Clearcutting and deer browsing intensity interact in controlling nitrification rates in forest floor[1]

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Abstract: Major forest disturbance such as clearcutting may increase nitrification rates in the forest floor, but the magnitude of this NO_3^- flush varies among different forest ecosystems. Here, we tested the hypothesis that this variation could partly be due to differences in deer-browsing intensity. More specifically, we hypothesized that nitrification rates would decrease as deer browsing increased and that this effect would be higher in clearcuts than in forests. Our experimental design consisted of 3 replicated blocks, each consisting of 3 plots (10–40 ha) in which white-tailed deer densities were kept at 0, 7.5, and 15 individuals·km^{-2} for 6 y and a fourth plot in which natural deer densities varied between 27 and 56 deer·km^{-2}. In the first year, 70% of mature balsam fir (*Abies balsamea*) forests in each plot were clearcut harvested. Average potential nitrification in forest floor samples was higher in clearcut than in forest plots. In clearcut plots, potential nitrification at the high deer density was about 2.5 times higher than at lower deer densities, thereby contradicting our first hypothesis. In forest plots, potential nitrification was negatively related to indices of soil available C but was unrelated to deer density. The shrub and herb vegetation in clearcut plots was dissimilar to, and more altered by, deer browsing than the understory vegetation in forest plots. In clearcut plots, increasing deer density reduced the percent cover of nitrophilous herbaceous species and increased the percent cover of graminoid plants. Possible mechanisms that could explain the interaction between forest disturbance and deer browsing intensity in controlling the magnitude of the NO_3^- flush are (1) soil N inputs via feces and urine, (2) loss of soil NO_3^- sinks due to the disappearance of nitrophilous plant species, and (3) browser-induced succession towards rangeland plant communities that stimulate rhizodeposition and soil N dynamics.

Keywords: clearcutting, deer browsing, forest floor, nitrification, plant community composition.

Résumé : Les perturbations forestières majeures comme la coupe à blanc peuvent faire augmenter les taux de nitrification dans le sol forestier, mais l'ampleur du flux de NO_3^- varie entre les différents écosystèmes. Nous avons évalué l'hypothèse selon laquelle cette variation pourrait en partie résulter de différences dans l'intensité du broutement par le cerf. Plus spécifiquement, nous avons formulé l'hypothèse que les taux de nitrification diminueraient lorsque le broutement par le cerf augmenterait et que cet effet serait plus important dans les coupes totales qu'en forêt. Notre plan expérimental comprenait 3 réplicats, chacun comprenant 3 parcelles (10–40 ha) dans lesquelles la densité de cerfs de Virginie était maintenue à 0, 7,5 et 15 individus·km^{-2} durant 6 ans et une quatrième parcelle où la densité de cerfs variait de façon naturelle entre 27 et 56 cerfs·km^{-2}. Au cours de la première année, 70 % des sapinières matures (*Abies balsamea*) de chaque parcelle a été récolté par coupe à blanc. La nitrification potentielle moyenne des échantillons de sol forestier était plus élevée dans les coupes totales que dans les parcelles forestières. Dans les parcelles de coupe totale, la nitrification potentielle à haute densité de cerfs était environ 2,5 fois plus élevée qu'à faible densité de cerfs, contredisant ainsi notre première hypothèse. Dans les parcelles forestières, la nitrification potentielle était reliée de façon inversement proportionnelle aux indices de disponibilité du C du sol, mais n'était pas reliée à la densité de cerfs. La végétation arbustive et herbacée des parcelles de coupe totale était différente et modifiée de façon plus importante par le broutement par le cerf que la végétation en sous-étage des parcelles forestière. Dans les parcelles de coupe totale, l'augmentation de la densité de cerfs a réduit le pourcentage de couverture des espèces herbacées nitrophiles et fait augmenter le pourcentage de couverture des plantes graminées. Les mécanismes possibles pouvant expliquer l'interaction entre la perturbation forestière et l'intensité du broutement par le cerf pour le contrôle de l'ampleur du flux de NO_3^- sont (1) les apports de N dans le sol par les fèces et l'urine (2) la perte des puits de NO_3^- du sol causée par la disparition d'espèces de plantes nitrophiles, ou (3) la succession causée par le broutement vers des communautés de plantes de pâturage qui stimulent la rhizodéposition et la dynamique du N du sol.

