

## AN ABSTRACT OF THE THESIS OF

Aaron L. Thiel for the degree of Master of Science in Forest Science presented on March 21, 2008.

Title: Nitrogen Dynamics Across Silvicultural Canopy Gaps in Young Forests of Western Oregon.

Abstract approved:

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Steven S. Perakis

Silvicultural canopy gaps are emerging as an alternative management tool to accelerate development of complex forest structure in young, even-aged forests of the Pacific Northwest. I investigated patterns of nitrogen (N) availability along transects through 0.1 and 0.4 ha silvicultural gaps in three 50-70 year old Douglas-fir forests of western Oregon. Six indices of N availability in forest floor and mineral soil and several factors related to N cycling were measured from November 2005 to February 2007, approximately 6-8 years after gap creation.

Results indicate that mineral soil pools of extractable ammonium ( $\text{NH}_4^+$ ) and nitrate ( $\text{NO}_3^-$ ), rates of net N mineralization and nitrification, and concentrations of ion-exchange resin  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were significantly elevated in gaps relative to adjacent forest. Gap-forest differences in forest floor layers were less clear. For the majority of response variables, magnitudes and trends were similar in the centers of both gap sizes. N availability in gap edge positions more often resembled levels in the

forest than in the gap interior, and there were few significant differences between positions north and south of gap centers. Forest floor and mineral soil percent moisture did not significantly differ along gap transects, nor did decomposition rates of wooden tongue depressors. Litterfall carbon (C) inputs and litterfall C:N ratios in gaps were significantly lower than in the forest. Reciprocal transfer incubations of mineral soil samples between gap and forest positions revealed that sample origin had a significant effect on net nitrification rates, while incubation environment did not. Variability of several indices of N availability also increased in gaps.

The overall increase of N availability in 6-8 year old silvicultural gaps may be due more to the quality and quantity of litterfall inputs than temperature and moisture conditions. Increased quality of litterfall in gaps, as indicated by lower C:N ratios, may increase rates of decomposition and net N mineralization, while overall lower litterfall C inputs may lead to C-limitation of microbial immobilization, resulting in increased accumulation of inorganic N in soil. While environmental factors have been shown to drive N availability soon after gap creation, litter inputs from early-seral species may perpetuate increased N availability into early stages of vegetative succession. From a management perspective, increased N availability in gaps may increase tree productivity, but at the same time, increase the likelihood of invasion by exotic species. Gap creation may also increase gap-scale heterogeneity of available N in the short-term, while increasing stand-scale heterogeneity in the long-term.

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Nitrogen Dynamics Across Silvicultural Canopy Gaps in Young Forests of Western  
Oregon

by  
Aaron L. Thiel

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I understand that my thesis will become part of the permanent collection of Oregon State Libraries. My signature below authorizes release of my thesis to any reader upon request.

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Aaron L. Thiel, Author

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For Mom and Dad...

...and maybe Shannon.

**Nitrogen Dynamics Across Silvicultural Canopy Gaps in Young Forests of  
Western Oregon**

## INTRODUCTION

Nitrogen (N) is widely considered the most critical nutrient that influences the structure and function of forest ecosystems. N is a limiting nutrient in many temperate forests (LeBauer and Treseder 2008), including those of western Oregon (Peterson and Hazard 1990). Subsequently, N availability can affect a wide range of biological factors, including tree growth and structural development (Pastor et al. 1984, Miller 1988), turnover of litter and woody debris (McClaugherty et al. 1985, Gholz et al. 2000), and vegetative (Wallace et al. 2007) and microbial (Carreiro et al. 2000, DeForest et al. 2004) diversity. Clearcutting, a traditional forest management practice, has been shown to increase soil N availability, resulting in the increased production and leaching of soluble nitrate ( $\text{NO}_3^-$ ) that can decrease both water quality and site productivity (Bormann et al. 1974, Vitousek et al. 1979, Feller and Kimmins 1984, Frazer et al. 1990). Understanding the impacts of management practices on N availability can therefore contribute to effective forest ecosystem decision-making.

As management objectives on federal lands of western Oregon shift from timber production to a broader set of goals, new management techniques are emerging. Alternatives to traditional forest practices are being developed to allow timber extraction while maintaining ecosystem viability (Swanson and Franklin 1992). One such practice is the creation of silvicultural canopy gaps in young, even-aged forests. Natural canopy gap formation, caused by the death of one to several hectares of dominant trees, is a major contributor to the structural and spatial heterogeneity in old-growth forests of the Pacific Northwest (Spies and Franklin 1989). By allowing resources such as light and water to penetrate to the understory, canopy gaps promote

the release of suppressed shade-tolerant tree species, thereby increasing species diversity of canopy trees (Spies and Franklin 1989, Spies et al. 1990). They also allow for multiple age classes to develop within a stand, resulting in a multi-storied canopy (Spies and Franklin 1989, Spies and Franklin 1991). By implementing silvicultural canopy gaps, forest managers hope to accelerate the development of old-growth habitat characteristics in stands that are currently dominated by young, even-aged trees.

The effects of canopy gaps on N availability are not fully understood. Small gaps, created by the death or removal of a single tree, have been shown to have little effect on N availability in tropical (Vitousek and Denslow 1986) and temperate coniferous forests (Parsons et al. 1994a, Prescott 1997, Hope et al. 2003, Prescott et al. 2003). Small gaps did, however, increase the net production of  $\text{NO}_3^-$  in a Wisconsin hemlock-hardwood forest (Mladenoff 1987). There is evidence that N availability increases as more adjacent trees are removed. Elevated N availability relative to adjacent forest has been detected in 15- and 30-tree gaps in a Wyoming pine forest (Parsons et al. 1994a), 30 m diameter gaps in a German hardwood forest (Bauhus and Barthel 1995), 0.1 ha gaps in a British Columbia spruce-fir forest (Prescott et al. 2003), and 300-2000  $\text{m}^2$  gaps in Wisconsin hardwood-hemlock forests (Scharenbroch and Bockheim 2007). While these results allude to a consistent increase in N availability in larger gaps, multi-site experimental designs are needed to make informed management decisions across broad geographical regions.

Although several studies have investigated general gap-forest differences in N availability, few have looked at finer-scale patterns of N availability across gaps and



into the adjacent forest. Due to the prevalence of the sun in the southern sky, solar radiation in high latitude forests of the northern hemisphere falls at an angle into gaps (Canham et al. 1990). Interception by trees along southern gap edges causes less radiation to fall on southern portions of gaps than on northern portions (Gray et al. 2002). The position of the sun may also cause more solar radiation to fall into the adjacent forest north of the gap than in the forest south of the gap (Canham et al. 1990, Chen et al. 1995). Elevated incidence of solar radiation can translate to elevated soil temperatures (Gray et al. 2002), which may lead to increased rates of N cycling (Nicolardot et al. 1994, Stark and Firestone 1996). Some studies of available N across gaps in northern temperate forests have detected evidence of increased N availability in northern gap positions and along northern gap edges (Bauhus 1996, Hope et al. 2003), while others have not (Redding 2001). In an old-growth coniferous forest of western Washington, Hayes (2002) saw a significant increase in inorganic N pools going from the south-facing edges of clearcuts into the adjacent forest, but detected no significant edge effects relating to north-facing edges. The existence of north-south available N gradients across gaps and into the adjacent forest could have repercussions on tree and understory species distributions and warrants further study (Ricklefs 1977, Denslow 1980).

Patterns of increased N availability in gaps are often attributed to reduced plant uptake of N and faster rates of decomposition due to warmer and moister soil conditions (Bormann et al. 1974, Vitousek and Matson 1985, Mladenoff 1987, Parsons et al. 1994a). Residual organic matter, such as dead roots, also provide a labile source of N for mineralization (Fahey et al. 1988, Chen et al. 2002). Some

studies suggest, however, that increased N availability in gaps may also be due to carbon (C) limitation of soil microbes resulting from decreased litterfall inputs (Hope et al. 2003, Prescott et al. 2003). Although these mechanisms are not mutually exclusive, further study is needed to understand the relative importance of environmental versus substrate control on N availability in gaps. In addition, most studies focus on changes in N availability for 1-3 years after gap creation, but it is less well understood whether and how changes in N availability persist over longer periods of time.

In the following study, I investigated N availability across two size classes of silvicultural canopy gaps in three young, even-aged forests of western Oregon. Silvicultural canopy gaps in these three sites were established and maintained by the Bureau of Land Management (BLM) as part of their Density Management Study (DMS), which is evaluating the impacts of alternative silvicultural techniques on a range of ecosystem characteristics in young, even-aged stands. My study was focused on four main research questions: 1.) Is there an overall difference in soil N availability between silvicultural canopy gaps and adjacent forest? 2.) Does gap size affect the magnitude of these differences? 3.) Is there a difference in N availability between northern and southern gap and forest positions? 4.) What factors drive patterns of N availability in silvicultural canopy gaps and the adjacent forest? Based on initial patterns in the data, I also performed a post-hoc evaluation of whether variability in available N differed in silvicultural canopy gaps compared to the adjacent forest.

## METHODS

### *Study Sites*

This study was conducted in three sites of the DMS (Cissel et al. 2006). One site (Green Peak) is located in the eastern foothills of the Oregon Coast Range, while the other two (Delph Creek and Keel Mountain) are located in the western foothills of the Oregon Cascades (Figure 2.1). All study sites are in the western hemlock (*Tsuga heterophylla*) forest zone and experience mild, temperate climates (Franklin and Dyrness 1973). Mean annual precipitation at these sites ranges from 1760 mm to 1874 mm, and mean annual minimum and maximum temperature ranges are 3.3-6.5° C and 14.0-17.4° C, respectively (Spatial Climate Analysis Service 2007). Soils at these sites are primarily Andic Dystrudepts derived from both sedimentary and volcanic sources (Soil Survey Staff 1975, 1985, 1987). Table 2.1 provides a summary of general site details, and Table 2.2 provides a summary of physical and chemical properties of forest floor and mineral soil at each site.

All sites were naturally regenerated after clearcutting and are currently dominated by 50-70 year-old Douglas-fir (*Pseudotsuga menziesii* Franco.), with a western hemlock component at Keel Mountain and Delph Creek (Cissel et al. 2006). Between 1998 and 2001, three thinning treatments (100, 200, and 300 trees per ha) were installed at each site, and within the 200 trees per ha treatment, three size classes of circular gaps (0.1, 0.2, and 0.4 ha) were installed by cutting and removing trees and associated logging slash with tractor and cable yarding. Operational constraints of logging determined the specific locations of gaps within a site. Western hemlock, Douglas-fir, western redcedar (*Thuja plicata*), and grand fir (*Abies grandis*) were

underplanted in the gaps approximately one year after gap creation. This study was focused on the 0.1 ha (small) and 0.4 ha (large) gaps.

### ***Study Design***

Three large gaps, three small gaps, and three forest reference plots were chosen at each site. Gaps were chosen based on several criteria: 1.) gaps were able to accommodate transect layout (see below) without encountering obstacles, such as streams, logging roads, and other gaps; 2.) gaps did not contain a major component of nitrogen-fixing plants; and 3.) gaps were not majorly disturbed by management activity (e.g., major soil compaction from logging machinery). Forest reference plots were 10 x 6 m plots placed within the surrounding thinned forest and kept at least 50 m from logging roads, gaps, streams, leave islands, and other thinning treatments.

Transects were run on a north-south bearing through the center point of each gap and continued 40 m from the gap edge into the forest on each side (Figure 2.2). Gap edges were defined as the line between the stems of the two nearest canopy trees along the gap boundary (Runkle 1982). In large gaps, nine 10 x 6 m plots were positioned along transects: one at the gap center (CG), two 20 m in each direction from the gap center (NG and SG), two 40 m from the gap center at the gap edge (NE and SE), two 20 m into the forest matrix (N20 and S20), and two 40 m into the forest matrix (N40 and S40). In small gaps, similar plots were placed at seven points along transects: one at the gap center (CG), two 20 m from the gap center at the gap edge (NE and SE), two 20 m into the forest matrix (N20 and S20), and two 40 m into the

forest matrix (N40 and S40). All plots were placed with their long edges perpendicular to the transect line.

### ***Sample Collection and Chemical Analyses***

#### **Forest Floor Mass and Mineral Soil Bulk Density**

Forest floor mass and mineral soil bulk density were determined at all transect positions in July 2007. Forest floor mass was determined on a composite of two randomly collected 20 x 20 cm samples after discarding freshly-fallen needles and cones, moss, and twigs > 1 cm diameter and drying at 105°C for 48 hrs. Mineral soil bulk density (0-10 cm) was determined from the composite mass of two randomly collected 6 cm diameter soil cores after sieving to 2 mm particle size and correcting for moisture by drying a 10 g subsample at 105°C for 48 hrs. Percent moisture in both forest floor and mineral soil samples were calculated as grams of water per gram of dry sample multiplied by 100. Measures of forest floor mass and mineral soil bulk density were used to convert concentration data into areal pool data.

#### **Available N**

For the purposes of this study, N is considered “available” if it is in forms and concentrations utilizable by plants (Bundy and Meisinger 1994). Inorganic N was considered the dominant form of plant available N, although evidence exists that some species of the Pacific Northwest can obtain smaller amounts of N directly from organic N compounds (Bennett and Prescott 2004). Several indices of N availability exist, each with advantages and disadvantages. In this study, I utilized extractable

inorganic N pools, rates of net N mineralization and nitrification, and ion-exchange resins (IER) as indices of N availability. Pools of extractable inorganic N provide a direct assessment of available N in soil at a single point in time, but can vary greatly both spatially and temporally and may overestimate the amount of N actually available to plants (Hart et al. 1994b). Net N mineralization and nitrification rates, which measure the net accumulation of inorganic N over time in the absence of plant roots, indicate the ability of soil to provide inorganic N to plants and are especially useful if measured *in situ* because they incorporate the effects of site temperature on microbial activity (Binkley and Hart 1989). IER provide a passive means to measure available N content in soil water. As soil water passes near the positive and negative exchange sites on IER,  $\text{NH}_4^+$  and  $\text{NO}_3^-$  ions adsorb and provide a relative index of available N integrated over time. IER inorganic N concentrations are considered a biologically meaningful measure of available N because most plants obtain nutrients from soil water, and they incorporate the effects of soil moisture, temperature, and microbial immobilization (Binkley 1984, Johnson et al. 2005). IER may also provide an index of possible N loss via leaching. Interpreted together, these indices of N availability provide a more complete picture of N cycling in soil.

#### *Extractable Inorganic N Pools and Net N Mineralization and Nitrification*

In both forest floor and mineral soil, extractable inorganic N pools and rates of net N mineralization and nitrification were determined at all transect positions in February, May, and August 2006 using buried-bag incubations (Eno 1960, Hart et al. 1994b). Two forest floor samples from each position were randomly collected using

30 cm x 30 cm square templates, with one half of each sample composited in a Ziploc bag for initial extractable N. The other half of each sample was sealed in a gas-permeable polyethylene bag and pinned in place near where it was collected. After a 28-day incubation, samples were collected, composited, and stored at 4° C for up to one week until processing. Gravimetric percent moisture was determined as above, and a sample of field-moist forest floor equivalent to 2.5 g dry weight was extracted with 35 mL of 0.5 M K<sub>2</sub>SO<sub>4</sub> for one hour on a shaker table and centrifuged at 5000 rpm for five minutes. The supernatant was then passed through a pre-rinsed filter (Whatman #20) and frozen until analysis.

Net N mineralization and nitrification in 0-10 cm mineral soil were determined from four randomly collected 3 cm diameter polyethylene soil cores at each transect position. Two of the cores were composited to determine initial extractable inorganic N. The remaining two cores were kept in their sleeves, sealed in gas-permeable polyethylene bags, incubated in their original holes for 30 days, and composited upon collection. Both initial and incubated samples were processed within 72 hrs of collection. Samples were sieved to 2 mm particle size, and gravimetric percent moisture was determined as above. A 7 g subsample was extracted with 35 mL of 0.5 M K<sub>2</sub>SO<sub>4</sub> on a shaker table for one hour, and after allowing the solution to settle for 40 minutes, the supernatant was filtered and frozen until analysis.

A series of transfer incubations were conducted on forest floor and 0-10 cm mineral soil collected from gap centers and forest positions 40 m south of gaps. Samples from gap centers were transferred to forest positions and vice versa, where

they were incubated, collected, and processed in the same manner as buried bag incubations described above.

Concentrations of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in forest floor and mineral soil extracts and extraction blanks were analyzed colorimetrically using a Lachat QuikChem 8000 flow-injection autoanalyzer (QuikChem Methods 12-107-06-2-E and 12-107-04-1-H, Lachat Instruments, Milwaukee, WI, USA). Extractable  $\text{NH}_4^+$  and  $\text{NO}_3^-$  pools were determined from initial extracts. Net N mineralization was calculated by subtracting  $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$  in initial extracts from incubated extracts, and similarly, net nitrification was calculated by subtracting  $\text{NO}_3^-\text{-N}$  in initial extracts from incubated extracts. Percent nitrification was calculated as the proportion of mineralized N that was nitrified during each incubation period, restricted to the range 0-100%.

### *Ion Exchange Resins*

Two ion-exchange resin (IER) bags were randomly deployed in six-month intervals from November 2005 until November 2006 at both the soil-forest floor interface and 10 cm mineral soil depth at all transect positions. IER bags were constructed of 7 cm of nylon stocking filled with 7 g (wet weight) cation-exchange resin (Dowex Marathon C-211, Dow Chemical Company, Midland, MI, USA) and 7 g (wet weight) anion-exchange resin (Dowex Marathon A, Dow Chemical Company, Midland, MI, USA). Before deployment, all IER bags were rinsed first with 10% HCl, then five times with Nanopure water, and finally once with 2 N NaCl. IER bags placed at the mineral soil-forest floor interface were laid flat and covered with forest floor. IER bags placed at 10 cm depth were inserted into a 45 degree slit created in the



mineral soil by a flat shovel. After incubation, IER bags were retrieved and stored at 4° C until processing.

In the laboratory, IER bags were carefully rinsed once with Nanopure water to remove soil and debris from the nylon. Bags that had lost >5% of resin by wet weight were discarded. Both IER bags from each sampling depth were placed in a single specimen cup and extracted with 100 mL of 2 M KCl for one hour on a shaker table. The supernatant was filtered, collected in 20 mL polyethylene vials, and frozen until analysis. Concentrations of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in IER extracts and sample blanks were analyzed colorimetrically using a Lachat QuikChem 8000 flow-injection autoanalyzer (QuikChem Methods 12-107-06-2-E and 12-107-04-1-H, Lachat Instruments, Milwaukee, WI, USA).

### **Extractable DOC and DON Pools**

Initial mineral soil extracts from the buried bag incubations were also analyzed for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) using a Shimadzu TOC-V CSH total organic carbon analyzer with a TNM-1 total nitrogen unit (Shimadzu Scientific Instruments, Columbia, MD, USA). Dissolved organic nitrogen (DON) was calculated by subtracting inorganic N from TDN.

Microbial biomass C and N in initial mineral soil samples from the buried bag incubations were determined using chloroform fumigation-direct extraction (Brookes et al. 1985). A 10 g subsample was weighed into an open 60 mL vial and placed in a dessicator containing moist paper towels and a flask filled with 50 mL of chloroform ( $\text{CHCl}_3$ ). The dessicator was evacuated four times with a motorized pump, sealed

under vacuum, and stored in the dark at room temperature ( $\sim 20^{\circ}\text{C}$ ). After 24 hours, the dessicator was vented to the atmosphere for 10 minutes. The samples were then extracted and analyzed as previously described for DOC and TDN. Microbial biomass C and N were calculated by subtracting DOC and TDN in unfumigated samples from fumigated samples. No correction factor was applied, so these values represent chloroform-labile microbial C and N.

### **Total Soil C and N**

Total soil C and N were determined on the same forest floor and mineral soil samples collected for initial extractable N from the buried bag incubations. 10 g subsamples were dried at  $65^{\circ}\text{C}$  for 48 hours, ground to fine powder on a roller mill, and analyzed on a Costech ECS-4010 elemental combustion analyzer (Costech Analytical, Valencia, CA, USA) against an atropine standard.

### **Litterfall C and N**

Freshly-fallen litter from each transect position was collected and analyzed to determine percent C and N of litterfall and C and N fluxes in litterfall. From November 2005 until February 2007, litterfall was collected and composited bi-monthly from two traps placed randomly within each plot. Traps were 37 x 25 x 14 cm plastic baskets fitted with 1.4 mm mesh netting. Traps were placed  $>1$  m from tree stems and adjusted so openings were level with the horizontal. To estimate litter inputs from plants that traps were covering, an area equal to the upper trap opening was flagged adjacent to each trap. During each collection, litter from each trap and

any plant material that had grown out of and died in the adjacent flagged area was removed, stored in paper bags, dried at 65°C for 48 hours, weighed, and subsampled for total C and N analysis, as described above. C and N fluxes in litterfall were calculated by multiplying the percent C and N values by the litterfall rate in each plot.

### **Decomposition**

To provide an index of decomposition, wooden tongue depressors (*Betula spp.*) were incubated in each plot from December 2005 to November 2006. First, all tongue depressors were dried at 105°C for 48 hours and weighed. Then, four tongue depressors were placed in the center of each plot at the soil-forest floor interface and covered with forest floor. After 90, 180, 270, and 330 days, a single tongue depressor was collected from each plot, rinsed of soil and debris, dried at 105°C for 48 hours, and reweighed. Percent mass loss of the last tongue depressor collected was calculated by dividing the post-incubation mass by the pre-incubation mass, subtracting the quotient from 1, and multiplying the difference by 100. Decomposition rate constants (k-values) were determined with the following model (Olsen 1963):

$$[1] \quad Y_t = Y_0 e^{-kt}$$

Where:

$Y_t$  = post-incubation mass

$Y_0$  = pre-incubation mass

$k$  = decomposition constant

$t$  = incubation time in years

Using data from the four tongue depressors incubated in each plot,  $k$  was calculated as the negative slope of the linear regression of the natural logarithm of percent mass remaining versus time. The resulting units were percent mass remaining  $\cdot \text{yr}^{-1}$ .

### **Temperature**

From January 2006 to January 2007, HOBO H8 Pro Series dual-channel temperature loggers (Onset Computer Corporation, Bourne, MA, USA) were deployed at each transect position across one large and one small gap at Keel Mountain. Each logger had an internal sensor in the main device body and another external sensor at the end of a flexible cord. The main body of the logger was fastened to a wooden stake at the center of the plot and buried in forest floor, while the external sensor was buried at a 10 cm mineral soil depth nearby. Hourly temperature data was downloaded from the loggers after 180 and 360 days in the field using a HOBO Shuttle data transporter (Onset Computer Corporation, Bourne, MA USA). BoxCar Pro 3.6 software (Onset Computer Corporation, Bourne, MA USA) was used to download the data from the data transporter and convert it into spreadsheets.

### ***Statistics***

To determine the effects of transect position on response variables, a blocked by site analysis of variance (ANOVA) with repeated measures in space (PROC MIXED in SAS 9.1) was used with the model:

$$[2] \quad Y_{ijk} = \mu + \beta_i + \lambda_{ij} + P_k + \varepsilon_{ijk}$$

Where:

$\mu$  = overall mean value of Y

$\beta_i$  = random effect due to site

$\lambda_{ij}$  = random effect due to variation among transects within site

$P_k$  = fixed effect due to position along transect

$\varepsilon_{ijk}$  = random effect due to variation among positions within transects,

where  $\varepsilon_{ijk} \sim \text{Multivariate Normal } (0, \Sigma)$ , and  $\Sigma$ =covariance matrix

Several structures exist for the above covariance matrix (Figure 2.3), so the Akaike Information Criteria (AIC, Akaike 1974) was used to determine which model best fit the data. Large and small gaps were analyzed separately. If position effect was significant, two sets of planned comparisons were made. The first was an environmental comparison, in which positions were grouped by environment (gap, edge, and forest) and all possible pair-wise comparisons were made between group means. The second set was a north-south position comparison, in which all positions equidistant from the gap center but in opposite direction along the transect (GN and GS in large gaps; NE and SE; N20 and S20; and N40 and S40) were compared. In large gaps, two additional comparisons were made between CG and the two other gap interior points, GN and GS. All comparison p-values were Bonferroni-adjusted.

The effects of gap size on response variables were determined by comparing values in large and small gap centers using a blocked by site ANOVA (PROC MIXED in SAS 9.1) with the model:

$$[3] \quad Y_{ijk} = \mu + \beta_i + \lambda_{ij} + S_k + \varepsilon_{ijk}$$

Where:

$\mu$  = overall mean value of Y

$\beta_j$  = random effect due to sites

$\lambda_{ij}$  = random effect due to variation among transects within site

$S_k$  = fixed effect due to gap size

$\varepsilon_{ijk}$  = residual error

The effects of incubation environment and sample origin on net N mineralization and nitrification rates in the transfer incubation experiment were determined using a blocked by site split plot ANOVA (PROC MIXED in SAS 9.1) with the model:

$$[4] \quad Y_{ijkl} = \mu + \beta_i + \lambda_{ij} + I_k + O_{kl} + \varepsilon_{ijkl}$$

Where:

$\mu$  = overall mean value of Y

$\beta_i$  = random effect due to sites

$\lambda_{ij}$  = random effect due to transects within sites

$I_k$  = fixed effect due to incubation environment

$O_{kl}$  = fixed effect due to sample origin within incubation environment

$\varepsilon_{ijkl}$  = residual error

If overall fixed effects for incubation environment were significant, pair-wise comparisons were made between samples originating from the same position but incubated at different positions. If overall fixed effects for sample origin were significant, pair-wise comparisons were made between samples originating from different positions but incubated at the same position. All comparison p-values were Bonferroni-adjusted.

Both standard deviations and coefficients of variation of replicates within sites were used to quantify variability of available N indices at each transect position. A blocked by site ANOVA (PROC MIXED in SAS 9.1) with repeated measures in space was then used to determine the effect of transect position on these measures of variability using the model:

$$[5] \quad Y_{jk} = \mu + \beta_i + P_j + \varepsilon_{jk}$$

Where:

$\mu$  = overall mean value of Y

$\beta_i$  = random effect due to site

$P_j$  = fixed effect due to position along transect

$\varepsilon_{ij}$  = random effect due to variation among positions within transects,

where  $\varepsilon_{ij} \sim \text{Multivariate Normal } (0, \Sigma)$ , and  $\Sigma$ =covariance matrix

AIC was used to select the best-fit model. If the position effect was significant, positions were grouped by environment, as above, and all pair-wise comparisons were made between group means. Comparison p-values were Bonferroni-adjusted.

All statistical analyses were performed using SAS version 9.1 (SAS Institute Inc. 2003). Analyses were focused mainly on data averaged across all collection periods, and analyses of individual collection periods, presented in Appendix Tables A1-A6, are considered as needed to interpret average responses. Average individual site data are also available in Appendix Tables B1-B6. Prior to analysis, data was checked for normality and equal variance; log transformations were made as necessary. For datasets that required log transformation and contained negative or zero values, a sufficient constant was added to all pre-transformed to make all values within the dataset positive. After analysis and back-transformation, the constant was subtracted from all estimates of medians (Field 2005). P-values of  $\leq 0.05$  were considered significant, and p-values  $> 0.05$  but  $\leq 0.10$  were considered marginally significant. In general, ANOVA results of net N mineralization and nitrification, extractable C and N, and total C and N were nearly identical whether expressed on a soil concentration or pool basis, so data presentation and discussion will focus on only pool data.



