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**Effect of harvest gap formation and thinning on soil
nitrogen cycling at the boreal-temperate interface**

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Abstract

In mixedwood forest, different types of commercial thinning that generate different gap sizes are being tested as alternatives to clearcutting to create forest stands with an irregular structure that would emulate the pre-industrial forests. The main goal of this study was to investigate the soil nitrogen dynamics in response to two partial harvesting treatments, used alone or in combination: commercial thinning creating tree size canopy gaps and harvest gaps creating 0.05 ha gaps. In a 30-year-old balsam fir (*Abies balsamea*) stand, both treatments, alone or in combination, as well as unharvested controls, were compared on replicated 0.75 ha plots. The most noticeable changes following treatments were observed in gaps while commercial thinning did not significantly influence any of the parameters assessed. In gaps, increases in N mineralization rates and mineral N concentrations and proportions (NO_3^- -N and NH_4^+ -N) relative to DON were observed. Our results suggest that these changes are caused by the increase in soil temperature and water content. In these forests, the response threshold of the N cycling regarding the size of the intervention would therefore be located between the removal of one or few trees (1-3 stems, 6-12 m²) and a gap of 500 m². Other studies conducted in different climate and forest types have showed that this threshold could be of equivalent or of a smaller size. These findings will contribute to optimizing our management strategies regarding partial cuts or small-scale clearcuts.

Key words: commercial thinning, canopy gap, nitrogen cycling, dissolved organic nitrogen, ammonium, nitrate.

Introduction

Among the nutrients essential to plant growth, nitrogen (N) is generally the one found to most often limit forest productivity in the northern temperate and boreal zones (Fisher and Binkley 2000; Maynard et al. 2007). Nitrogen cycling in these biomes is seasonally patterned and generally achieved at low rates owing to the limited microbial activity at low temperature and the acidic, highly lignified form of the boreal forest litter (Attiwill and Adams 1993). In addition, nitrogen cycling varies at a fine spatial scale in the forest soil and is influenced by natural and anthropogenic disturbances (Bélanger and Van Rees 2007). Among these, harvesting can alter several soil properties that are likely to influence N dynamics, such as temperature (Dalias et al. 2002; Grenon et al. 2004), water content (Barg and Edmonds 1999), organic matter content (Hazlett et al. 2007) and decomposition (Prescott et al. 2003). The interaction among these soil factors along with the large diversity in logging practices (extent of cutting areas, technique, equipment, etc.) explain why forest harvesting effects on N dynamics are highly variable. In their review of logging effects on boreal soil biogeochemistry, Kreutzweiser et al. (2008) observed that forest cuts had no significant effect on NH_4^+ -N and NO_3^- -N pools or fluxes in 73% of the soil studies reviewed. This large variability in the effect of tree cutting on the dissolved inorganic forms of N (DIN) available for plant growth, plus the scarcity of studies measuring dissolved organic N (DON), indicate that a clear comprehension of the effect of forest management on N dynamics is yet to come. In addition to DIN, DON contributes significantly to N uptake by plants in northern temperate and boreal ecosystems (Averill and Finzi 2011; Schimel and Bennett 2004). In these ecosystems, the depolymerization of complex molecules containing N is generally considered as the limiting step in the N cycle. Because both DON and DIN contribute to tree nutrition, Kranabetter et al. (2007) proposed using the sum of these forms in soil solution as an

indicator of soil N availability, noting that the ratio of DIN/DON was also related to N dynamics.

Among studies of the effects of tree cutting on soil N dynamics, some were performed in the context of gap (cutting of trees over a restricted area) or partial cutting, including thinning (cutting of individual stems in a stand). Gaps measuring 15 to 30 m in diameter allowed an increased amount of solar radiation to reach the soil surface and increase soil temperature. In addition, in a temperate climate, soil moisture is generally higher in the gaps (Bauhus and Bartsch 1995; Ritter et al. 2005; Muscolo et al. 2014) due to reduced rain interception and evapotranspiration by trees. These changes in local climatic controls and reduced litter inputs have often been associated with altered N dynamics in gaps, but the effect of gaps on N dynamics remains variable. For instance, the throughfall NH_4^+ -N input decreases according to size in gaps ranging from 0 (control) to 0.06 ha (Schliemann and Bockheim 2014). In a Mediterranean climate where soil humidity may be limiting N mineralization processes, increases in NH_4^+ -N and NO_3^- -N soil content are higher in smaller (0.04 ha) than in larger (0.15 ha) gaps, compared with soil under forest canopy (Muscolo et al. 2007). In the temperate climate of Denmark, Ritter (2005) reports a higher nitrification, net N mineralization and total N concentration in soil from gaps as small as 0.02 ha, and this trend is most pronounced at the centre than at the edge of the gap (Ritter and Vesterdal 2006). Significant increases in soil NO_3^- -N have been reported 3 to 7 years after logging in gaps ranging from 0.1 to 10 ha in size, but such an effect was not apparent in thinning, presumably because trees that are in close proximity are able to sequester the excess N (Prescott et al. 2003). Thinning had no effect on net ammonification, total N mineralization, or soil microbial biomass in a Douglas-fir forest of western America (Barg and Edmonds 1999), but other studies found that thinning in a coniferous stand induced a sudden postlogging increase in

NH_4^+ -N, NO_3^- -N and microbial N that quickly returned to control values afterward (Baeumler and Zech 1998; Thibodeau et al. 2000). The thinning of 58% of the stems induced a significant increase in soil NH_4^+ -N compared with the control in a Korean *Pinus densiflora* stand (Oh et al. 2012), but no such effect was observed on NH_4^+ -N or NO_3^- -N in a *Cryptomeria japonica* plantation in Taiwan (Zhuang et al. 2014).