Mots-clés : broutement par le cerf, composition de la communauté végétale, coupe à blanc, nitrification, sol forestier.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

Early studies at the Hubbard Brook Experimental Watershed demonstrated that clearcutting followed by extensive herbicide application increased the export of soil NO_3^- to groundwater and streams by large amounts (*e.g.*, Likens *et al*., 1970). Since then, the effect of forest disturbance on the flow and fate of this key soil mineral N form has received considerable attention. Over time, it has become apparent that the magnitude of the post-disturbance soil NO_3^- flush varies considerably among different forest ecosystems (*e.g.*, Grenon *et al*., 2004). This variability has been attributed to various edaphic factors such as soil temperature and moisture (Barg & Edmonds, 1999), humus form, root density and soil available C (Lavoie & Bradley, 2003), soil pH (Paavolainen & Smolander, 1998), soil NH_4^+ concentrations (Bradley, 2001), and soil enzyme expression (Joanisse *et al*., 2007) and to whether soil nitrifiers are predominantly autotrophic or heterotrophic (Bradley & Parsons, 2007). Linkages have been drawn between these edaphic factors and attributes of the plant community following disturbance, such as the chemical quality of the litter produced by early seral herbaceous vegetation (Bradley, Kimmins & Martin, 2002), the partial retention of trees (Lapointe, Bradley & Shipley, 2005), and the production of secondary metabolites by ericaceous shrubs (Joanisse, Bradley & Preston, 2008). No studies to our knowledge have attempted, however, to show a relationship between browsing intensity by large herbivores and the magnitude of the post-harvest soil NO_3^- flush in forest ecosystems.

It is well documented that large herbivores such as moose, elk, bison, and deer can affect soil nitrification rates, although the direction of these effects varies among ecosystems. Positive effects are mainly observed in grasslands (*e.g.*, Frank *et al*., 2000) where grazing is believed to increase rhizodeposition (*i.e.*, soil available carbon) and microbial activity, which leads to positive feedbacks through soil food-webs and a concomitant increase in nitrification. By contrast, grazing commonly reduces nitrification rates in forest ecosystems, because, as Pastor *et al*. (1993) suggested, the less palatable plant species that are not consumed are those that produce low-quality litter and decrease soil nutrient cycling. Thus, the effect of herbivores on forest floor nitrification rates following clearcutting ostensibly depends on the nature of the plant community, which in turn is controlled by the intensity of browsing. Given that clearcutting also changes the understory plant community (Kimmins, Martin & Bradley, 2002), we predicted an interaction between this form of forest disturbance and deer browsing intensity in controlling soil nitrification rates.

Here, we report on a controlled grazing experiment where we tested for such an interaction using white-tailed deer (*Odocoileus virginianus*) enclosure and exclosure plots, comprising both mature balsam fir (*Abies balsamea*) forests and clearcuts. The study was conducted on Anticosti Island, Canada, where the population of white-tailed deer, introduced over a century ago, has risen to > 20 deer·km^{-2} in the absence of predators (Rochette & Gingras, 2007) and may be > 50 deer·km^{-2} in some areas (Tremblay, Huot &

Potvin, 2006). The effects of this natural deer density on the shrub and herbaceous vegetation, and on nitrification rates in the forest floor, were compared to experimental densities of 0, 7.5, and 15 deer·km^{-2} that were maintained over a 6-y period. We focussed on the forest floor rather than mineral soil horizons, because this is where we find the highest fine-root biomass for nutrient uptake in coniferous forests (Pietikäinen *et al*., 1999). We initially hypothesized that potential nitrification rates in both forests (McInnes *et al*., 1992) and regenerating clearcuts (Harrison & Bardgett, 2004) would decrease as deer browsing intensity increased. We also hypothesized that the impact of browsing would be higher in clearcuts than in forests, because we expected more palatable herbaceous species and higher nitrification rates in the non-browsed clearcuts. Results contradicted our first hypothesis, as we observed higher nitrification rates in clearcuts with high deer densities. We offer alternative explanations in light of observed shifts in the abundance of nitrophilous and graminoid plants, and in soil available C, due to the interaction between clearcutting and deer browsing intensity.

Methods

STUDY SITE DESCRIPTION AND HISTORY

Anticosti Island covers an area of about 8000 km^2 and is located in the Gulf of the St. Lawrence River (49.1–50.0° N, 61.7–64.5° W), Quebec, Canada. The sub-boreal maritime climate is characterized by cool summers (15 °C in July) and cold winters (–10 °C in January). Annual precipitation generally exceeds 1000 mm, of which 40% falls as snow. The area belongs to the Eastern Balsam Fir–White Birch bioclimatic zone, according to Quebec's ecological classification system (Grondin *et al*., 1996). The most abundant tree species are balsam fir and white spruce (*Picea glauca*).