## RESULTS

### *Transect Position Effects on Response Variables*

#### **Forest Floor Mass, Mineral Soil Bulk Density, Percent Moisture, and Total Soil C and N**

There was a significant position effect on forest floor mass only along large gap transects (Table 3.1, Figure 3.1), where values in gaps positions were 61% lower than in forest positions ( $t_{16}=3.88$ ,  $p=0.001$ ) and a marginally significant 35% lower than in edge positions ( $t_{16}=2.06$ ,  $p=0.056$ ). All north-south comparisons were non-significant. The position effect on mineral soil bulk density was not significant along transects of either gap size (Table 3.2). The position effect on percent moisture in both forest floor (Table 3.1) and mineral soil (Table 3.2) was not significant along transects of either gap size. Position effects on total C, total N, and C:N ratios in forest floor and mineral soil were all non-significant (Tables 3.1 and 3.2).

#### **Extractable Inorganic N Pools**

Inorganic N pools in forest floor and mineral soil were strongly dominated (> 90%) by  $\text{NH}_4^+$  at all transect positions. In forest floor, the only significant position effect was on  $\text{NO}_3^-$  pools along small gap transects (Table 3.1, Figure 3.2). Planned comparisons, however, were all non-significant. In mineral soil, position effects on  $\text{NH}_4^+$  pools along both gap sizes were significant (Table 3.2, Figure 3.3). Values in large gap positions were 72% greater than in edge positions ( $t_{16}=3.76$ ,  $p=0.002$ ) and 96% greater than in forest positions ( $t_{16}=4.87$ ,  $p<0.001$ ). Similarly,  $\text{NH}_4^+$  pools in small gap positions were 146% greater than in edge positions ( $t_{12}=6.14$ ,  $p<0.001$ ) and

188% greater than in forest positions ( $t_{12}=6.27$ ,  $p<0.001$ ). Position effects on mineral soil  $\text{NO}_3^-$  pools were significant along both large and small gap transects (Table 3.2, Figure 3.4). In large gaps,  $\text{NO}_3^-$  pools in gap positions were 154% greater than in edge positions ( $t_{16}=3.35$ ,  $p=0.004$ ) and 158% greater than in forest positions ( $t_{16}=4.07$ ,  $p=0.001$ ), and in small gaps,  $\text{NO}_3^-$  pools in gap positions were 480% greater than in edge positions ( $t_{12}=5.84$ ,  $p<0.001$ ) and 422% greater than in forest positions ( $t_{12}=5.1035$ ,  $p<0.001$ ). For mineral soil  $\text{NH}_4^+$  and  $\text{NO}_3^-$  pools along transects of both gap sizes, all north-south comparisons were non-significant.

### **Net N Mineralization and Nitrification**

In forest floor, position effects on net N mineralization and nitrification and percent nitrification were non-significant along transects of both gap sizes (Table 3.1). In mineral soil, however, there were several significant position effects on the same variables along transects of both gap sizes (Table 3.2; Figures 3.5-3.7). Along large gap transects, net N mineralization in gap positions was 109% greater than in forest positions ( $t_{16}=2.38$ ,  $p=0.030$ ), but not significantly different from edge positions ( $t_{16}=1.73$ ,  $p=0.104$ ). In large gaps, net nitrification in gap positions was 400% greater than in edge and forest positions ( $t_{16}=5.05$ ,  $p<0.001$ ;  $t_{16}=4.25$ ,  $p=0.001$ ), while along small gap transects, net nitrification in gap positions was 1119% greater than in edge plots ( $t_{12}=3.27$ ,  $p=0.007$ ) and 560% greater than in forest plots ( $t_{12}=2.86$ ,  $p=0.014$ ). Additionally, net nitrification rates in center gap positions of large gaps were 3% greater than in north gap positions ( $t_{12}=2.25$ ,  $p=0.039$ ) and 4% greater than in the south gap positions ( $t_{12}=3.10$ ,  $p=0.007$ ). In large gaps, percent nitrification in gap

positions was significantly greater than in edge ( $t_{16}=4.35$ ,  $p=0.001$ ) and forest positions ( $t_{16}=3.37$ ,  $p=0.004$ ), and in small gaps, percent nitrification in gap positions was also significantly greater than in both edge ( $t_{12}=2.53$ ,  $p=0.027$ ) and forest positions ( $t_{12}=3.08$ ,  $p=0.009$ ). All north-south comparisons of net N mineralization and nitrification and percent nitrification along transects of both gap sizes were non-significant.

### **Ion Exchange Resins**

In forest floor, significant position effects on IER  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations were detected only along transects of large gaps (Table 3.1; Figures 3.8-3.9). IER  $\text{NH}_4^+$  concentrations in gap plots were 22% greater than in edge plots ( $t_{16}=2.86$ ,  $p=0.01$ ) and 35% greater than in forest plots ( $t_{16}=4.59$ ,  $p<0.001$ ), but all north-south position comparisons were non-significant. All planned comparisons of IER  $\text{NO}_3^-$  concentrations along large gap transects were non-significant.

In mineral soil, significant position effects on IER  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations were detected along transects of both gap sizes (Table 3.2; Figures 3.10-3.11). Along large gap transects, IER  $\text{NH}_4^+$  concentrations in gap positions were 104% greater than in edge positions ( $t_{16}=2.50$ ,  $p=0.024$ ) and 169% greater than in forest positions ( $t_{16}=4.30$ ,  $p=0.001$ ), while along small gap transects, IER  $\text{NH}_4^+$  concentrations in gap positions were 386% greater than in edge positions ( $t_{12}=3.21$ ,  $p=0.007$ ) and 436% greater than in forest positions ( $t_{12}=3.58$ ,  $p=0.004$ ). All planned comparisons of IER  $\text{NO}_3^-$  concentrations along large gap transects were non-significant. Along small gap transects, IER  $\text{NO}_3^-$  concentrations in gap positions were

24 times greater than in edge plots ( $t_{12}=4.97$ ,  $p<0.001$ ) and 20 times greater than in forest plots ( $t_{12}=6.67$ ,  $p<0.001$ ). All north-south position comparisons of mineral soil IER  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations were non-significant.

### **Extractable DOC and DON Pools**

In mineral soil, there was not a significant position effect on most DOC and DON pools along transects of either gap size (Table 3.2). The exception was DON pools along small gap transects (Figure 3.12), where pools in gap positions were 49% greater than in forest positions ( $t_{12}=2.29$ ,  $p=0.036$ ), but not significantly different from edge positions ( $t_{12}=1.09$ ,  $p=0.292$ ). Additionally, DON in forest positions 40 m north of gaps were 33% lower than in forest positions 40 m south of gaps ( $t_{12}=-2.25$ ,  $p=0.044$ ).

While there was not a significant position effect on microbial C and N pools in mineral soil along transects of either gap size (Table 3.2), microbial biomass C:N ratios were significantly lower in gap positions than in edge and forest positions along transects of both gap sizes (Table 3.2; Figure 3.13). North-south comparisons, however, were non-significant.

### **Litterfall C and N**

Position effects were significant for litterfall C fluxes in both gap sizes and litterfall N fluxes in large gaps (Table 3.3; Figures 3.14-3.15). Litterfall C flux in large gap positions were 53% lower than in edge positions ( $t_{16}=-3.01$ ,  $p=0.008$ ) and 146% lower than in forest positions ( $t_{16}=-7.03$ ,  $p<0.001$ ). Additionally, edge positions

had 60% lower total litterfall C flux than forest positions ( $t_{16}=-4.55$ ,  $p<0.001$ ).

Litterfall C flux in small gap and edge positions were 70% ( $t_{12}=-3.30$ ,  $p=0.006$ ) and 38% ( $t_{12}=-3.13$ ,  $p=0.009$ ) lower than in forest positions, respectively, but were not significantly different from each other ( $t_{12}=-1.17$ ,  $p=0.264$ ). Litterfall N flux in large gap and edge positions were 90% ( $t_{16}=5.62$ ,  $p<0.001$ ) and 63% ( $t_{16}=5.97$ ,  $p<0.001$ ) lower than in forest positions, respectively, but not significantly different from each other ( $t_{16}=1.27$ ,  $p=0.222$ ). All north-south comparisons of litterfall C and N flux were non-significant.

There was a significant position effect on litterfall percent N only along small gap transects (Table 3.3; Figure 3.16), where values in gap positions were 37% greater than in edge positions ( $t_{12}=5.04$ ,  $p<0.001$ ) and 40% greater than in forest positions ( $t_{12}=5.89$ ,  $p<0.001$ ). There were no significant north-south position differences. Along transects of both gap sizes, there was a significant position effect on litterfall C:N ratios (Table 3.3; Figure 3.17). C:N ratios were lower in gap positions than in edge (large gaps:  $t_{16}=-3.72$ ,  $p=0.002$ , small gaps:  $t_{12}=-4.11$ ,  $p<0.001$ ) and forest (large gaps:  $t_{16}=-5.23$ ,  $p<0.001$ , small gaps:  $t_{12}=-6.12$ ,  $p<0.001$ ) positions, but north-south comparisons were all non-significant.

### **Decomposition Rates**

In most cases, there was not a significant position effect on decomposition of tongue depressors along transects of either gap size (Table 3.3). The exception was a marginally significant position effect on decomposition constants along small gap transects (Table 3.3; Figure 3.18), where values in gap positions were 123% greater

than in edge positions ( $t_{12}=2.32$ ,  $p=0.039$ ) and 120% greater than in forest positions ( $t_{12}=2.97$ ,  $p=0.012$ ). The determination coefficients ( $R^2$ ) of the regressions for decomposition constants ranged from 0.05 to 0.99 along large gap transects and from 0.34 to 0.99 along small gap transects.

### **Temperature**

Over the course of the study, mean daily temperatures and mean daily minimum temperatures in forest floor did not vary greatly along the large or small gap transect, while mean daily maximum temperatures showed more of a partitioning between gap and forest plots (Figure 3.19). This difference was greater along the large gap transect. Along the small gap transect, there was 5°C difference between plots at the cooler south edge and the warmer north edge. Similar north-south differences were not seen in the large gap. Mean daily mineral soil temperatures showed little variation across either the small or large gap transect (Figure 3.19). The range between mean daily minimum and maximum temperatures was smaller than in the forest floor, yet mineral soil mean daily temperatures were only approximately 1°C lower than in the forest floor.

### ***Gap Size Effects on Response Variables***

There were few significant differences in forest floor, mineral soil, litterfall, or decomposition response variables between large and small gap centers (Table 3.4). Forest floor C:N ratios were the only exception, where ratios in large gap centers were marginally significantly lower than in small gap centers ( $F_{1,2}=15.50$ ,  $p=0.059$ ). In

several cases, however, response variables tended to be greater in the center of small gaps than in large gaps, despite the lack of statistical differences. In terms of available N,  $\text{NO}_3^-$  pools, net nitrification rates, and IER  $\text{NO}_3^-$  concentrations were elevated in small gaps relative to large gaps. A similar pattern was also detected in litterfall C and N and decomposition constants.

### ***Mineral Soil and Forest Floor Transfer Incubations***

In transfer incubations of forest floor material between gap centers and forest positions, neither site of sample origin nor incubation environment had a significant effect on net N mineralization or nitrification rates (Table 3.5). In mineral soil, site of origin did have a significant effect on net nitrification, but not on net N mineralization (Table 3.5, Figure 3.20). In the centers of both large and small gaps, net nitrification of samples collected and incubated *in situ* was over 8 times greater than of samples transferred from forest to gaps (large gaps:  $t_4=3.18$ ,  $p=0.033$ , small gaps:  $t_4=3.41$ ,  $p=0.03$ ). In forest positions of large gap transects, net nitrification was a marginally significant 4.8 times greater in samples transferred from the gap than in samples collected and incubated *in situ* ( $t_4=2.38$ ,  $p=0.08$ ). In forest positions of small gap transects, net nitrification rates were 4.3 times greater in transferred gap samples than in samples collected and incubated *in situ* ( $t_4=3.00$ ,  $p=0.04$ ).

### ***Transect Position Effects on Variability of N Availability***

In several cases, the standard deviations of available N response variables were greater in gaps than in the forest (Table 3.6). In forest floor, there was a significant

position effect on the standard deviations of inorganic N pools in small gaps and a marginally significant effect on the standard deviations of net N mineralization and nitrification rates in large gaps. Multiple comparisons showed that in each case, standard deviations in gaps were significantly greater than in the adjacent forest. In mineral soil, there was a significant position effect on the standard deviations of net N mineralization and IER  $\text{NH}_4^+$  concentrations in large gaps and  $\text{NO}_3^-$  pools and net nitrification in small gaps. Marginally significant position effects were detected on standard deviations of net N mineralization rates and IER  $\text{NH}_4^+$  concentrations in small gaps. As in the forest floor, most multiple comparisons between environmental group means showed that standard deviations of mineral soil N availability were greater in gaps than in the forest.

There was not a significant position effect on the coefficients of variation of most forest floor and mineral soil available N response variables (Table 3.7). Mineral soil  $\text{NO}_3^-$  pools and net nitrification rates in small gaps were the only exceptions, and in both cases, coefficients of variance in gaps were greater than in the adjacent forest.



## DISCUSSION

### *Patterns of N Availability Across Gaps*

Differences in N availability between gaps and the adjacent forest were most prevalent in the surface mineral soil, with fewer differences observed in the forest floor. For the most part, mineral soil inorganic N pools, net N mineralization and nitrification, and IER inorganic N concentrations were significantly greater in gaps than in the adjacent forest. The only exception was net N mineralization along small gap transects, where values were four-fold elevated in gap plots, but not significantly different from forest values. Mineral soil N availability along gap edges most often resembled levels in the forest. Results of this study are, for the most part, in accordance with several other studies investigating N availability in silvicultural gaps. Parsons et al. (1994a) detected increases in  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations and net N mineralization and nitrification rates in 15- and 30-tree gaps 1-3 years after gap creation in a Wyoming lodgepole pine (*Pinus contorta* ssp. *Latifolia* [Engelm. Ex Wats.] Critchfield) forest. Bauhus and Barthel (1995) saw a significant increase in net N mineralization in the center of 30 m-diameter gaps relative to adjacent forest one year after gap creation in a German beech (*Fagus sylvatica*) forest. One year later, however, net N mineralization in gaps was significantly lower than in the forest. Prescott et al. (2003) observed initial increases in  $\text{NH}_4^+$  pools followed by increases in  $\text{NO}_3^-$  pools in 0.1, 1, and 10 ha gaps created in a high-elevation Engelmann Spruce (*Picea engelmannii* Parry ex. Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forest of British Columbia. In contrast, Hope et al. (2003) did not see consistent differences in mineral soil inorganic N concentrations between 1.7 ha gaps and uncut

forest 2-7 years after gap creation in a British Columbia Douglas-fir forest, possibly due to low treatment replication. In general, there seems to be a consistent gap-forest difference in short-term (1-8 years after gap creation) mineral soil N availability across a range of systems.

Significant differences in forest floor N availability were found along only large gap transects, where IER  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations in gaps were elevated relative to the adjacent forest. Several studies from British Columbia report evidence of increased N availability in gap forest floors. Redding (2001) observed higher forest floor  $\text{NO}_3^-$  concentrations in a 1 ha gap than in the adjacent forest, but differences in  $\text{NH}_4^+$  concentrations and net N mineralization were less consistent and highly variable. Similar to their findings in mineral soil, Prescott et al. (2003) observed a short-term increase in forest floor  $\text{NH}_4^+$  concentrations in 0.1, 1, and 10 ha gaps soon after gap creation, followed by an increase in  $\text{NO}_3^-$  concentrations several years later. Over a 5 year period, Hope et al. (2003) detected an inconsistent trend of increased  $\text{NO}_3^-$  concentrations in the forest floor of 1.7 ha gaps. I expected to see relatively greater differences in forest floor than mineral soil response variables across gaps, because the forest floor is often considered more responsive to perturbations than mineral soil (Currie 1999). A possible reason for the lack of definitive differences may be the relatively high C:N ratios of forest floor material. The mean C:N ratio of forest floor along transects of both gap sizes was approximately 48, which is well above the critical ratio ( $\sim 30$ ) for net N mineralization (Chapin et al. 2002). With plentiful C available, mineralized N may have been immobilized by microbes. In contrast, the average mineral soil C:N across sites was 30, close to the critical ratio for

net N mineralization. The relatively stronger response of mineral soil than forest floor N cycling to gap creation may be explained if the C:N of belowground litter inputs across transects resembles patterns observed in aboveground litterfall (Newman and Hart 2006), thus depositing relatively N-rich litter into mineral soils that are already close to the critical C:N for net N mineralization. Regardless of the mechanism, my work supports the idea that belowground processes associated with roots and mycorrhizae are more important mediators of forest responses to gap creation than generally recognized (Parsons et al. 1994b).

For the most part, magnitudes of N availability in large and small gap centers were not significantly different. In the cases of  $\text{NO}_3^-$  pools, net nitrification rates, and IER  $\text{NO}_3^-$  concentrations, however, measures were markedly, if not significantly, greater in small gap centers. Several other factors, such as litterfall C and N fluxes and decomposition constants, also followed this trend. Higher quality litterfall and faster decomposition rates in small gaps may create conditions conducive to greater production of  $\text{NO}_3^-$  (Pastor et al. 1984, McLaugherty et al. 1985). Taken together, these results suggest that subtle differences in environmental factors and litterfall inputs between gap sizes may be responsible for modest increases in nitrification in small gaps.

Other studies have shown that once beyond a certain threshold, gap size may not have a major effect on N availability. Single tree selection and thinning have shown to have little effect on N availability (Knight et al. 1991, Parsons et al. 1994a, Prescott 1997, Bargs and Edmonds 1999, DeLuca and Zouhar 2000, Hope et al. 2003). When more adjacent trees are removed, however, gap-forest differences begin to

emerge. Parsons et al. (1994a) saw net N mineralization and  $\text{NO}_3^-$  concentrations begin to increase with the removal of 15 trees. Prescott et al. (2003) first observed elevated forest floor and mineral soil  $\text{NO}_3^-$  concentrations when gap size reached 0.1 ha, and  $\text{NO}_3^-$  concentrations in subsequently larger gaps did not significantly differ. These findings and the results of the current study suggest that once conditions are met for increased N availability in gap interiors, gap size becomes less of a relevant factor.

Aspect of gap edges had little effect on N availability in gaps. Due to the high northern latitudes of the study sites, it was expected that the effective light gap would be shifted to the north, making solar radiation more intense and longer lasting in the northern half of the gap and along the northern gap edge (Canham et al. 1990, Van Pelt and Franklin 1999, Gray et al. 2002). This would lead to increased soil temperatures (Gray and Spies 1997, Gray et al. 2002) and increased rates of N cycling (Nicolardot et al. 1994, Stark and Firestone 1996). For the most part, our results showed little north-south differentiation within large gap interiors, although there were some non-significant trends of elevated mineral soil percent nitrification in the northern half of large gaps and elevated mineral soil IER  $\text{NH}_4^+$  concentrations in the southern half of large gaps. Prior studies investigating the effect of within gap position on N availability provide some suggestive evidence of north-south differences. In a German beech forest, Bauhus (1996) saw a significant decrease in mineralizable N in forest floor and mineral soil in northern gap and northern edge positions two years after gap creation. This decrease was attributed to increased N mineralization depleting labile N after gap creation. Hope et al. (2003) observed that the proportion of inorganic N as  $\text{NO}_3^-$  concentrations increased near the northern edge

of a 10 ha clearcut, indicating the possibility of increased nitrification rates. Due to a lack of replication, however, they were not able to statistically compare values between gap positions.

It was also hypothesized that intense solar radiation would extend into the adjacent forest north of gaps (Canham et al. 1990, Chen et al. 1995), possibly creating conditions conducive to increased N cycling. Our results, however, show little evidence of north-south differentiation in forest plots adjacent to gaps. In fact, there is little evidence of a major gap influence extending into the forest at all. N availability at gap edges was often more similar to forest plots than gap interiors. This is contrary to Hayes (2002), who saw a significant increase in overall  $\text{NH}_4^+$  pools along transects going from the edges of 20 year old clearcuts into adjacent old-growth forest. Additionally, edge effects extended further into the forest at south-facing edges than at north-facing edges. The overall decrease along edges was attributed to reduced N inputs from litterfall and continued N uptake by trees in the adjacent forest (Hayes 2002). In the current study, a shift in N availability often occurred 3-17 m into the gap from the gap edge, regardless of edge aspect. These findings of a relatively abrupt transition zone between gap and forest conditions are in accordance with Redding (2001), who saw forest floor  $\text{NO}_3^-$  concentrations increase 4-6 m into a 1 ha clearcut from both north and south gap edges. Hope et al. (2003) also saw evidence of increased nitrification within 16 m of the north and south gap edges within a 1.7 ha gap. Such an abrupt transition zone within the gap could be due in part to root infiltration and uptake from trees along the gap perimeter.

### ***Drivers of N Availability Across Gaps***

N availability in forest soils is the product of many processes, including decomposition of organic matter, ammonification of DON, nitrification of  $\text{NH}_4^+$ , microbial immobilization, plant uptake, and retention of N on soil ion-exchange sites (Chapin et al. 2002). In turn, these processes are affected by several biological, chemical and physical factors, including temperature, moisture, quality and quantity of litter inputs, microbial biomass and composition, and the presence of plant roots (Chapin et al. 2002).

Elevated N availability in soil following large-scale tree removal is often attributed to increased decomposition, N mineralization, and nitrification brought about by increased temperature and moisture (Bormann et al. 1974, Matson and Vitousek 1981, Frazer et al. 1990). Several findings of this and other studies, however, indicate that moisture and temperature may not be the main drivers of N availability in 6-8 year old silvicultural gaps (Bradley et al. 2000, Hope et al. 2003, Prescott et al. 2003). Results of the reciprocal transfer incubations show that incubation environment did not have a significant effect on net N mineralization or nitrification rates in either forest floor or mineral soil samples. Additionally, temperature loggers detected less than a 1°C gap-forest difference in daily mean forest floor and mineral soil temperatures in a large and small gap at Keel Mountain. These results indicate that gap and forest temperature regimes may not be sufficiently different to induce a difference in N cycling rates. Other studies examining soil temperatures in gaps or clearcuts several years after tree removal have detected few differences from uncut forests (Griffiths and Swanson 2001, Hope et al. 2003). A

substantial temperature difference in soil between gaps and the forest may exist soon after gap creation (Gray and Spies 1997, Gray et al. 2002); however, once a vegetative layer becomes established within the gap, as is the case in gaps of this study, the forest floor and mineral soil may be buffered from direct sunlight, effectively reducing gap-forest temperature differences (Van Pelt and Franklin 1999).

Moisture also did not differ in most cases between gaps and the forest. No significant differences in average forest floor or mineral soil percent moisture were detected along transects of either gap size. Seasonal analysis, however, revealed two exceptions to this trend (Appendix Tables A3 and A6), where August percent moisture values in forest floor and mineral soil were 9% and 4% greater, respectively, in gap positions than in forest positions ( $t_{12}=4.55$ ,  $p<0.001$ ;  $t_{12}=3.77$ ,  $p=0.003$ ). This overall lack of a major gap-forest moisture difference agrees with several other studies investigating soil moisture in gaps or clearcuts for prolonged periods after harvest. Hope et al. (2003) detected few consistent differences in moisture between 1.7 ha gaps and uncut forest 2-7 years after tree removal in British Columbia. In western Washington, Bargs and Edmonds (1999) saw no significant moisture increases in 2-5 year-old clearcuts relative to uncut forest. In a chronosequence of western Oregon clearcuts, Griffiths and Swanson (2001) saw no moisture differences between old-growth forest and 5-40 year old clearcuts. Prescott et al. (2003) saw summer moisture actually decrease in larger (0.1-10 ha) gaps 2-7 years after tree removal, most likely due to increased rates of evaporation. Although a temporary increase in soil moisture often accompanies tree removal (Bormann et al. 1974, Parsons et al. 1994a, Gray et al. 2002), water uptake from establishing vegetation in gaps may draw down soil

moisture to a level comparable to forest conditions, diminishing gap-forest differences over time.

Increased decomposition rates of tongue depressors were not detected in large gaps, but were detected in small gaps. The use of a primarily cellulose material may not accurately simulate the decomposition of litterfall, but it does assess the effect of environmental conditions on the decomposition of a standardized substrate. My results imply that moisture and temperature conditions in large gaps may not be sufficiently different from those of the forest to cause differences in decomposition rates. Small gap conditions, however, may be subtly more favorable for decomposition than those in large gaps and adjacent forest. Whether this is due to gap-forest differences in temperature and moisture not detected by my analyses or another factor, such as microbial community composition, is not known. As mentioned above, this difference in decomposition rates between gap sizes may contribute to modestly elevated  $\text{NO}_3^-$  accumulation detected in small gap centers. Other studies investigating the decomposition rates of various litter types between gaps or clearcuts and uncut forest have detected few or no differences (Yin et al. 1989, Prescott 1997, Hope et al. 2003, Prescott et al. 2003).

My results indicate that patterns of N availability in 6-8 year old gaps may be driven by the litterfall inputs of early-seral plants. N-rich litterfall, as indicated by a low C:N ratio, is often correlated with faster decomposition (Enriquez et al. 1993, Gholz et al. 2000) and increased net N mineralization rates (Pastor et al. 1984). Lower litterfall C:N ratios detected in gaps brought about by the presence of early-seral species may therefore play a role in elevating N availability, particularly if



belowground litterfall C:N values are lowest in gap centers as found for aboveground litterfall. Overall lower litterfall C inputs in gaps may also contribute to increased N availability in through the C-limitation of microbial immobilization. In a comparison of gross and net N cycling in mature forests, Davidson et al. (1992) suggested that low net N mineralization and net nitrification rates in mature forests may be caused by the rapid assimilation of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  by microbes rather than overall low rates of N cycling. With plentiful labile C coming from the canopy, microbial demand for N is high, so  $\text{NH}_4^+$  and  $\text{NO}_3^-$  would be immobilized in microbial biomass rather than accumulate in soil. In gaps and clearcuts, as logging residues and dead roots decompose, litterfall inputs become the main source of labile C for microbes (Prescott 2002). The reduction of fresh litter inputs may bring about C-limitation of microbial communities, causing inorganic N, especially in the form of  $\text{NO}_3^-$ , to accumulate in soil (Hart et al. 1994a, Bradley et al. 2000, Prescott et al. 2003). If C-limitation was occurring in gaps of this study, lower levels of labile DOC would have been expected. Analysis of bulk extractable DOC pools, however, did not reveal such a forest-gap difference. One explanation could be that bulk DOC pool values include both labile and recalcitrant forms of C, so changes in labile forms would be difficult to detect. The results of our transfer incubation are consistent with the possibility of C-limitation in that net nitrification in mineral soil samples originating in gaps was significantly greater than in samples taken from the forest, regardless of incubation environment.

