Nitrogen Deposition in Western National Parks

with Special Reference

to

Elk Island National Park

Final Report

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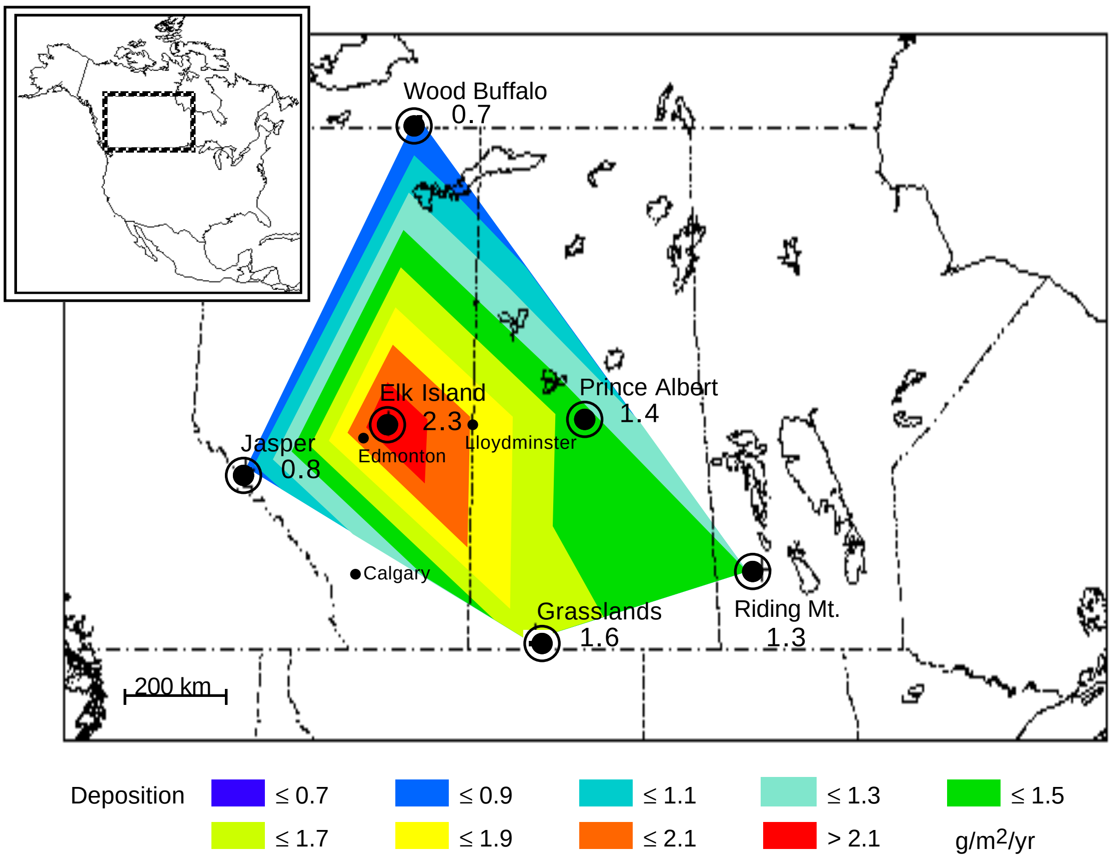
Deposition of Mineral Nitrogen from the Atmosphere ($g/m^2/yr$)



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Abstract

Vegetation changes in Elk Island National Park are consistent with effects of atmospheric mineral nitrogen (N) deposition on vegetation in central Europe. We measured the deposition of atmospheric mineral N and availability of mineral soil N in six western national parks continuously for two years using ion exchange resins. Deposition rates were highest in Elk Island National Park (2.3 g N/m^2/yr) and lowest in parks in non-industrialized areas (0.7-0.8 g N/m^2/yr). Availability of soil N was also highest in Elk Island (0.7 mg N/sample/yr) and lowest in parks in non-industrialized areas (0.3 mg N/sample/yr). At Elk Island, management practices (burning, grazing), soil type (brunisol, luvisol), and vegetation type (forest, shrubland, grassland) had no significant effect on N deposition. Availability of soil N, however, was highest in burned ungrazed sites, intermediate in burned and unburned grazed sites, and lowest in unburned ungrazed sites.

We also measured N storage in vegetation and soil in Elk Island and in a park with low N deposition, Jasper. N storage was similar in both parks. We assume that differences in N storage due to higher deposition in Elk Island were obscured by initial differences between parks and high variation among sites within parks.

Introduction

Nitrogen (N) is the nutrient that usually limits productivity in temperate terrestrial vegetation (Tamm 1991). Increased nitrogen supply can increase plant productivity (DiTommaso & Aarssen 1989), litter decomposition rate (Hunt et al. 1988), and microbial activity (Schimel 1986). Secondary effects include changes in plant-plant interactions (Wilson & Tilman 1995), higher grazing rate (Day & Detling 1990), higher fire susceptibility of prairie (Knapp & Seastedt 1986), and shading (Hogbom & Hogberg 1991). In combination or alone, these factors can cause the replacement of one vegetation type by another (Schulze et al. 1989, Berendse & Elberse 1990, Tamm 1991).

The Nitrogen Cycle

Nitrogen is the third most abundant element in biomass. N occurs as dinitrogen (N_2) in the atmosphere where it is by far the most abundant gas (78%). However, the molecular structure of N_2 prevents most species from using atmospheric N_2 directly. Only some bacteria and cyanobacteria are capable of converting N_2 into organic molecules such as proteins. N in this form is called "organic N". Eventually, N in dead organic matter is used by some bacteria to produce energy. Organic N is decomposed in several steps into "mineral N" (nitrate, NO_3^-, and ammonium, NH_4^+). Mineral N dissolved in soil water ("available N") is mostly taken up by plants and microbes. N in plants is returned to the soil as leaf or root litter where it is mineralized by micro-organisms and re-enters the nitrogen cycle. Plants may be eaten by animals and the N in faeces or carcasses is mineralized and returned to the soil.

In most temperate ecosystems there is less available mineral N in the soil than plants could take up. Consequently, the provision of additional mineral N, e.g., as fertilizer, increases plant growth.