In 1896, 220 white-tailed deer were introduced on the island, and in the absence of natural predators the population rapidly grew. Historical surveys estimate that deer populations across different sectors of the island have remained at 20–50 individuals·km^{-2} for the past 80 y (Gingras, Potvin & Rochette, 1993; Potvin *et al*., 2000). These high densities maintain a thriving sport hunting industry, the mainstay of the local economy. Balsam fir is the principal winter forage for deer on Anticosti Island, and consequently there is little natural regeneration of this species (Tremblay, Huot & Potvin, 2007). For this reason, senescing balsam fir stands that were established before the introduction of deer on the island are being replaced mainly by white spruce (Potvin, Beaupré & Laprise, 2003), a species that is generally shunned by the deer (Sauvé & Côté, 2007). Thus, it is feared that when the existing balsam fir forests have fallen, the deer population will crash (Potvin, Beaupré & Laprise, 2003). In order to maintain deer populations and sustain balsam fir regeneration, commercial logging operations began in 1995. These operations included various silvicultural systems designed to conserve the natural diversity of plant species while creating a mosaic of food and cover habitats for the deer (Potvin & Boots, 2004). Among these, temporary deer exclosures up to 27 km^2 in size have been erected at various locations on the island to

allow balsam fir regeneration to grow above the maximum browsing height of the deer.

EXPERIMENTAL DESIGN AND FIELD SAMPLING

The design consisted of 3 replicated blocks, located 4 to 71 km apart and occurring over flat topography, each consisting of 4 experimental units. The first unit in each block consisted of a 10-ha exclosure from which all deer were removed (0 deer·km^{-2}). The second and third units consisted of 40-ha (7.5 deer·km^{-2}) and 20-ha (15 deer·km^{-2}) enclosures, each stocked for 6 consecutive years (2002–2007) with 3 yearling deer. The fourth unit in each block consisted of an unfenced 30-ha area where natural deer densities were estimated each year from line transect surveys of summer fecal pellets (Buckland *et al.*, 2001), using DISTANCE 5.0 software (Thomas *et al.*, 2002). For the 3 blocks, these estimated *in situ* densities were respectively 56, 56, and 27 deer·km^{-2} over the 6 years. In summer 2001, clearcutting was performed in a random pattern in the area where each block was to be located by harvesting all trees > 9 cm diameter at breast height. The experimental units were later positioned such that 30% of each unit was composed of residual forest cover. Given the random location of these forest patches, we are confident that the clearcut and forest plots within each experimental unit were not located in areas that predisposed them to different nitrification rates. The resulting split-plot design included, therefore, 8 treatments (*i.e.*, 4 deer densities × 2 vegetation cover types), each replicated 3 times (see Tremblay *et al.*, 2005 for a complete description). Deer were introduced into the enclosures immediately following snowmelt (early May) and were removed at the onset of snowfall (late October), since we were chiefly interested in the effects of deer on the recovery of the ground and shrub layer following a long history of browsing. All enclosure and exclosure plots were bounded with 3-m-high wire game fencing.

Between July 6th and August 2nd 2007, 20 random quadrats (1 m^2) were established in each of the 24 plots. Around the periphery of each quadrat, we collected 6 cores (~20 cm^3) of F-layer forest floor material (Soil Classification Working Group, 1998). The cores from each quadrat were pooled into 1 sample, passed through a 5-mm mesh sieve, placed in a plastic bag over ice, and transported to the University of Sherbrooke for further analyses. As part of a related study, we noted the percent cover of all herbaceous and shrub species in each of the 480 quadrats.

SOIL ANALYSES

Potential nitrification rates were measured in all 480 forest floor samples using an aerobic incubation technique similar to that used by Harrison and Bardgett (2004) in a similar study on red deer (*Cervus elaphus*). We first determined moisture content by weight loss after drying 5–10 g subsamples at 101 °C for 72 h. We then weighed 25–30 g of fresh forest floor material directly into mason jars and covered these with polyethylene film to prevent desiccation and allow gas exchange with ambient air. The jars were incubated for 30 d in the dark at 22 °C. We then added 100 mL of 1N KCl solution to each jar and stirred these for 60 min on a rotary shaker. Solutions were passed through

Whatman No.5 filter paper and the filtrates were analyzed colorimetrically for NO_3^--N concentrations (Cd-reduction + sulphanilamide) using a Technicon Autoanalyser (Pulse Instrumentation, Saskatoon, Saskatchewan, Canada).