Plant and mycorrhizal uptake are also important determinants of N availability in soils. After tree removal, the death of living roots can increase N availability by providing a labile source of nutrients (Fahey et al. 1988, Chen et al. 2002) and

reducing plant competition for mineralized N (Vitousek and Matson 1985). Although root biomass was not measured in this study, other studies have seen a rapid recovery of fine roots in clearcuts across a variety of systems (Raich 1980, Yin et al. 1989, Messier and Kimmins 1991, Fahey and Hughes 1994). This rapid recovery may be due to sprouting from the residual root system or stumps (Yin et al. 1989) or rapid colonization of shrubs and trees (Mou et al. 1993). In addition, root death results in the destruction of associated mycorrhizal communities that provide trees with greatly increased access to nutrients in exchange for photosynthetic products (Parsons et al. 1994b, Griffiths and Swanson 2001). Although this study did not specifically test for the presence of fungal hyphae, during soil collection I observed them more often in the forest than in gaps (*personal observation*). Also, microbial biomass C:N ratios in the mineral soil of gaps were significantly lower than in forests, possibly indicating a slight shift from a fungal-dominated microbial community with high C:N ratios to a more bacterial-dominated community with lower C:N ratios (Paul and Clark 1996, Chapin et al. 2002). Reductions of mycorrhizal hyphae after gap creation may also persist for many years. In a chronosequence of clearcuts in Douglas-fir forests of western Oregon, Griffiths and Swanson (2001) saw a near total loss of ectomycorrhizal mats in a 5 year-old clearcut relative to nearby old-growth. In the same study, ectomycorrhizal mats in a 40-year-old clearcut had recovered to only 50% of old growth levels. Reappearance of mycorrhizae in smaller-sized gaps may be somewhat faster. In a Wyoming lodgepole pine forest, Parsons et al. (1994b) saw ectomycorrhizal root tips disappear from the center of 30-tree gaps soon after gap creation. After 5 years, however, ectomycorrhizal root tips were again present in gap

centers. In our study of 6-8 year old gaps, a rapid recovery of fine roots combined with a slower recovery of mycorrhizal networks could account, in part, for a gap-forest difference in N availability but the lack of a gap-forest difference in moisture.

### ***Variability of N Availability Across Gaps***

When measured as standard deviations, the variability of available N was often greater in gaps than in the adjacent forest. Fewer gap-forest differences were detected when coefficients of variation were analyzed. These results indicate that there is a greater spread of available N values in gaps but also that this increase may be associated with greater mean effects. Regardless, standard deviations provide an ecologically meaningful measure of variability because plant and microbial communities respond to absolute changes in available N.

Other studies have also detected increased variability of available N in gaps. Parsons et al. (1994a) saw the variance of  $\text{NO}_3^-$  concentrations in lysimeter water increase in 15- and 30-tree gaps relative to the adjacent forest. In a chronosequence of clearcuts, Griffiths and Swanson (2001) saw greater coefficients of variation of  $\text{NH}_4^+$  concentrations in 5 year old clearcuts than in old growth forest, although differences were not statistically significant.

Several mechanisms may increase the variability of available N after tree removal. First, the root networks in gaps may lack the complexity of those in the forest (Griffiths and Swanson 2001). As mentioned above, root networks and their associated mycorrhizae take time to establish after tree removal. The root networks of establishing early-seral species may not fully extend throughout the gap interior 6-8

years after gap creation. This patchiness of belowground root colonization could translate into elevated variability of available N throughout the gap by creating local-scale differences in N demands. Plant community composition may be another reason for increased variability of available N in gaps. In a study of four DMS sites, including Keel Mountain, Fahey (2005) found that plant species diversity increased in silvicultural gaps relative to the adjacent forest. Although spatial heterogeneity of available N has been positively linked to plant diversity (Ricklefs 1977, Tilman 1982, McKane et al. 2002) a cause-and-effect relationship cannot be ascertained from the current study. The existence of a diverse plant community, however, may help maintain the detected patterns of spatial heterogeneity. In the forest, canopy trees are the prime source of litter inputs, providing a relatively uniform substrate to soil microbes (Prescott 2002). On the other hand, a diverse plant community throughout gaps may result in a spatial diversity of litter inputs both above- and below-ground, which could lead to greater spatial heterogeneity of available N.

### ***Management Implications***

Increased N availability in gaps may increase the productivity of regenerating canopy trees. A positive relationship has been shown between Douglas-fir productivity and available N in western Washington and Oregon (Chappell et al. 1991). Across a wide range of soil N capital, the sustained, dramatic increases of available N detected in gaps of this study may therefore play an important role in the expedient growth of underplanted or naturally regenerating trees. This may be particularly true of sites with low soil N capital (Chappell et al. 1991). Faster tree

growth, in turn, may speed the development of a structurally complex multi-storied canopy.

While elevated N availability may increase overall productivity in gaps, it may also increase the risk of invasion by exotic plant species. A plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources (Davis et al. 2000). When access to an essential resource, such as light, water, or nutrients, increases, competition between species decreases, making the establishment of a new species more likely (Davis et al. 1998). Several studies have shown a positive relationship between N availability and invasibility (Kay and Evans 1965, Huenneke et al. 1990, McLendon and Redente 1994, Trent et al. 1994), especially when disturbance is involved (Hobbs and Mooney 1985, Burke and Grime 1996). Increased available N in silvicultural gaps may contribute to the establishment of exotic species that compete effectively for the same resources with native species.

The increased production of  $\text{NO}_3^-$  detected in gaps of this study may be accompanied by an increase in N leaching (Parsons et al. 1994a). According to inorganic N pool and IER data, mineral soil  $\text{NO}_3^-$  increased in gaps, but the proportion of inorganic N as  $\text{NO}_3^-$  was consistently very low regardless of transect position. These  $\text{NH}_4^+$ -dominated conditions are not usually conducive to major N losses via leaching (Vitousek et al. 1982). The highly elevated levels of percent nitrification in gaps, however, indicate that  $\text{NO}_3^-$  is being produced much more rapidly than reflected in pool and IER data. A possible explanation for this discrepancy is the preferential uptake of  $\text{NO}_3^-$  by early-seral species. Several species of *Rubus*, a genus commonly found in gaps of the DMS (Fahey 2005), have a high capacity to produce nitrate

reductase in their leaves in the presence of elevated soil  $\text{NO}_3^-$  (Truax et al. 1994, Claussen and Lenz 1999). Nitrate reductase is energetically costly to produce, but allows plants to reduce  $\text{NO}_3^-$  into more biologically viable forms of N (Raven et al. 1998). A prevalence of species with this adaptation could draw down  $\text{NO}_3^-$  to levels reflected in inorganic N pool and IER data. To definitively assess N loss from gaps, however, measurement of soil water below rooting depth would be necessary.

Many of the patterns of N availability detected across gaps in this study could be short-lived. As canopy species emerge and begin to fill the gap, decreased light resources will not favor species with high light demands, including many ruderal and early-seral species. As canopy trees establish over time, the development of complex rooting systems may increase the efficiency of N uptake and subsequently reduce the availability and variability of N (Griffiths and Swanson 2001). Aboveground, increased inputs of low-quality litter could have a similar effect. As gap-scale effects diminish, however, larger scale effects may be taking place. Gap creation may cause a shift in dominant tree species, and such a shift could increase or decrease N availability in the former gap relative to the adjacent forest, depending on the species involved (Prescott 2002). If species effects are dissimilar enough, gap creation could increase long-term stand-scale spatial heterogeneity of N availability.

While gap creation seems to have impacted N availability in gaps, several other important soil properties were not as affected. As discussed above, soil moisture and temperature in gaps were very similar to levels in the forest. Mineral soil bulk density also did not increase in gaps, meaning tree extraction methods may not have caused major soil compaction. This, however, must be taken with the caveat that

sampling methods avoided roads and skid trails. One important soil property that did change in gaps, however, was forest floor mass, which decreased in large gaps.

Although conditions for decomposition were similar across large gaps, reduced litterfall inputs over time may have caused a net loss of forest floor mass (Prescott 1997). Small gap interiors may have enough lateral movement of litter from trees at gap edges to offset detectable losses (Bauhus 1996). As the stand ages and the canopy closes, however, forest floor mass in large gaps may return to forest levels (Griffiths and Swanson 2001).

## CONCLUSIONS

The results of this study provide convincing evidence that the creation of silvicultural canopy gaps can influence N availability in western Oregon forests. Patterns of elevated N availability in gaps were prevalent to a greater extent in the upper mineral soil than in the forest floor layer, and gap-forest differences did not seem to be influenced greatly by gap size. Expected differences between northern and southern positions in gaps and adjacent forest were not detected. Analysis of variables related to N cycling indicated that patterns of N availability in 6-8 year old gaps may be driven more by the litterfall of early-seral species and reduced plant uptake than by altered temperature and moisture conditions. Variability analysis also provided evidence that spatial heterogeneity of N availability may increase in gaps. Whether this is a direct effect of gap creation or the indirect effect of a diverse plant community is not known. As silvicultural canopy gaps emerge as an alternative management tool in western Oregon, the results of this study will directly aid forest managers in making sound forest ecosystem management decisions.



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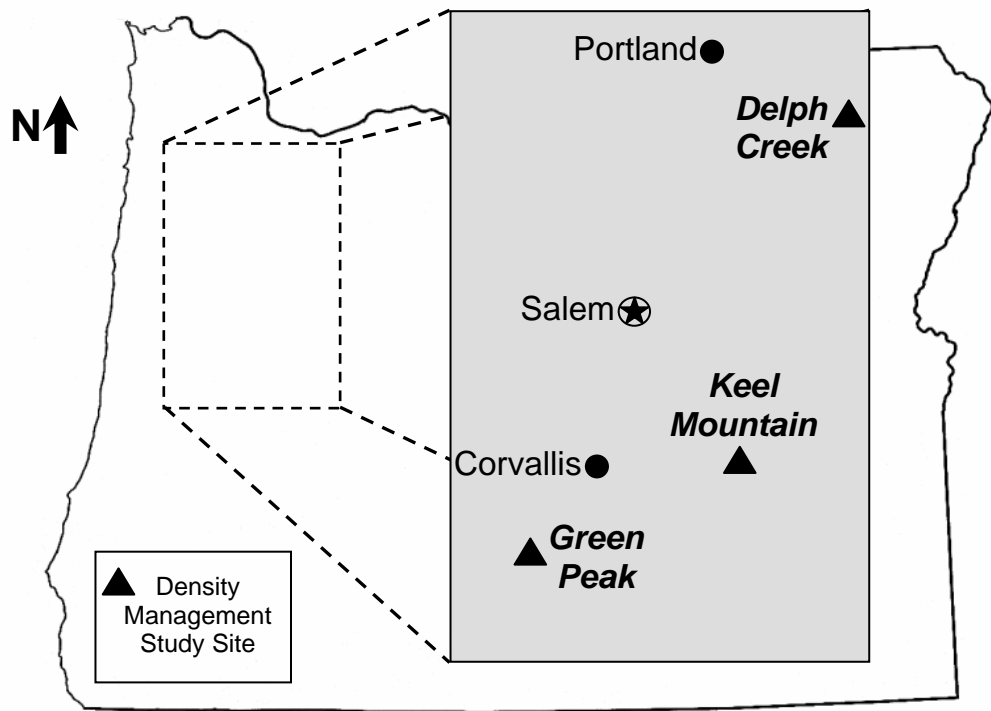


Figure 2.1. Locations of Density Management Study (DMS) sites selected for this study.

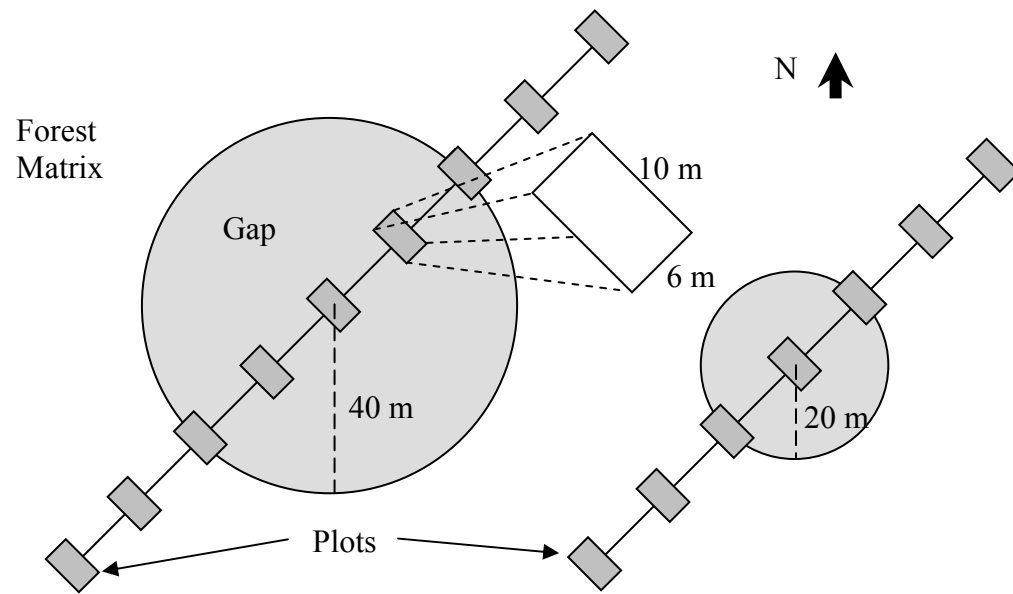


Figure 2.2. Transect layout across large (0.4 ha, left) and small (0.1 ha, right) gaps.

Unstructured

	1	2	3	4	5	6	7
1	1	$\rho_{2,1}$	$\rho_{3,1}$	$\rho_{4,1}$	$\rho_{5,1}$	$\rho_{6,1}$	$\rho_{7,1}$
2	$\rho_{1,2}$	1	$\rho_{3,2}$	$\rho_{4,2}$	$\rho_{5,2}$	$\rho_{6,2}$	$\rho_{7,2}$
3	$\rho_{1,3}$	$\rho_{2,3}$	1	$\rho_{4,3}$	$\rho_{5,3}$	$\rho_{6,3}$	$\rho_{7,3}$
4	$\rho_{1,4}$	$\rho_{2,4}$	$\rho_{3,4}$	1	$\rho_{5,4}$	$\rho_{6,4}$	$\rho_{7,4}$
5	$\rho_{1,5}$	$\rho_{2,5}$	$\rho_{3,5}$	$\rho_{4,5}$	1	$\rho_{6,5}$	$\rho_{7,5}$
6	$\rho_{1,6}$	$\rho_{2,6}$	$\rho_{3,6}$	$\rho_{4,6}$	$\rho_{5,6}$	1	$\rho_{7,6}$
7	$\rho_{1,7}$	$\rho_{2,7}$	$\rho_{3,7}$	$\rho_{4,7}$	$\rho_{5,7}$	$\rho_{6,7}$	1

Toeplitz

	1	2	3	4	5	6	7
1	1	$\rho_2$	$\rho_3$	$\rho_4$	$\rho_5$	$\rho_6$	$\rho_7$
2	$\rho_2$	1	$\rho_2$	$\rho_3$	$\rho_4$	$\rho_5$	$\rho_6$
3	$\rho_3$	$\rho_2$	1	$\rho_2$	$\rho_3$	$\rho_4$	$\rho_5$
4	$\rho_4$	$\rho_3$	$\rho_2$	1	$\rho_2$	$\rho_3$	$\rho_4$
5	$\rho_5$	$\rho_4$	$\rho_3$	$\rho_2$	1	$\rho_2$	$\rho_3$
6	$\rho_6$	$\rho_5$	$\rho_4$	$\rho_3$	$\rho_2$	1	$\rho_2$
7	$\rho_7$	$\rho_6$	$\rho_5$	$\rho_4$	$\rho_3$	$\rho_2$	1

Compound Symmetry

	1	2	3	4	5	6	7
1	1	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$
2	$\rho$	1	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$
3	$\rho$	$\rho$	1	$\rho$	$\rho$	$\rho$	$\rho$
4	$\rho$	$\rho$	$\rho$	1	$\rho$	$\rho$	$\rho$
5	$\rho$	$\rho$	$\rho$	$\rho$	1	$\rho$	$\rho$
6	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$	1	$\rho$
7	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$	$\rho$	1

Autoregressive Order 1

	1	2	3	4	5	6	7
1	1	$\rho$	$\rho^2$	$\rho^3$	$\rho^4$	$\rho^5$	$\rho^6$
2	$\rho$	1	$\rho$	$\rho^2$	$\rho^3$	$\rho^4$	$\rho^5$
3	$\rho^2$	$\rho$	1	$\rho$	$\rho^2$	$\rho^3$	$\rho^4$
4	$\rho^3$	$\rho^2$	$\rho$	1	$\rho$	$\rho^2$	$\rho^3$
5	$\rho^4$	$\rho^3$	$\rho^2$	$\rho$	1	$\rho$	$\rho^2$
6	$\rho^5$	$\rho^4$	$\rho^3$	$\rho^2$	$\rho$	1	$\rho$
7	$\rho^6$	$\rho^5$	$\rho^4$	$\rho^3$	$\rho^2$	$\rho$	1

Figure 2.3. Covariance structures for ANOVA with repeated measures in space. Numbered rows and columns represent the seven positions along a small gap transect.  $\rho$  represents the correlation between two points along the transect given a specific covariance structure.

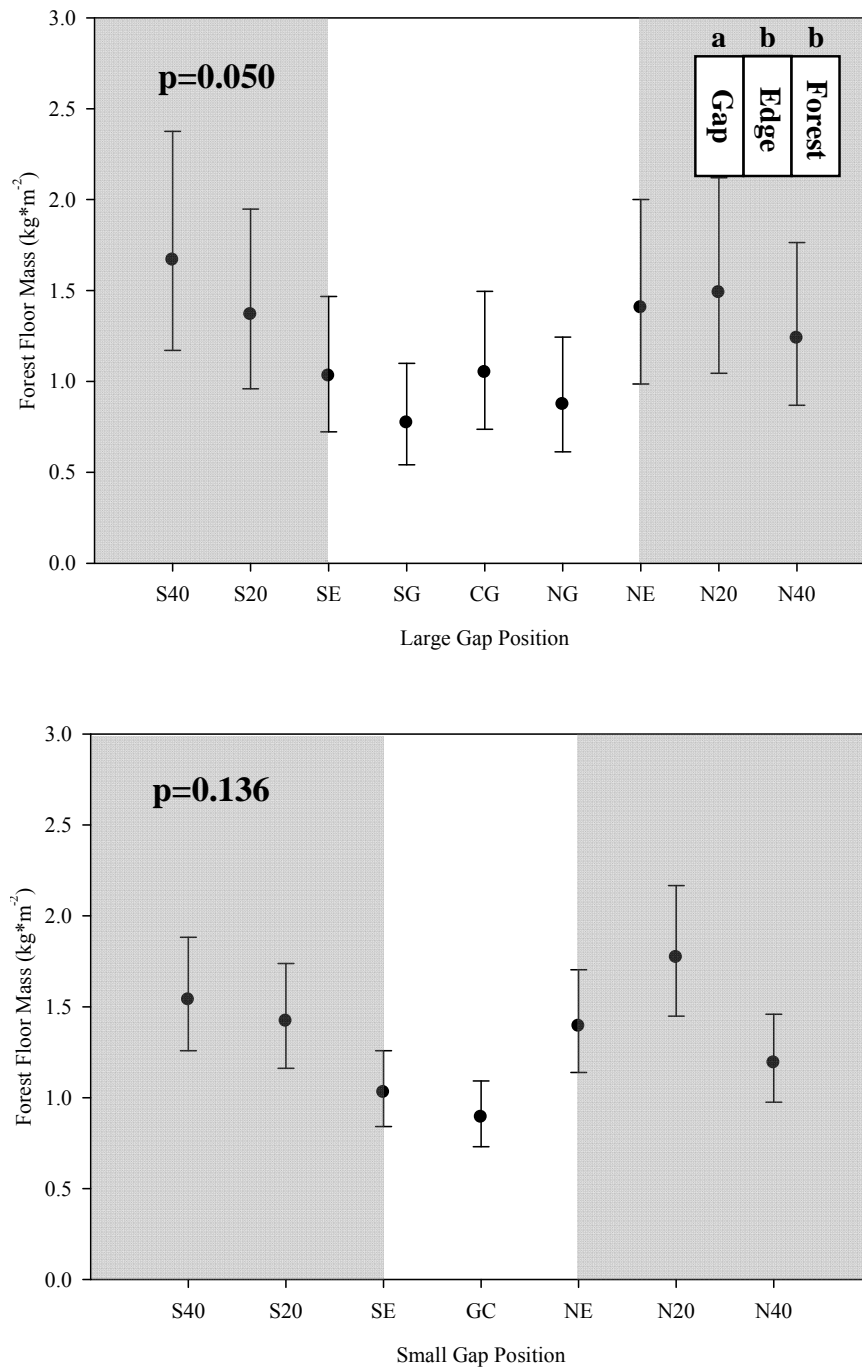


Figure 3.1. Forest floor mass across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm$  1 standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

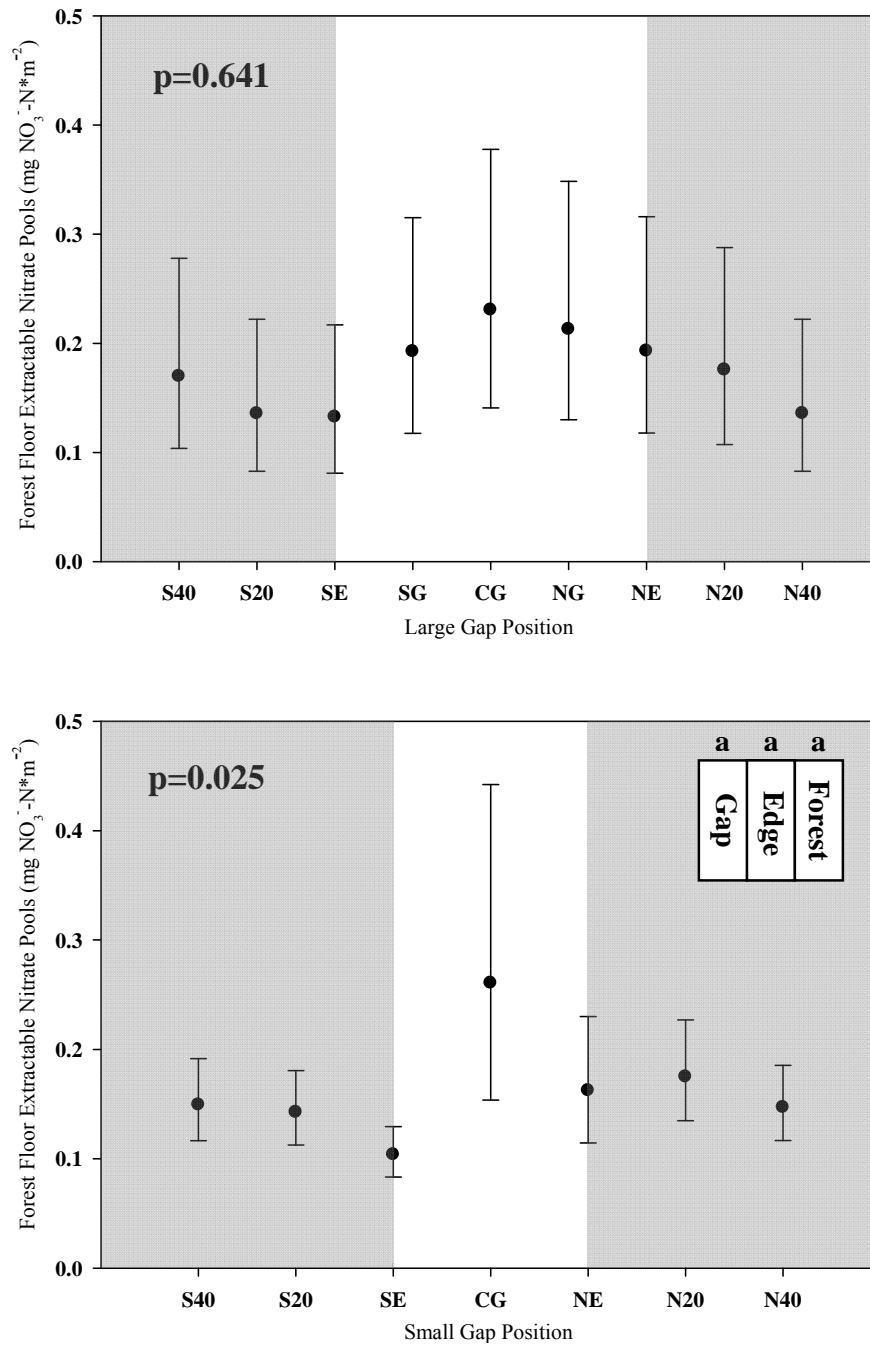


Figure 3.2. Forest floor extractable  $\text{NO}_3^-$  pools across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

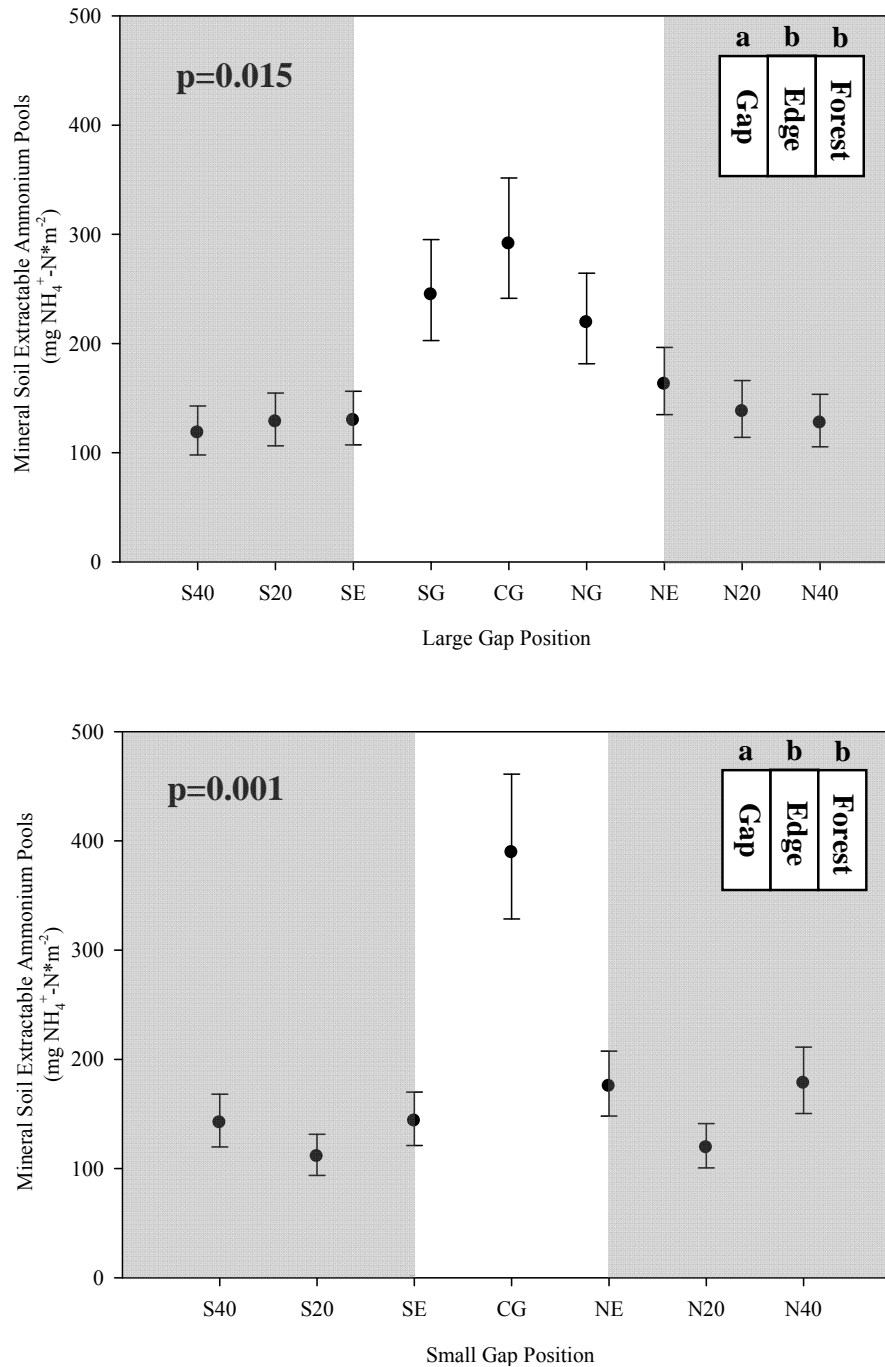


Figure 3.3. Mineral soil extractable  $\text{NH}_4^+$  pools across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