Most studies on the effect of tree cutting on N cycling were done in the context of large clearcuts, focusing on the medium- or long-term effects, and only a few of them considered the DON component (Kreutzweiser et al. 2008; Thiel and Perakis 2009). To our knowledge, very few studies address the effect of tree cutting on N cycling in the very short term, particularly for partial cuts. In addition, the only N dynamics study that specifically addresses N dynamics in the cold soils of the southeastern Canadian boreal forest focused on the effect of precommercial thinning (Thibodeau et al. 2000). Therefore, the main objective of this study was to identify the short-term effects (from the first post-treatment growing season) of commercial thinning and 0.05 ha canopy gaps on NH_4^+ -N and NO_3^- -N and DON net fluxes and pools in the soil of a young coniferous forest. A secondary objective was to identify the relationships between several physicochemical parameters (organic layer depth, soil density, water content, pH, total N, total C, C:N ratio) and nitrogen pools and fluxes.

Materials and methods

Study area

The study area (67°9'20" W, 48°33'0" N) is located on the Appalachian Plateau of eastern Canada at an altitude of 420 m. It sits on the Grenville sedimentary bedrock, covered by glacial deposits that are more than 1 m deep from which a Humo-ferric Podzol has developed. The texture of the B layer varied from a loam to a silty loam and drainage ranged from good to

moderate. Data (1971 to 1997) from the Amqui meteorological station located about 22 km away indicate that the average annual temperature is 2.0°C with the warmest (July) and coldest (January) months reaching averages of 17.0°C and -15.0°C, respectively. Average annual precipitation is 1032 mm, a third of which falls as snow. The growing season extends for 160 days and has an average of 1324 growing degree-days >5°C. The site is located within the 5h ecological region, in the eastern balsam fir and white birch forests subdomain (MRN 2005) and can be associated with the balsam fir-yellow birch ecological type that is recognized as relatively fertile (Grondin et al. 2000). The current vegetation is a young even-aged forest of 2300 trees per ha with a dominant mean height of 14.9 m, regenerated after clearcutting that occurred in 1979. The tree basal area (29.5 m²·ha⁻¹) is 80% dominated by balsam fir (*Abies balsamea* (L.) Mill.) accompanied by white spruce (*Picea glauca* (Moench) Voss.) and white birch (*Betula papyrifera* Marsh.).

Experimental set-up and sampling

The experiment took place in a partly nested design (Quinn and Keough 2002) that included eight homogeneous blocks of 0.75 ha crossed by two skid trails dividing the blocks into three subblocks of 0.25 ha (Fig. 1). In four blocks, a partial cut of 35% of the basal area including the skid trails was made, whereas no thinning treatment was performed within the other four blocks (controls). Thinning involved the cutting of every third stem according to the MSCR selection criterion (Boulet 2007) so that one to three neighbouring stems were harvested, leaving a canopy opening of 6 to 12 m². In each block, a canopy gap of 0.05 ha was made in the centre of one subblock per block (n=8), leaving one subplot with a gap and one without a gap per block, for a total of 16 experimental units. All harvesting operations were carried out by manual felling in the fall of 2008.

The *in situ* incubation technique with buried bags was used twice during the season (summer 2009 and fall 2009) to assess net N mineralization and net depolymerization (DEPO) rates following Bélanger et al. (2007). In summer 2009, the first series of incubations started June 8 and finished July 28, while the last series of incubation started on June 16 and finished on August 6. The fall incubation series began at the same time summer incubations finished. During fall, the first series of incubations started on July 28 and finished on October 6, while the last series of incubations started on August 5 and finished on October 9. Within each experimental unit without gaps, two transects of six sampling points spaced 10 m apart were established, while for experimental units with a canopy gap, three sampling points were made 3 m from the centre of the gap at three equally spaced azimuths of 360°, 120° and 240° for the first series of incubations, and at 40°, 160° and 280° for the second series of incubations.

At each sampling point, a pair of samples was taken at 0.75 m on either side of the transect line in subblocks or along the bearing line in gaps. Square samples (width = 17.5 cm) of organic layer were cut and care was taken to delicately remove the litter (L) from the sample to keep the fibric (F) and humic (H) layers only. One soil sample was brought to the laboratory on ice in a cooler while the other was replaced with minimum disturbance in the soil after placing it in a polyethylene bag. The thickness of the F and H layers was measured to the nearest millimetre at the four corners of the square and the sample was placed in a polyethylene bag. In the hole thus created, an 18 cm deep mineral soil core was removed with a soil probe 5 cm in diameter, and the same process was repeated. Finally, the whole set-up was covered with about 2 cm of litter to protect the bag from direct insulation. These samples were left in the forest for incubation for 8 weeks. The plastic bags used for incubations and samples (whirl-pack® by Nasco, Salida, CA) were sterile and were 76.2 µm thick.

Using temperature data loggers (iButton© Temperature Logger, Maxim Integrated, San Jose, CA), soil temperature (5 cm deep in the mineral layer, under the H layer) was measured every 2 h in three control subblocks, three thinned subblocks and three canopy gaps. These data were used to calculate soil daily average temperature and daily temperature variability.

Laboratory analyses

From the time they were removed from the ground, samples were kept cool at around 4°C and processed within 24 h. In the laboratory, each of the samples of known volume were weighed in order to make possible the calculation of the bulk density, then sieved at 6 mm (organic) and 4 mm (mineral). Five grams of dry weight equivalent were placed in a 250 mL Erlenmeyer flask with 50 mL of KCl at 2 M (ratio $m/v = 1/10$). The samples were mixed for 1 h with a wrist-action shaker (Burrell Scientific©, Pittsburgh, PA) and then vacuum-filtered with a Whatman No. 42 filter. The filtered solution was stored in the freezer until NH_4^+ -N, NO_3^- -N and DON contents were analyzed by FIA (Quickchem 8500, Lachat Instruments, Loveland, CO) using the method described by Maynard et al. (2007). To measure DON concentration, samples had been previously placed in contact with an oxidative solution containing persulfate ($\text{K}_2\text{S}_2\text{O}_8$) and boric acid (H_3BO_4) at 121°C and 135 kPa in an autoclave. This has the effect of oxidizing all nitrogen forms until formation of NO_3^- -N, which concentration was determined by FIA (Cabrera and Beare 1993; Chantigny et al. 2007). Net nitrification, ammonification and DEPO rates were calculated as the net change in nitrate, ammonium or DON, respectively, between the pre- and post-incubation samples on an 8-week incubation period basis.

