aerts, R, Berendse, F and Devisser, W. 1992. Nitrogen mineralisation in heathland ecosystems dominated by different plant species. *Biogeochemistry* ***16***, 151–166.