

Nitrogen deposition and forest expansion in the northern Great Plains

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Summary

1 Atmospheric nitrogen (N) deposition has become one of the most important agents of vegetation change in densely populated regions. It may also contribute to forest expansion into grasslands at the northern edge of the North American Great Plains.

2 We measured N deposition and available soil N with ion-exchange resin over 2 years in six national parks in areas varying in population density and industrialization. N deposition was significantly higher in four parks in densely populated regions than in two remote parks.

3 Available soil N increased significantly with N deposition across all parks.

4 We measured N mass and ^{15}N abundance ($\delta^{15}\text{N}$) in vegetation and soil in two parks: Elk Island, receiving $22 \text{ kg N ha}^{-1} \text{ year}^{-1}$, and Jasper, receiving $8 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Differences between parks in tissue N concentrations were small, but forest expansion over five decades resulted in the mass of N in vegetation increasing by 74% in Elk Island but by only 26% in Jasper. $\delta^{15}\text{N}$ in forest vegetation was significantly lower in Elk Island than in Jasper, suggesting that anthropogenic sources contribute significantly to the high rates of N entering that ecosystem.

5 We determined the rate of forest expansion within parks using six decades of aerial photographs. Parks in aspen parkland and boreal forest showed a strong positive relationship between forest expansion and N deposition. The relationships found between N deposition, available soil N and forest expansion suggest that even comparatively low rates of N deposition may accelerate the expansion of forest into temperate grasslands.

Key-words: terrestrial eutrophication, invasion, grassland, nitrogen deposition, forest

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Introduction

Terrestrial eutrophication caused by nitrogen (N) deposition is receiving considerable attention because it changes species composition and lowers diversity over wide areas (Vitousek *et al.* 1997; Bobbink *et al.* 1998). Studies of N deposition have naturally focused on areas receiving high inputs, such as the north-eastern United States and Europe. Vegetation change, however, is not restricted to areas with dense human populations. The grasslands of the Great Plains of North America, for example, have relatively small human populations and, presumably, low rates of N deposition, and yet are characterized by invasions of woody species

(Archibold & Wilson 1980; Kleb & Wilson 1997). Our objective was to test for variability in N deposition across the sparsely populated northern edge of the Great Plains, and to determine whether deposition and rates of tree invasion are related.

In this region, relatively low mean temperatures reduce evapotranspiration compared with more southern locations, and the limiting soil resource is therefore usually N (Tilman 1987). This situation may be analogous to that in Europe where, at similar latitude and with ample water, the single most important agent of vegetation change in nature reserves is N deposition (Vitousek *et al.* 1997). High amounts of deposited N are correlated with the increase of tall species in nutrient-poor European grasslands and heathlands (Bobbink *et al.* 1998). Due to their height, trees and shrubs can intercept more airborne particulate N than grasses and they should therefore benefit most from N deposition (Kellman & Carty 1986; Binkley 1995). Fertilization also increases the water-use efficiency of woody invaders (Bert *et al.* 1997) and this may enable them to

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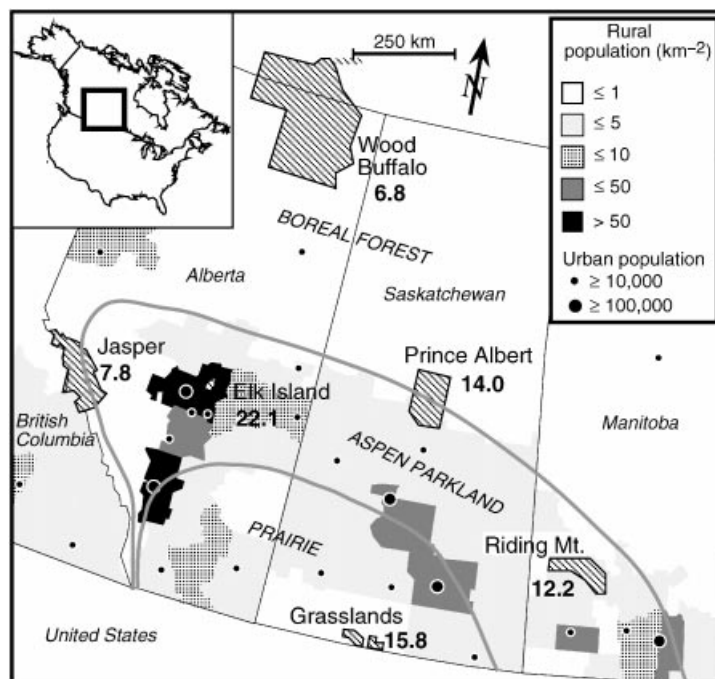