Indices of available C were derived by soil respirometry (Bradley & Fyles, 1995a) and included measurements of basal respiration rate and microbial biomass. Basal respiration rate was determined by weighing 5 g (dry wt. equiv.) of forest floor material from each quadrat into 73-mL gas sampling jars, allowing 5 d for soils to condition to room temperature, flushing the headspace with ambient air for 5 min, sealing the jars with air-tight lids equipped with rubber septa, and sampling aliquots of headspace air with a needle and syringe after 4 h. Air samples were analyzed for CO_2 concentrations using a model CP-2002 P Micro-GC (Chrompack, Middelburg, The Netherlands) equipped with a thermal conductivity detector (TCD), with He as carrier gas. Room temperature was noted during each measurement, and ambient CO_2 concentration was measured several times daily. For each measurement, ambient CO_2 concentration was subtracted from sampled CO_2 concentration and the difference was adjusted according to Ideal Gas Laws and centred at 22 °C using $Q_{10} = 2$.

Microbial biomass (MB) was determined by weighing 5 g (dry wt. equiv.) of forest floor material from each quadrat into 500-mL plastic containers and amending these with ground and sieved (65 μm) glucose (1500 μg C·g soil^{-1}) (Bradley & Fyles, 1995a). The amendments were applied as 250-mg mixtures with talc and dispersed throughout the samples using a kitchen handmixer with 1 beater. The glucose-amended forest floor samples were then transferred into 125-mL gas sampling jars and left uncovered for 100 min to reach optimum substrate induced respiration (SIR) rates (Anderson & Domsch, 1978). These were then flushed for 5 min with ambient air and sealed for 30 min, and headspace air was analyzed for CO_2 concentration using the GC (as described above). SIR rates were converted to MB using equations derived by Anderson and Domsch (1978).

STATISTICAL ANALYSES

For each treatment, we computed potential nitrification rate, basal respiration rate, and microbial biomass in the forest floor by averaging values of the 20 sample quadrats in each plot. Skewness in the nitrification data could not be removed by transformation; therefore, we used DISTLM v.5 software (Anderson, 2004a), which is a distribution-free permutation-based ANOVA, to test the effects of deer density, forest cover, and their interaction on this variable. The experimental layout was a split-plot design, with deer density as the whole-plot factor and forest cover as the subplot factor. Where significant interactions were found, we compared the effects of deer density within each level of forest cover using simple main effects contrasts (Woodward, Bonett & Brecht, 1990). Relationships between indices of available C and log-transformed values of potential nitrification in clearcut and forest plots were analyzed using simple linear regressions (SAS Institute, 2003).

In order to compare the relative impact of deer densities on plant communities in forest *versus* clearcut plots, we

averaged the percent cover of each plant species within each treatment plot and analyzed these by principal component analysis (PCA) using the "vegan" library in "R" statistical software (Oksanen *et al.*, 2008). The dispersion of first and second principal component scores for forest and clearcut plots were then compared using Levene's test for equality of variances (Levene, 1960). We also compared the dispersion of these data within each cover type using PERMDISP software (Anderson, 2004b), a non-parametric permutation-based multivariate test for equality of variances. Rare species accounting for less than 1% of total cover were removed from these analyses because they contributed many zero values to the data matrix. The relationships between deer densities in clearcut plots, the 3 most abundant nitrophilous (Godefroid, 2001; Sujetoviene, 2007) species (*Chamerion angustifolium*, *Fragaria virginiana*, and *Rubus pubescens*), and the sum of the 8 graminoid taxa (*Agropyron* sp., *Carex* sp., *Calamagrostis canadensis*, *Luzula acuminata*, *Phleum pratense*, *Poa* sp., *Schizachne purpurascens*, and unidentified Poaceae) were analyzed using linear and logarithmic regression models (SAS Institute, 2003).

Results

Potential nitrification rates were higher in clearcut (61.9 ± 11.2 μg $NO_3^-{\cdot}g$ N^{-1}) than in forest plots (25.7 ± 3.6 $\mu g{\cdot}g^{-1}$), but the response to cutting depended strongly on deer population density ($F_{interaction} = 6.73$, $P < 0.01$, 8 df). More specifically, potential nitrification in clearcut plots was significantly ($F = 31.49$, $P < 0.001$, 8 df) higher at the highest (*i.e.*, natural) deer density, whereas deer density had no effect on potential nitrification in forest plots (Figure 1). Deer density had no effect on indices of available C in forest plots, but potential nitrification rate decreased as microbial biomass ($P < 0.05$) and basal respiration rate ($P < 0.01$) increased (Figure 2a,b). In contrast, potential nitrification in clearcut plots increased with microbial biomass ($P < 0.10$), but only after eliminating 1 outlier (Figure 2c).