A subsample from the sieved soil was used to measure the pH in water following the method by Hendershot and Lalonde (2007) with a ratio $m/v = 1/2$ for the mineral soil and 1/10 for the organic layer. Another subsample of approximately 10 g was weighed, then dried for 24 h at

65°C for the organic layer and at 105°C for the mineral soil. After cooling in a desicator, another weighing was done in order to determine water content. Total C and N were measured using combustion with an elemental analyzer (ECS 4010, Costech Analytical Technologies, Valencia, CA), with helium as the carrier gas. Control of the system, data acquisition and processing were performed using the EAS32 software (Costech). The standard curve was prepared using the acetanilide standard (Costech) with at least four calibration points in a range of about 0.2 mg to 1.2 mg. Prior to analysis, samples were sieved at 2 mm, finely ground (<100 mesh) and dried all night at 50°C, and then cooled in a desiccator.

Statistical analysis

Soil nitrogen

The effects of treatments on soil N parameters (Table S1) were modeled with mixed ANOVA with three fixed factors of two levels: thinning [THN], comparing thinned (THINNING) and unthinned controls (CONTROLS), gap [GAP], comparing gaps (GAP) with areas outside of gaps, being either thinned or unthinned (FOREST), and season [SN], comparing summer and fall periods and a random factor of eight levels: block [BLOCK(THN)]. To account for repeated measures, we added an autoregressive (AR(1)) correlation structure in the error term ϵ_{ijklm} . The homogeneity of variance and the normality of data were verified and the data were log-transformed when not corresponding to the conditions of the analysis. The package *nlme* (Pinheiro et al. 2012) of the R software version 2.15.1 (R Core Team 2012) was used for the analysis. The model corresponds to the following formula:

$$Y_{ijklm} = \mu + THN_i + GAP_j + SN_k + BLOCK_{l(i)} + (THN*GAP*SN)_{ijk} + \epsilon_{ijklm}$$

where i = presence or absence of thinning (thinning or control);
 j = presence or absence of gap (gap or forest);

k = for concentrations (Y = DON, NH_4 or NO_3): June or August
for fluxes (Y = DEPO, AMO or NIT): June to August or August to October;
and
 l = block number.

Soil physicochemistry

The effect of soil physicochemistry (Table S1) on soil N cycling was analyzed using a canonical redundancy analysis (RDA), an approach that allows ordination of a matrix of N parameters constrained by a matrix of treatments and a matrix of soil physicochemistry parameters. Two partial RDAs were performed for each of the layers, one for the treatment matrix and one for the soil physicochemistry matrix. The factors of the treatment matrix were previously transformed into quantitative variables using Helmert contrasts (Legendre and Anderson 1999; Venables and Ripley 2002). For each of these two partial RDAs, a selection of models using the Akaike information Criterion (AIC) was performed (Godínez-Domínguez and Freire 2003) in order to construct two models that are both explanatory and parsimonious. The final RDA was constructed from all the variables selected by AIC for each of the two partial RDAs.

Finally, variance partitioning allowed us to assess the proportion of the total variance explained by each of the explanatory variables matrices, in the same way as the one common to both matrices (Peres-Neto et al. 2006). The *vegan* package (Oksanen et al. 2012) from the R software version 2.15.1 (R Core Team 2012) was used for these analyses.

Temperature

A limited number of thermal sensors were placed in the experimental site (Fig. 1) to compare soil temperature (T_{mean} and ΔT) between controls, commercial thinnings and canopy gaps using a mixed model for repeated measures. This combination becomes possible and does

not bias the interpretation of results since the interaction GAP*THN is not significant for each of the soil N parameters studied. The analysis, performed with the *nlme* package (Pinheiro et al. 2012) of the R software version 2.15.1 (R Core Team 2012), was done on contrasts of the TREAT factor, comparing controls, thinning and gaps, based on the number of incubation days as the quantitative variable and the block as the random factor with nine levels.

Results

Soluble soil N

In the control, over 80% of the soil extractable N pool ($\text{kg}\cdot\text{ha}^{-1}$) is situated in the mineral layers, and the DON fraction accounts for about 98% of it; NH_4^+ -N accounts for about 2% of it, while NO_3^- -N is almost nonexistent (Table 1). The DON pool decreased significantly in fall compared with summer in the mineral ($p = 0.0017$) and organic layers ($p < 0.0001$), while the NH_4^+ -N pool increased in both layers ($p < 0.0001$) (Tables 1 and 2). Net DEPO rates switched from negative to positive from summer to fall (Table 1), while net ammonification increased in the organic layer only (Table 1). The net ammonification rate was the most important soil net N flux measured in this experiment, averaging 16.9 and 20.4 $\text{kg}\cdot\text{ha}^{-1}$ per 8 weeks in summer and fall, respectively (Table 1).

Treatments had a significant effect on soil N pools and cycling rates in the organic layer (Fig. 2a). Between June and August, DON remained almost stable or weakly increased in GAP while it decreased in FOREST. As a result, in the fall, DON was significantly higher in GAP than in FOREST. DEPO rates did not show any significant difference among treatments, although negative rates were observed, but only in summer in gaps within thinning areas. Net ammonification rate was significantly higher in gaps, even more so during the fall, at the same time NH_4^+ -N concentrations reached significantly higher values in gaps than under forest cover

($p < 0.05$). June measurements showed that gaps already had a higher NH_4^+ -N concentration in the organic layer than in control and thinning areas ($p < 0.05$).