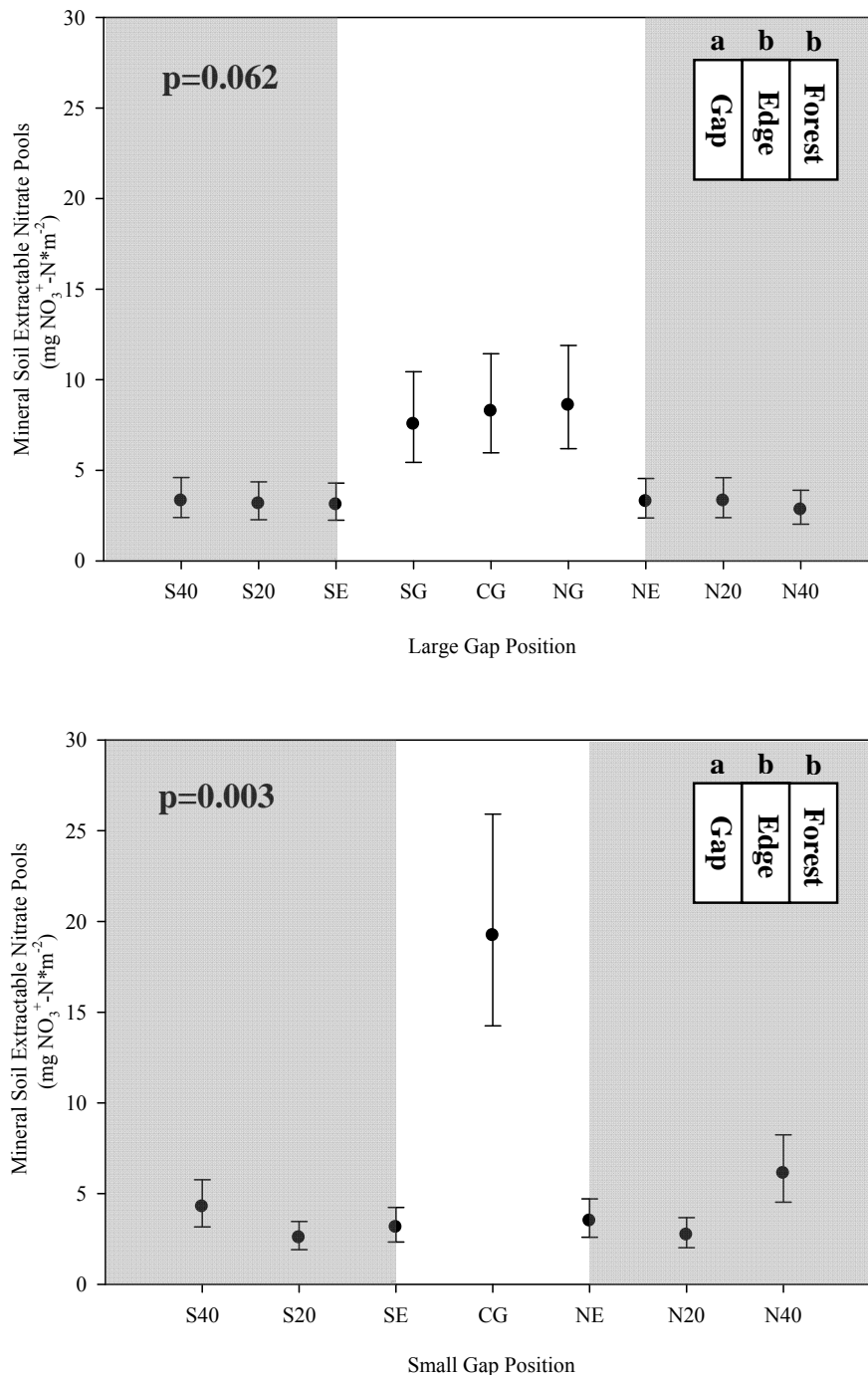


Figure 3.4. Mineral soil extractable  $\text{NO}_3^-$  pools across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

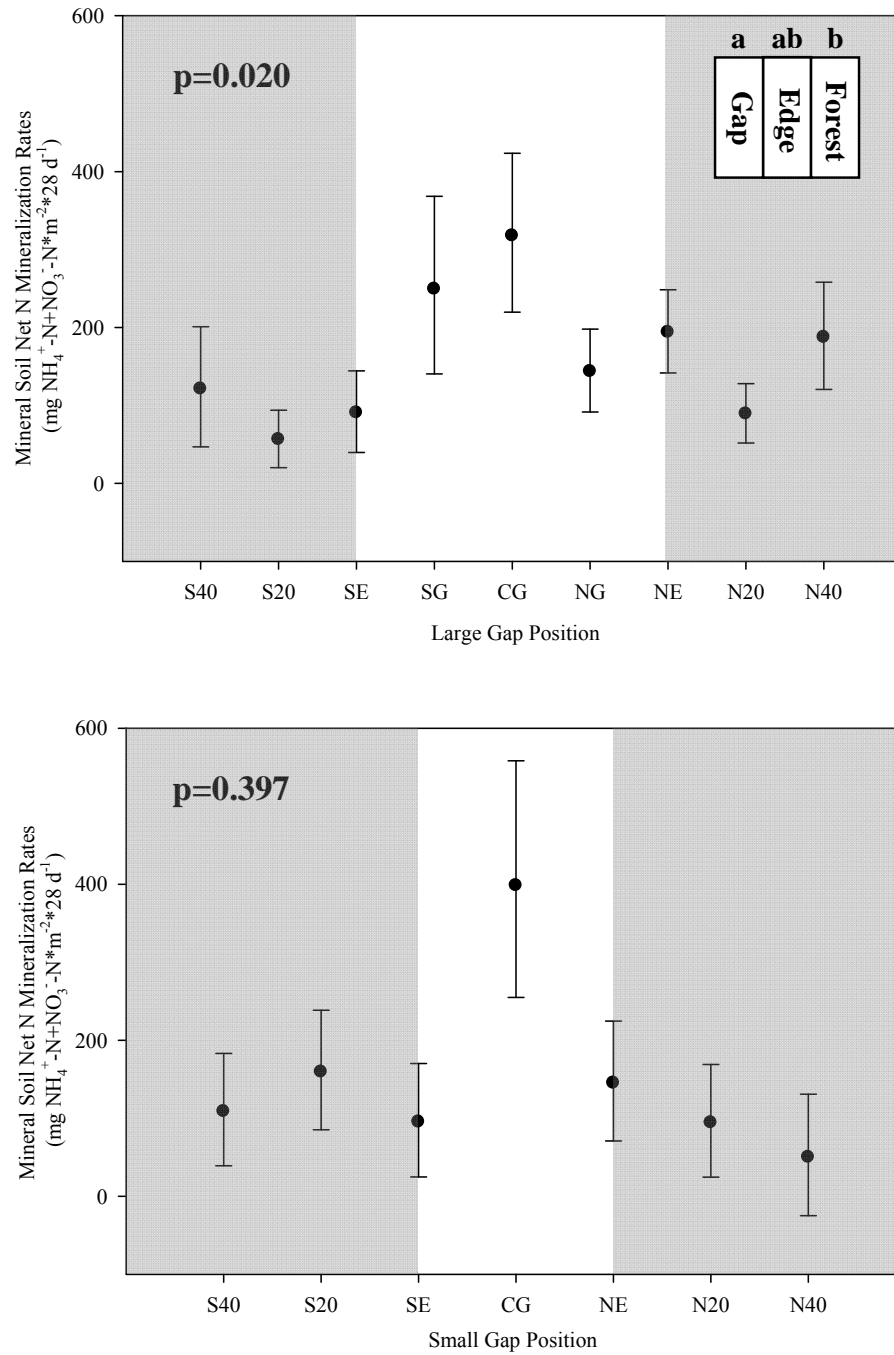


Figure 3.5. Mineral soil net N mineralization rates across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.



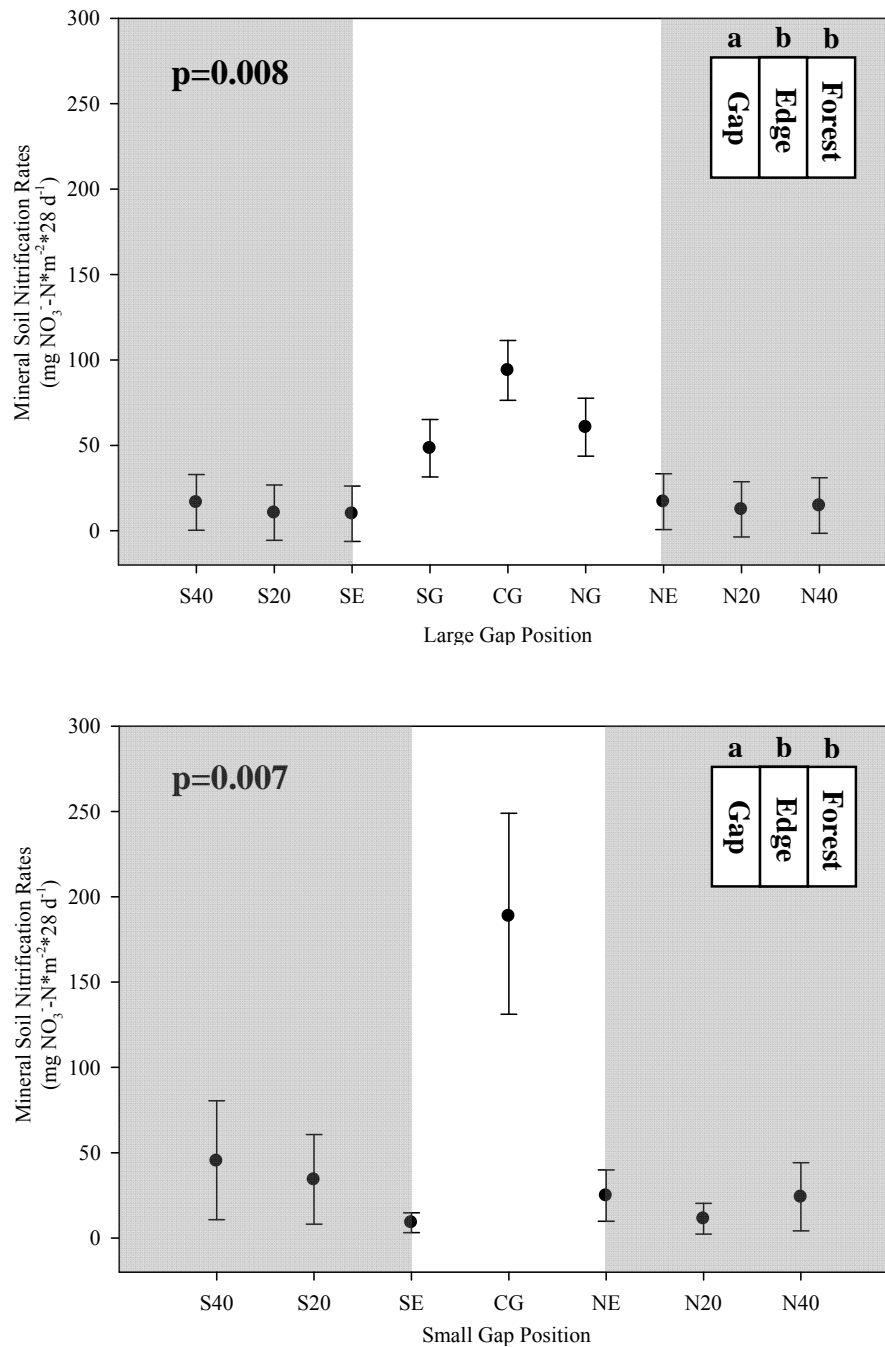


Figure 3.6. Mineral soil net nitrification rates across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

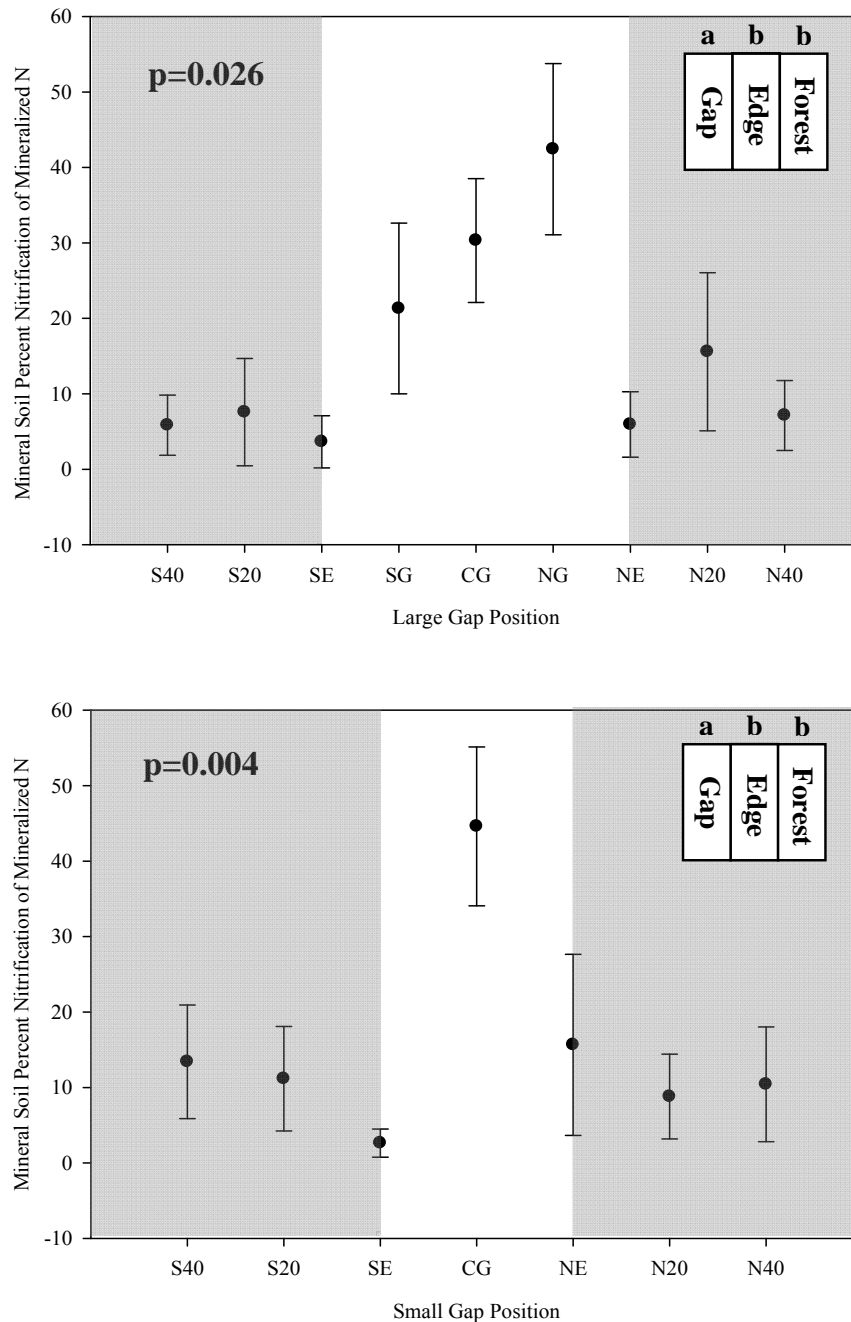


Figure 3.7. Mineral soil percent nitrification of mineralized N across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are mean estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

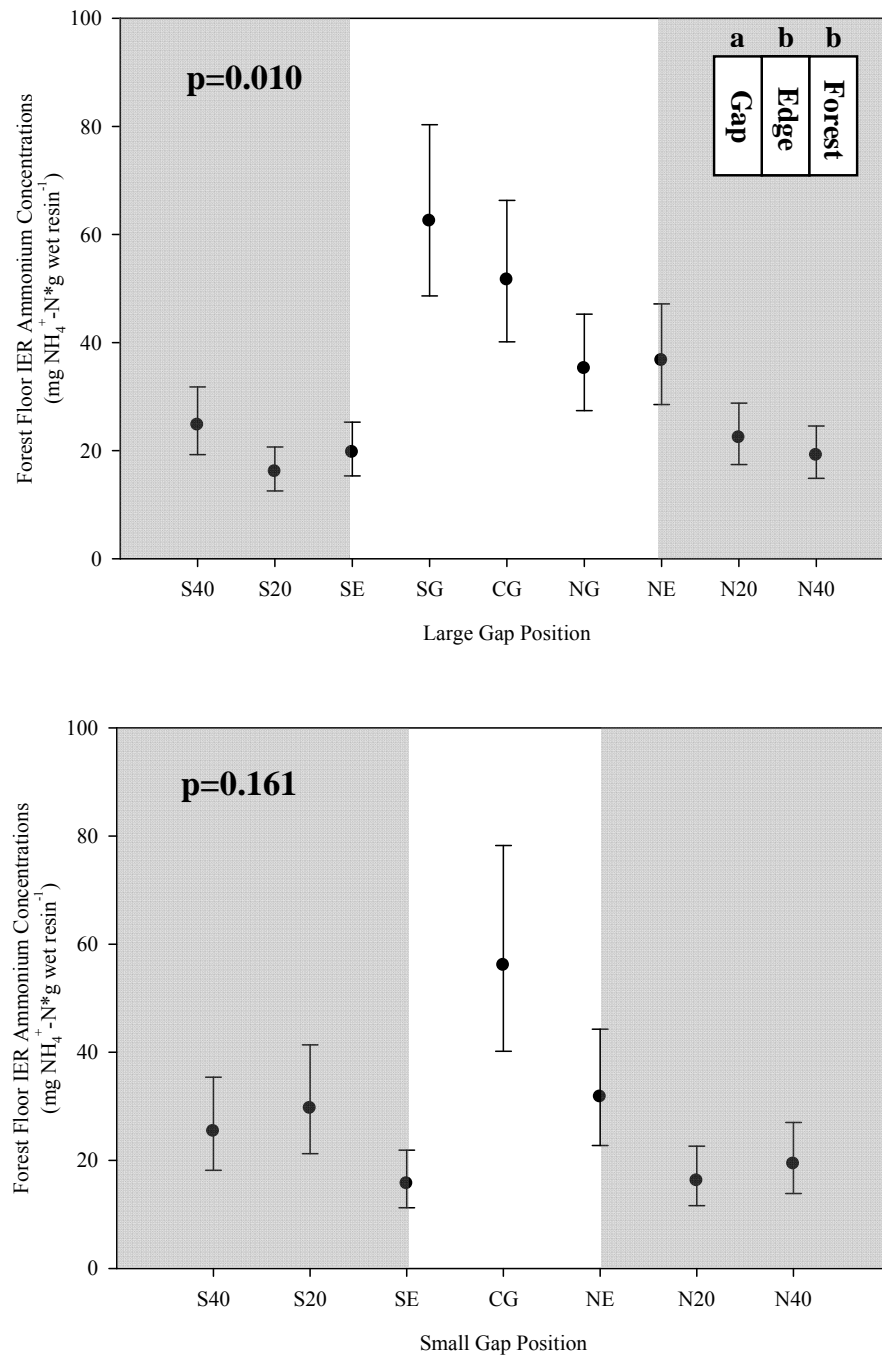


Figure 3.8. Forest floor IER  $\text{NH}_4^+$  concentrations across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

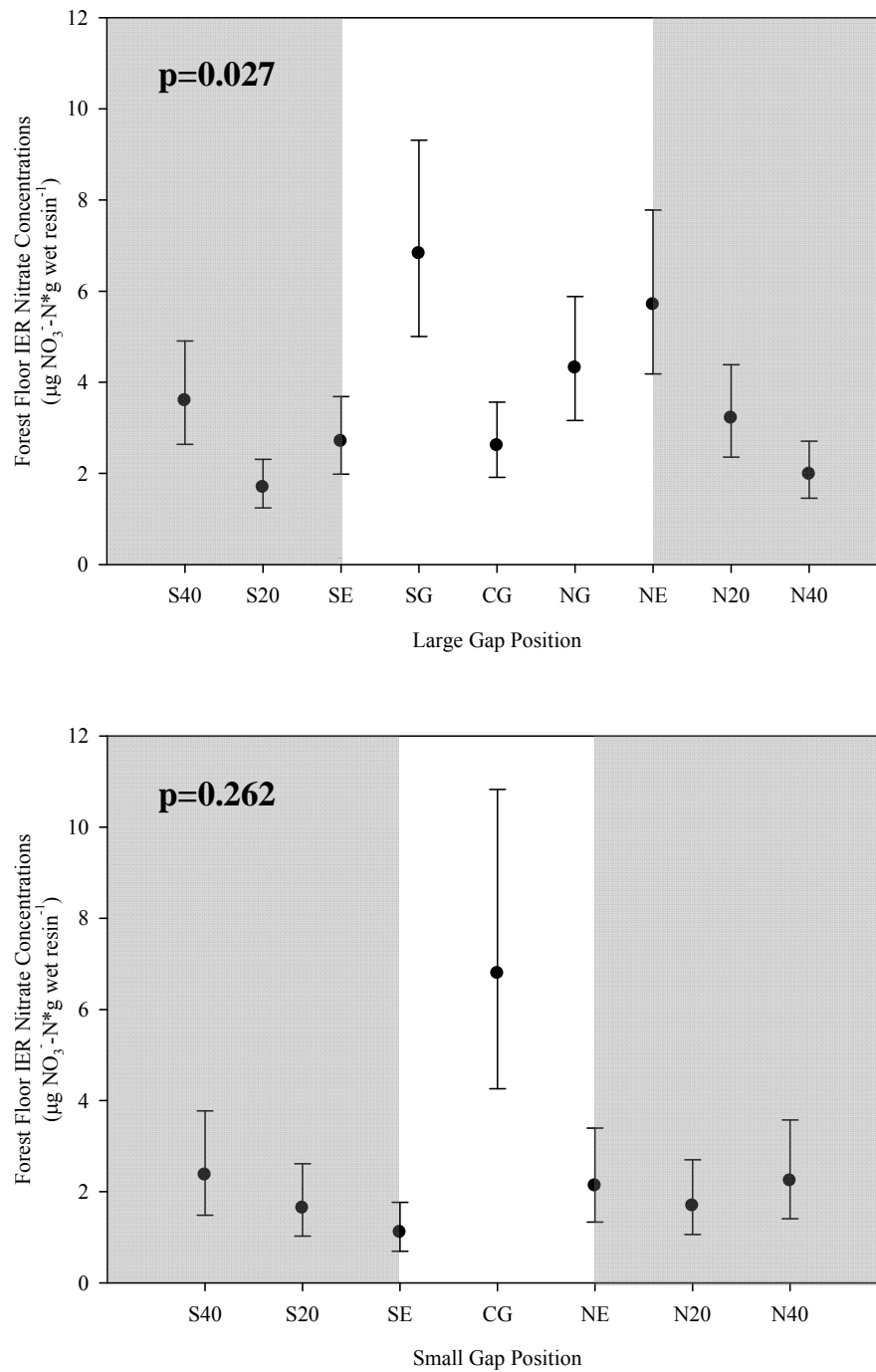


Figure 3.9. Forest floor IER  $\text{NO}_3^-$  concentrations across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

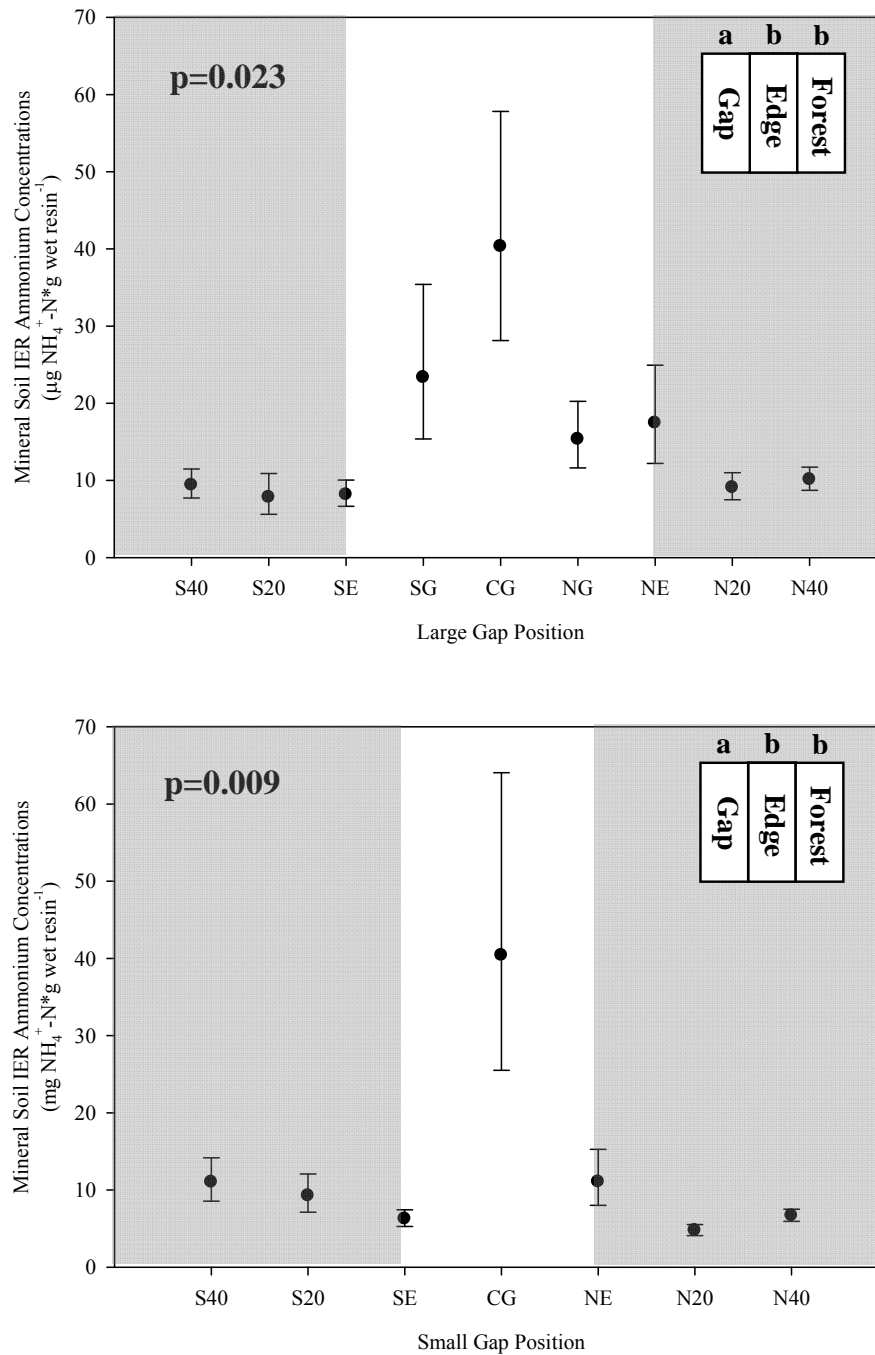


Figure 3.10. Mineral soil IER  $\text{NH}_4^+$  concentrations across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