Results from PCA based on vegetation inventory data showed a clear segregation of clearcut and forest plots along
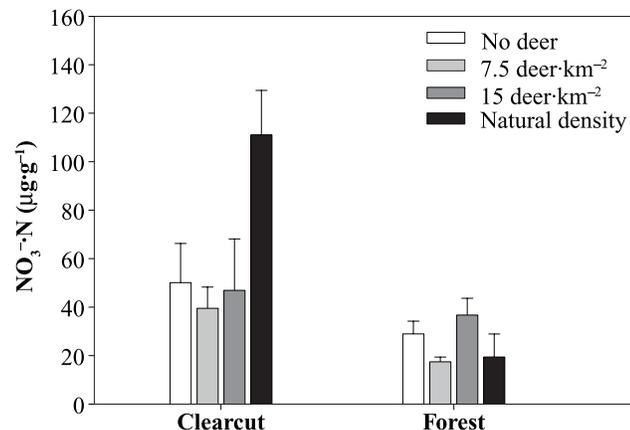
the first principal component, which accounted for 30% of the total variability in the data set (Figure 3). Levene's test revealed a greater variability of first principal component scores ($P = 0.05$, $F = 4.19$, 1 df) among clearcut than among forest plots. On the other hand, PERMDISP analysis, which uses all of the information in the data set, revealed a lower significance level ($P = 0.11$, $F = 2.68$, 1 df) for this comparison. The 3 most common nitrophilous herbaceous species found in clearcut plots decreased as deer density increased (Figure 4a–c). The estimated sum of their cover was 30% in the absence of deer and only 3% at the highest deer density (Figure 4d). In contrast, when the sum of graminoid plant cover was regressed against deer density, it increased from 2% in the absence of deer to 18% at the highest deer density (Figure 4e).

Discussion

Our results show that a soil NO_3^- flush is detectable 6 y after clearcutting on Anticosti Island and that the magnitude of this flush is influenced by deer density. Given that natural deer densities may vary considerably from year to year due to factors such as winter severity, predation rate, and hunting kills, our results suggest that regional differences in the timing and magnitude of the post-disturbance soil NO_3^- flush can be partly attributed to temporal variations in the top-down effects of large herbivores such as white-tailed deer. Based on evidence obtained from this and other studies, we propose and discuss the merits of possible mechanisms that could explain this interaction between forest disturbance and deer browsing intensity.

Pastor *et al.* (1993) proposed that moose browsing reduces the quantity and chemical quality of plant litter in forest ecosystems, which in turn depresses C and N cycling in the forest floor. In our study, however, there was no relationship between deer browsing and these 2 variables in forest plots. Results from PCA and PERMDISP imply that the vegetation response to a reduction in deer browsing pressure is faster in clearcut than in forest plots, which may explain why deer density had no effect on potential nitrification in forest plots. The fact that available C and potential nitrification were negatively correlated (Figure 2a,b) suggests that net nitrification in forest plots was controlled more by microbial immobilization of NO_3^- (Hart *et al.*, 1994) than by deer browsing effects on gross nitrification rates.

In clearcut plots, high deer densities had the opposite effect on potential nitrification than we had predicted based on results from previous studies (Pastor *et al.*, 1993; Harrison & Bardgett, 2004), which suggests that intense browsing either increased litter quality or triggered alternative mechanisms that led to higher potential nitrification rates. Higher litter quality induced by browsing is unlikely, given the high correlation between digestibility and decomposability of plant material (Cornelissen *et al.*, 2004). Feces and urine constitute an easily decomposable, nutrient-rich resource that can stimulate soil C and N mineralization (Molvar, Bowyer & van Ballenberghe, 1993) and might therefore provide an alternative mechanism leading to higher potential nitrification rates. To corroborate this hypothesis, we would need to show that deer defecated more

FIGURE 1. Effect of white-tailed deer density on potential nitrification in the forest floor of clearcut and forest plots in balsam fir–dominated stands of Anticosti Island, Quebec, Canada. Bars represent the mean value of 3 replicate plots; vertical lines = 1 SD.

Forest plots

a) $Y = -0.067x + 1.31$
$r^2 = 0.44$, $P < 0.05$

Clearcut plots

c) ⊙ outlier
$Y = 0.18x + 0.23$
$r^2 = 0.23$, $P < 0.10$

Log(1+[NO$_3^-$])

Microbial biomass (mg C$_{mic}$·soil g^{-1})

b) $Y = -0.19x + 1.57$
$r^2 = 0.49$, $P < 0.01$

d) ns

Log(1+[NO$_3^-$])