In the mineral layer, DON concentrations decreased in August compared with June in FOREST, whereas no significant difference was observed in GAP (Fig. 2b). This trend in DON pool between June and August was paralleled by net DEPO rates that shifted from negative values in summer to positive values in fall, particularly in forest areas that were thinned, where this shift is significant. Net ammonification was higher in gaps than outside, and this difference increased in fall, especially among gaps made in thinned forests ($p < 0.05$). This resulted in a significant increase in NH_4^+ -N concentration in gaps in August compared with thinning and control areas. The net nitrification rate was consistently higher in gaps compared with non-gaps and this difference increased in fall, especially among gaps in control areas ($p < 0.05$). These dynamics paralleled the NO_3^- -N concentrations that increased in August compared with June, especially in gaps.

Soil physicochemistry

Only a few physicochemical properties (Table 3) met the AIC to be retained in the parsimonious model and were used as inputs for the partial RDA (Table 4). Among these parameters, Z_ORG, DENS and H₂O were retained for the organic layer, and H₂O and PH were retained for the mineral layer. For various treatments, only SN, GAP and their interaction (SNxGAP) were retained for the organic layer, and only the SN and GAP variables were retained for the mineral layer. Based on the AIC and the absence of correlation between THN variables and their interactions with other variables (THNxSN, GAPxTHN or SNxTHNxGAP), THN did not appear to have any effect on N cycling in the context of this study.

The RDA performed for the organic layer (Fig. 3a and b) has three significant axes (RDA1: $p = 0.005$; RDA2: $p = 0.005$ and RDA3: $p = 0.025$) which together explained 58% of the variability (R^2) existing in the relations between N parameters and the soil and treatment variables. Axis 1 expresses a humidity gradient of the sites, from the most xeric, associated with low organic matter thicknesses (Z_ORG) to the left, to more humid sites on the right. This axis also expresses the effect of gaps, which are strongly related to soil humidity (H2O). Axis 2 expresses mainly the season effect (SN) whereas axis 3 is associated with an increasing aeration gradient of the organic layer, as expressed by compacted organic material (DENS) that opposes thicker organic layer (Z_ORG).

Some relationships between variables appeared particularly robust in the ordination space of these three axes. For instance, the position of DON remained near H2O and, to a lesser extent, GAP (Fig. 3a and b), which is congruent with the positive correlation between DON, H2O and GAP. The position of the AMO rate and NH_4^+ -N pool remained positively related to H2O and GAP, and negatively correlated to Z_ORG in both projections (Fig. 3a and b); in addition, the NH_4^+ -N pool was positively correlated to SN and SNxGAP (Table 4). Net DEPO does not appear to be strongly related to any variable except GAP, to which it was weakly negatively correlated ($r = -0.31$; $p = 0.084$).

The RDA performed for the mineral layer (Fig. 3c) had two significant axes (RDA1: $p = 0.005$ and RDA2: $p = 0.005$) explaining 34% of the variance (R^2). The configuration of the vectors at 45° compared with the axes of ordination expresses on the one hand a negative relationship between PH and SN, and on the other hand, a positive relationship between H2O and GAP, which is orthogonal. In this ordination space, DON is close to the variables H2O and PH and opposed to SN, which is congruent with the significant correlations between these variables

(Table 4). The ordination space demonstrated that DEPO was positively related to SN and negatively to PH (Fig. 3c), which was confirmed by a significant correlation (Table 4). In the ordination space, NH_4^+ -N is located between variables SN and GAP, reflecting its positive correlation with these variables and their interaction (GAP $\times$ SN) (Table 4). The position of NO_3^- -N in the ordination reflects the high values observed in gap areas in August (Figs. 2b and 3c), although NO_3^- -N was positively correlated with season only (Table 4).

Globally, the RDA performed for the organic layer explained 37% of data variability (adjusted R^2 , Fig. 3d). Of this explained variability, 28% concerns the soil physicochemistry and 19% the treatments with 10% of overlap. For the mineral layer, it is 46% of the data variability that is explained. Soil physicochemistry explains 34%, treatments 36% and the overlap proportion is 25%.

Temperature

The compilation of temperature variables according to the number of incubation days (Fig. 4) clearly indicates that the average daily temperature of soil was higher in gaps than in controls, and this relationship was observed during summer ($T_5 = 7.098$; $p < 0.001$) and fall ($T_5 = 12.885$; $p < 0.001$) as well. The average daily temperature of soil also tended to be higher in thinnings than in controls, although this difference was less significant in summer ($T_5 = 1.878$; $p = 0.061$) than in fall ($T_5 = 2.992$; $p = 0.003$). However, this temperature difference in thinning compared with control areas decreases towards the end of the fall incubation period ($T_5 = -2.238$; $p = 0.026$).

Daily temperature variation (Fig. 4) was significantly higher in gaps than in controls, as much in summer ($T_5 = 4.714$; $p < 0.001$) as in fall ($T_5 = 6.450$; $p < 0.001$), but this day to night difference decreased towards the end of the fall incubation period ($T_5 = -6.952$; $p < 0.001$).

Discussion

Study site nutritional regime

This study documents some major components of net N turnover during a period that encompasses the growing season and extends into the fall in a northern temperate forest ecosystem. In seasonally cold biomes, up to 40% of annual cumulative gross N mineralization (ammonification + nitrification) and almost 100% of net N mineralization may occur during the growth period (Wu et al. 2012). The net N mineralization rate measured here may poorly represent the gross production of mineral N available for plant-microbe uptake (Vervaeke et al. 2004; Wu et al. 2012). Nevertheless, along with the net depolymerization rate (DEPO), it constitutes a useful index of soil N cycling (Schimel and Bennett 2004) and availability to plants (Farrell et al. 2013; Kranabetter et al. 2007). The overwhelming dominance of DON in the soil's extractable N pool, as observed in other northern forest ecosystems (Kranabetter et al. 2007), suggests that the N mineralization rate is not limited by DON availability and hence by the DEPO rate at our site. However, because DON can play a role in plant nutrition, the rate of DEPO can still be of importance to tree nutrition.