Nitrogen Emissions

The atmosphere contains minute amounts of mineral N produced by forest and grassland fires, lightning, volatilization from animal faeces, and microbial activity. The amount of mineral N in the atmosphere due to natural processes may be increased up to 100 times as the result of human activity, especially from combustion processes in vehicles, power plants, and furnaces, from the production and application of fertilizer, and from intensive livestock breeding (Legge 1988, Taylor et al. 1994).

Nitrogen Deposition

Rain, fog, gravity, and diffusion return atmospheric mineral N to the biosphere where it is deposited on vegetation and soil (Söderlund 1981, Lovett 1994). The wash-out of mineral N from the atmosphere by precipitation (wet deposition) can be measured by collecting and analyzing rainfall. Mineral N that gravitates or diffuses to surfaces (dry deposition) is hard to measure because the process is affected by many factors including surface roughness, surface chemistry, and particle size (Davidson & Wu 1992, Lovett 1994). As a rule of thumb, dry deposition to inert surfaces is about the same amount as wet deposition (Linsey et al. 1987, van Breemen & van Dijk 1988, Fangmeier et al. 1994). In most regions, total (wet + dry) deposition of atmospheric mineral N is increasing with industrialization and traffic unless rigorous measures to reduce emissions are taken (Torrens 1987, Manitoba Environment 1995).

Effects of Nitrogen Deposition

Changes in species composition of vegetation in Elk Island National Park are consistent with vegetation changes in other areas exposed to fertilization by atmospheric mineral nitrogen: species such as *Poa pratensis* (Kentucky blue-grass) and *Urtica dioica* (stinging nettle) have increased (Tamm 1991, Caporn et al. 1994) and understorey biomass in Elk Island is similar to that in experiments in which N has been added to prairie (Wilson & Tilman 1991).

The deposition of high amounts of additional N in Europe and western North-America over recent decades has affected ecosystems (Ulrich 1989, Lovett 1994, Taylor et al. 1994). Observed or expected effects include increase of pioneer and weed-type species and species that are better competitors at higher N levels (e.g., *Urtica dioica*, *Rubus idaeus*, *Populus* sp., *Betula* sp.), decline of nutrient-poor heath-lands and bogs (Kellner & Mårshagen 1991, Berendse 1994), increase of evapotran-spiration due to increased production (Hofmann et al. 1990), decline of mosses and lichens (Rodenkirchen 1992, Morecroft et al. 1994, Fangmeier et al. 1994), decrease of species diversity (Kirchner 1977), increase of nutrients leaching from soil (Dise & Wright 1995), and decline of mycorrhiza (Hofmann et al. 1990).

Objectives of Study

We tested whether atmospheric N deposition and availability of soil N differed between national parks in agro-industrial and natural landscapes in western Canada. Further, we tested whether management practices (grazing, fire), soil type, or vegeta-tion type at Elk Island have an effect on nitrogen deposition and availability.

Lastly, we tested whether biomass, nitrogen, and carbon content of vegetation at Elk Island differ from those at Jasper, a park with less atmospheric N deposition.

Methods

Nitrogen Deposition and Availability

We measured nitrogen deposition and available soil N in six national parks in western Canada. Three parks were in agro-industrial landscapes (Elk Island, Riding Mountain, Grasslands) and three parks in more natural landscapes (Prince Albert, Jasper, Wood Buffalo). We determined N deposition as total dryfall and wetfall of nitrate and ammonium. Available soil N was determined as the total amount of un-bound nitrate and ammonium in the soil.

N was collected using ion-exchange resin bags (3 cm × 3 cm), each containing 1.1 g (≈1 cm^3) mixed-bed (anionic and cationic) ion-exchange resin (BioRad® AG 501-X8) with an ion-exchange capacity of 1 meq/g (Binkley & Hart 1989). Thus, the total ion-exchange capacity of each bag was 1.2 eq/m^2. Bags were washed in 2 M NaCl and rinsed in double-distilled water to remove dyes and excessive N from the resin.

Bags to collect N deposited from the atmosphere were put in flat 2 mm-mesh stainless steel hardware cloth cages (10 cm × 10 cm) and fixed to the ground by stainless steel pins to discourage mammals from removing the bags (Fig. 1). The cages were put in places that minimized tree canopy interception. Available soil N was measured by burying a resin bag about 10 cm deep in undisturbed vegetation (Fig. 2). Surface and belowground bags were paired and <20 m apart from each other. In all parks, except Elk Island, ten pairs of bags were put at 1-2 km intervals along roadsides with little traffic (Appendix 1). In Elk Island, N deposition and available soil N were measured in 21 sites (Appendix 1) representing all combinations of two soil types (luvisol and brunisol), two ungulate grazing regimes (grazed and ungrazed), two fire regimes (burned and not burned within the previous 15 years), and three vegetation types (forest, shrub, and grass). Burned, ungrazed forest, shrubland, and grassland on brunisol did not occur in Elk Island. Four pairs of bags were deployed for four

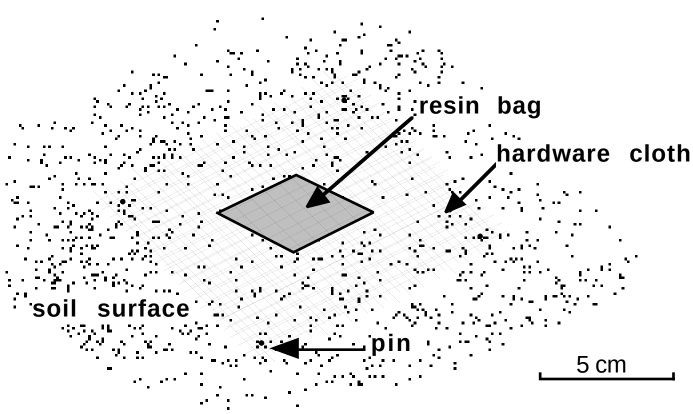

Fig. 1. Surface resin bag for measuring deposition of atmospheric mineral N (NO_3^- and NH_4^+).