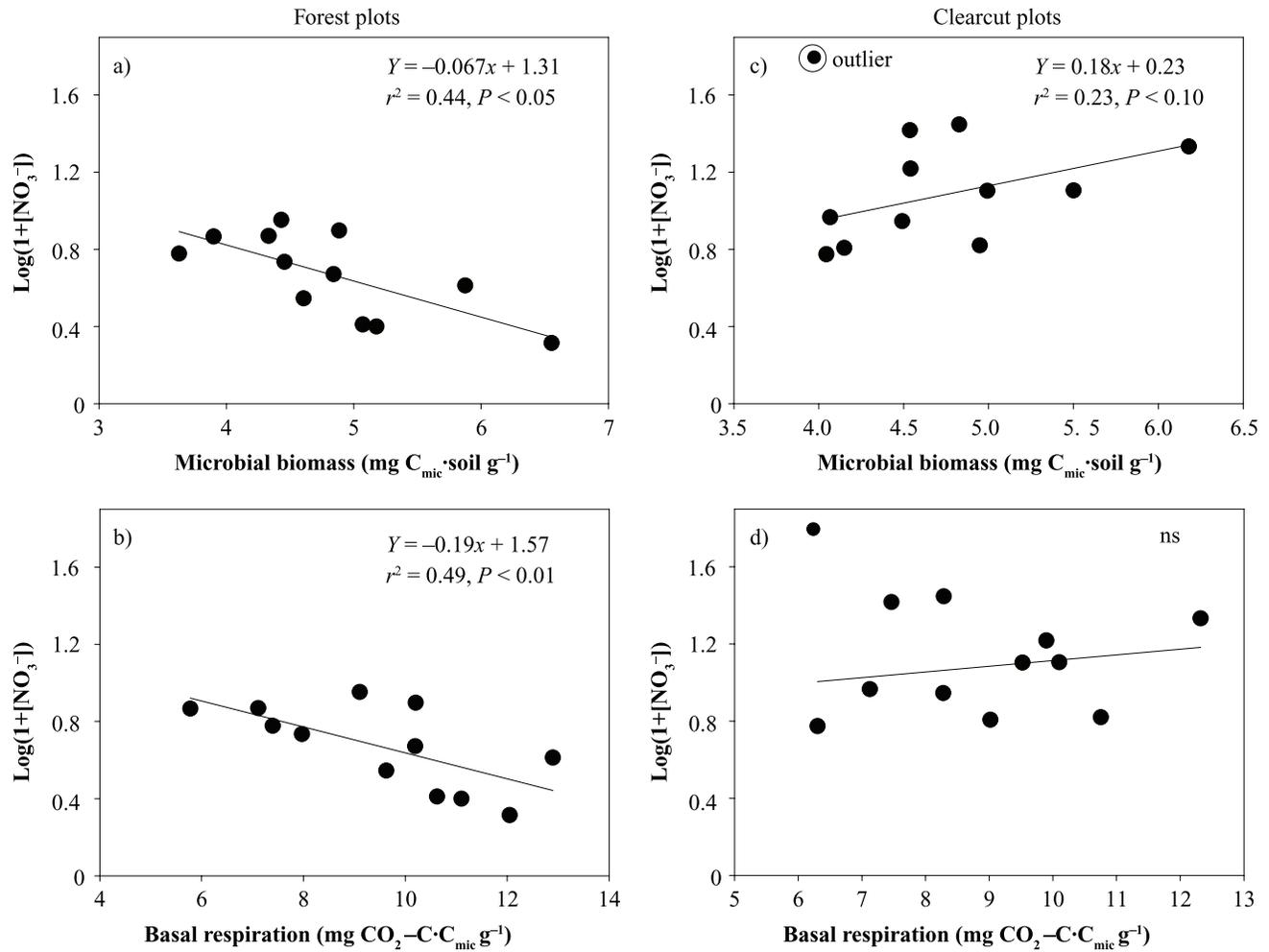Basal respiration (mg CO$_2$−C·C$_{mic}$ g^{-1})

FIGURE 2. Relationship between 2 indices of available C (microbial biomass and basal respiration rate) and potential nitrification in the forest floor of clearcut and balsam fir–dominated forest plots. Outlier point shown in frame (c) was excluded from linear regression analysis. Regression model (solide line) of data in frame (d) is non-significant (ns = $P > 0.10$).

frequently in clearcut than in forest plots, as the effect of deer densities on potential nitrification occurred only in clearcut plots. In a prior study, Coulombe (2006) concluded that deer in these experimental plots spent roughly the same amount of time per area in clearcut and forest plots during summer, but data are lacking on their defecation habits. Even if deer were to defecate more in clearcut plots, some have argued that N inputs via feces and urine of large herbivores are too small to compensate for negative effects of browsing on N cycling in forest ecosystems (Pastor *et al.*, 1988; Hobbs, 2006). To verify this, we gleaned data from Pletscher (1987), who estimated annual soil N inputs via the feces and urine of a mature white-tailed deer to be about 5.62 kg·y^{-1}. Extrapolating these estimates further, total soil N inputs via feces and urine in our highest natural density plots would be about 3.14 kg·ha^{-1}·y^{-1}, or 2 orders of magnitude lower than recommended forest N fertilization rates (Strengbom & Nordin, 2008). It has also been argued that the effect of deer fecal droppings is very local, which would reduce the likelihood of establishing sampling quadrats exactly where droppings occur (Augustine & Frank, 2001). However, white-tailed deer defecate on average 12.7 times per day (Eberhart & van Etten, 1956), and assuming that