Fig. 1 N deposition rate (bold numbers; kg ha⁻¹ year⁻¹) in six national parks (hatched areas) in western Canada. Natural vegetation zones (forest, parkland, prairie) are as shown. Population density is based on electoral regions (Köchy 1999). The inset shows the location of the study area in North America.

colonize temperate grasslands on dry, coarsely textured soils. Accelerated N cycling following deposition (Högbom & Högberg 1991; Berendse 1994; Carreiro *et al.* 2000) decreases competition for N and increases competition for light (Wilson & Tilman 1991), and may give further advantage to tall or fast growing trees (Aerts 1999). Overall, therefore, increased deposition rates may result in a self-maintaining positive feedback that allows trees to establish in grasslands (Wilson 1998).

The southern limit of forest in our region appears to have been relatively stable for the last 2000 years of the Holocene (Campbell *et al.* 1994; Hickman & Schweger 1996) but has been extending into the Great Plains since the first historical records (Archibold & Wilson 1980). Although this expansion is commonly attributed to reductions in bison grazing and fire frequency (Campbell *et al.* 1994; Archer 1996; Schwarz & Wein 1997), which may be necessary for forest expansion, other factors may accelerate the advance of forest into grassland (Archer 1996). On the Great Plains, European colonization, industrialization and the increase of atmospheric anthropogenic N appear to be temporally correlated with the expansion of forest.

N deposition varies on a continental scale (NADP 1996) but the effects of N deposition on ecosystems have mostly been studied on small scales in regions of high deposition (e.g. Potter *et al.* 1991; Aber *et al.* 1993; Magill *et al.* 1997) and dense populations (NADP 1996; Vitousek *et al.* 1997). We therefore examined patterns of N deposition and vegetation change over a large, sparsely populated area at the northern edge of the Great Plains (Fig. 1) where N deposition rates are likely to be relatively low.

The isotopic composition of anthropogenic N emissions differs from that of atmospheric dinitrogen (N₂), with a lower ¹⁵N : ¹⁴N ratio in vehicle exhaust than in N₂ (Heaton 1990). Vehicle exhausts are the largest source of total N emissions in the Canadian prairie provinces (34.3%; Environment Canada 1997, 1998), followed by petrochemical refining (33.9%), power and heat production (15.7%) and forest fires (9.6%). Given the high contribution of vehicles to N emissions in this region and the ubiquity of this source, the ¹⁵N abundance of deposited N should tend to be lower than that of organic N biologically fixed from N₂.

Here we relate 2 years of continuous measurements of N deposition made along the northern edge of the Great Plains to values of soil N availability. We compared ¹⁵N abundance of vegetation in a park with high deposition with that in a park with low deposition and explored whether the source of N deposition can be deduced from the ¹⁵N signal. Lastly, we used six decades of aerial photographs to test whether forest invasion rates are related to N deposition rates.

Methods

STUDY SITES

We measured atmospheric nitrogen deposition, available soil N and forest invasion in six national parks in western Canada (Fig. 1, Table 1) for 25 months during 1994–96. The parks vary in proximity to large cities and in regional population density. All parks included both forest and grassland areas. Four parks (Jasper, Elk Island, Prince Albert, Riding Mountain) are close