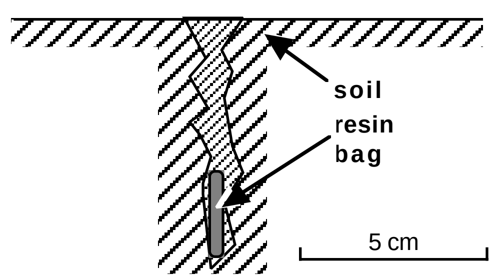

Fig. 2. Belowground resin bag for measuring available soil N (NO_3^- and NH_4^+).

seasons for two years (eight sampling periods) at each site.

Bags were set out during 13-25 June, 14-24 August, 5-12 October 1994, 26 April - 2 May, 14-24 June, 16-23 August, 4-11 October 1995 and 8-14 May 1996. Bags were retrieved when the next set of bags was set out. The last set was retrieved during 3-10 July 1996. Sampling periods correspond to summer, fall, winter, and spring. Some bags were not retrieved in April/May because the ground was still frozen or snow made the location inaccessible. These bags were retrieved in June/July.

The amount of N collected by the resin was assessed by removing the resin from retrieved bags and extracting the resin in 30 ml 2 M KCl (Giblin et al. 1994). The concentration of N in the extract was then measured using an ion-selective electrode (Orion, Boston, Massachusetts, USA). Results for surface bags were divided by mean bag area to calculate deposition per area. We added known amounts of nitrate and ammonia to unused bags to determine an extraction rate. We determined actual N uptake by bags used in the field by multiplying amounts of extracted N by extraction rate.

We calculated mean daily rates of deposited N (expressed as $g/m^2/yr = 10$ kg/ha/yr) and available soil N (expressed as mg/bag/yr) for each sampling period. Rates were compared among parks using four-factor analysis of variance (ANOVA) with year as a random factor and season and type of landscape, i.e., agro-industrial vs. natural, as fixed factors. Parks were nested as a random factor within landscape. For comparisons within Elk Island we summed deposition and soil N amounts over season and compared annual deposition rates using five-factor ANOVA with year as a random factor and fire, grazing, vegetation type, and soil type as fixed factors. For reasons of comparability we used only data from ungrazed forest vegetation at Elk Island in comparisons among parks because the grazed areas at Elk Island appeared to be more heavily grazed than those of other parks. We assumed that samples with an equivalent of ≥ 10 g $N/m^2/yr$ (≥ 100 kg N/ha/yr) had been contaminated and excluded them from analyses.

Nitrogen Storage

At Elk Island and Jasper we measured the mass of each of the following vegetation and soil compartments: standing crop (tree leaves, tree stems, shrub leaves, shrub stems, herbs), litter, roots at 0-15 cm and 15-50 cm depth, and soil at 0-15 cm and 15-50 cm depth. Each compartment was measured in 10 forest, 10 shrubland, and 10 grassland plots. Forest plot size was 10 m × 10 m, shrubland plot size was 1 m × 2 m, and grassland plot size was 0.1 m × 1 m. We used 1 m × 2 m plots to sample shrubs within the centre of forest plots and we used 0.1 × 1 m plots to sample herbaceous shoots and litter in the centre of the plots for all vegetation types. Root and soil mass were sampled with a 2-cm diameter soil corer at 0-15 cm and 15-50 cm depth. Three soil cores were taken from each plot and depth and mixed. In some plots rocks prevented us from taking soil and root samples from the 15-50 cm soil layer.

We determined tree stem and leaf mass by measuring tree height and diameter at breast height (1.3 m) and calculating mass according to the equations given by Peterson & Peterson (1992). We determined shrub stem and leaf mass by measuring basal stem diameter and calculating mass according to regression equations. The equations for snowberry (*Symphoricarpos occidentalis*), buffaloberry (*Shepherdia canadensis*) and hazel (*Corylus cornuta*) were established from 30 shrubs per species growing just outside the plots. Equations for wolfwillow (*Elaeagnus commutata*) and rose (*Rosa acicularis* sp.) were established from 30 shrubs per species growing in natural prairie near Regina, Saskatchewan. The regression equation for wild red raspberry (*Rubus idaeus*) was taken from Brown (1976). Biomass samples were dried to constant mass at 70 °C.

We took randomly selected subsamples of all vegetation compartments of each plot for analysis of tissue N and C content. Subsamples were one stem core and five leaves of each of five trees, stems and leaves of five shrubs, ten subsamples of forb leaves, grass leaves, and herbaceous stems from 0.1 × 1 m^2 plots, and ten subsamples of soil and roots. Subsamples for each compartment in each plot were pooled, ground, and analyzed by the Stable Isotope Facility at the University of Saskatchewan. Carbon and nitrogen concentrations were multiplied by compartment mass to calculate C and N storage. Results for subcompartments of standing crop (tree leaves and stems, shrub leaves and stems, herbs) are reported in Appendix 2.

Budget data were analyzed using a mixed-effects ANOVA with park, vegetation type, and compartment as fixed effects and plot as a random effect.

Statistical Details

Mean squares were calculated with JMP 3.1.6 (SAS Institute 1996) and F and p values with Excel 4.0 (Microsoft 1992) according to the formulas in Zar (1974) because SAS Institute calculates F values in a non-standard way (Ayres & Thomas 1990). Data were checked for homogeneity of variances and normality and log-transformed to meet assumptions for ANOVA. Due to missing data we could not always calculate all F-tests in a full-factorial ANOVA. In those cases we pooled non-significant factors ($p \geq 0.20$) with the error term (Kirk 1968). We report significance as *: $p \leq 0.05$, **: $p \leq 0.01$, and ***: $p \leq 0.001$.

Results

Nitrogen Deposition

Deposition rates differed significantly among parks ($F_{4,407} = 7.05$***, Fig. 3). Elk Island received the highest amount of N from the atmosphere, Wood Buffalo the lowest. Deposition rates for parks in agro-industrial landscapes (1.7 g/m^2/yr) were twice those of parks in natural landscapes (1.0 g/m^2/yr), but the difference was not significant due to high deposition rates at Prince Albert, which were similar to those in agro-industrial landscapes.