In northern temperate forests, it is mainly the ectomycorrhizae that perform net DEPO (Schimel and Bennett 2004) and they can contribute to N immobilization or to N transfer to their hosts, according to N availability (Averill et al. 2014; Näsholm et al. 2013). When the first incubation started on June 8, the mineral soil had not completely warmed up, barely reaching 6°C on average. At such an early time in the growing season, the proteolytic efficiency of residual

ectomycorrhizal hyphae and extracellular enzymes in the incubation bags might have been reduced (Brzostek and Finzi 2011) at the same time soil microbial biomass was building up (Wu et al. 2012). Therefore, it can be speculated that microbial communities would have immobilized DON at the beginning of summer, hence the negative DEPO, and it is only later that fungal communities and enzymes would have begun to fulfill their proteolytic role and resume a positive DEPO rate.

Effects of silvicultural treatments on the N cycling

Results from this study indicate that thinning had no significant effect on the N cycling parameters assessed, whereas gaps of 500 m² did affect N cycling. This general trend is well depicted by the RDA. It shows a close overlap between sites in control and thinning areas on the left side of the ordination space, and sites in gap areas, which are distinctly positioned on the right side, along with every N cycling parameters assessed here with the exception of DEPO in the organic layer, which remains associated with sites in control and thinning areas. Indeed, the removal of trees in GAP induced an increase in ammonification rates and NH₄⁺-N pools to a level that is not observed in thinning, both in the mineral layers and the forest floor (Fig. 2, Tables 2 and 3). Differences were more apparent in fall than in summer, hence the further distancing of GAP sites from THN sites in the RDA ordination space.

The light effect of thinning on soil N cycling parameters and the most significant one in the gap depicted by the RDA ordinations resemble the situation documented by Prescott et al. (2003) in a study that included thinning and gap. There, the thinning of 30% of trees in a spruce-fir forest resulted in increased mineral N and NH₄⁺-N concentrations in the forest floor and mineral soil, but these increases were accentuated in gaps of 0.1 ha and 1 ha, reaching a significance level only in 1 ha and 10 ha gaps during the second growing season following tree removal. Although

not significant in our experiment, thinning has a stimulating effect on N mineralization in several types of conifer-dominated ecosystems, including Mediterranean (Wic-Baena et al. 2013) and subtropical humid (Oh et al. 2012) pine forests. Under bioclimatic conditions close to those studied here, the thinning of high density (14,000 trees ha⁻¹) regenerating balsam fir stands brought down to 3000 trees ha⁻¹, was associated with a significant increase in the concentration of NH₄⁺-N at the beginning of the first growing season following tree cutting (Thibodeau et al. 2000). The thinning of 30-40% of trees in a mature *Picea* and *Abies* mountainous forest in the fall resulted in a significant increase in mineral N in the soil solution (Baeumler and Zech 1998). For our intermediate-aged stand, a similar percentage of thinning may represent a smaller nutrient input to the soil in the form of foliage or dead roots. Besides mineral N, we report here for the first time some results on the effect of thinning and gap on DON and the DEPO rate of organic matter. While thinning had no effect on DON (Table 1), it is noteworthy that mineral soil DON concentration decreased from June to August only in treatments where a tree cover remained (control and thinning), while net DEPO rates increased, suggesting a heavy use of this N form by soil microbes or plants during the growing season.

Our results indicate that gaps of 500 m² had a significant effect on almost all N cycling parameters analyzed here, the effect of gaps on DEPO being almost significant in mineral (p = 0.08) and organic (p = 0.14) layers. From summer to fall, in the gaps, there was an increase in NH₄⁺-N and NO₃⁻-N mineral soil pools that are paralleled by increased rates of ammonification and nitrification, suggesting that gaps had a stimulating effect on mineral N turnover during the growing season. Because thinnings that create a canopy opening of 6 to 12 m² had no effect on those parameters, this suggests that the minimal size for gaps to have a significant effect on soil N cycling in the study area would be between 12 and 500 m². However, in the range of 25 m² to

590 m², gap size was unrelated to forest floor NH₄⁺-N and NO₃⁻-N leacheates in the northern hardwood forest of Michigan and not different from the control, but this was 6 years following gap formation (Schlieman and Bockheim 2014). The effect of gap on NH₄⁺-N and NO₃⁻-N was not related to their size, which ranged from 230 m² to 1520 m², in forest dominated by *Fagus* (Ritter et al. 2005, Ritter 2005) or Mediterranean *Pinus* (Muscolo et al. 2007). In the gaps of our study site, the net ammonification and net nitrification almost doubled in summer and nearly tripled in fall, although the NO₃⁻-N concentration increased to a detectable level only by the end of the growing season (August). It may be that the latter has been actively sequestered by the profuse growth of two strongly nitrophilous species, namely *Rubus idaeus* (Jobidon 1993) and *Galeopsis tetrahit* (Thimonier et al. 1992), in the gaps of the study area.

Factors involved in the observed changes

Among the environmental factors that vary between treatment conditions, soil humidity and temperature are likely to have a strong influence on N dynamics. An increase in soil humidity following gap creation is the rule in a large variety of forest types (Ritter and Vesterdal 2006; Muscolo et al. 2014). When soil aeration remains adequate (Castellano et al. 2012), there is a correlation between the increase in soil humidity and microbial activity (Barg and Edmonds 1999). In our study, water content is nearly one and a half times higher in gaps than in controls and represents 250% of the organic layer dry weight. Changes in net ammonification, net nitrification and in DON and NH₄⁺-N concentrations in canopy gaps are strongly correlated to an increase in soil water content, which appears to be associated with the gradient control < thinning < gap.