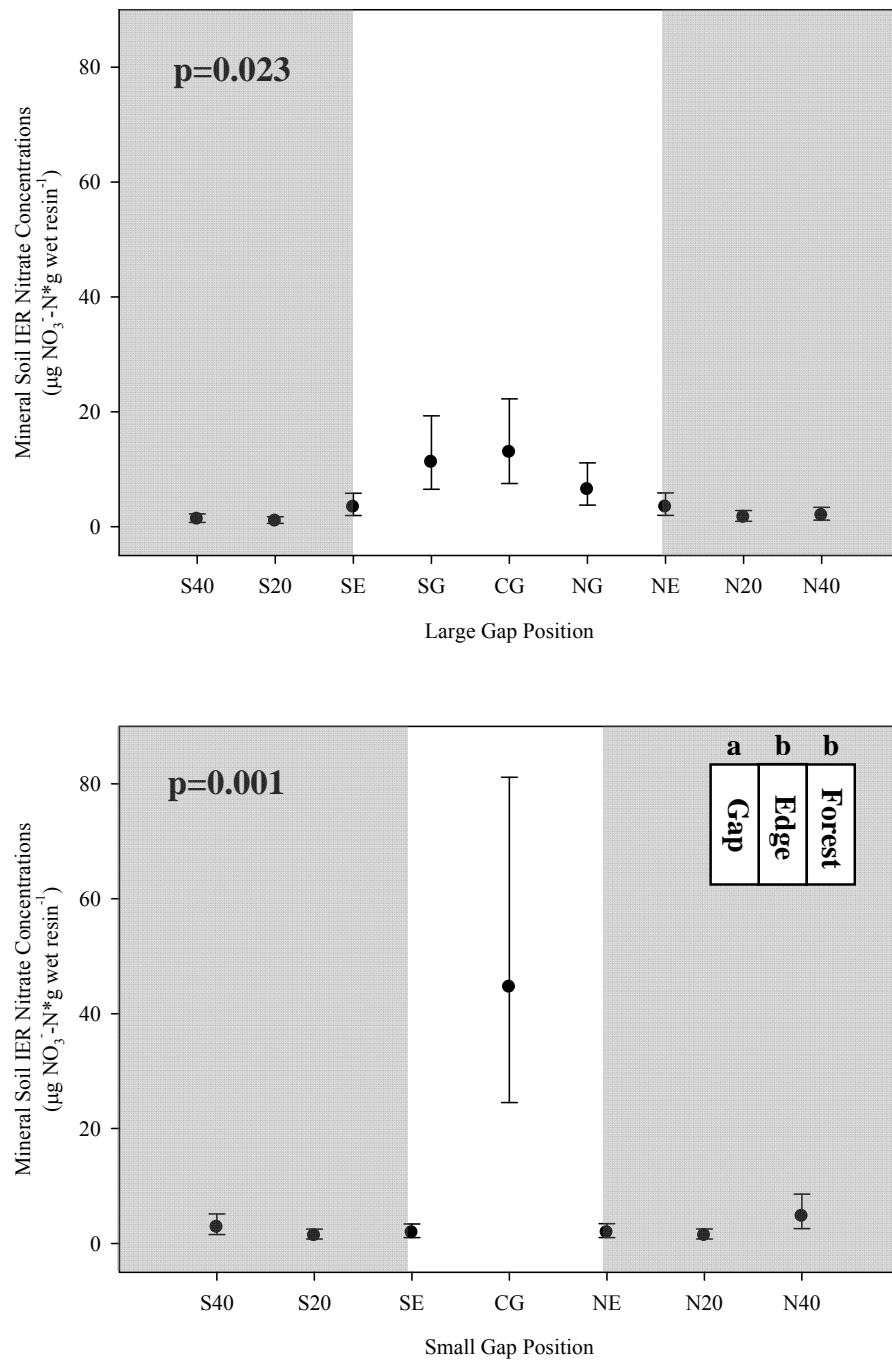


Figure 3.11. Mineral soil IER  $\text{NO}_3^-$  concentrations across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

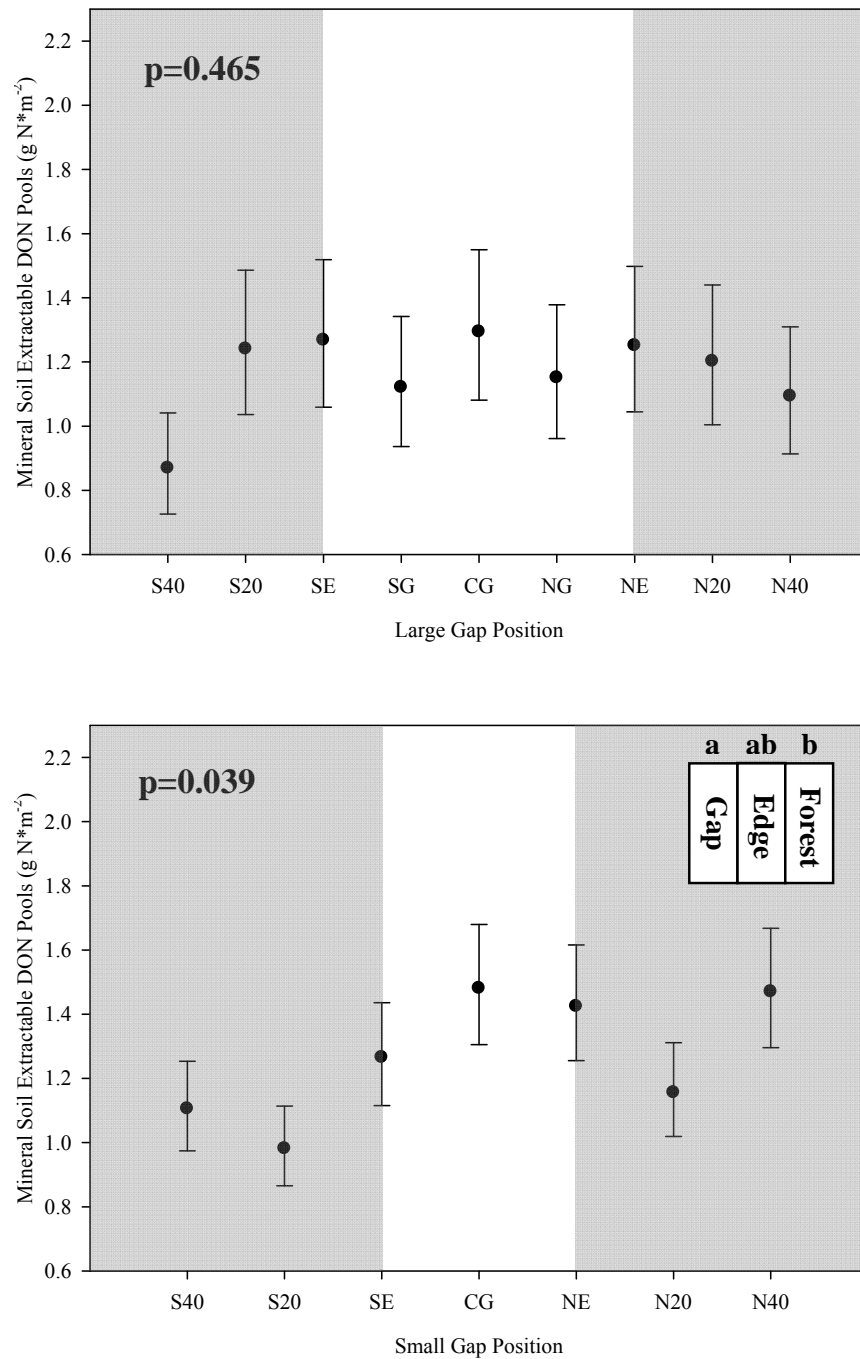


Figure 3.12. Mineral soil extractable DON pools across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

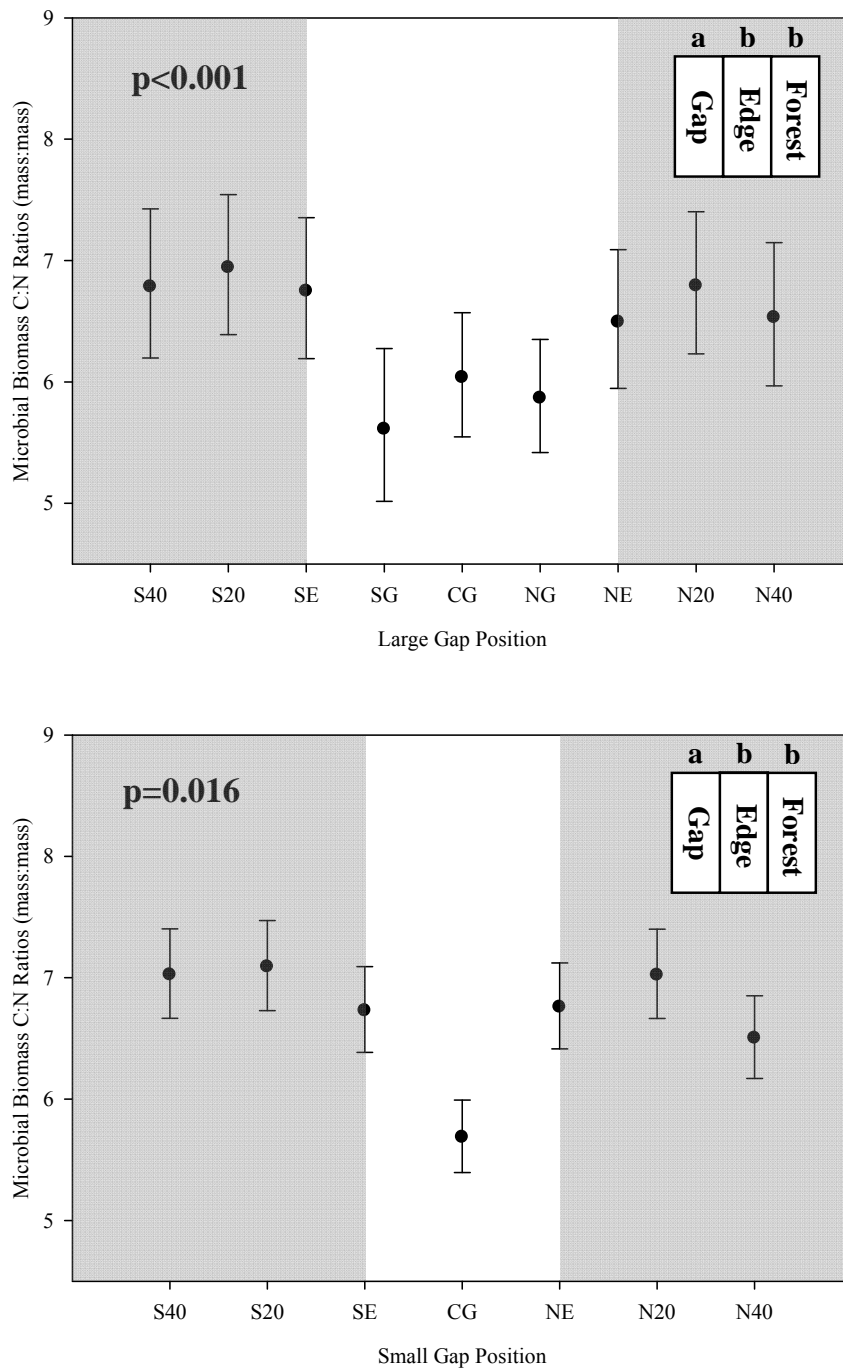


Figure 3.13. Microbial biomass C:N ratios across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are back-transformed median estimates  $\pm 1$  standard error.  $p$ -values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.



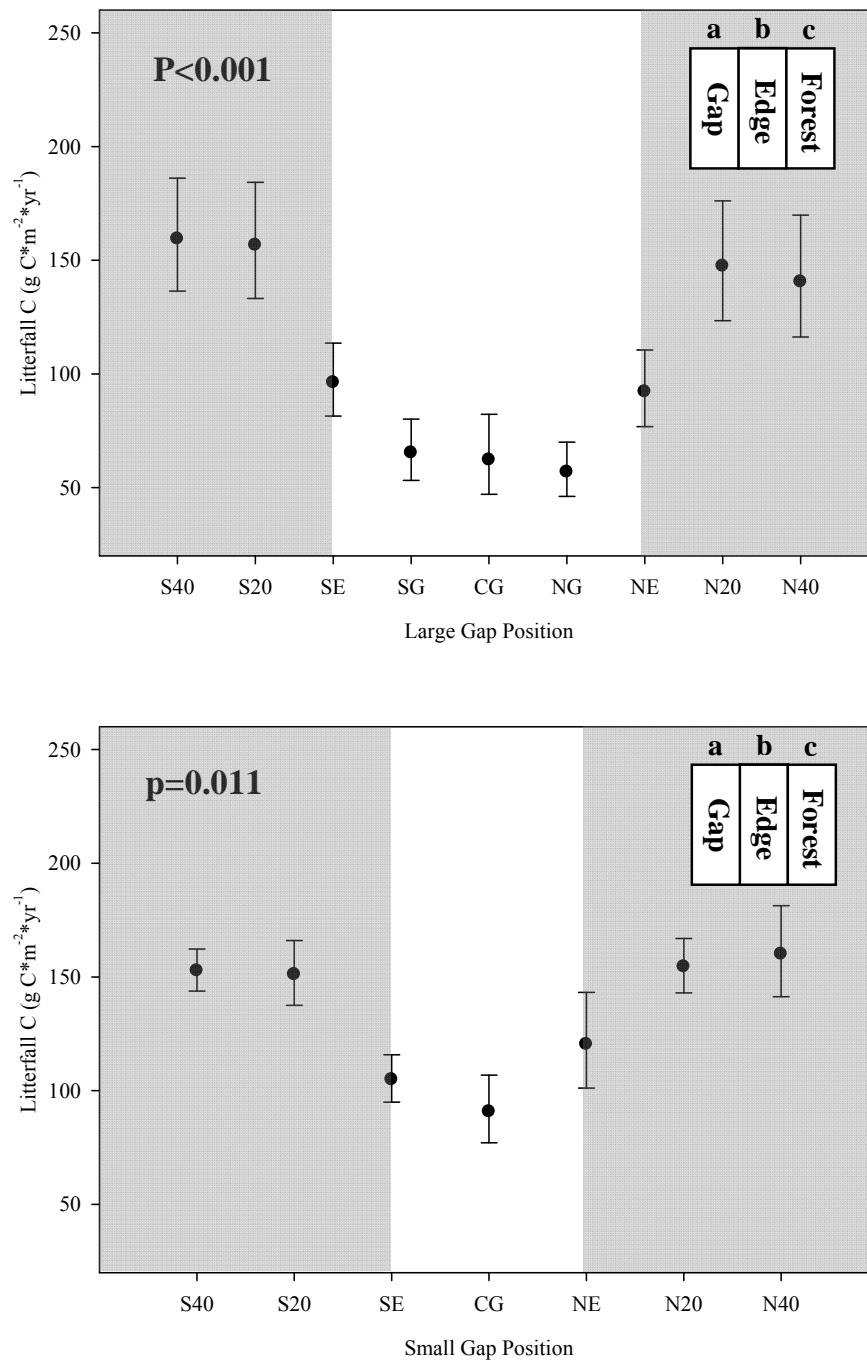


Figure 3.14. Litterfall C across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

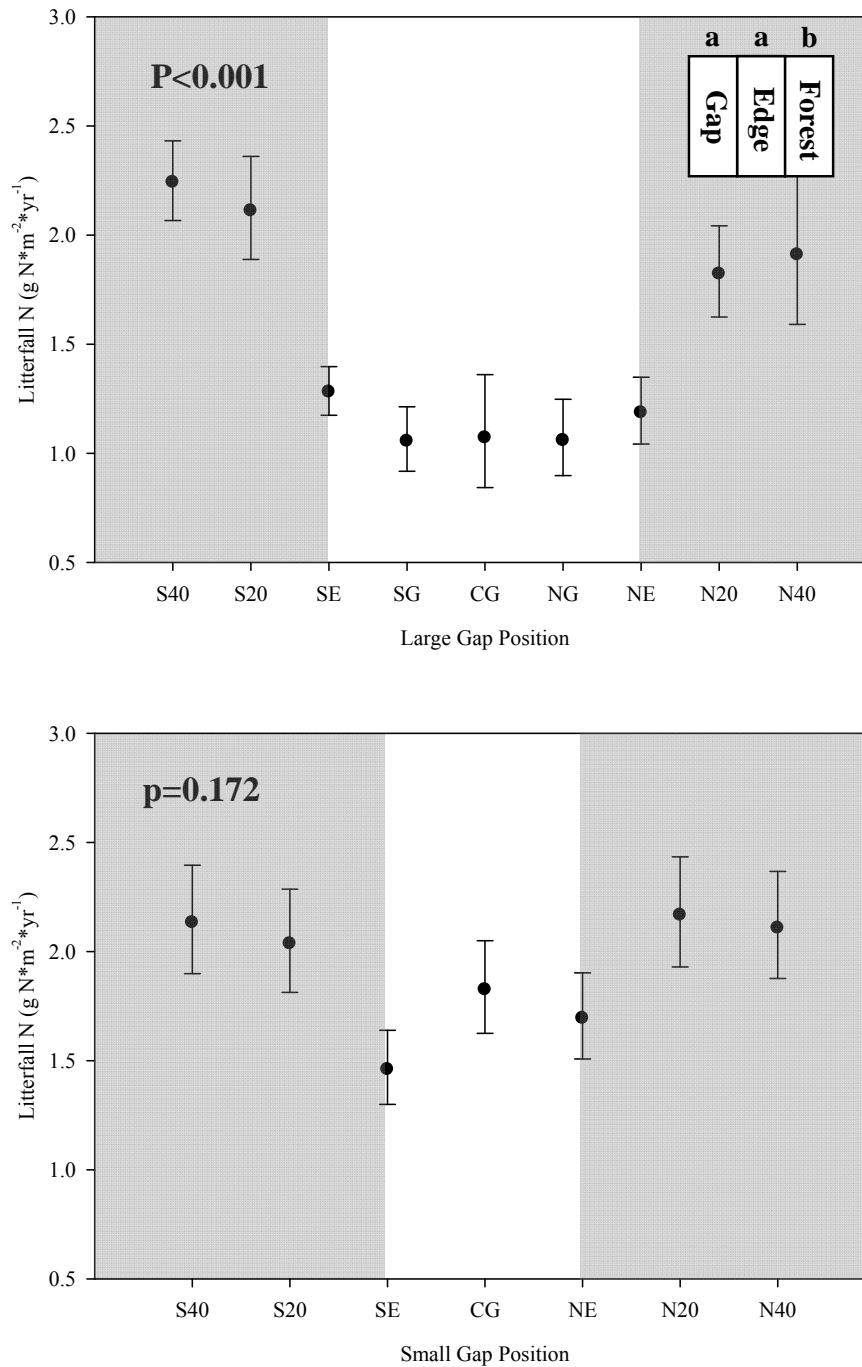


Figure 3.15. Litterfall N across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

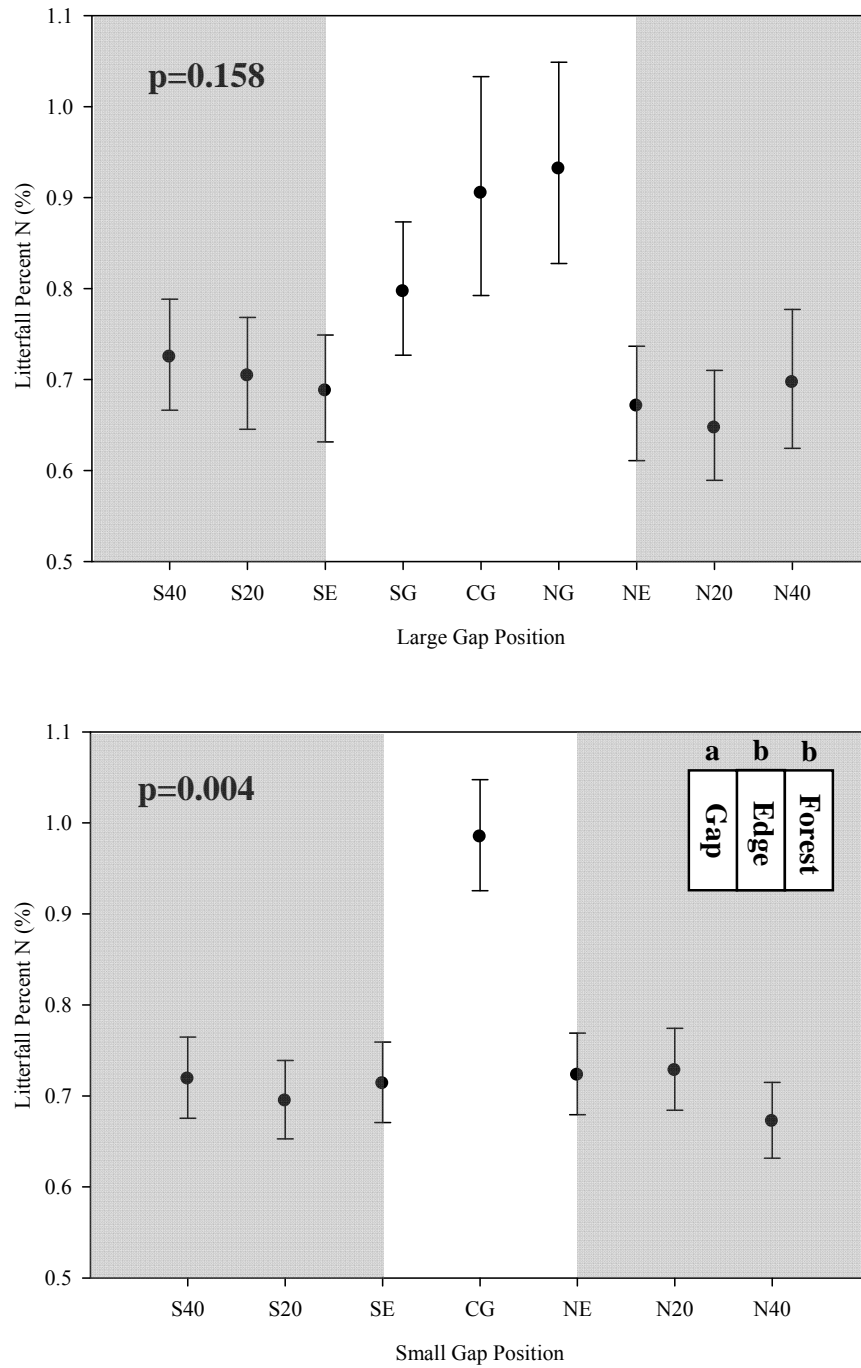


Figure 3.16. Percent litterfall N across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

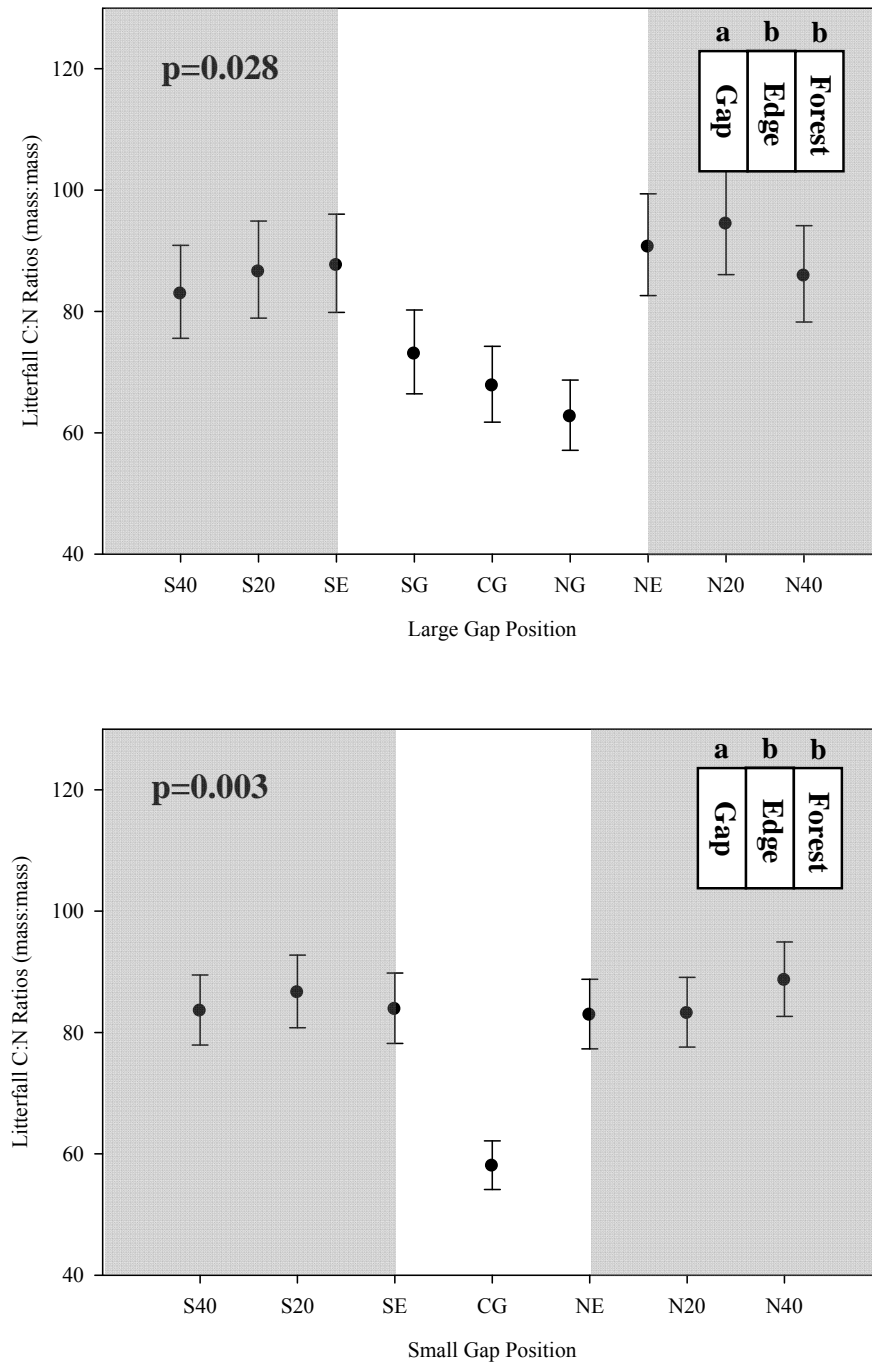


Figure 3.17. Litterfall C:N ratios across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