Deposition rates differed among seasons ($F_{3,3.72} = 11.57$*, Fig. 3). Rates were on average lowest in winter and peaked in summer. The seasonal pattern differed among parks ($F_{12,407} = 2.97$***, Fig. 3) with Elk Island and Grasslands receiving their highest

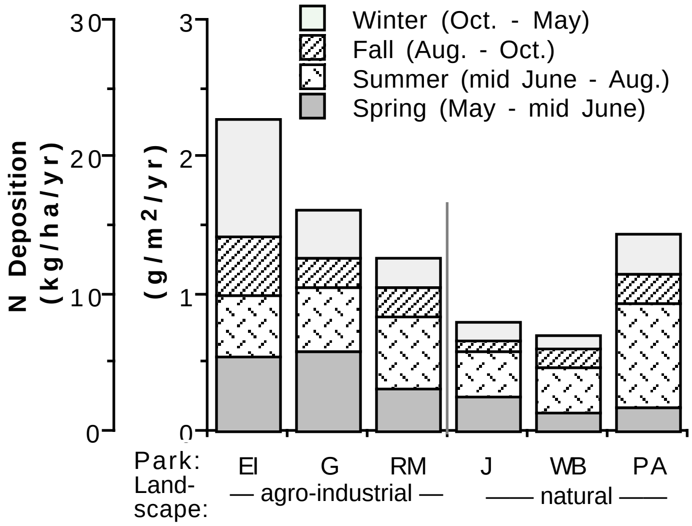

Fig. 3. Annual and seasonal rates of atmospheric mineral N deposition in western Canadian parks (daily rates times length of season). Park abbrevia-tions: EI: Elk Island, G: Grasslands, RM: Riding Mountain, J: Jasper, WB: Wood Buffalo, PA: Prince Albert.

daily N input in spring. Prince Albert was also exceptional in that it received 1.44 g/m^2/yr in summer, a higher average than in any other season in any of the parks. Deposition rates showed a geographical pattern with high rates southeast of Edmonton (Fig. 4).

At Elk Island, grazing, fire, soil type, and vegetation type, individually or as interactions, did not affect deposition rates.

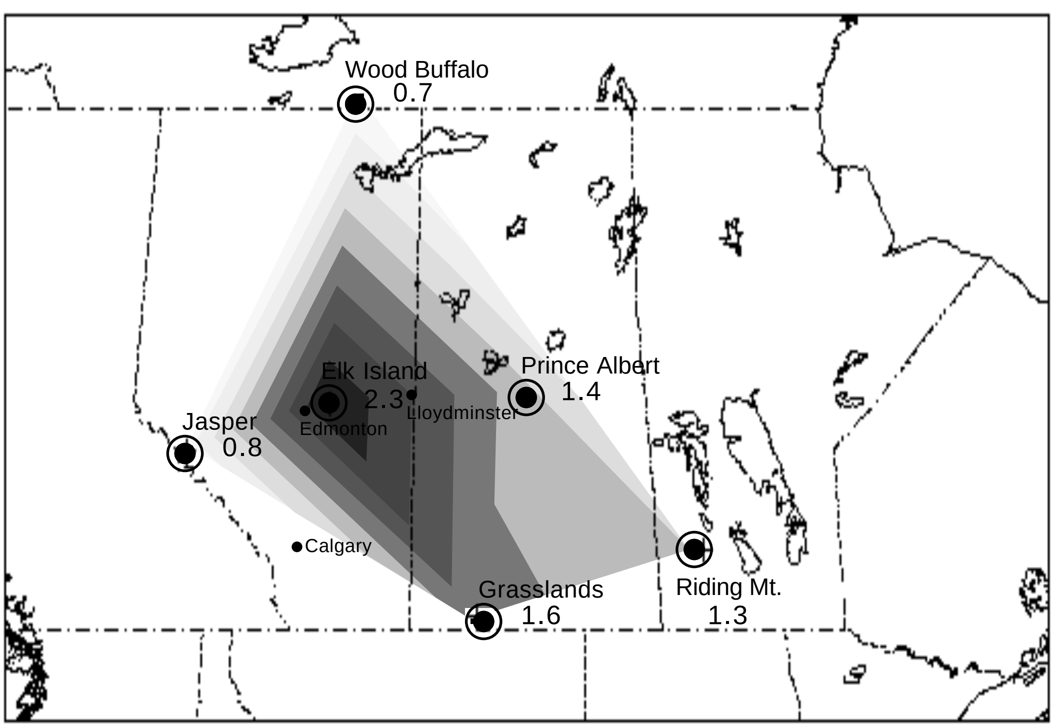

Fig. 4. Geographical distribution of deposition rates of atmospheric mineral N (g N/m^2/yr).

Available Soil Nitrogen

Available soil N differed significantly among parks ($F_{4,400}$ = 8.06***). The highest rate was measured at Elk Island, the lowest at Jasper, but there was no significant difference between agro-industrial and natural landscapes (Fig. 5). Rates of available N were on average highest in spring and declined during the vegetation period. Differences among seasons, however, were not significant ($F_{3,2.36}$ = 13.75, p = 0.07, Fig. 5). At Elk Island, available soil N varied significantly with the interaction between fire and grazing ($F_{1,17}$ = 18.09***, Fig. 6). This occurred because grazing increased available soil N in unburned vegetation but decreased soil N in burned vegetation.

Available soil N increased significantly with N deposition. The relationship was stronger among parks (R^2 = 0.417, $F_{1,46}$ = 23.76***, Fig. 7) than within Elk Island (R^2 = 0.173, $F_{1,158}$ = 32.99***, Fig. 8).

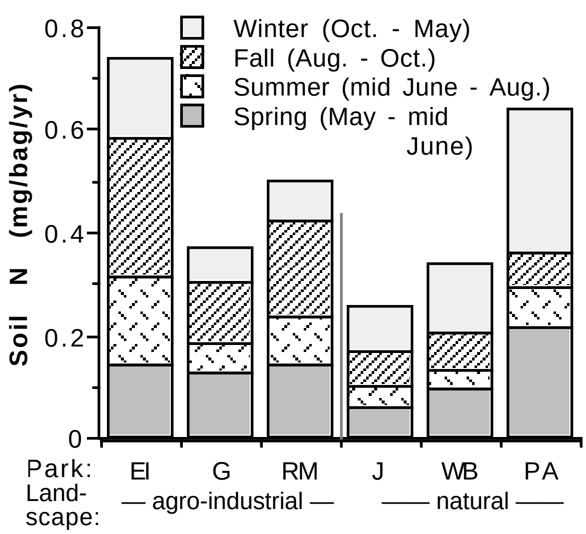

Fig. 5. Annual and seasonal rates of available mineral N in soils in western Canadian parks (daily rates times length of season). Abbreviations as in Fig. 3.