Our results show a significant increase in the soil temperature of canopy gaps and, to a lesser extent, in thinned blocks, compared with control blocks. Several studies have demonstrated

that temperature has a positive effect on some N cycling processes (Brzostek et al. 2012; Guntinas et al. 2012), although there are exceptions (D'Orangeville et al. 2013). Indeed, it is widely recognized that an increase in soil temperature is likely to promote the microbial activity responsible for nutrient cycling, especially net ammonification (Dalias et al. 2002; Grenon et al. 2004). Net DEPO is relatively constant between treatments; it is more or less sensitive to temperature and varies mostly according to the quality of the protein substrate (Brzostek and Finzi 2011), which can be considered rather homogeneous across treatments. In this study, soil temperature and humidity increased to levels that enhanced N cycling, especially in gaps and, to lesser extent, in thinning areas. However, they were not the only factors involved.

Among the other soil physicochemical properties that were analyzed using RDA, thickness of the organic layer, soil density and pH seem to be the variables that have the strongest influence on N dynamics, but these factors act in different layers. In the organic layer, it seems that density and thickness are the factors that best explain the variability measured after the silvicultural treatments. Thick organic layers had a low bulk density. A low bulk density and a greater thickness may provide a greater insulation and lower summer temperatures. Thick organic layers can also indicate a lower organic matter quality (Côté et al. 2000). The negative correlations between Z_ORG and NH_4^+-N or AMO could be related to the low decomposition rate of a thick organic layer. Variance partitioning suggests that treatments explained a similar portion of RDA model variability in the mineral (11%) and organic (9%) layers, while the physicochemistry of soil horizons explained more RDA model variability in the organic (18%) than in the mineral (9%) layer. As a whole, the effects of physicochemical factors on RDA projections were less influenced by treatments in the organic layer (10%) than in the mineral (25%) layer, which

suggests that N dynamics are more profoundly disrupted by thinning and gaps in the mineral than in the organic layer.

Conclusion

In the studied forests, the extractable N pool was largely dominated by DON. Major treatment effects on N cycling occurred only in gaps, while thinning did not cause any significant change. Those changes were reflected primarily by an increase in the mineral forms of N, which appear related to an increase in soil temperature and water content as well as a decrease in uptake by plants, although this last item was not assessed. Thinned sites (without gaps) were similar to controls. The effects of commercial thinning and canopy gaps documented during this study provide a better understanding of how harvest intensity affects soil processes and, incidentally, the growth and establishment of regenerating trees as well as companion or competing species. Although limited to one forest type, this study illustrates that the intensity of biomass removal could have a threshold response pattern for soil processes. The literature suggests that time since disturbance, ecosystem types and intensity of tree removal have an impact on this threshold. The verification of such a threshold in other forest ecosystem types could guide the development of silvicultural systems. Increasing the proportion of mineral N in the soil solution may be desirable or not, depending on the context. A better understanding of the thresholds of tree removal intensity that would create changes in soil N cycling could help to better understand the implication of silvicultural practices that aim to maintain a partial cover.

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Tables

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Table 1. Extractable pools and fluxes of N and total pools of C and N in organic (O) and top 18 cm of the mineral (M) soil with season and canopy treatments. DON: dissolved organic nitrogen DEPO: net depolymerization rate, AMO: net ammonification rate, NIT: net nitrification rate.

		DON pool (kg·ha ⁻¹)			NH ₄ ⁺ -N pool (kg·ha ⁻¹)			NO ₃ ⁻ -N pool (kg·ha ⁻¹)			Total extractable N pool (kg·ha ⁻¹)			
		O	M	O+M	O	M	O+M	O	M	O+M	O	M	O+M	
Summer														
	Forest/control	18.2	108.2	126.3	0.4	2.3	2.7	0.0	0.1	0.0	18.5	110.5	129.1	
	Forest/thinning	20.5	105.9	126.5	0.5	2.5	3.0	0.0	0.1	0.1	21.0	108.5	129.6	
	Gap/control	18.5	136.8	155.3	0.6	4.4	5.0	0.0	0.1	0.1	19.1	141.3	160.3	
	Gap/thinning	20.7	127.5	148.2	0.9	3.3	4.2	0.0	0.0	0.0	21.6	130.8	152.3	
Fall														
	Forest/control	14.8	81.5	96.4	0.4	2.4	2.8	0.0	0.2	0.2	15.3	84.1	99.4	
	Forest/thinning	17.6	83.0	100.6	0.6	3.3	4.0	0.0	0.1	0.1	18.3	86.4	104.7	
	Gap/control	19.9	105.1	125.0	2.9	12.2	15.1	0.0	0.4	0.4	22.8	117.7	140.5	
	Gap/thinning	16.8	107.3	124.2	3.0	15.6	18.6	0.0	0.5	0.6	19.9	123.5	143.4	
		DEPO Net depolymerization (kg·ha ⁻¹ per 8 weeks)			AMO Net ammonification (kg·ha ⁻¹ per 8 weeks)			NIT Net nitrification (kg·ha ⁻¹ per 8 weeks)						
		O	M	O+M	O	M	O+M	O	M	O+M				
Summer														
	Forest/control	3.6	-14.1	-10.5	3.0	6.6	9.6	0.0	1.8	1.9				
	Forest/thinning	6.8	-9.6	-2.8	4.5	6.9	11.4	0.1	2.2	2.3				
	Gap/control	2.0	-0.2	1.8	6.6	16.9	23.5	0.0	3.9	4.0				
	Gap/thinning	3.5	-12.0	-8.6	10.2	12.9	23.1	0.0	5.4	5.4				
Fall														
	Forest/control	5.1	-1.0	4.1	2.9	6.2	9.1	0.0	1.8	1.8				
	Forest/thinning	2.4	0.5	2.9	4.8	9.1	13.9	0.0	2.4	2.4				
	Gap/control	3.7	13.6	17.3	9.5	14.7	24.2	0.0	5.0	5.0				
	Gap/thinning	2.8	15.6	18.4	9.4	25.0	34.5	0.0	5.3	5.4				
		Total N (kg·ha ⁻¹)			Total C (kg·ha ⁻¹)									
		O	M	O+M	O	M	O+M							
Summer														
	Forest/control	542	2 829	3 370	14 275	50 623	64 897							
	Forest/thinning	404	2 013	2 418	10 347	50 617	60 964							
	Gap/control	625	2 543	3 169	17 364	48 273	65 636							
	Gap/thinning	595	2 980	3 575	15 274	55 589	70 863							
Fall														
	Forest/control	530	2 451	2 981	14 025	42 911	56 937							
	Forest/thinning	531	2 628	3 159	12 857	46 510	59 367							
	Gap/control	493	2 754	3 247	13 429	47 822	61 250							
	Gap/thinning	425	4 459	4 884	10 179	41 946	52 125							