Table 1 Description of study sites: six national parks in western Canada

	Elk Island	Grasslands	Prince Albert	Riding Mountain	Jasper	Wood Buffalo
Elevation (m)	750	800	650	650	1000	500
Climate type ¹	Arid, temperate- boreal, continental	Arid, temperate continental	Arid, temperate- boreal, continental	Arid temperate- boreal continental	Montane within temperate- boreal	Boreal, continental
Annual precipitation (mm) ²	412	312	456	508	394	353
Annual mean temperature (°C) ²	2.6	3.5	0.3	0.0	3.1	-3.0
Trees	Aspen ³	Aspen	Aspen, spruce	Aspen, spruce ⁴	Spruce, aspen ⁵	Aspen ⁶
Dominant grasses	<i>Poa pratensis</i>	Mixed-grass prairie ⁷	<i>Festuca scabrella</i> ⁸	<i>Festuca scabrella</i> ⁹	<i>Koeleria</i> ⁵	Northern prairie ^{6,10}
Soil types ¹¹	Gray Luvisol	Brown Chernozemic and Solonchic	Gray Luvisol	Black Chernozemic	Regosol	Gley- Fibri- Bruni- Cryosols

¹Mean annual precipitation and temperature, Walter & Lieth (1967); ²Environment Canada (1993); ³Bork *et al.* (1997); ⁴Dickson (1909); ⁵Holland & Coen (1982); ⁶Raup (1935); ⁷Coupland (1950); ⁸Carbyn (1971); ⁹Blood (1966); ¹⁰Schwarz & Wein (1997); ¹¹National Atlas of Canada (1974).

to the natural boundary between aspen parkland and boreal forest, while Grasslands, which is further south, is dominated by grassland and Wood Buffalo, which is further north, is dominated by forest.

The expanding woody species in all parks is aspen (*Populus tremuloides* Michx.), a clonal tree. Aspen invasion is typically preceded by the establishment of shrubs, including *Symphoricarpos occidentalis* Hook., *Shepherdia canadensis* (L.) Nutt., *Corylus cornuta* Marsh., *Elaeagnus commutata* Bernh. and *Rosa* spp. In most parks the grassland is mixed-grass or fescue prairie (Coupland 1950) with *Stipa* spp., *Festuca campestris* Rydb. (= *F. scabrella* Torr.), *Koeleria gracilis* Pers., *Agropyron* spp. and *Poa* spp. (Table 1), but at Elk Island grassland is dominated by *Poa pratensis* L. and *Calamagrostis canadensis* (Michx.) Beauv. Most parks are unmanaged save for the suppression of wildfires. Elk Island vegetation is managed by prescribed burns and is grazed by high densities of bison (*Bison bison* L.), moose (*Alces alces* L.), elk (*Cervus elaphus* L.) and deer (*Odocoileus* spp.) (Bork *et al.* 1997).

N DEPOSITION AND AVAILABLE SOIL N

We measured N deposition and available soil N with ion-exchange resin bags (Lindberg *et al.* 1986; Binkley & Hart 1989). Measurements of N deposition using resin bags may be more relevant to plants than conventional meteorological measurements because resin, like leaves, is not inert and captures N through adsorption and absorption (Lindberg *et al.* 1986; Davidson & Wu 1990). Resin bags collect wet and dry deposition, and presumably also collect N deposited as coarse particles that are not measured by most other methods but contribute considerably to dry deposition (Lovett &

Lindberg 1993; Shachak & Lovett 1998). Measurements of N deposition using resin bags have not yet been calibrated with other methods. Therefore, our measurements are comparable within our study but may not be directly comparable with results obtained using other methods. Measurements of available soil N with resin bags may also be more relevant to plants than other methods because resin measurements integrate over time, are sensitive to the different mobility of nitrate and ammonium ions in the soil, and are sensitive to soil moisture (Giblin *et al.* 1994).

Resin bags (3 × 3 cm, made from nylon stockings) each contained 2 cm³ ion-exchange resin (anionic and cationic, AG 501-X8, Bio-Rad, Hercules, California, USA), an amount sufficient to take up ions during each measurement period without becoming saturated (Köchy & Wilson 1997). Bags were washed before deployment in 2 mol/L NaCl and rinsed in double-distilled water to remove dyes and background N.