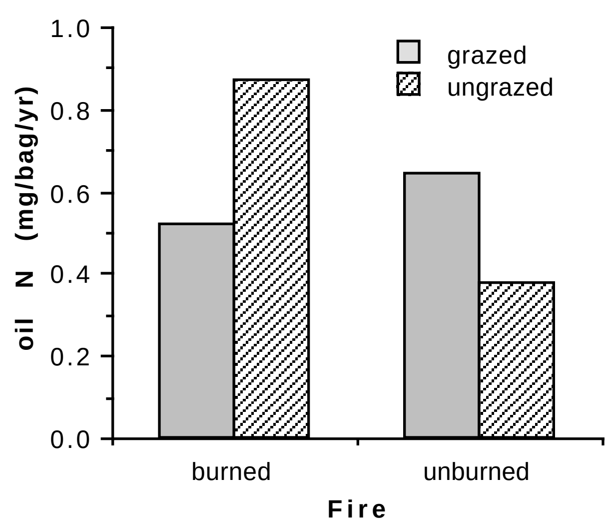

Fig. 6. Available mineral N in soil in Elk Island National Park: fire × grazing interaction.

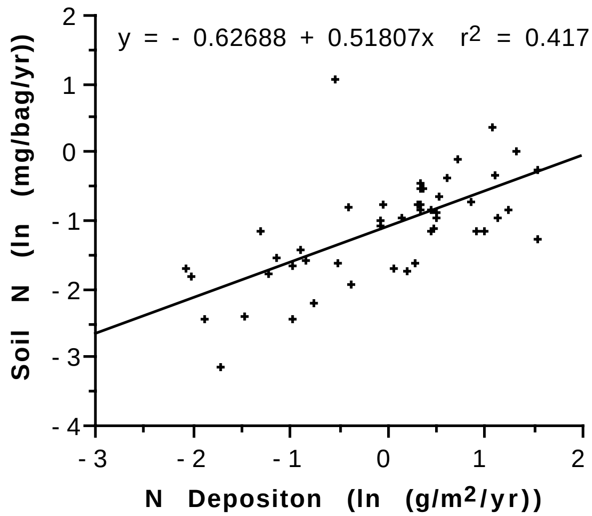

Fig. 7. Available mineral N in soil in western Canadian parks as a function of mineral N deposition (n = 48).

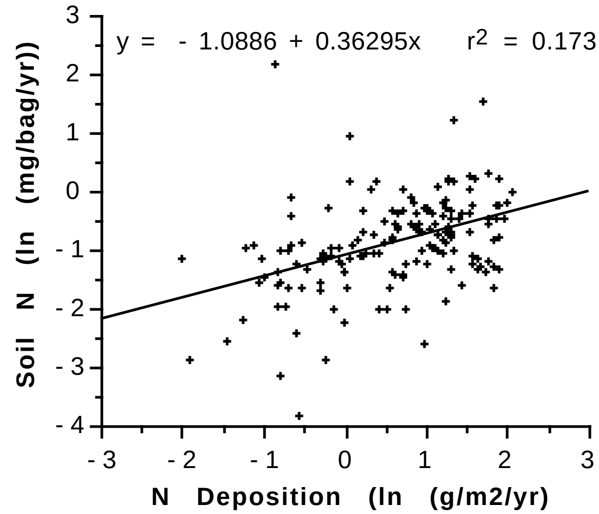

Fig. 8. Available mineral N in soil in Elk Island National Park as a function of mineral N deposition (n = 160).

Nitrogen storage

Averaged over vegetation types, the total amount of N in the ecosystem (vegetation plus soil) at Elk Island (0.127 kg/m^2) was not significantly different from the amount at Jasper (0.144 kg/m^2). N in biomass was also not significantly different between parks. In both parks, forest had the highest amount of N and shrubland had a lower amount than prairie (Fig. 9). At Elk Island, the amount of N in shrubland and

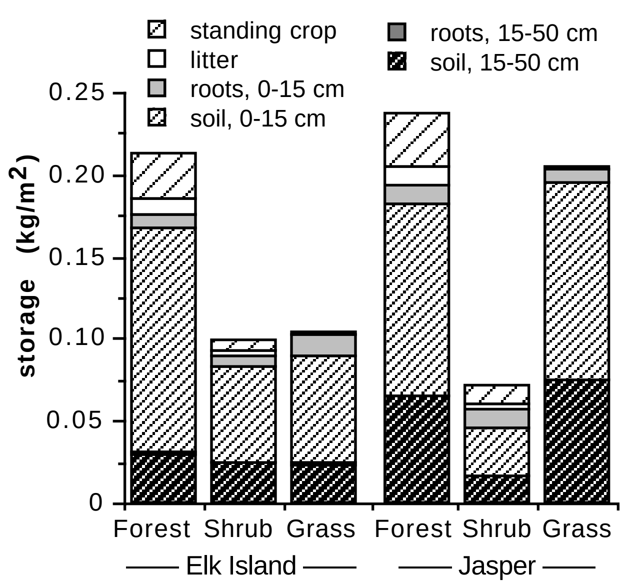

Fig. 9. Amount of nitrogen in standing crop, litter, roots, and soil of forest, shrubland, and prairie in Elk Island and Jasper National Parks.