Clearcut plots   Forest plots
○ No deer   △ No deer
◐ 7.5 deer·km^{-2} ◭ 7.5 deer·km^{-2}
◑ 15 deer·km^{-2} ◮ 15 deer·km^{-2}
● Natural density   ▲ Natural density
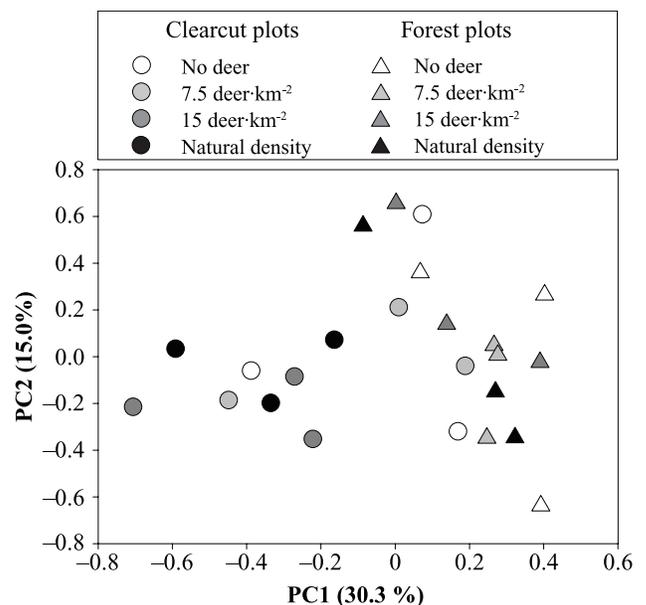
PC2 (15.0%)

PC1 (30.3 %)

FIGURE 3. Ordination biplot of the 24 sample plots resulting from principal component analysis (PCA) of understory plant community composition.

each dropping affects an area of about 1 m², it is possible for 26% of the total area in our high deer density plots to be littered annually with fecal droppings. Furthermore,
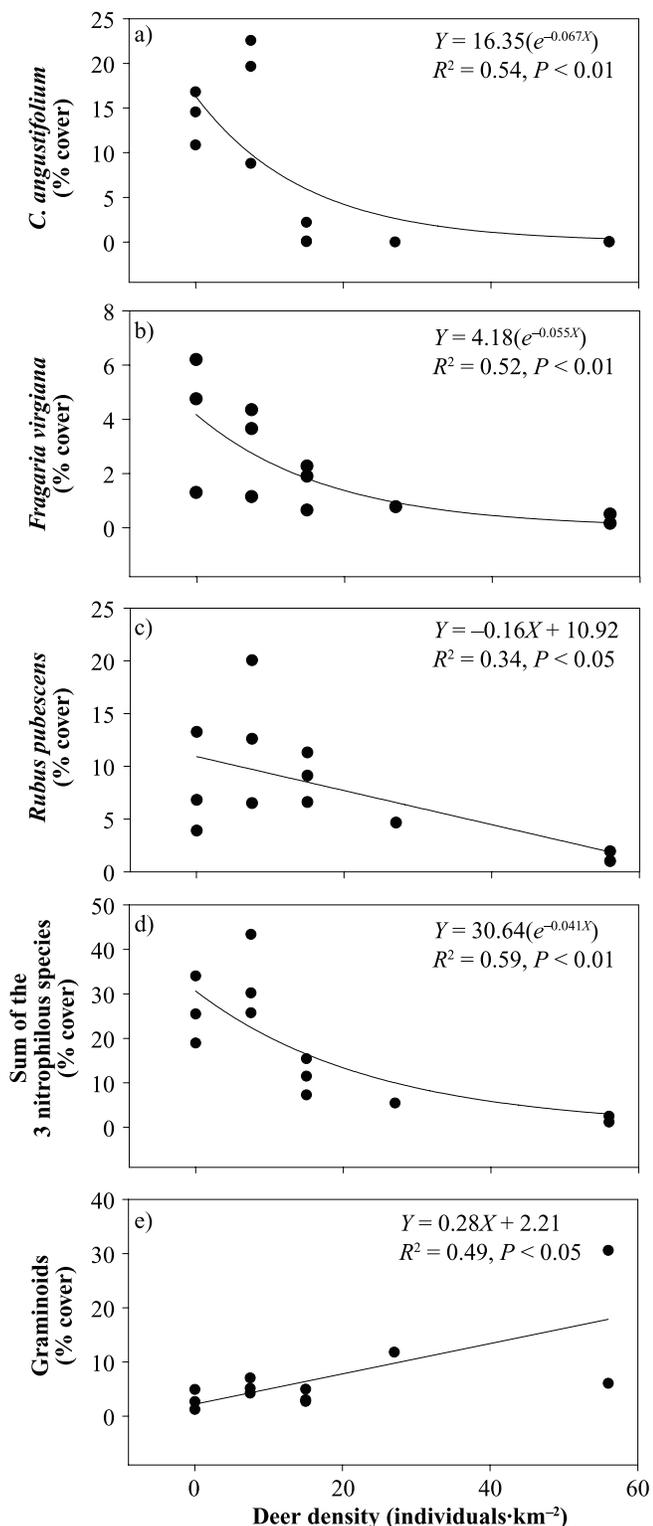