We collected N deposited from the atmosphere with resin bags in flat stainless steel cages (10 × 10 × 0.5 cm, 2-mm mesh) fixed to the ground with stainless steel pins. Cages were designed to reduce disturbance from animals. We placed these surface bags ≥ 4 m from tree canopies and ≥ 1 m from shrubs to reduce the effect of canopy leaching on N deposition measurements (Lindberg *et al.* 1986; Potter *et al.* 1991). A comparison of deposition in forest, shrubland and grassland in Elk Island found no significant differences among vegetation types (Köchy 1999), suggesting that variation among sites in the height of vegetation near resin bags had no effect on deposition rates measured by the bags.

We measured available soil N with resin bags buried in the A horizon, about 10 cm below the soil surface, in undisturbed vegetation. Each buried bag was < 20 m

from a surface bag. Ten pairs of surface and soil bags were distributed at 1–2 km intervals along roads in each park (traffic was negligible for most of the year and presumably had no effect on N deposition). Surface bags were installed *c.* 10 m from the road edge.

We sampled N in summer (mid-June–August), fall (August–October), winter (October–May) and spring (May–mid-June) in 1994–96. We retrieved bags from the current season when we set out bags for the next season.

Retrieved bags were cleaned of dirt by hand and stored individually in clean plastic bags at 4 °C for up to 5 months. Microbial mineralization of remaining organic soil particles on the bags may have continued and slightly increased measured available soil N, but this overestimation is presumably small compared with the exposure time of the bags in the soil (> 6 weeks). We let the resin bags air-dry protected from dust for 2 days before removing the resin and extracting it in 30 mL of 2 mol/L KCl for 60 min (Binkley & Hart 1989). The solution was frozen until analysis. Nitrate in the solution was reduced to ammonium with TiCl_3 , and this, together with ammonium collected directly by the resin, was converted to ammonia by increasing pH of the solution with 10 mol/L NaOH. The concentration of N in the extract was measured with an ion-selective electrode for ammonia (Orion, Boston, Massachusetts, USA) to give a combined value for nitrate and ammonium. We added known amounts of nitrate and ammonium ranging from 0.05 to 5 mmol/L to unused bags to determine an extraction rate and the regression $N_{\text{extracted}} = 0.6902 \cdot \ln(N_{\text{added}} + 1)$ ($R^2 = 0.85$, $n = 204$) was used to determine the amount of N collected by resin in the field.

We measured nitrate and ammonium together because previous studies show very little ammonium deposition in this region. The relative abundance of these two forms of available N varies geographically (Högberg 1997), but industrial ammonium emissions in western Canada constitute < 5% of NO_x -N emissions (Environment Canada 1997, 1998) and atmospheric ammonia concentrations are usually below detectable levels (Myrick & Hunt 1998).

Daily N deposition rates were calculated by dividing solution concentrations from surface bags by mean bag area and length of sampling period. We compared deposition rates among parks using a fully factorial repeated-measures analysis of variance (ANOVA), with year as a random factor and season and park as fixed factors. Means of deposition and available soil N were compared among parks using the Newman-Keuls method ($\alpha = 0.05$, Lorenzen & Anderson 1993). Heteroscedastic and skewed data were ln-transformed data to meet the assumptions of ANOVA. Statistics were calculated with JMP 3.2 (SAS Institute 1996). *F*-values were calculated with Excel 4.0 according to Lorenzen & Anderson (1993). Deposition data are reported as annual rates ($\text{kg ha}^{-1} \text{ year}^{-1}$, calculated as average daily rates multiplied by season length). Soil available N collection rates were examined the same way.