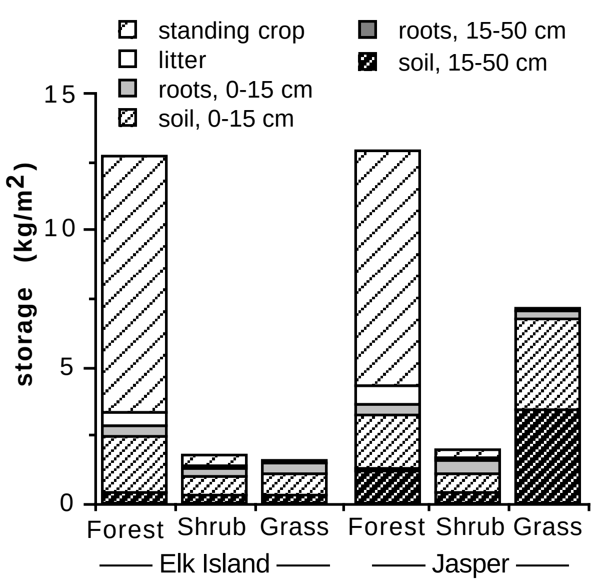

Fig. 10. Amount of carbon in standing crop, litter, roots, and soil of forest, shrubland, and prairie in Elk Island and Jasper National Parks.

prairie was very similar, at roughly half the amount of forest. In Jasper, in contrast, the amount of N in shrubland was about a third the amount in prairie and forest. In both parks, most of the N was stored in the soil at 0-15 cm depth ($F_{5,45}$ = 353.23***).

Total carbon (C) storage averaged over vegetation types was lower in Elk Island (5.136 kg/m^2) than Jasper (6.294 kg/m^2, $F_{1,9}$ = 33.42***). Prairie in Elk Island had only about a fifth of the total C in Jasper ($F_{2,18}$ = 32.53***, Fig. 10). Most C in all vegetation types was stored in the upper soil layer ($F_{5,45}$ = 203.60***, Fig. 10).

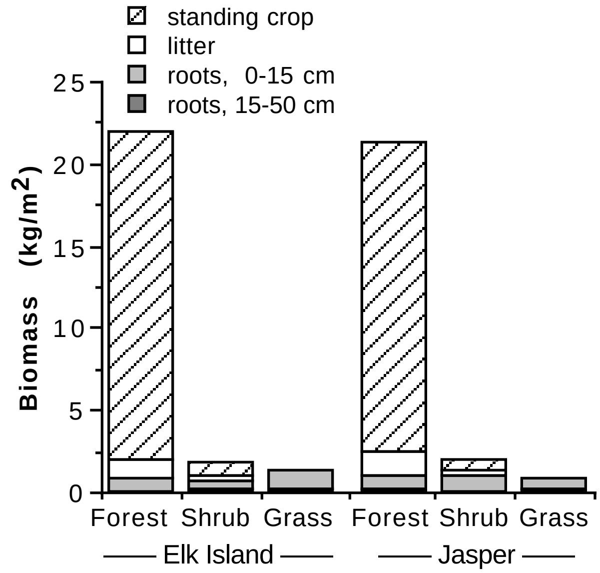

Fig. 11. Biomass of standing crop, litter, roots, and soil of forest, shrubland, and prairie inElk Island and Jasper National Parks.

Biomass averaged over vegetation type was similar in both parks (Elk Island: 8.335 kg/m^2, Jasper: 8.000 kg/m^2). In both parks, forest had the highest biomass (21.594 kg/m^2, average of both parks), shrubland about a tenth of forest (1.868 kg/m^2), and grassland about half of shrubland (1.039 kg/m^2; $F_{2,18}$ = 667.56***; Fig. 11).

Discussion

Elk Island: Atmospheric and Soil Nitrogen

Elk Island had the highest rate of N deposition (Fig. 3, 4) and the highest rate of available soil N (Fig. 5) for all parks. The general correlation of N deposition and available soil N (Fig. 7, 8) supports the hypothesis of a causal relationship between the two processes.

High N input in Elk Island is presumably caused by high nitrate emissions from the Edmonton area (>20µg nitrate/m^3/yr compared to <1 µg/m^3/yr in northern Alberta, Legge 1988, Fig. 4). The largest sources of nitrate emissions in Edmonton are power plants, petroleum industry, urban establishments, and traffic (Legge 1988).

Prince Albert, although categorized as park in natural landscape, received high rates of N deposition comparable to those in agro-industrial landscape (Fig. 3). The high deposition rate is reflected in a high rate of available soil N (Fig. 5). As at Elk Island, grassland at Prince Albert is being invaded by forest (M. Fitzsimmons, *pers. comm.*). Both cases may be related to high N deposition rates. High N input in Prince Albert may originate from long-distance transport from oil refineries in Lloydminster, in addition to emissions from Edmonton (Fig. 4). The peak rate of N deposition in Prince Albert occurred in summer (Fig. 3), suggesting an effect of forest fire frequency or tourism traffic.

High deposition rates at Grasslands (Fig. 3, 4) may be caused by fertilizer application in southern Alberta and southwest Saskatchewan in the first place or by long-distance transport from Calgary which also emits >20 µg nitrate/m^3/yr (Legge 1988).

At Elk Island, soil N varied with the interaction between fire and grazing (Fig. 6). The interaction is partly caused by high soil N in one location (Oxbow Trail exclosure) where the herb and shrub vegetation had not yet regrown after a forest fire. It is likely that high amounts of N in the soil are due to breakdown of organic matter from fire, increased microbial mineralization, and a lack of uptake by vegetation from the upper soil layer (Risser & Parton 1982, Stock & Lewis 1986). Two months later, soil N at the same site was no longer unusually high. On burned and unburned grazed sites, soil N may be higher than on unburned ungrazed sites because plants take up more N to compensate for losses by grazing (Risser & Parton 1982).

Growth of temperate natural vegetation is usually limited by availability of N (Tamm 1991). Therefore, addition of N by deposition would enhance plant growth. Available soil N was about a third of N deposition (Fig. 7, 8), suggesting that most of the deposited N enters the N cycle and is taken up by the vegetation. N storage, however, did not differ between Elk Island and Jasper (Fig. 9). On the other hand, available soil N was much higher in Elk Island than in Jasper (Fig. 5). This relation suggests that vegetation change in Elk Island is more related to high availability of soil N than to total N in the system (Aber et al. 1991). If growth of aspen at Elk Island is more limited by N than is the growth of grasses, or if aspen uses N less efficiently, then additional N from atmospheric deposition could favour aspen and cause a shift from grassland to forest (cf. Wedin & Tilman 1990, Hobbie 1992, Berendse 1994). Two lines of evidence suggest that this should happen: (1) aspen is associated with soils with high rates of available N (Wilson 1993, Wilson & Kleb 1996), and (2) growth form of aspen allows it to scour air for N more than grasses do (van Breemen & van Dijk 1988, Binkley 1995).