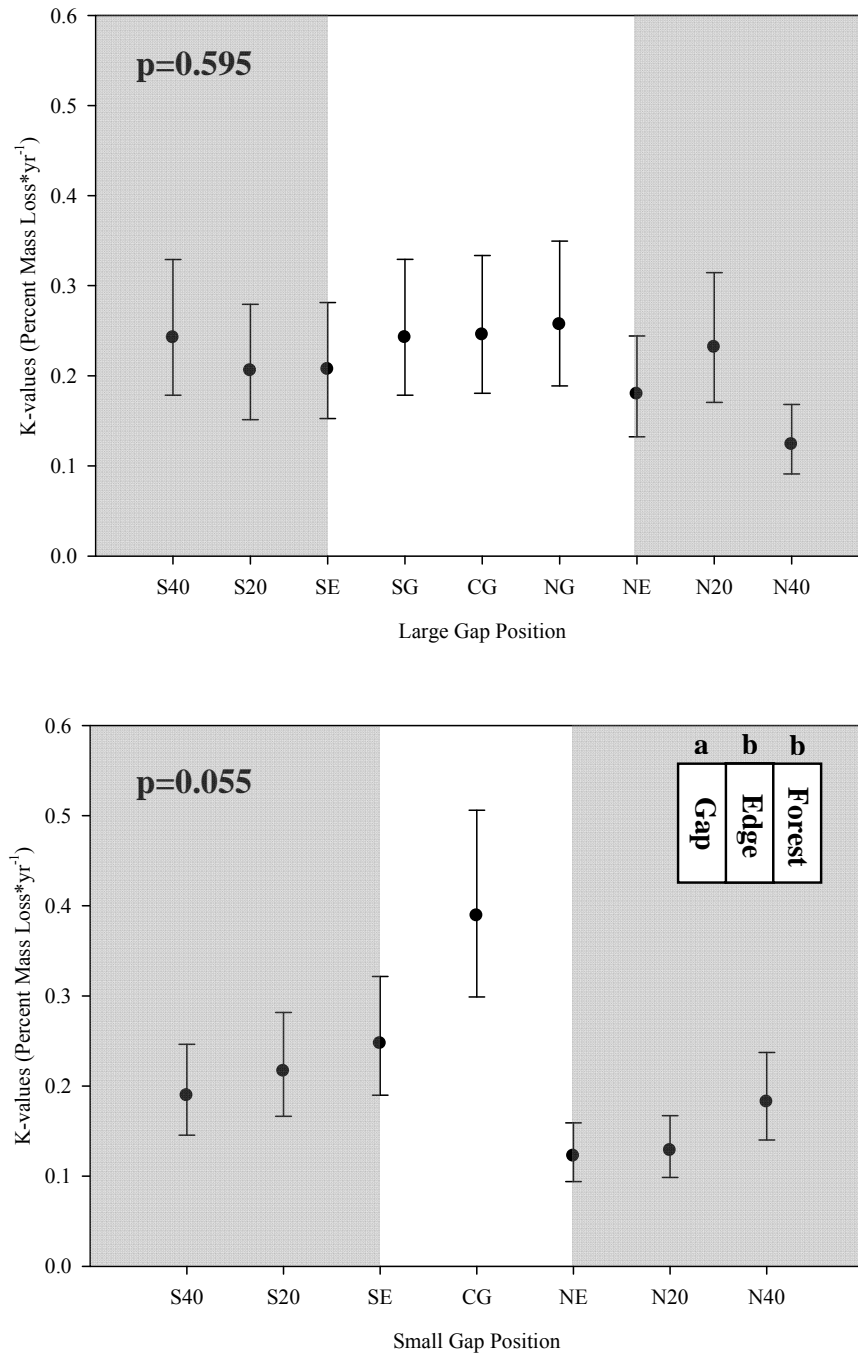


Figure 3.18. Decomposition constants (k-values) across gaps. White areas indicate the gap, while shaded areas indicate the forest. Values are median estimates  $\pm$  1 standard error. p-values in the upper left corner indicate the significance of a position effect on the response variable from an ANOVA with repeated measures in space. Labeled boxes in the upper right corner indicate results of multiple comparisons between group means of gap, edge, and forest positions. Different letters indicate significant pair-wise differences between group means (Bonferroni-adjusted,  $p \leq 0.05$ ). Group mean comparisons were carried out only if the position effect was significant.

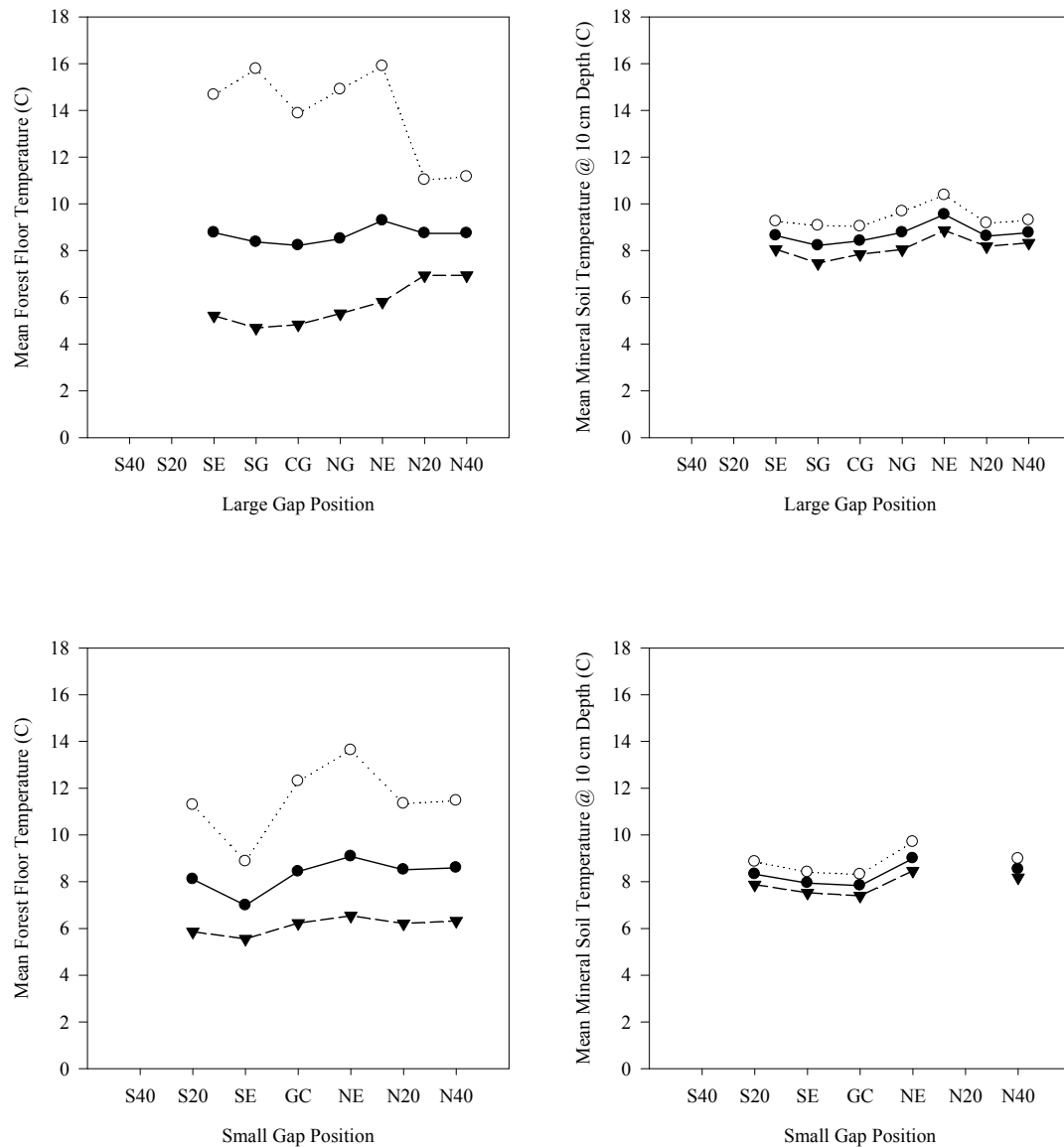


Figure 3.19. Mean daily forest floor and mineral soil temperatures from January 2006 to January 2007. Open circles indicate mean daily maximum temperature, closed circles indicate mean annual daily temperature, and closed triangles indicate mean daily minimum temperatures. Missing data points at transect positions indicate datalogger malfunction.

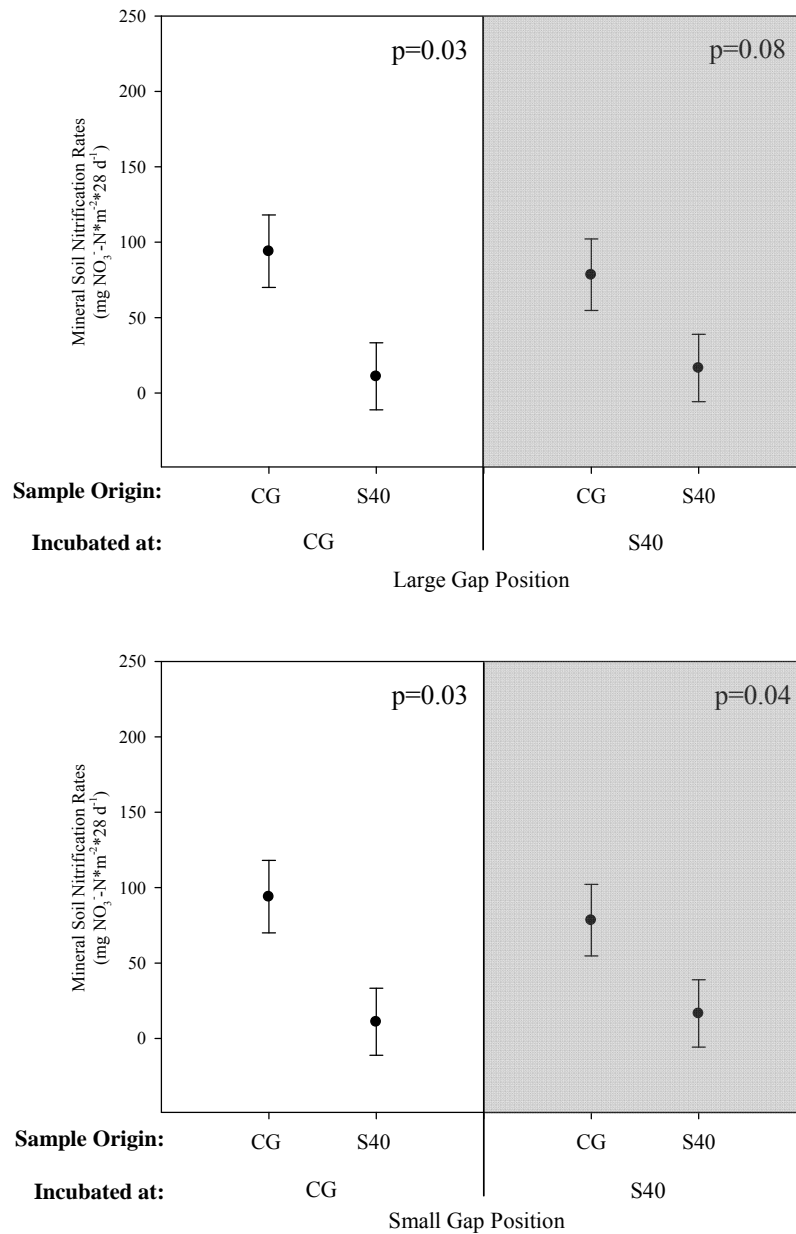


Figure 3.20. Mineral soil net nitrification rates of reciprocal transfer incubation samples. White areas indicate gap incubation positions, while shaded areas indicate forest positions. p-values indicate the significance of comparisons between samples incubated at the same gap position, but originating from different gap positions. All comparisons were Bonferroni-adjusted.

Table 2.1. General site characteristics.

Property	SITE		
	Delph Creek	Green Peak	Keel Mountain
Latitude <sup>€</sup>	45° 15' 56.0"	44° 22' 00.0"	44° 31' 41.0"
Longitude <sup>€</sup>	122° 9' 33.0"	123° 27' 30.0"	122° 37' 55.0"
Elevation (m) <sup>€</sup>	557-704	472-741	660-770
Aspect <sup>€</sup>	NW N W	SE E NE	SW W N
Parent Material <sup>\$</sup>	Mixed sedimentary and volcanic	Sedimentary	Mixed sedimentary and volcanic
Soil Subgroups <sup>\$</sup>	Andic Dystrudepts	Andic Dystrudepts Typic Dystrudepts	Andic Dystrudepts
Mean Annual Maximum Temperature (°C) <sup>£</sup>	14.0	17.4	15.3
Mean Annual Minimum Temperature (°C) <sup>£</sup>	3.3	6.5	4.5
Mean Annual Precipitation (mm) <sup>£</sup>	1874	1830	1760
Dominant Plant Associations <sup>€</sup>	Tsuga heterophylla/Oxalis oregana	Tsuga heterophylla/Mahonia nervosa-Oxalis oregana	Tsuga heterophylla/Oxalis oregana
Stand Age (yrs) <sup>€</sup>	72	74	60
Year of Gap Creation <sup>€</sup>	2000	2000	1998
Logging System <sup>€</sup>	Tractor yarding	Cable yarding	Tractor yarding
Site Index (Kings at 50 years) <sup>€</sup>	122	123	127

€ Cissell et al. 2006

\$ Natural Resource Conservation Service 1975, 1985, and 1987

£ Spatial Climate Analysis Service 1895-2007



Table 2.2. Physical and chemical characteristics of forest floor and mineral soil.

Material	Property	SITE		
		Delph Creek	Green Peak	Keel Mountain
Forest Floor	Mass ( $\text{kg}\cdot\text{m}^{-2}$ )	1.73	1.09	1.66
	Total C ( $\text{g C}\cdot\text{m}^{-2}$ )	881 (50.8%)	492 (45.3%)	798 (47.0%)
	Total N ( $\text{g N}\cdot\text{m}^{-2}$ )	20.9 (1.20%)	13.7 (1.26%)	19.4 (1.19%)
	C:N Ratio (mass:mass)	42.2	36.0	41.2
Mineral Soil	pH	5.09	6.06	5.26
	0-10 cm Bulk Density ( $\text{g}\cdot\text{cm}^{-3}$ )	0.76	1.18	0.73
	Total C ( $\text{g C}\cdot\text{m}^{-2}$ )	5390 (7.25%)	9330 (8.24%)	7830 (10.82%)
	Total N ( $\text{g N}\cdot\text{m}^{-2}$ )	185 (0.25%)	365 (0.32%)	220 (0.30%)
	C:N Ratio (mass:mass)	29.1	25.5	35.6

Note: Values are means of forest reference plots (n=3). Values in parentheses are a percentage of total mass.

Table 3.1. Results of ANOVA with repeated measures in space for forest floor response variables along transects.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p
Large	<b>Forest Floor Mass</b>	kg·m <sup>-2</sup>	TOEP(1)	8	16	2.59	<b>0.050</b>
	% Moisture <sup>€</sup>	%	AR(1)	8	16	0.76	0.641
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	1.45	0.251
	Total N	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.43	0.260
	C:N Ratio	mass:mass	TOEP(1)	8	16	0.67	0.715
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	AR(1)	8	16	0.76	0.641
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	8	16	0.20	0.988
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(2)	8	16	1.53	0.223
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	1.21	0.356
	% Nitrification <sup>€</sup>	%	TOEP(9)	8	16	1.79	0.153
	<b>IER NH<sub>4</sub><sup>+</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	TOEP(2)	8	16	3.87	<b>0.010</b>
	<b>IER NO<sub>3</sub><sup>-</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	TOEP(9)	8	16	3.05	<b>0.027</b>
Small	Forest Floor Mass	kg·m <sup>-2</sup>	TOEP(1)	6	12	2.06	0.136
	% Moisture <sup>€</sup>	%	TOEP(1)	6	12	1.75	0.193
	Total C	g C·m <sup>-2</sup>	AR(1)	6	12	0.92	0.512
	Total N	g N·m <sup>-2</sup>	TOEP(3)	6	12	1.53	0.251
	C:N Ratio	mass:mass	TOEP(2)	6	12	1.49	0.262
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	6	12	1.14	0.397
	<b>Extractable NO<sub>3</sub><sup>-</sup></b>	mg N·m <sup>-2</sup>	UN(1)	6	12	3.73	<b>0.025</b>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(2)	6	12	1.23	0.355
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	1.20	0.372
	% Nitrification <sup>€</sup>	%	UN(1)	6	12	1.36	0.304
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	AR(1)	6	12	1.90	0.161
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	TOEP(1)	6	12	1.49	0.262

€ Response variable not natural log-transformed.

Note: Covariance structure abbreviations denote the following: AR(1) = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. Boldface type denotes a significant (p≤0.05) transect position effect. Italicized type denotes a marginally significant (p≤0.1) transect position effect.

Table 3.2. Results of ANOVA with repeated measures in space for mineral soil response variables along transects.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p
Large	Bulk Density	kg·m <sup>-2</sup>	AR(1)	8	16	0.69	0.696
	% Moisture <sup>€</sup>	%	TOEP(7)	8	16	0.37	0.920
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	1.45	0.251
	Total N	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.43	0.260
	C:N Ratio	mass:mass	TOEP(1)	8	16	0.67	0.715
	<b>Extractable NH<sub>4</sub><sup>+</sup></b>	mg N·m <sup>-2</sup>	AR(1)	8	16	3.52	<b>0.015</b>
	<i>Extractable NO<sub>3</sub><sup>-</sup></i>	mg N·m <sup>-2</sup>	TOEP(1)	8	16	2.43	<i>0.062</i>
	<b>Net N Mineralization</b>	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	3.30	<b>0.020</b>
	<b>Net Nitrification</b>	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	AR(1)	8	16	4.11	<b>0.008</b>
	<b>% Nitrification<sup>€</sup></b>	%	UN(1)	8	16	3.09	<b>0.026</b>
	<b>IER NH<sub>4</sub><sup>+</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	AR(1)	8	16	3.20	<b>0.023</b>
	<b>IER NO<sub>3</sub><sup>-</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	TOEP(2)	8	16	3.17	<b>0.024</b>
	Extractable DOC	g C·m <sup>-2</sup>	AR(1)	8	16	1.28	0.322
	Extractable DON	g N·m <sup>-2</sup>	TOEP(3)	8	16	1.65	0.187
	Microbial C	g C·m <sup>-2</sup>	TOEP(1)	8	16	1.05	0.439
	Microbial N	g N·m <sup>-2</sup>	AR(1)	8	16	0.74	0.653
	<b>Microbial C:N</b>	mass:mass	UN(1)	8	16	11.68	<b>&lt;0.001</b>
Small	Bulk Density	kg·m <sup>-2</sup>	TOEP(1)	6	12	1.82	0.178
	Percent Moisture <sup>€</sup>	%	TOEP(1)	6	12	1.26	0.344
	Total C	g C·m <sup>-2</sup>	AR(1)	6	12	0.92	0.512
	Total N	g N·m <sup>-2</sup>	TOEP(3)	6	12	1.53	0.251
	C:N Ratio	mass:mass	TOEP(2)	6	12	1.49	0.262
	<b>Extractable NH<sub>4</sub><sup>+</sup></b>	g N·m <sup>-2</sup>	AR(1)	6	12	9.10	<b>0.001</b>
	<b>Extractable NO<sub>3</sub><sup>-</sup></b>	g N·m <sup>-2</sup>	UN(1)	6	12	9.24	<b>0.001</b>
	Net N Mineralization	g N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	1.14	0.398
	<b>Net Nitrification</b>	g N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(2)	6	12	5.28	<b>0.007</b>
	<b>Percent Nitrification<sup>€</sup></b>	%	UN(2)	6	12	6.00	<b>0.004</b>
	<b>IER NH<sub>4</sub><sup>+</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	UN(1)	6	12	4.89	<b>0.009</b>
	<b>IER NO<sub>3</sub><sup>-</sup></b>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	AR(1)	6	12	8.83	<b>0.001</b>
	DOC	g C·m <sup>-2</sup>	TOEP(1)	6	12	0.69	0.664
	<b>DON</b>	g N·m <sup>-2</sup>	AR(1)	6	12	3.24	<b>0.039</b>
	Microbial C	g C·m <sup>-2</sup>	TOEP(1)	6	12	0.08	0.997
	Microbial N	g N·m <sup>-2</sup>	AR(1)	6	12	0.49	0.807
	<b>Microbial C:N</b>	mass:mass	AR(1)	6	12	4.27	<b>0.016</b>

€ Response variable not natural log-transformed.

Note: Covariance structure abbreviations denote the following: AR(1) = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. Boldface type denotes a significant (p≤0.05) transect position effect. Italicized type denotes a marginally significant (p≤0.1) transect position effect.

Table 3.3. Results of ANOVA with repeated measures in space for litterfall and decomposition response variables along transects.

Material	Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p
Litter	Large	<b>C inputs</b>	g C·m <sup>-2</sup>	UN(1)	8	16	8.66	<b>&lt;0.001</b>
		<b>N inputs</b>	g N·m <sup>-2</sup>	UN(1)	8	16	13.62	<b>&lt;0.001</b>
		% N	%	UN(1)	8	16	1.77	0.158
		<b>C:N Ratio</b>	mass:mass	TOEP(1)	8	16	3.04	<b>0.028</b>
	Small	<b>C inputs</b>	g C·m <sup>-2</sup>	UN(1)	6	12	4.71	<b>0.011</b>
		N inputs	g N·m <sup>-2</sup>	AR(1)	6	12	1.85	0.172
		% N	%	TOEP(1)	6	12	6.23	<b>0.004</b>
		<b>C:N Ratio</b>	mass:mass	TOEP(1)	6	12	6.59	<b>0.003</b>
Wood	Large	Percent mass remaining after 330 days	%	UN(1)	8	16	1.30	0.310
		k-values	yr <sup>-1</sup>	TOEP(9)	8	16	0.82	0.595
	Small	Percent mass remaining after 330 day	%	TOEP(3)	6	12	1.43	0.282
		<i>k-values</i>	yr <sup>-1</sup>	AR(1)	6	12	2.90	<i>0.055</i>

Note: All variables were log-transformed. Covariance structure abbreviations denote the following: AR(1) = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. Boldface type denotes a significant ( $p \leq 0.05$ ) transect position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect.

Table 3.4. Results of ANOVA for forest floor, mineral soil, litterfall, and decomposition response variables in large and small gap centers.

Material	Variable	Units	F <sub>1,2</sub>	p
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	0.36	0.611
	% Moisture <sup>€</sup>	%	6.64	0.123
	Total C	g C·m <sup>-2</sup>	0.47	0.565
	Total N	g N·m <sup>-2</sup>	0.01	0.920
	C:N Ratio	mass:mass	15.50	0.059
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	0.39	0.595
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.02	0.890
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.17	0.717
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.02	0.899
	% Nitrification <sup>€</sup>	%	1.70	0.323
	IER NH <sub>4</sub> <sup>+</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	0.06	0.827
	IER NO <sub>3</sub> <sup>-</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	6.11	0.132
Mineral Soil	Bulk Density	kg·m <sup>-2</sup>	0.47	0.565
	% Moisture <sup>€</sup>	%	0.16	0.728
	Total C	g C·m <sup>-2</sup>	0.19	0.707
	Total N	g N·m <sup>-2</sup>	0.12	0.759
	C:N Ratio	mass:mass	2.31	0.268
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	3.76	0.192
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	7.65	0.110
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.26	0.664
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	3.25	0.213
	% Nitrification <sup>€</sup>	%	1.20	0.388
	IER NH <sub>4</sub> <sup>+</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	0.00	0.998
	IER NO <sub>3</sub> <sup>-</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	2.86	0.233
	Extractable DOC	g C·m <sup>-2</sup>	0.62	0.514
	Extractable DON	g N·m <sup>-2</sup>	1.39	0.359
	Microbial C	g C·m <sup>-2</sup>	0.24	0.673
	Microbial N	g N·m <sup>-2</sup>	0.89	0.446
	Microbial C:N Ratio	mass:mass	2.84	0.234
Litter	C inputs	g·m <sup>-2</sup>	1.71	0.321
	N inputs	g·m <sup>-2</sup>	3.73	0.193
	Total N	%	0.50	0.551
	C:N Ratio	mass:mass	2.19	0.277
Tongue Depressors	Mass remaining after 330 days	%	0.01	0.936
	k-values	yr <sup>-1</sup>	0.62	0.515

€ Response variable not natural log-transformed.

Note: Boldface type denotes a significant ( $p \leq 0.05$ ) gap size effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect.

Table 3.5. Results of split-plot ANOVA for forest floor and mineral soil reciprocal transfer incubations.

Material	Gap Size	Variable	Incubation Environment		Sample Origin	
Forest Floor	Large	Net N mineralization	$F_{1,4}=0.58$	$p=0.490$	$F_{2,4}=0.12$	$p=0.888$
		Net nitrification	$F_{1,4}=0.06$	$p=0.819$	$F_{2,4}=0.58$	$p=0.602$
	Small	Net N mineralization	$F_{1,4}=0.91$	$p=0.395$	$F_{2,4}=0.85$	$p=0.493$
		Net nitrification	$F_{1,4}=0.01$	$p=0.912$	$F_{2,4}=0.68$	$p=0.557$
Mineral Soil	Large	Net N mineralization	$F_{1,4}=0.55$	$p=0.613$	$F_{2,4}=2.26$	$p=0.207$
		Net nitrification	$F_{1,4}=0.03$	$p=0.872$	$F_{2,4}=7.87$	<b><math>p=0.041</math></b>
	Small	Net N mineralization	$F_{1,4}=0.08$	$p=0.793$	$F_{2,4}=3.22$	$p=0.147$
		Net nitrification	$F_{1,4}=0.20$	$p=0.674$	$F_{2,4}=10.30$	<b><math>p=0.026</math></b>

Note: All variables were log-transformed. Boldface type denotes a significant ( $p \leq 0.05$ ) fixed effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) fixed effect.

Table 3.6. Results of ANOVA with repeated measures in space for the standard deviations of forest floor and mineral soil response variables along transects.