Table 2. ANOVA results of the six parameters of the N cycle in organic and mineral layers. DON: dissolved organic nitrogen DEPO: net depolymerization rate, AMO: net ammonification rate, NIT: net nitrification rate.

Dependent variable	Season (SN)		Thinning (THN)		Gap (GAP)		SN * THN		SN * GAP		THN * GAP		SN * THN * GAP	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Organic layer														
DEPO	1.98	0.1608	0.05	0.8286	2.23	0.1368	1.86	0.1746	0.00	0.9543	0.13	0.7184	0.02	0.8641
DON	15.48	0.0001	0.00	0.9651	15.39	0.0001	0.05	0.8222	4.45	0.0362	0.83	0.3624	0.15	0.7023
AMO	5.54	0.0196	3.39	0.1153	57.47	<.0001	1.56	0.2131	0.56	0.4561	1.14	0.2876	0.50	0.4811
NH ₄ ⁺ -N	29.20	<.0001	0.60	0.4679	105.30	<.0001	0.37	0.5416	27.84	<.0001	1.86	0.1747	0.33	0.5665
NIT							Not available							
NO ₃ ⁻ -N							Not available							
Mineral layer														
DEPO	24.63	<.0001	0.21	0.6621	3.10	0.0795	0.43	0.5119	0.00	0.9491	0.24	0.6247	0.23	0.6286
DON	49.44	<.0001	0.12	0.7369	5.14	0.0244	1.15	0.2852	2.02	0.1564	1.60	0.2065	0.38	0.5338
AMO	4.10	0.0440	0.76	0.4171	18.11	<.0001	3.34	0.0691	0.24	0.6255	0.65	0.4193	3.01	0.0843
NH ₄ ⁺ -N	23.35	<.0001	0.32	0.5924	94.79	<.0001	1.20	0.2746	34.33	<.0001	2.49	0.1157	0.00	0.9333
NIT	0.67	0.4117	0.17	0.69	24.72	<.0001	0.28	0.5957	0.14	0.7045	0.00	0.9733	2.00	0.1590
NO ₃ ⁻ -N	62.00	<.0001	0.79	0.4093	7.79	0.0057	1.67	0.1974	16.76	<.0001	0.10	0.7508	0.36	0.5470

Table 3. Mean (standard deviation) of physicochemical parameters of soil based on treatments.

Treatments	Z_ORG (mm)	DENS (mg/cm ³)	H ₂ O (g _{water} /g _{soil})	pH	N% (gN/gsoil)	C% (gC/gsoil)	C:N
Organic layer							
<i>Summer</i>							
forest/control	52.4 (29.9)	122 (64)	1.69 (0.61)	3.6 (0.6)	0.009 (0.005)	0.264 (0.137)	34 (14)
forest/thinning	68.6 (34.4)	135 (84)	1.96 (0.72)	3.8 (0.6)	0.012 (0.004)	0.332 (0.133)	35 (15)
gap/control	53.3 (28.2)	117 (52)	2.27 (0.79)	4 (0.8)	0.01 (0.005)	0.299 (0.153)	33 (11)
gap/thinning	53.5 (16.6)	117 (23)	2.34 (0.51)	3.7 (0.6)	0.012 (0.002)	0.36 (0.097)	34 (7)
<i>Fall</i>							
forest/control	53.9 (37.9)	102 (56)	1.89 (0.65)	2.6 (0.3)	0.015 (0.007)	0.366 (0.109)	30 (8)
forest/thinning	55.3 (30.2)	109 (47)	1.94 (0.69)	2.9 (0.6)	0.013 (0.005)	0.377 (0.123)	34 (7)
gap/control	45.2 (20.8)	112 (37)	2.79 (0.68)	3 (0.3)	0.014 (0.004)	0.379 (0.093)	32 (9)
gap/thinning	41.3 (14.6)	110 (37)	2.56 (0.55)	3.2 (0.3)	0.014 (0.006)	0.327 (0.091)	30 (7)
Mineral layer							
<i>Summer</i>							
forest/control	54.1 (32.2)	1 032 (232)	0.49 (0.11)	3.7 (0.6)	0.004 (0.004)	0.076 (0.104)	22 (7)
forest/thinning	72.4 (38)	1 003 (222)	0.53 (0.12)	3.8 (0.7)	0.003 (0.002)	0.048 (0.022)	21 (6)
gap/control	53.3 (26.9)	1 121 (312)	0.52 (0.09)	3.7 (0.5)	0.002 (0.001)	0.039 (0.016)	19 (7)
gap/thinning	53.7 (15.9)	1 127 (208)	0.47 (0.11)	3.6 (0.8)	0.003 (0.001)	0.037 (0.025)	17 (8)
<i>Fall</i>							
forest/control	53.8 (36.4)	987 (205)	0.48 (0.18)	2.9 (0.5)	0.003 (0.004)	0.033 (0.013)	18 (9)
forest/thinning	52.9 (28.2)	968 (233)	0.44 (0.09)	3 (0.6)	0.002 (0.001)	0.037 (0.017)	19 (4)
gap/control	45.5 (19.9)	1 001 (238)	0.59 (0.17)	3 (0.5)	0.003 (0.001)	0.046 (0.023)	19 (4)
gap/thinning	66.2 (87.4)	1 107 (170)	0.44 (0.05)	3 (0.5)	0.002 (0.001)	0.033 (0.012)	18 (7)

Table 4. Pearson’s correlation coefficients between N cycle parameters, soil physicochemical variables and treatments. DON: dissolved organic nitrogen DEPO: net depolymerisation rate, AMO: net ammonification rate, NIT: net nitrification rate.