Assuming that N storage in the organic mass of a vegetation type is related to long-term (decades to centuries) availability of soil N (Fig. 9, Rode 1993), we predict that, with increasing N deposition and in the absence of recurring disturbance (fire, grazing, avalanches, etc.), vegetation types tend to develop towards forest. Forest may take up more N per root mass (Fig. 9, 11), may produce more leaves, and potentially shade out competing herbaceous vegetation (Hogbom & Hogberg 1991).

Deposition Rates

The seasonal pattern of daily deposition rates (Fig. 3) seems to correlate roughly with seasonal temperatures. Monthly data of wet deposition for 1990-1993 (M. Shaw, Environment Canada, *pers. comm.*) collected by the only two monitoring stations in the prairie provinces, Esther, Alberta (51° 40' N, 110° 12' W), and McCreary, Manitoba (50° 43' N, 99° 31' W), show a similar seasonal pattern with a peak in May or June. Peaks in spring or early summer may result from high farming activity with fertilizer application.

At Elk Island, deposition rates did not vary with grazing or fire history. Ammonia released from ungulate urine deposits (Redmann 1975) is small compared with among-site variation in N deposition. Vegetation type also had no significant effect on deposition rate. Although denser vegetation may "comb" the air more effectively (Binkley 1995) and increase deposition rates locally, deposition in grassland was similar to that in forest (see also Heil et al. 1988, van Dam 1990).

Soils are a potential source of atmospheric mineral N as a product of protein decomposition and anaerobic microbial denitrification (Firestone & Tiedje 1979, Tamm 1991). Differences between soil types, however, were much smaller than variation within the same type.

Our measurements of N deposition are not directly comparable to those obtained by climatological methods (precipitation collection), because ion-exchange resin bags measure deposition and soil N in a way that may be more relevant to plants. In our study area there are only two stations run by Environment Canada (CAPMoN programme, M. Shaw, *pers. comm.*) that measure wet deposition of atmospheric mineral. Annual wet deposition of total N (nitrate-N + ammonium-N) for 1990-1993 was 0.13 $g/m^2/yr$ at Esther, Alberta, and 0.30 $g/m^2/yr$ at McCreary, Manitoba. Applying published wet:dry deposition ratios from northwestern Ontario (Linsey et al. 1987), annual wet + dry deposition of total N in the grainbelt would range between approximately 0.2 and 0.5 $g/m^2/yr$. For comparison, total annual deposition in The Netherlands was estimated to be 4.1 $g/m^2/yr$ (van Breemen & van Dijk 1988).

Our measurements are about four times higher than estimates based on wet deposition (e.g. CAPMoN data) partly because we actually included dry deposition in our measurements while most other studies have estimated dry deposition. Our results are higher than climatological measurements because we did not use an inert receptor surface. A non-inert surface such as leaves or ion-exchange resins can increase deposition rates through adsorption and absorption (Ulrich et al. 1979, Davidson & Wu 1990). Our measurements are also higher because resin bags were underneath the canopy where deposition is enriched by N that is washed or leached from the vegetation (e.g., Lovett et al. 1985, Nihlgård 1985, Lindberg et al. 1986, Potter et al. 1991).

Available Soil Nitrogen

Elk Island and Prince Albert had the highest rates of available soil N of parks in agro-industrial and, respectively, natural landscape (Fig. 5). This is a similar pattern as for deposition rates (Fig. 3). Most remarkable is a high rate of soil N in Prince Albert in spring. Spring rates in other parks were either low or comparable to rates in other seasons (Fig. 5). This indicates that high soil N in Prince Albert is due to site-specific factors, e.g., subsurface drainage of nitrate-rich soil water as the result of high decomposition rates and a low capacity of microbes and vegetation to assimilate nitrogen.

Nitrogen Storage

Nitrogen storage at Elk Island did not differ significantly from that at Jasper. We do not know the pre-industrial level of N storage in either park and therefore cannot tell whether N from atmospheric N is accumulating in the biomass. The higher amount of N deposited from the atmosphere at Elk Island is probably incorporated into the N cycle and not lost rapidly from the ecosystem because most natural temperate vegetation types are N-limited (Tamm 1991). We may have overlooked N stored at greater depth than 50 cm, but that amount is presumably very small (Dormaar & Lutwick 1966).

We estimated the amount of N that Elk Island may have received from anthropogenic N deposition by summing the difference between the deposition rates of Elk Island and Jasper over 100 years. We used three scenarios: quadratic, linear, and inverse-quadratic increase of deposition rates. We calculated that within the past 100 years 50-100 g N/m^2 may have been added to Elk Island vegetation on top of natural input. The variability of N storage among plots, however, was in the same order of magnitude (standard deviation in forests $\approx$60 g/m^2) and obscured differences between parks.

N and C storage in Elk Island soils were lower than in Jasper. This may be a reflection of Elk Island's woody vegetation (Dormaar & Lutwick 1966), since forest soils store less N and C than grassland soils. Our data do not reflect the spatial extent of each vegetation type in each park. Thus, Elk Island as a park may have more N and C in the ecosystem because more of Elk Island is forest than is the Athabasca valley sampled in Jasper.

Conclusions

Higher deposition rates, increases in available soil N, and vegetation change are consistent with patterns of ecosystem effects of N deposition in central Europe. There, high amounts of deposited N (5-20 g N/m^2/yr, Diederen & Duyzer 1988 in Pearson & Stewart 1993) are correlated with the increase of tall species in nutrient-poor grassland (Bobbink et al. 1988, Ellenberg 1985, 1987), heathland (Berendse 1994), and forest understorey (Kellner & Mårshagen 1991, Hofmann et al. 1990). There was also an increase of species typical of N-rich but acidic sites (Tyler 1987, Ellenberg 1988, Bobbink et al. 1992) in forests. Trees in exposed forests in Europe first showed accelerated growth, as is observed for aspen in Elk Island, but later the damaging acidifying effects of N deposition prevailed (Heinsdorf & Lützke 1982, Nihlgård 1985, Hofmann et al. 1990, Bobbink et al. 1992).