Type	Gap Size	Variable	Covariance Structure	Num df	Den df	F	p	Gap	Edge	Forest
Forest Floor	Large	Extractable $\text{NH}_4^+$	AR(1)	8	16	0.35	0.930			
		Extractable $\text{NO}_3^-$	AR(1)	8	16	1.11	0.407			
		Net N Mineralization	AR(1)	8	16	2.19	<i>0.086</i>	a	a	b
		Net Nitrification	AR(1)	8	16	2.57	<i>0.052</i>	a	ab	b
		Resin $\text{NH}_4^+$	TOEP(1)	8	16	1.70	0.175			
		Resin $\text{NO}_3^-$	TOEP(1)	8	16	2.04	0.108			
	Small	<b>Extractable <math>\text{NH}_4^+</math></b>	TOEP(1)	6	12	3.84	<b>0.023</b>	a	a	b
		<b>Extractable <math>\text{NO}_3^-</math></b>	TOEP(1)	6	12	3.94	<b>0.021</b>	a	a	b
		Net N Mineralization	AR(1)	6	12	1.34	0.313			
		Net Nitrification	AR(1)	6	12	1.13	0.401			
		Resin $\text{NH}_4^+$	AR(1)	6	12	1.53	0.250			
		Resin $\text{NO}_3^-$	AR(1)	6	12	0.80	0.585			
Mineral Soil	Large	Extractable $\text{NH}_4^+$	TOEP(1)	8	16	1.28	0.318			
		Extractable $\text{NO}_3^-$	AR(1)	8	16	1.12	0.400			
		<b>Net N Mineralization</b>	AR(1)	8	16	3.32	<b>0.020</b>	a	a	b
		Net Nitrification	AR(1)	8	16	1.83	0.144			
		<b>Resin <math>\text{NH}_4^+</math></b>	TOEP(2)	8	16	3.19	<b>0.023</b>	a	a	b
		Resin $\text{NO}_3^-$	TOEP(1)	8	16	1.19	0.363			
	Small	Extractable $\text{NH}_4^+$	TOEP(1)	6	12	0.91	0.522			
		<b>Extractable <math>\text{NO}_3^-</math></b>	AR(1)	6	12	4.20	<b>0.017</b>	a	b	ab
		Net N Mineralization	AR(1)	6	12	2.42	<i>0.091</i>	a	a	b
		<b>Net Nitrification</b>	TOEP(1)	6	12	3.38	<b>0.035</b>	a	a	b
		Resin $\text{NH}_4^+$	TOEP(2)	6	12	2.81	<i>0.060</i>	a	a	b
		Resin $\text{NO}_3^-$	AR(1)	6	12	1.56	0.242			

Note: All variables were log-transformed. Covariance structure abbreviations denote the following: AR(1) = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. Boldface type denotes a significant ( $p \leq 0.05$ ) transect position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect. Different letters in a row denote significant differences ( $p \leq 0.05$ ) among group means of the standard deviations of response variables, with those labeled "a" exceeding those labeled "b."

Table 3.7. Results of ANOVA with repeated measures in space for the coefficients of variance of forest floor and mineral soil response variables along transects.

Type	Gap Size	Variable	Covariance Structure	Num df	Den df	F	p	Gap	Edge	Forest
Forest Floor	Large	Extractable $\text{NH}_4^+$	AR(1)	8	16	0.37	0.924			
		Extractable $\text{NO}_3^-$	TOEP(1)	8	16	1.64	0.189			
		Net N Mineralization	AR(1)	8	16	0.85	0.572			
		Net Nitrification	TOEP(1)	8	16	0.96	0.499			
		Resin $\text{NH}_4^+$	TOEP(1)	8	16	0.42	0.892			
		Resin $\text{NO}_3^-$	AR(1)	8	16	0.91	0.531			
	Small	Extractable $\text{NH}_4^+$	TOEP(1)	6	12	1.72	0.201			
		Extractable $\text{NO}_3^-$	TOEP(1)	6	12	2.18	0.118			
		Net N Mineralization	AR(1)	6	12	0.66	0.685			
		Net Nitrification	AR(1)	6	12	0.77	0.608			
		Resin $\text{NH}_4^+$	AR(1)	6	12	2.05	0.137			
		Resin $\text{NO}_3^-$	TOEP(2)	6	12	0.87	0.543			
Mineral Soil	Large	Extractable $\text{NH}_4^+$	AR(1)	8	16	1.50	0.235			
		Extractable $\text{NO}_3^-$	AR(1)	8	16	1.33	0.297			
		Net N Mineralization	AR(1)	8	16	1.12	0.401			
		Net Nitrification	AR(1)	8	16	0.95	0.507			
		Resin $\text{NH}_4^+$	AR(1)	8	16	1.23	0.346			
		Resin $\text{NO}_3^-$	TOEP(1)	8	16	0.80	0.612			
	Small	Extractable $\text{NH}_4^+$	AR(1)	6	12	1.53	0.249			
		<b>Extractable <math>\text{NO}_3^-</math></b>	TOEP(1)	6	12	<b>4.03</b>	<b>0.019</b>	a	b	b
		Net N Mineralization	AR(1)	6	12	1.78	0.185			
		<b>Net Nitrification</b>	TOEP(1)	6	12	<b>2.99</b>	<b>0.050</b>	a	ab	b
		Resin $\text{NH}_4^+$	AR(1)	6	12	1.22	0.360			
		Resin $\text{NO}_3^-$	TOEP(1)	6	12	0.44	0.839			

Note: All variables were log-transformed. Covariance structure abbreviations denote the following: AR(1) = autoregressive with all positions correlated, UN(x) = unstructured with x positions correlated, TOEP(x) = banded toeplitz with x positions correlated. Boldface type denotes a significant ( $p \leq 0.05$ ) transect position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect. Different letters in a row denote significant differences ( $p \leq 0.05$ ) among group means of the coefficients of variance of response variables, with those labeled "a" exceeding those labeled "b."



## **APPENDICES**

## **Appendix A. Seasonal Analyses**

Appendix Table A1. Results of ANOVA with repeated measures in space for forest floor response variables along transects in February 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>€</sup>	%	AR(1)	8	16	1.98	0.116	77.8 (76.2, 79.4)	74.0 (72.4, 75.6)	74.6 (73.0, 76.2)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	2.42	0.063	420 (289, 609)	570 (393, 826)	679 (468, 985)
	Total N	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.56	0.212	11.5 (7.8, 16.9)	13.5 (9.2, 19.9)	16.6 (11.3, 24.3)
	Total C:N	mass:mass	TOEP(1)	8	16	1.29	0.317	42.6 (39.5, 45.8)	49.1 (45.6, 52.9)	47.8 (44.4, 51.5)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	8	16	1.23	0.345	7.73 (4.72, 12.67)	7.01 (4.28, 11.48)	8.99 (5.49, 14.73)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(2)	8	16	1.61	0.198	0.144 (0.100, 0.207)	0.141 (0.098, 0.202)	0.163 (0.113, 0.234)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	1.51	0.229	12.47 (3.80, 21.22)	1.69 (-6.89, 10.34)	1.24 (-7.34, 9.89)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(4)	8	16	0.98	0.484	1.354 (0.093, 2.220)	0.208 (0.001, 0.415)	0.433 (0.003, 0.862)
	% Nitrification <sup>€</sup>	%	TOEP(6)	8	16	0.29	0.958	5.63 (0.90, 10.36)	5.92 (1.19, 10.65)	2.44 (-2.29, 7.17)
Small	% Moisture <sup>€</sup>	%	TOEP(1)	6	12	0.77	0.608	77.6 (75.3, 80.0)	74.8 (72.4, 77.1)	75.4 (73.0, 77.7)
	<b>Total C</b>	g C·m <sup>-2</sup>	UN(1)	6	12	3.72	<b>0.025</b>	381 (276, 526) <b>a</b>	563 (450, 704) <b>a</b>	697 (537, 904) <b>a</b>
	<b>Total N</b>	g N·m <sup>-2</sup>	TOEP(5)	6	12	3.34	<b>0.036</b>	11.0 (8.8, 13.9) <b>a</b>	14.5 (11.6, 18.2) <b>ab</b>	17.9 (14.3, 22.5) <b>b</b>
	Total C:N	mass:mass	AR(1)	6	12	1.38	0.297	40.2 (38.1, 42.5)	45.3 (42.9, 47.8)	45.8 (43.3, 48.4)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	6	12	1.10	0.414	7.03 (5.33, 9.26)	6.45 (4.90, 8.51)	9.38 (7.12, 12.36)
	<b>Extractable NO<sub>3</sub><sup>-</sup></b>	mg N·m <sup>-2</sup>	UN(1)	6	12	3.26	<b>0.038</b>	0.120 (0.088, 0.165) <b>a</b>	0.138 (0.110, 0.173) <b>a</b>	0.174 (0.135, 0.223) <b>a</b>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	0.77	0.607	21.97 (2.68, 41.63)	4.41 (1.02, 7.80)	2.78 (-1.33, 6.92)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	0.73	0.637	0.547 (0.116, 0.978)	0.323 (0.010, 0.636)	0.019 (-0.001, 0.038)
	% Nitrification <sup>€</sup>	%	UN(1)	6	12	1.53	0.250	1.33 (0.64, 2.02)	3.35 (1.56, 5.14)	1.34 (0.52, 2.16)

€ Response variable not natural log-transformed.

Note: Boldface type denotes a significant ( $p \leq 0.05$ ) position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect. Different letters in a row denote significant differences ( $p \leq 0.05$ ) among group means of response variables. Ranges of standard errors are in parentheses.

Appendix Table A2. Results of ANOVA with repeated measures in space for forest floor response variables along transects in May 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>€</sup>	%	AR(1)	8	16	1.18	0.369	52.7 (37.9, 67.4)	56.7 (41.9, 71.4)	54.6 (39.9, 69.4)
	Total C	g C·m <sup>-2</sup>	TOEP(2)	8	16	2.27	0.077	425 (292, 619) <i>a</i>	569 (393, 824) <i>ab</i>	677 (466, 984) <i>b</i>
	Total N	g N·m <sup>-2</sup>	TOEP(3)	8	16	2.37	0.068	10.3 (6.9, 15.2) <i>a</i>	12.5 (8.5, 18.5) <i>ab</i>	16.5 (11.2, 24.4) <i>b</i>
	Total C:N	mass:mass	TOEP(1)	8	16	1.93	0.125	49.1 (45.3, 53.3)	53.1 (49.1, 57.3)	48.0 (44.3, 51.9)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	8	16	2.01	0.112	2.83 (2.15, 3.73)	4.89 (3.71, 6.44)	5.56 (4.22, 7.32)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	8	16	0.76	0.638	0.157 (0.091, 0.255)	0.141 (0.090, 0.220)	0.135 (0.094, 0.193)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	1.69	0.176	121.2 (44.6, 240.8)	159.1 (83.7, 239.8)	43.7 (-7.8, 97.8)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	1.78	0.155	3.859 (-0.237, 10.252)	-0.062 (-0.136, 0.012)	0.706 (0.017, 1.396)
	% Nitrification <sup>€</sup>	%	UN(1)	8	16	1.78	0.155	5.22 (0.76, 9.67)	1.24 (0.10, 2.39)	1.33 (0.43, 2.24)
Small	% Moisture <sup>€</sup>	%	TOEP(1)	6	12	0.80	0.588	51.3 (35.8, 66.9)	50.4 (34.8, 65.9)	52.4 (36.9, 68.0)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	6	12	2.09	0.130	426 (349, 519)	586 (478, 718)	704 (576, 860)
	Total N	g N·m <sup>-2</sup>	TOEP(1)	6	12	1.38	0.298	11.2 (9.0, 13.9)	14.5 (11.6, 18.1)	16.5 (13.2, 20.5)
	Total C:N	mass:mass	TOEP(2)	6	12	1.22	0.360	44.4 (41.8, 47.2)	47.6 (44.7, 50.6)	49.6 (46.6, 52.7)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(6)	6	12	0.45	0.830	6.52 (4.63, 9.19)	4.11 (2.92, 5.79)	4.74 (3.37, 6.68)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	6	12	2.77	0.063	0.144 (0.084, 0.247) <i>a</i>	0.107 (0.080, 0.142) <i>a</i>	0.131 (0.097, 0.177) <i>a</i>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(2)	6	12	1.18	0.380	136.5 (43.6, 237.7)	107.5 (56.3, 161.3)	25.3 (5.8, 45.1)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	0.96	0.493	1.759 (0.302, 3.218)	0.103 (0.023, 0.183)	0.305 (0.054, 0.556)
	% Nitrification <sup>€</sup>	%	UN(1)	6	12	1.13	0.403	2.66 (1.23, 4.10)	1.85 (0.46, 3.23)	4.49 (1.37, 7.62)

€ Response variable not natural log-transformed.

Note: Boldface type denotes a significant ( $p \leq 0.05$ ) position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect. Different letters in a row denote significant differences ( $p \leq 0.05$ ) among group means of response variables. Ranges of standard errors are in parentheses.

Appendix Table A3. Results of ANOVA with repeated measures in space for forest floor response variables along transects in August 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>€</sup>	%	TOEP(4)	8	16	1.97	0.118	18.3 (15.4, 21.1)	17.0 (14.2, 19.9)	20.2 (17.3, 23.0)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	2.47	0.059	422 (297, 601)	560 (394, 798)	677 (475, 963)
	<b>Total N</b>	g N·m <sup>-2</sup>	TOEP(7)	8	16	4.80	<b>0.004</b>	10.4 (7.1, 15.2) <b>a</b>	12.3 (8.4, 17.9) <b>ab</b>	16.2 (11.1, 23.7) <b>b</b>
	Total C:N	mass:mass	TOEP(1)	8	16	1.81	0.149	47.4 (44.7, 50.3)	53.2 (50.2, 56.5)	48.7 (45.9, 51.7)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	8	16	0.55	0.804	10.60 (6.53, 17.21)	9.45 (5.82, 15.34)	9.27 (5.71, 15.04)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	8	16	0.76	0.640	0.162 (0.085, 0.298)	0.148 (0.093, 0.235)	0.150 (0.101, 0.224)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(1)	8	16	0.83	0.588	10.7 (-3.3, 24.9)	13.6 (-0.4, 27.9)	11.2 (-2.8, 25.4)
	<b>Net Nitrification</b>	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(2)	8	16	3.21	<b>0.022</b>	0.571 (0.220, 1.140) <b>a</b>	0.044 (-0.053, 0.141) <b>b</b>	0.233 (0.057, 0.410) <b>ab</b>
	% Nitrification <sup>€</sup>	%	UN(1)	8	16	1.98	0.117	2.76 (0.86, 4.66)	2.51 (0.76, 4.26)	0.30 (0.08, 0.51)
Small	% Moisture <sup>€</sup>	%	TOEP(3)	6	12	8.45	<b>&lt;0.001</b>	28.4 (25.3, 31.6) <b>a</b>	20.2 (17.1, 23.3) <b>b</b>	19.8 (16.7, 22.9) <b>b</b>
	<b>Total C</b>	g C·m <sup>-2</sup>	UN(1)	6	12	3.97	0.020	420 (316, 559)	564 (475, 669)	689 (561, 846)
	<b>Total N</b>	g N·m <sup>-2</sup>	AR(1)	6	12	1.85	0.172	11.3 (8.9, 14.3)	12.6 (9.9, 16.0)	16.5 (13.0, 20.9)
	Total C:N	mass:mass	TOEP(1)	6	12	1.25	0.347	43.4 (40.3, 46.7)	52.1 (48.4, 56.1)	48.8 (45.3, 52.5)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	CS	8	16	0.55	0.804	21.72 (15.58, 30.29)	7.41 (5.31, 10.33)	9.31 (6.68, 12.99)
	<b>Extractable NO<sub>3</sub><sup>-</sup></b>	mg N·m <sup>-2</sup>	UN(1)	6	12	3.23	<b>0.040</b>	0.930 (0.311, 2.783) <b>a</b>	0.125 (0.090, 0.173) <b>a</b>	0.141 (0.111, 0.179) <b>a</b>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	1.04	0.447	-117.9 (-243.4, 28.5)	14.8 (0.5, 29.2)	10.0 (3.6, 16.5)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(1)	6	12	0.95	0.494	-133.5 (-180.3, -84.0)	0.3 (-53.8, 57.5)	0.2 (-53.9, 57.4)
	% Nitrification <sup>€</sup>	%	UN(7)	6	12	5.96	<b>0.004</b>	0 (0, 0) <b>a</b>	0.30 (0.17, 0.44) <b>a</b>	1.27 (0.21, 2.33) <b>a</b>

€ Response variable not natural log-transformed.

Note: Boldface type denotes a significant ( $p \leq 0.05$ ) position effect. Italicized type denotes a marginally significant ( $p \leq 0.1$ ) transect position effect. Different letters in a row denote significant differences ( $p \leq 0.05$ ) among group means of response variables. Ranges of standard errors are in parentheses.

Appendix Table A4. Results of ANOVA with repeated measures in space for mineral soil response variables along transects in February 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>ε</sup>	%	TOEP(6)	8	16	0.54	0.812	42.6 (39.6, 45.5)	42.6 (39.6, 45.6)	41.2 (38.2, 44.2)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	0.99	0.481	6220 (5190, 7450)	6890 (5760, 8260)	5360 (4470, 6420)
	Total N	g N·m <sup>-2</sup>	UN(2)	8	16	0.76	0.645	209 (182, 247)	222 (190, 260)	180 (157, 206)
	Total C:N	mass:mass	TOEP(4)	8	16	1.26	0.328	34.7 (31.7, 37.8)	36.1 (33.1, 39.5)	34.8 (31.8, 38.0)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(3)	8	16	4.60	<b>0.005</b>	268 (212, 338) <b>a</b>	136 (108, 172) <b>b</b>	119 (94, 150) <b>b</b>
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	8	16	3.71	<b>0.012</b>	6.86 (4.64, 9.81) <b>a</b>	3.45 (2.93, 4.08) <b>b</b>	2.98 (2.50, 3.54) <b>c</b>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	1.10	0.415	82.3 (2.7, 177.7)	78.9 (8.1, 154.6)	89.0 (39.8, 140.6)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(9)	8	16	2.18	<i>0.088</i>	37.02 (25.05, 49.13) <i>a</i>	8.18 (-3.46, 19.96) <i>b</i>	6.24 (-5.38, 17.99) <i>b</i>
	% Nitrification <sup>ε</sup>	%	UN(1)	8	16	3.65	<b>0.013</b>	35.81 (23.29, 48.33) <b>a</b>	3.15 (1.23, 5.06) <b>b</b>	7.12 (1.69, 12.56) <b>b</b>
	Extractable DOC	g C·m <sup>-2</sup>	AR(1)	8	16	0.61	0.759	19.6 (14.7, 26.2)	22.0 (16.5, 29.3)	19.6 (14.7, 26.2)
	Extractable DON	g N·m <sup>-2</sup>	AR(1)	8	16	0.85	0.577	1.52 (1.26, 1.83)	1.39 (1.15, 1.67)	1.20 (0.99, 1.44)
	Microbial C	g C·m <sup>-2</sup>	AR(1)	8	16	1.13	0.395	18.7 (15.9, 22.1)	25.1 (21.3, 29.5)	20.1 (17.0, 23.7)
	Microbial N	g N·m <sup>-2</sup>	TOEP(3)	8	16	1.01	0.464	3.23 (2.63, 3.98)	3.83 (3.12, 4.72)	2.87 (2.33, 3.53)
	Microbial C:N	mass:mass	TOEP(6)	8	16	3.78	<b>0.011</b>	6.76 (6.05, 7.55) <b>a</b>	7.62 (6.82, 8.52) <b>b</b>	7.82 (7.00, 8.75) <b>b</b>
Small	% Moisture <sup>ε</sup>	%	TOEP(1)	6	12	1.26	0.344	41.6 (39.2, 44.0)	41.3 (38.9, 43.7)	41.0 (38.6, 43.4)
	Total C	g C·m <sup>-2</sup>	AR(1)	6	12	0.42	0.854	6260 (5400, 7260)	5930 (5120, 6880)	5350 (4620, 6210)
	Total N	g N·m <sup>-2</sup>	AR(1)	6	12	0.80	0.586	239 (204, 280)	219 (187, 256)	193 (165, 226)
	Total C:N	mass:mass	TOEP(3)	6	12	1.83	0.175	30.6 (28.8, 32.5)	31.6 (29.8, 33.7)	32.3 (30.4, 34.3)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	6	12	9.43	<b>0.001</b>	456 (363, 572) <b>a</b>	147 (117, 184) <b>b</b>	128 (102, 161) <b>b</b>
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(2)	6	12	14.7	<b>0.000</b>	14.83 (9.62, 22.88) <b>a</b>	3.77 (2.97, 4.78) <b>a</b>	3.16 (2.47, 4.04) <b>a</b>
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(1)	6	12	0.56	0.751	172.6 (70.7, 284.2)	86.2 (-8.2, 189.6)	86.4 (-8.1, 189.8)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	3.62	<b>0.027</b>	138.2 (105.4, 171.9) <b>a</b>	11.9 (0.7, 23.2) <b>b</b>	42.5 (3.7, 82.7) <b>b</b>
	% Nitrification <sup>ε</sup>	%	UN(3)	6	12	4.09	<b>0.018</b>	50.89 (37.89, 63.88) <b>a</b>	5.43 (1.55, 9.32) <b>b</b>	8.21 (1.17, 15.24) <b>b</b>
	DOC	g C·m <sup>-2</sup>	TOEP(1)	6	12	1.64	0.220	20.5 (16.1, 26.1)	22.6 (17.7, 28.7)	18.4 (3.8, 4.8)
	DON	g N·m <sup>-2</sup>	TOEP(1)	6	12	2.11	0.127	1.51 (1.31, 1.73)	1.48 (1.29, 1.70)	1.17 (1.01, 1.16)
	Microbial C	g C·m <sup>-2</sup>	CS	6	12	0.18	0.978	22.1 (17.6, 27.8)	25.4 (20.2, 31.9)	23.6 (18.8, 29.6)
	Microbial N	g N·m <sup>-2</sup>	TOEP(2)	6	12	0.36	0.892	3.81 (2.95, 4.94)	3.76 (2.90, 4.86)	3.31 (2.56, 4.28)
	Microbial C:N	mass:mass	TOEP(1)	6	12	2.41	<i>0.092</i>	6.77 (6.34, 7.23) <i>a</i>	7.89 (7.38, 8.43) <i>b</i>	8.30 (7.77, 8.87) <i>b</i>

<sup>ε</sup> Response variable not natural log-transformed.

Note: Boldface type denotes a significant (p≤0.05) position effect. Italicized type denotes a marginally significant (p≤0.1) transect position effect. Different letters in a row denote significant differences (p≤0.05) among group means of response variables. Ranges of standard errors are in parentheses.

Appendix Table A5. Results of ANOVA with repeated measures in space for mineral soil response variables along transects in May 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>€</sup>	%	AR(1)	8	16	0.46	0.868	23.8 (21.1, 26.5)	23.5 (20.8, 26.2)	24.0 (21.3, 26.8)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	1.30	0.310	6310 (5320, 7480)	5970 (5040, 7080)	5330 (4500, 6320)
	Total N	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.09	0.417	215 (183, 253)	205 (174, 241)	182 (155, 214)
	Total C:N	mass:mass	TOEP(5)	8	16	0.48	0.853	34.2 (32.2, 36.2)	34.0 (32.1, 36.0)	34.2 (32.2, 36.2)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(2)	8	16	1.36	0.287	157 (125, 196)	131 (104, 164)	106 (84, 132)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	TOEP(2)	8	16	1.01	0.468	4.38 (3.11, 6.17)	2.49 (1.76, 3.51)	2.62 (1.86, 3.69)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	3.24	<b>0.022</b>	136.8 (69.4, 189.8) <b>a</b>	83.7 (49.4, 119.1) <b>a</b>	77.3 (25.4, 131.9) <b>a</b>
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(8)	8	16	0.94	0.514	10.81 (2.73, 18.96)	5.27 (-2.76, 13.38)	4.14 (-3.89, 12.23)
	% Nitrification <sup>€</sup>	%	TOEP(4)	8	16	0.83	0.593	9.41 (3.63, 15.20)	5.37 (-0.41, 11.16)	3.98 (-1.81, 9.76)
	Extractable DOC	g C·m <sup>-2</sup>	TOEP(3)	8	16	1.50	0.232	44.8 (39.4, 51.0)	48.7 (42.8, 55.4)	43.3 (38.0, 49.2)
	Extractable DON	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.17	0.373	4.61 (4.08, 5.19)	4.65 (4.12, 5.24)	4.20 (3.72, 4.73)
	Microbial C	g C·m <sup>-2</sup>	TOEP(1)	8	16	0.75	0.648	22.6 (19.4, 26.2)	24.3 (20.9, 28.2)	22.3 (19.2, 25.9)
	Microbial N	g N·m <sup>-2</sup>	TOEP(3)	8	16	0.69	0.698	3.19 (2.75, 3.70)	3.19 (2.75, 3.70)	2.94 (2.53, 3.40)
	Microbial C:N	mass:mass	TOEP(5)	8	16	1.86	0.139	8.25 (7.72, 8.82)	8.88 (8.31, 9.49)	8.85 (8.28, 9.46)
Small	% Moisture <sup>€</sup>	%	TOEP(1)	6	12	3.15	<b>0.043</b>	25.2 (22.0, 28.4) <b>a</b>	24.6 (21.4, 27.8) <b>b</b>	23.5 (10.1, 13.3) <b>b</b>
	Total C	g C·m <sup>-2</sup>	TOEP(1)	6	12	0.67	0.677	6850 (5820, 8070)	5790 (4920, 6810)	5290 (4490, 6220)
	Total N	g N·m <sup>-2</sup>	AR(1)	6	12	1.07	0.432	244 (210, 284)	204 (176, 237)	190 (164, 220)
	Total C:N	mass:mass	AR(1)	6	12	1.16	0.386	32.7 (30.7, 34.8)	33.0 (31.0, 35.2)	32.5 (30.5, 34.6)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(1)	6	12	6.53	<b>0.003</b>	290 (242, 347) <b>a</b>	126 (106, 151) <b>b</b>	107 (89, 128) <b>b</b>
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	6	12	2.20	0.116	7.47 (4.70, 11.87)	2.57 (2.20, 3.00)	3.48 (2.42, 4.99)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	0.97	0.486	204.7 (71.4, 354.6)	111.7 (47.7, 179.6)	46.4 (1.0, 93.9)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	1.34	0.312	32.55 (16.35, 49.01)	1.53 (0.43, 2.64)	-2.02 (-15.29, 11.43)
	% Nitrification <sup>€</sup>	%	TOEP(1)	6	12	1.28	0.336	17.04 (9.65, 24.43)	1.78 (-5.61, 9.17)	8.77 (1.38, 16.16)
	DOC	g C·m <sup>-2</sup>	TOEP(1)	6	12	1.15	0.393	53.8 (46.6, 62.1)	50.7 (44.0, 58.6)	43.6 (37.8, 50.4)
	DON	g N·m <sup>-2</sup>	TOEP(1)	6	12	4.86	<b>0.010</b>	6.20 (5.39, 7.13) <b>a</b>	4.72 (4.10, 5.42) <b>b</b>	4.36 (3.79, 5.02) <b>b</b>
	Microbial C	g C·m <sup>-2</sup>	UN(1)	6	12	0.49	0.801	26.4 (22.3, 31.2)	18.7 (13.4, 25.9)	22.7 (19.3, 26.7)
	Microbial N	g N·m <sup>-2</sup>	TOEP(1)	6	12	1.49	0.261	4.39 (3.68, 5.23)	3.06 (2.57, 3.65)	3.09 (2.59, 3.69)
	Microbial C:N	mass:mass	UN(1)	6	12	3.19	<b>0.041</b>	7.02 (6.64, 7.42) <b>a</b>	7.11 (5.44, 9.30) <b>ab</b>	8.56 (8.18, 8.96) <b>b</b>

€ Response variable not natural log-transformed.

Note: Boldface type denotes a significant (p≤0.05) position effect. Italicized type denotes a marginally significant (p≤0.1) transect position effect. Different letters in a row denote significant differences (p≤0.05) among group means of response variables. Ranges of standard errors are in parentheses.