	Soil physicochemistry										Treatments ¹							
	Z_ORG	DENS	H ₂ O	pH	Npct	Cpct	CN	SN	THN	GAP	GAPxTHN	GAPxSN	THNxSN	GAPxTHNxSN				
<i>Organic layer</i>																		
DON	-0.11	ns	-0.02	ns	0.62	****	0.20	ns	0.15	ns	-0.02	ns	-0.17	ns	-0.07	ns	-0.14	ns
DEPO	0.22	ns	-0.39	*	-0.18	ns	-0.23	ns	0.00	ns	0.17	ns	0.25	ns	0.04	ns	-0.31	x
NH ₄ ⁺ -N	-0.45	*	-0.15	ns	0.66	****	-0.14	ns	0.26	ns	0.14	ns	-0.20	ns	0.48	**	0.08	ns
AMO	-0.36	*	-0.01	ns	0.40	*	0.05	ns	-0.04	ns	-0.09	ns	-0.06	ns	0.25	ns	0.19	ns
NO ₃ ⁻ -N											Not available							
NIT											Not available							
<i>Mineral layer</i>																		
DON	0.12	ns	0.06	ns	0.55	**	0.42	*	0.03	ns	0.31	x	0.18	ns	-0.59	***	-0.18	ns
DEPO	-0.38	*	0.13	ns	-0.03	ns	-0.57	***	-0.10	ns	-0.20	ns	-0.08	ns	0.56	***	-0.03	ns
NH ₄ ⁺ -N	-0.08	ns	0.01	ns	0.25	ns	-0.14	ns	-0.01	ns	-0.09	ns	-0.26	ns	0.46	**	-0.04	ns
AMO	-0.32	x	0.01	ns	0.18	ns	-0.26	ns	-0.07	ns	-0.05	ns	0.07	ns	0.13	ns	0.15	ns
NO ₃ ⁻ -N	-0.18	ns	-0.31	x	0.34	x	-0.27	ns	0.19	ns	0.14	ns	-0.08	ns	0.63	****	-0.15	ns
NIT	-0.07	ns	0.19	ns	0.17	ns	-0.04	ns	0.02	ns	0.04	ns	-0.09	ns	0.02	ns	0.06	ns

ns : $p > 0.1$ x : $0.5 < p < 0.1$ * : $0.01 < p < 0.5$ ** : $0.001 < p < 0.01$ *** : $0.0001 < p < 0.001$ **** : $p < 0.0001$
¹ The factors of the treatments matrix were previously converted into quantitative variables by performing Helmert contrasts (Legendre and Anderson 1999; Venables and Ripley 2002).

Figures

- Fig. 1.** Map of the experimental site in Blais township.
- Fig. 2.** Concentrations (mg kg^{-1}) and fluxes ($\text{mg kg}^{-1} \text{ day}^{-1}$) of N in organic (A) and mineral (B) layers as a function of seasons, gaps and thinnings. Letters that are different indicate a significant difference (ANOVA, $p < 0.05$). DON: Dissolved organic nitrogen. DEPO: depolymerisation. AMO: net ammonification. NIT: net nitrification.
- Fig. 3.** Canonical redundancy analysis for the organic layer (A: axes 1 and 2, B: axes 1 and 3) and the mineral layer (C: axes 1 and 2) and variance partitioning (D) between the physicochemical variables and the silvicultural treatments for the organic and mineral layers using the adjusted R^2 (Peres-Neto et al. 2006). Dotted lines refer to soil physicochemical variables and solid lines to treatment variables. Within the RDA, polygons correspond to sites (green: controls, blue: thinnings, red: gaps).
- Fig. 4.** Soil temperature at a 5 cm depth in the mineral layer during the summer and fall soil incubation period for different silvicultural treatments (solid line: controls, large dotted line: commercial thinning, thin dotted line: gaps).

A) Organic

B) Mineral

Mineral layer

Variance partitioning (adjusted R^2)

Table S1. Description of variables

Variable	Description
<i>Parameters of the N cycle</i>	
DON	Dissolved organic nitrogen (mg/kg)
DEPO	Net depolymerization rate (mg/kg/8 weeks)
NH ₄ ⁺	Ammonium (mg/kg)
AMO	Net ammonification (mg/kg/8 weeks)
NO ₃ ⁻	Nitrate (mg/kg)
NIT	Net nitrification (mg/kg/8 weeks)
<i>Treatments</i>	
SN	Season (random factor with 2 levels)
THN	Thinning (random factor with 2 levels)
GAP	Gap (random factor with 2 levels)
BLOC	Block (fixed factor with 8 levels)
<i>Soil physicochemistry</i>	
Z_ORG	Depth of the organic layer (cm)
DENS	Sample density (g/cm ³)
H ₂ O	Water content (weight in water/dry weight , expressed in %)
PH	Water pH-H ₂ O
Npct	Total nitrogen (%)
Cpct	Total carbon (%)
CN	Carbon/nitrogen ratio
<i>Temperature</i>	
Tmean	Average daily temperature
ΔT	Daily temperature variation
TREAT	Silvicultural treatment (random factor with 3 levels)

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