Deposition rates in Elk Island are approaching a region of 1-7.5 g N/m^2/yr (measured as wet deposition) where detrimental effects on ecosystems beyond vegetation change such as toxicity or nitrate leaching can be expected or have been observed in some cases (Hyder et al. 1975, Grennfelt & Thörnelöf 1992, Pearson & Stewart 1993, Dise & Wright 1995). The threshold region, however, is not universal (cf. Wittig et al. 1985, Nilsson et al. 1988, Becker et al. 1992).

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Appendix 1

Study sites:

Elk Island National Park

UTM zone 12 (UQ) W4M

3762E	59527N	brunisol/grazed/unburned/forest, shrub, grass
		luvisol/grazed/unburned/forest, shrub, grass
3752E	59468N	luvisol/ungrazed/burned/shrub, grass (outside park)
		luvisol/grazed/burned, shrub, grass
3752E	59467N	luvisol/grazed/burned/forest
3752E	59466N	luvisol/grazed/burned/shrub, grass
3825E	59464N	brunisol/ungrazed/unburned/forest, shrub, grass (outside park)
3803E	59445N	brunisol/ungrazed/unburned/forest
		brunisol/grazed/unburned/forest, shrub, grass
3727E	59394N	luvisol/ungrazed/unburned/grass
		luvisol/grazed/unburned/grass
3748E	59394N	luvisol/ungrazed/unburned/grass
3782E	59381N	luvisol/ungrazed/unburned/forest, shrub, grass
3754E	59335N	brunisol/burned/grazed/forest, shrub, grass

Grasslands National Park

West block, between km 0 and 8 from northern gate

Jasper National Park

Celestine Lake road on two-lane part

Prince Albert National Park

Kingsmere Road between Waskesiu and Point View

Riding Mountain National Park, Manitoba

Highway 10 between Beach Ridges and Moon Lake

Wood Buffalo National Park

Ft. Smith - Peace Point road between km 24 and 42

Appendix 2

Table 1. N storage (g/m^2) in forest, shrubland, and grassland in Elk Island and Jasper National Parks.

	Elk Island			Jasper		
Compartment	Forest	Shrubland	Grassland	Forest	Shrubland	Grassland
Tree Leaves	11.100			11.559		
Tree Stems	15.918			16.947		
Shrub Leaves	0.089	3.403		0.332	2.927	
Shrub Stems	0.238	3.517		0.431	7.741	
Herbs	1.341	0.314	1.910	2.329	0.401	0.934
Standing Crop	*28.687*	*7.233*	*1.910*	*31.597*	*11.069*	*0.934*
Litter	9.739	3.589	0.109	12.620	2.841	0.382
Roots, 0-15 cm	8.222	5.866	13.060	9.948	11.215	8.195
Roots, 15-50 cm	0.250	0.713	1.034	1.172	0.011	1.026
Biomass	*46.898*	*17.401*	*16.114*	*55.337*	*25.137*	*10.537*
Soil, 0-15 cm	136.323	58.257	64.166	117.156	30.606	119.701
Soil, 15-50 cm	29.954	24.063	23.335	64.126	15.631	74.292
Total	*213.176*	*99.721*	*103.614*	*236.618*	*71.374*	*204.530*

Table 2. C storage (g/m^2) in forest, shrubland, and grassland in Elk Island and Jasper National Parks.

	Elk Island			Jasper		
Compartment	Forest	Shrubland	Grassland	Forest	Shrubland	Grassland
Tree Leaves	371.816			417.608		
Tree Stems	19590.770			18179.400		
Shrub Leaves	12.497	123.146		17.959	84.954	
Shrub Stems	57.275	598.513		99.131	639.945	
Herbs	80.656	14.874	98.782	114.683	39.857	40.414
Standing Crop	*20113.013*	*736.533*	*98.782*	*18828.781*	*764.756*	*40.414*
Litter	1086.676	324.741	9.101	1446.385	273.952	36.936
Roots, 0-15 cm	768.506	555.026	1125.438	857.739	969.784	668.981
Roots, 15-50 cm	21.221	110.135	123.964	106.103	1.061	89.127
Biomass	*21989.416*	*1726.436*	*1357.285*	*21239.008*	*2009.553*	*835.458*
Soil, 0-15 cm	37549.110	41721.410	41579.330	37411.070	39243.260	37595.260
Soil, 15-50 cm	42791.460	45216.240	45728.930	38006.730	39077.840	42565.110

Table 3. Mass (g/m^2) of forest, shrubland, and grassland in Elk Island and Jasper National Parks.

	Elk Island			Jasper		
Compartment	Forest	Shrubland	Prairie	Forest	Shrubland	Prairie
Tree Leaves	174.052			195.954		
Tree Stems	9124.045			8251.223		
Shrub Leaves	1.338	54.161		8.312	39.214	
Shrub Stems	7.462	263.846		46.938	284.819	
Herbs	33.262	6.150	42.431	46.807	18.619	17.482
Standing Crop	*9340.159*	*324.157*	*42.431*	*8549.233*	*342.652*	*17.482*
Litter	489.122	145.922	3.772	670.814	128.147	15.692
Roots, 0-15 cm	359.546	237.235	448.505	391.669	425.006	271.372
Roots, 15-50 cm	9.679	42.658	48.645	47.411	0.500	40.157
Biomass	*10198.506*	*749.972*	*543.353*	*9659.126*	*896.305*	*344.703*
Soil, 0-15 cm	2055.163	714.279	718.880	1968.363	725.472	3320.491
Soil, 15-50 cm	402.240	257.808	263.116	1184.731	359.516	3407.166
Total	*12655.908*	*1722.060*	*1525.349*	*12812.220*	*1981.293*	*7072.360*