Appendix Table A6. Results of ANOVA with repeated measures in space for mineral soil response variables along transects in August 2006.

Gap Size	Variable	Units	Covariance Structure	Num df	Den df	F	p	ENVIRONMENT		
								Gap	Edge	Forest
Large	% Moisture <sup>ε</sup>	%	AR(1)	8	16	0.46	0.868	23.8 (21.1, 26.5)	23.5 (20.8, 26.2)	24.0 (21.3, 26.8)
	Total C	g C·m <sup>-2</sup>	TOEP(1)	8	16	1.30	0.310	6310 (5320, 7480)	5970 (5040, 7080)	5330 (4500, 6320)
	Total N	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.09	0.417	215 (183, 253)	205 (174, 241)	182 (155, 214)
	Total C:N	mass:mass	TOEP(5)	8	16	0.48	0.853	34.2 (32.2, 36.2)	34.0 (32.1, 36.0)	34.2 (32.2, 36.2)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	TOEP(2)	8	16	1.36	0.287	157 (125, 196)	131 (104, 164)	106 (84, 132)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	TOEP(2)	8	16	1.01	0.468	4.38 (3.11, 6.17)	2.49 (1.76, 3.51)	2.62 (1.86, 3.69)
	<b>Net N Mineralization</b>	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	8	16	3.24	<b>0.022</b>	136.8 (69.4, 189.8) <b>a</b>	83.7 (49.4, 119.1) <b>a</b>	77.3 (25.4, 131.9) <b>a</b>
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	TOEP(8)	8	16	0.94	0.514	10.81 (2.73, 18.96)	5.27 (-2.76, 13.38)	4.14 (-3.89, 12.23)
	% Nitrification <sup>ε</sup>	%	TOEP(4)	8	16	0.83	0.593	9.41 (3.63, 15.20)	5.37 (-0.41, 11.16)	3.98 (-1.81, 9.76)
	Extractable DOC	g C·m <sup>-2</sup>	TOEP(3)	8	16	1.50	0.232	44.8 (39.4, 51.0)	48.7 (42.8, 55.4)	43.3 (38.0, 49.2)
	Extractable DON	g N·m <sup>-2</sup>	TOEP(1)	8	16	1.17	0.373	4.61 (4.08, 5.19)	4.65 (4.12, 5.24)	4.20 (3.72, 4.73)
	Microbial C	g C·m <sup>-2</sup>	TOEP(1)	8	16	0.75	0.648	22.6 (19.4, 26.2)	24.3 (20.9, 28.2)	22.3 (19.2, 25.9)
	Microbial N	g N·m <sup>-2</sup>	TOEP(3)	8	16	0.69	0.698	3.19 (2.75, 3.70)	3.19 (2.75, 3.70)	2.94 (2.53, 3.40)
	Microbial C:N	mass:mass	TOEP(5)	8	16	1.86	0.139	8.25 (7.72, 8.82)	8.88 (8.31, 9.49)	8.85 (8.28, 9.46)
Small	<b>% Moisture<sup>ε</sup></b>	%	TOEP(1)	6	12	3.15	<b>0.043</b>	25.2 (22.0, 28.4) <b>a</b>	24.6 (21.4, 27.8) <b>b</b>	23.5 (10.1, 13.3) <b>b</b>
	Total C	g C·m <sup>-2</sup>	TOEP(1)	6	12	0.67	0.677	6850 (5820, 8070)	5790 (4920, 6810)	5290 (4490, 6220)
	Total N	g N·m <sup>-2</sup>	AR(1)	6	12	1.07	0.432	244 (210, 284)	204 (176, 237)	190 (164, 220)
	Total C:N	mass:mass	AR(1)	6	12	1.16	0.386	32.7 (30.7, 34.8)	33.0 (31.0, 35.2)	32.5 (30.5, 34.6)
	<b>Extractable NH<sub>4</sub><sup>+</sup></b>	mg N·m <sup>-2</sup>	TOEP(1)	6	12	6.53	<b>0.003</b>	290 (242, 347) <b>a</b>	126 (106, 151) <b>b</b>	107 (89, 128) <b>b</b>
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	UN(1)	6	12	2.20	0.116	7.47 (4.70, 11.87)	2.57 (2.20, 3.00)	3.48 (2.42, 4.99)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	0.97	0.486	204.7 (71.4, 354.6)	111.7 (47.7, 179.6)	46.4 (1.0, 93.9)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	UN(1)	6	12	1.34	0.312	32.55 (16.35, 49.01)	1.53 (0.43, 2.64)	-2.02 (-15.29, 11.43)
	% Nitrification <sup>ε</sup>	%	TOEP(1)	6	12	1.28	0.336	17.04 (9.65, 24.43)	1.78 (-5.61, 9.17)	8.77 (1.38, 16.16)
	DOC	g C·m <sup>-2</sup>	TOEP(1)	6	12	1.15	0.393	53.8 (46.6, 62.1)	50.7 (44.0, 58.6)	43.6 (37.8, 50.4)
	<b>DON</b>	g N·m <sup>-2</sup>	TOEP(1)	6	12	4.86	<b>0.010</b>	6.20 (5.39, 7.13) <b>a</b>	4.72 (4.10, 5.42) <b>b</b>	4.36 (3.79, 5.02) <b>b</b>
	Microbial C	g C·m <sup>-2</sup>	UN(1)	6	12	0.49	0.801	26.4 (22.3, 31.2)	18.7 (13.4, 25.9)	22.7 (19.3, 26.7)
	Microbial N	g N·m <sup>-2</sup>	TOEP(1)	6	12	1.49	0.261	4.39 (3.68, 5.23)	3.06 (2.57, 3.65)	3.09 (2.59, 3.69)
	<b>Microbial C:N</b>	mass:mass	UN(1)	6	12	3.19	<b>0.041</b>	7.02 (6.64, 7.42) <b>a</b>	7.11 (5.44, 9.30) <b>ab</b>	8.56 (8.18, 8.96) <b>b</b>

<sup>ε</sup> Response variable not natural log-transformed.

Note: Boldface type denotes a significant (p≤0.05) position effect. Italicized type denotes a marginally significant (p≤0.1) transect position effect. Different letters in a row denote significant differences (p≤0.05) among group means of response variables. Ranges of standard errors are in parentheses.



**Appendix B. Average Individual Site Data**

Appendix Table B1. Average forest floor, mineral soil, litterfall, and decomposition data along large gap transects at Delph Creek.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	0.904 (0.112)	1.502 (0.346)	1.372 (0.045)
	% Moisture	%	53.4 (1.3)	51.3 (0.5)	53.5 (0.4)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	13.69 (5.34)	15.08 (3.95)	9.40 (0.97)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.858 (0.410)	0.321 (0.118)	0.160 (0.032)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	92.5 (16.2)	160.3 (40.7)	53.0 (11.9)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	5.651 (1.596)	0.173 (0.240)	1.223 (1.065)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	77.0 (17.6)	30.3 (4.8)	27.6 (7.8)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	8.62 (3.83)	4.13 (1.63)	4.35 (1.14)
	Total C	g C·m <sup>-2</sup>	439 (54)	734 (173)	666 (31)
	Total N	g N·m <sup>-2</sup>	11.6 (1.4)	17.6 (4.0)	16.1 (0.8)
	C:N Ratio	mass:mass	43.0 (1.9)	48.8 (0.8)	48.2 (0.6)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	0.769 (0.043)	0.569 (0.017)	0.518 (0.075)
	% Moisture	%	35.3 (1.1)	34.1 (0.5)	35.9 (0.7)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	282 (70)	101 (5)	108 (19)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	17.87 (8.46)	2.33 (0.05)	2.43 (0.28)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	357 (90)	193 (87)	115 (59)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	70.63 (26.09)	9.04 (8.43)	7.63 (4.08)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	28.0 (11.5)	28.1 (10.2)	15.1 (3.1)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	39.78 (29.27)	5.66 (1.69)	3.49 (1.40)
	Extractable DOC	g C·m <sup>-2</sup>	42.9 (4.4)	37.0 (0.9)	36.3 (5.3)
	Extractable DON	g N·m <sup>-2</sup>	0.300 (0.078)	0.103 (0.005)	0.111 (0.019)
	Microbial C	g C·m <sup>-2</sup>	20.5 (2.2)	20.0 (2.1)	19.4 (3.0)
	Microbial N	g N·m <sup>-2</sup>	3.75 (0.46)	3.15 (0.36)	3.01 (0.58)
	Microbial C:N Ratio	mass:mass	6.41 (0.42)	7.44 (0.22)	7.58 (0.20)
	Total C	g N·m <sup>-2</sup>	6190 (770)	4410 (250)	4360 (550)
	Total N	g N·m <sup>-2</sup>	215 (21)	161 (16)	159 (27)
	C:N Ratio	mass:mass	33.3 (2.2)	32.4 (1.8)	32.5 (1.4)
Litterfall	C inputs	g N·m <sup>-2</sup>	76.8 (21.3)	104.5 (8.0)	179.9 (7.6)
	N inputs	g N·m <sup>-2</sup>	1.52 (0.34)	1.21 (0.14)	2.24 (0.13)
	% N	%	1.110 (0.043)	0.619 (0.044)	0.661 (0.060)
	C:N Ratio	mass:mass	50.1 (3.5)	87.7 (5.3)	83.9 (8.5)
Tongue Depressor	Mass remaining after 330 days	%	77.3 (4.6)	78.5 (4.8)	78.0 (3.5)
	k-values	yr <sup>-1</sup>	0.363 (0.078)	0.343 (0.059)	0.363 (0.078)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Ranges of standard errors are in parentheses.

Appendix Table B2. Average forest floor, mineral soil, litterfall, and decomposition data along small gap transects at Delph Creek.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	1.05 (0.38)	1.50 (0.13)	1.56 (0.10)
	% Moisture	%	55.5 (0.9)	52.4 (2.8)	50.7 (1.1)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	17.92 (14.05)	8.64 (1.38)	8.97 (0.24)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	1.301 (1.128)	0.248 (0.094)	0.137 (0.010)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	70.8 (37.1)	114.1 (10.8)	27.7 (15.9)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	2.480 (2.271)	0.628 (0.287)	0.124 (0.035)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	104.0 (37.6)	54.4 (20.7)	21.7 (3.8)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	17.58 (3.45)	2.02 (0.09)	2.83 (1.02)
	Total C	g C·m <sup>-2</sup>	14.6 (5.7)	17.7 (1.4)	18.4 (1.0)
	Total N	g N·m <sup>-2</sup>	508 (199)	696 (57)	766 (59)
	C:N Ratio	mass:mass	40.4 (1.0)	45.9 (1.9)	48.7 (1.1)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	1.05 (0.38)	1.50 (0.13)	1.56 (0.10)
	% Moisture	%	39.6 (1.6)	36.3 (0.9)	35.8 (0.9)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	329 (80)	138 (14)	130 (35)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	48.30 (20.67)	2.78 (0.24)	2.65 (0.63)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	280.5 (132.0)	126.0 (51.2)	51.1 (20.3)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	176.29 (78.41)	9.07 (4.59)	6.46 (4.57)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	23.8 (8.1)	18.3 (12.2)	13.6 (6.4)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	163.36 (69.85)	2.48 (0.81)	2.41 (0.43)
	Extractable DOC	g C·m <sup>-2</sup>	45.2 (5.6)	38.3 (5.7)	37.6 (4.4)
	Extractable DON	g N·m <sup>-2</sup>	1.40 (0.18)	1.19 (0.06)	1.07 (0.19)
	Microbial C	g C·m <sup>-2</sup>	20.7 (4.3)	18.2 (2.9)	19.3 (2.8)
	Microbial N	g N·m <sup>-2</sup>	3.70 (0.78)	2.86 (0.55)	2.90 (0.55)
	Microbial C:N Ratio	mass:mass	6.54 (0.06)	7.67 (0.05)	8.05 (0.50)
	Total C	g N·m <sup>-2</sup>	7200 (1460)	4950 (360)	4410 (780)
	Total N	g N·m <sup>-2</sup>	251 (57)	180 (7)	169 (36)
	C:N Ratio	mass:mass	33.7 (1.0)	32.1 (1.3)	31.5 (1.5)
Litterfall	C inputs	g N·m <sup>-2</sup>	1.193 (0.203)	0.728 (0.043)	0.694 (0.009)
	N inputs	g N·m <sup>-2</sup>	78.0 (30.0)	110.2 (3.9)	161.1 (5.1)
	% N	%	1.92 (0.81)	1.52 (0.07)	2.11 (0.06)
	C:N Ratio	mass:mass	43.8 (8.0)	72.9 (4.3)	76.6 (1.3)
Tongue Depressor	Mass remaining after 330 days	%	0.811 (0.041)	0.771 (0.065)	0.812 (0.035)
	k-values	yr <sup>-1</sup>	0.276 (0.087)	0.367 (0.121)	0.299 (0.070)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Standard errors are in parentheses.

Appendix Table B3. Average forest floor, mineral soil, litterfall, and decomposition data along large gap transects at Green Peak.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	0.663 (0.099)	0.571 (0.178)	0.930 (0.069)
	% Moisture	%	37.9 (1.6)	39.7 (1.6)	38.1 (0.8)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	7.26 (3.36)	3.46 (0.25)	7.39 (1.20)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.538 (0.223)	0.111 (0.055)	0.100 (0.011)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	9.18 (2.95)	4.33 (3.43)	6.10 (1.11)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.074 (0.120)	0.007 (0.032)	0.009 (0.008)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	36.9 (11.4)	36.5 (12.6)	20.8 (5.6)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	3.34 (0.81)	9.90 (4.64)	5.03 (0.17)
	Total C	g C·m <sup>-2</sup>	316 (42)	251 (72)	425 (32)
	Total N	g N·m <sup>-2</sup>	7.01 (0.99)	5.41 (1.14)	10.44 (1.21)
	C:N Ratio	mass:mass	54.4 (3.3)	52.2 (5.1)	48.5 (3.6)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	0.716 (0.182)	0.940 (0.091)	0.841 (0.069)
	% Moisture	%	32.0 (2.7)	28.7 (2.5)	28.6 (1.6)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	300 (63)	185 (28)	166 (30)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	18.52 (7.66)	4.30 (0.46)	5.02 (1.55)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	245.0 (142.1)	211.0 (46.3)	185.1 (37.3)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	106.89 (48.31)	32.24 (23.24)	27.45 (11.96)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	63.26 (44.36)	9.59 (2.93)	9.44 (1.68)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	39.41 (20.53)	7.07 (3.36)	8.49 (6.04)
	Extractable DOC	g C·m <sup>-2</sup>	36.0 (6.3)	49.1 (5.3)	42.8 (2.3)
	Extractable DON	g N·m <sup>-2</sup>	0.863 (0.099)	1.213 (0.183)	1.050 (0.119)
	Microbial C	g C·m <sup>-2</sup>	21.8 (3.9)	29.4 (2.3)	25.9 (1.2)
	Microbial N	g N·m <sup>-2</sup>	3.91 (0.54)	5.00 (0.60)	4.44 (0.30)
	Microbial C:N Ratio	mass:mass	6.47 (0.24)	6.99 (0.58)	6.87 (0.16)
	Total C	g N·m <sup>-2</sup>	209 (16)	271 (45)	226 (23)
	Total N	g N·m <sup>-2</sup>	6100 (530)	7860 (1760)	6260 (400)
	C:N Ratio	mass:mass	33.9 (1.5)	33.6 (2.6)	32.4 (1.1)
Litterfall	C inputs	g N·m <sup>-2</sup>	50.9 (15.0)	77.8 (11.2)	114.5 (8.0)
	N inputs	g N·m <sup>-2</sup>	0.86 (0.29)	1.25 (0.13)	1.72 (0.15)
	% N	%	0.854 (0.046)	0.847 (0.040)	0.773 (0.020)
	C:N Ratio	mass:mass	59.7 (2.6)	61.6 (3.1)	66.8 (1.8)
Tongue Depressor	Mass remaining after 330 days	%	0.854 (0.025)	0.804 (0.084)	0.848 (0.040)
	k-values	yr <sup>-1</sup>	0.199 (0.058)	0.281 (0.131)	0.202 (0.069)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Standard errors are in parentheses.

Appendix Table B4. Average forest floor, mineral soil, litterfall, and decomposition data along small gap transects at Green Peak.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	0.920 (0.211)	0.956 (0.236)	1.218 (0.240)
	% Moisture	%	38.8 (3.2)	34.7 (1.4)	38.6 (1.6)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	11.44 (6.96)	6.03 (1.12)	7.37 (1.46)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.441 (6.121)	8.026 (4.359)	8.664 (3.118)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.44 (6.12)	8.03 (4.36)	8.66 (3.12)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.242 (0.169)	0.109 (0.070)	0.176 (0.139)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	27.8 (3.2)	21.9 (1.2)	39.3 (11.7)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	2.61 (0.48)	4.11 (1.71)	3.17 (0.54)
	Total C	g C·m <sup>-2</sup>	423 (70)	446 (111)	571 (124)
	Total N	g N·m <sup>-2</sup>	10.1 (2.4)	10.3 (2.9)	13.9 (3.2)
	C:N Ratio	mass:mass	50.6 (2.0)	52.3 (3.1)	48.6 (0.6)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	1.053 (0.124)	0.936 (0.143)	0.900 (0.147)
	% Moisture	%	28.7 (2.6)	27.2 (1.7)	27.9 (0.8)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	352 (40)	267 (72)	171 (17)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	16.54 (3.80)	4.58 (0.49)	19.22 (9.05)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	524 (165)	184 (66)	231 (53)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	223.6 (94.3)	41.2 (21.7)	69.2 (12.9)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	23.61 (7.03)	11.79 (1.38)	9.26 (1.89)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	32.7 (14.4)	19.6 (10.1)	11.6 (4.3)
	Extractable DOC	g C·m <sup>-2</sup>	48.5 (5.8)	53.2 (4.1)	50.7 (4.8)
	Extractable DON	g N·m <sup>-2</sup>	1.29 (0.12)	1.29 (0.13)	1.21 (0.04)
	Microbial C	g C·m <sup>-2</sup>	26.9 (1.8)	31.7 (0.6)	33.4 (3.4)
	Microbial N	g N·m <sup>-2</sup>	4.81 (0.36)	5.23 (0.40)	5.11 (0.57)
	Microbial C:N Ratio	mass:mass	6.55 (0.07)	7.26 (0.40)	7.68 (0.25)
	Total C	g N·m <sup>-2</sup>	6140 (200)	6530 (350)	6560 (390)
	Total N	g N·m <sup>-2</sup>	242 (9)	256 (14)	253 (16)
	C:N Ratio	mass:mass	29.7 (1.8)	29.8 (0.8)	30.2 (0.6)
Litterfall	C inputs	g N·m <sup>-2</sup>	124 (24)	114 (31)	142 (20)
	N inputs	g N·m <sup>-2</sup>	2.14 (0.17)	1.71 (0.43)	2.23 (0.34)
	% N	%	0.886 (0.109)	0.766 (0.013)	0.782 (0.015)
	C:N Ratio	mass:mass	57.2 (7.4)	65.8 (1.1)	64.5 (1.1)
Tongue Depressor	Mass remaining after 330 days	%	0.667 (0.103)	0.890 (0.009)	0.878 (0.005)
	k-values	yr <sup>-1</sup>	0.633 (0.185)	0.116 (0.020)	0.148 (0.014)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Standard errors are in parentheses.

Appendix Table B5. Average forest floor, mineral soil, litterfall, and decomposition data along large gap transects at Keel Mountain.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	1.65 (0.22)	3.28 (1.58)	2.74 (0.32)
	% Moisture	%	57.5 (0.8)	56.7 (0.1)	57.7 (2.0)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	17.4 (8.1)	17.6 (7.9)	18.4 (1.4)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.245 (0.083)	0.341 (0.161)	0.312 (0.050)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	65.1 (48.8)	34.3 (25.5)	1.6 (1.7)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	0.172 (0.092)	0.008 (0.005)	0.152 (0.125)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	78.8 (23.9)	29.3 (4.5)	21.7 (5.0)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	7.33 (1.81)	5.20 (1.36)	1.62 (0.37)
	Total C	g C·m <sup>-2</sup>	21.3 (4.0)	31.6 (13.3)	32.8 (3.8)
	Total N	g N·m <sup>-2</sup>	770 (110)	1620 (820)	1340 (160)
	C:N Ratio	mass:mass	43.3 (2.0)	54.2 (3.4)	48.2 (1.2)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	0.782 (0.137)	0.743 (0.078)	0.694 (0.074)
	% Moisture	%	39.1 (0.1)	40.7 (1.0)	38.7 (0.6)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	242 (28)	189 (24)	156 (39)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	4.17 (0.32)	3.50 (0.41)	3.67 (0.88)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	180.3 (70.4)	45.3 (18.7)	68.0 (35.4)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	31.11 (28.13)	0.46 (0.37)	6.36 (6.32)
	IER NH <sub>4</sub> <sup>+</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	50.51 (26.87)	20.24 (9.92)	8.86 (0.87)
	IER NO <sub>3</sub> <sup>-</sup>	µg N·g <sup>-1</sup> ·yr <sup>-1</sup>	20.87 (14.83)	6.18 (5.47)	1.17 (0.51)
	Extractable DOC	g C·m <sup>-2</sup>	53.5 (9.3)	61.4 (8.1)	53.6 (5.6)
	Extractable DON	g N·m <sup>-2</sup>	1.75 (0.29)	1.74 (0.16)	1.50 (0.18)
	Microbial C	g C·m <sup>-2</sup>	21.9 (5.0)	25.3 (3.2)	22.2 (3.7)
	Microbial N	g N·m <sup>-2</sup>	3.31 (0.79)	3.38 (0.52)	2.83 (0.64)
	Microbial C:N Ratio	mass:mass	7.78 (0.30)	9.03 (0.30)	9.57 (0.34)
	Total C	g N·m <sup>-2</sup>	7840 (1460)	8560 (1070)	6630 (970)
	Total N	g N·m <sup>-2</sup>	253 (46)	243 (13)	209 (39)
	C:N Ratio	mass:mass	36.0 (0.3)	41.2 (3.0)	37.9 (1.2)
Litterfall	C inputs	g N·m <sup>-2</sup>	78.4 (12.9)	112.9 (6.6)	185.6 (10.2)
	N inputs	g N·m <sup>-2</sup>	1.19 (0.17)	1.35 (0.08)	2.48 (0.38)
	% N	%	0.745 (0.057)	0.612 (0.043)	0.675 (0.068)
	C:N Ratio	mass:mass	68.1 (4.7)	84.5 (6.0)	78.1 (7.6)
Tongue Depressor	Mass remaining after 330 days	%	0.769 (0.042)	0.918 (0.015)	0.859 (0.031)
	k-values	yr <sup>-1</sup>	0.370 (0.067)	0.165 (0.087)	0.226 (0.026)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Standard errors are in parentheses.

Appendix Table B6. Average forest floor, mineral soil, litterfall, and decomposition data along small gap transects at Keel Mountain.

Material	Variable	Units	ENVIRONMENT		
			Gap	Edge	Forest
Forest Floor	Forest Floor Mass	kg·m <sup>-2</sup>	1.15 (0.48)	1.57 (0.35)	2.23 (0.25)
	% Moisture	%	63.1 (2.5)	58.3 (0.9)	58.2 (1.0)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	34.71 (15.57)	9.35 (1.93)	13.57 (2.21)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	0.830 (0.427)	0.175 (0.035)	0.273 (0.058)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	151.0 (99.9)	21.8 (21.7)	4.2 (1.1)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	2.212 (2.099)	0.004 (0.004)	0.219 (0.199)
	IER NH <sub>4</sub> <sup>+</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	96.9 (39.5)	22.6 (9.3)	24.8 (3.0)
	IER NO <sub>3</sub> <sup>-</sup>	μg N·g resin <sup>-1</sup> ·yr <sup>-1</sup>	9.74 (4.99)	1.71 (1.07)	3.51 (1.32)
	Total C	g C·m <sup>-2</sup>	554 (242)	760 (185)	1077 (122)
	Total N	g N·m <sup>-2</sup>	16.7 (6.8)	18.9 (3.6)	26.8 (4.0)
	C:N Ratio	mass:mass	38.3 (2.3)	46.8 (2.4)	47.2 (2.6)
Mineral Soil	Bulk Density	g·cm <sup>-3</sup>	0.925 (0.218)	0.747 (0.136)	0.754 (0.156)
	% Moisture	%	40.2 (2.3)	38.7 (0.6)	38.5 (0.6)
	Extractable NH <sub>4</sub> <sup>+</sup>	mg N·m <sup>-2</sup>	545 (11)	160 (39)	161 (50)
	Extractable NO <sub>3</sub> <sup>-</sup>	mg N·m <sup>-2</sup>	13.48 (3.53)	3.34 (0.59)	6.91 (4.25)
	Net N Mineralization	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	534.2 (397.7)	68.5 (17.7)	56.9 (43.2)
	Net Nitrification	mg N·m <sup>-2</sup> ·28 d <sup>-1</sup>	186.3 (95.0)	2.3 (2.2)	17.1 (17.1)
	IER NH <sub>4</sub> <sup>+</sup>	μg N·g <sup>-1</sup> ·yr <sup>-1</sup>	328.72 (250.29)	7.50 (1.63)	6.85 (0.81)
	IER NO <sub>3</sub> <sup>-</sup>	μg N·g <sup>-1</sup> ·yr <sup>-1</sup>	43.08 (25.66)	0.50 (0.02)	8.83 (5.13)
	Extractable DOC	g C·m <sup>-2</sup>	58.1 (2.7)	61.3 (11.0)	54.0 (4.3)
	Extractable DON	g N·m <sup>-2</sup>	1.85 (0.07)	1.70 (0.35)	1.44 (0.14)
	Microbial C	g C·m <sup>-2</sup>	24.5 (3.8)	27.1 (5.2)	22.5 (3.2)
	Microbial N	g N·m <sup>-2</sup>	4.14 (0.37)	3.58 (0.73)	3.10 (0.63)
	Microbial C:N Ratio	mass:mass	6.84 (0.41)	8.97 (0.39)	8.63 (0.50)
	Total C	g N·m <sup>-2</sup>	7150 (620)	7190 (1450)	6010 (320)
	Total N	g N·m <sup>-2</sup>	258 (19)	237 (41)	207 (41)
	C:N Ratio	mass:mass	32.9 (4.1)	35.6 (3.1)	36.0 (4.6)
Litterfall	C inputs	g N·m <sup>-2</sup>	93.7 (14.1)	148.2 (49.3)	173.8 (3.6)
	N inputs	g N·m <sup>-2</sup>	1.89 (0.46)	1.97 (0.61)	2.18 (0.27)
	% N	%	0.967 (0.128)	0.677 (0.063)	0.657 (0.084)
	C:N Ratio	mass:mass	52.7 (8.5)	77.5 (6.4)	81.5 (9.5)
Tongue Depressor	Mass remaining after 330 days	%	0.756 (0.084)	0.847 (0.033)	0.832 (0.041)
	k-values	yr <sup>-1</sup>	0.424 (0.165)	0.223 (0.057)	0.286 (0.074)

Note: Values are means of three transects calculated after environmental group means were determined within transects. Standard errors are in parentheses.