FIGURE 4. The effect of deer population size on the percent cover of 3 nitrophilous plant species (a–c), on the sum of their cover (d), and on total percent cover of 8 graminoid plant species (e) in 7–y–old clearcut plots following 6 consecutive years of controlled grazing.

this may be a conservative estimate, as it excludes the area affected by urine inputs. Thus, although the total annual N-input by feces and urine appears to be modest, each quadrat in the high density plots likely had a 1-in-4 probability of being established over an area locally affected by current-year droppings. In short, there are grounds not to dismiss soil N inputs via feces and urine as a possible explanation for differences in potential nitrification among our experimental plots, but more research is required to validate this claim.

A second plausible explanation for observing higher NO_3^- concentrations in high deer density clearcut plots is a shift in plant community composition in these plots that would stimulate potential nitrification. Although several studies have reported an increase in the recruitment of white spruce due to browsing (McInnes *et al*., 1992; Rooney & Waller, 2003), which would ostensibly reduce soil nitrification, such is not the case on Anticosti Island, where white spruce recruitment is as high in deer exclosures as in natural deer density plots following 8 decades of chronic heavy browsing (Tremblay, Huot & Potvin, 2007). Even if white spruce recruitment had been higher in high deer density plots, the relatively slow growth and high needle longevity of this species implies that its presence would have little effect on soil nutrient cycling in the first decade following disturbance. It is essential to understand that the potential nitrification assay we used considers the initial (*i.e.*, pre-incubation) soil NO_3^- pool to be part of the NO_3^- pool that is potentially available (Powers, 1980). Hence, the elimination of fast-growing early-seral nitrophilous species such as *C. angustifolium*, *F. Virginiana*, and *R. pubescens* at high deer densities may have increased pre-incubation soil NO_3^- pools and, consequently, potential nitrification in clearcut plots. The importance of the vegetation sink in controlling forest floor NO_3^- following clearcutting has been inferred from various root trenching experiments (*e.g.*, Vitousek *et al*., 1979) and N budget studies (Kimmins, Martin & Bradley, 2002).

A third plausible explanation for the higher soil NO_3^- concentrations measured on high deer density clearcut plots concerns the progressive conversion of early-seral forest vegetation to graminoid rangeland plant communities. Given the small size of our sampling quadrats, the data shown in Figure 4e do not represent the full extent of this phenomenon. In a recent landscape-level study of plant community dynamics on Anticosti Island, Barrette (2009) concluded that about two-thirds of recently disturbed forest sites have regressed toward an open rangeland structure dominated by graminoids, notably *Calamagrostis canadensis*. Although some have claimed that grasses are rarely consumed by white-tailed deer (*e.g.*, Horsley, Stout & DeCalesta, 2003), visual observations of their feeding habits on Anticosti Island have confirmed that *C. canadensis* is extensively browsed, especially the young shoots (Tesky, 1992). This perennial grass species is tolerant to browsing because of its basal leaf meristem (Gloser, 2002), and like most grasses it is expected to shunt a large proportion of its photosynthate belowground (Jackson, Mooney & Schulze, 1997). Increased rhizodeposition, resulting from a browser-induced succession towards rangeland plant communities,

could stimulate microbial growth and soil nitrogen dynamics (Bradley & Fyles, 1995b; Frank *et al.*, 2000).

In summary, our results confirm that clearcutting on Anticosti Island may increase nitrification rates in the forest floor. We have also shown that differences in deer-browsing intensity may significantly affect the magnitude of this NO_3^- flush. We conclude, therefore, that the size of large herbivore populations should be factored into conceptual or predictive model calculations of forest soil N cycling.

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