^{15}N AND N MASS AT HIGH AND LOW N DEPOSITION

We measured the ^{15}N abundance and N concentrations in soil and vegetation in one park with high deposition (Elk Island) and one with low deposition (Jasper, Fig. 1), in June and July 1995. We assessed tree leaves, tree stems, shrub leaves, shrub stems, herbs, litter, roots 0–15 cm deep (the main rooting depth) and 15–50 cm deep, and soil 0–15 cm and 15–50 cm deep. Each compartment was sampled in 10 forest, 10 shrubland and 10 grassland plots. Trees were sampled in 10×10 m plots and shrubs in a 1×2 m subplot centred within each tree plot. Herbs and litter were collected in a 0.1×1 m subplot centred within each shrub subplot. Roots and soil were sampled within each subplot using a 2-cm diameter soil corer. Three soil cores were taken at each depth in each subplot and were combined. Rocks prevented sampling the deep layer in some plots. We calculated tree mass based on tree height and stem diameter at breast height using regression equations (Petersen & Petersen 1992), and shrub mass using regression equations based on basal stem diameter (Brown 1976 for *Rubus idaeus*; Köchy 1999 for all others).

Biomass and soil samples were dried to constant mass at 70 °C and weighed. Subsamples analysed for N were one stem core and five leaves of each of five trees from each plot, stems and leaves of five shrubs from each subplot, and 10 subsamples of forb leaves, grass leaves, herbaceous stems, and soil and root cores from each subplot. Subsamples for each compartment were pooled, ground and analysed for ^{15}N abundance ($^{15}\text{N}/(^{15}\text{N} + ^{14}\text{N})$, atom percentage) and total N concentration using a continuous-flow mass spectrometer (Europa, Crewe, UK). ^{15}N abundance (*A*) is expressed in reference to the abundance in standard atmospheric dinitrogen (N_2) of 0.36637% as:

$$\delta^{15}\text{N} = ((A_{\text{sample}} - A_{\text{standard}})/A_{\text{standard}}) \times 1000\text{‰}$$

We calculated average $\delta^{15}\text{N}$ values and N concentrations for woody (tree and shrub stems) and herbaceous tissue (all leaves and herbaceous stems) by multiplying the $\delta^{15}\text{N}$ value and the N concentration of each compartment by the compartment mass and dividing the sum by the total mass of the pooled compartments. For $\delta^{15}\text{N}$ this is equivalent to first calculating the average ^{15}N abundance across compartments and then converting it to $\delta^{15}\text{N}$.

We compared $\delta^{15}\text{N}$ values, N concentrations and N mass (N concentration \times biomass) between parks and among vegetation types and compartments with ANOVAs where park and vegetation type were crossed, fixed factors, compartment was nested as a fixed factor within vegetation type and crossed with park (McKone & Lively 1993), and plot was nested as a random factor within park \times vegetation type. $\delta^{15}\text{N}$ data were homoscedastic and normal. N concentration data were arcsine-square-root transformed to reduce

heteroscedasticity. N mass data were ln-transformed to achieve homoscedasticity and normality. We excluded N mass data for the 15–50 cm layer from analysis because of the small sample size in some treatment groups caused by rocky soil.

FOREST EXPANSION

We calculated forest expansion in all parks from sequences of ≥ 4 aerial photographs from 1930 to 1995 (National Air Photo Library, Ottawa, Canada; for details of photographs see Köchy 1999). For each park we selected one area of *c.* 3.5 km² that included contiguous areas of grassland and forest. The photographs were digitized such that the selected area within each park was covered by approximately 10⁶ pixels. On average, each pixel represented an area of 3.1 m² (SD = 1.0 m², *n* = 34). The images were analysed by density-slicing, i.e. shades of grey were manually assigned to either forest or grassland and the number of pixels of each vegetation type counted. We plotted forest area against year: high slopes indicate high expansion rates. We used analysis of covariance to test whether slopes differed among parks. We also tested whether forest expansion rates varied with annual N deposition, mean annual precipitation, long-term change of annual precipitation, mean annual temperature, or the long-term change of mean annual temperature, using annual data for 1942–92 from the weather station closest to each park (Environment Canada, Ottawa, Canada). No historical data are available for N deposition that are comparable to those for forest expansion but, assuming that population density influences N deposition (NADP 1996), we examined the pattern of human population growth in the study area (the provinces of Alberta, Saskatchewan and Manitoba; Statistics Canada, Ottawa, Canada) over the period covered by aerial photographs.

Results

N DEPOSITION AND SOIL AVAILABLE N

N deposition varied significantly among parks (Table 2) and was highest in Elk Island, Prince Albert,

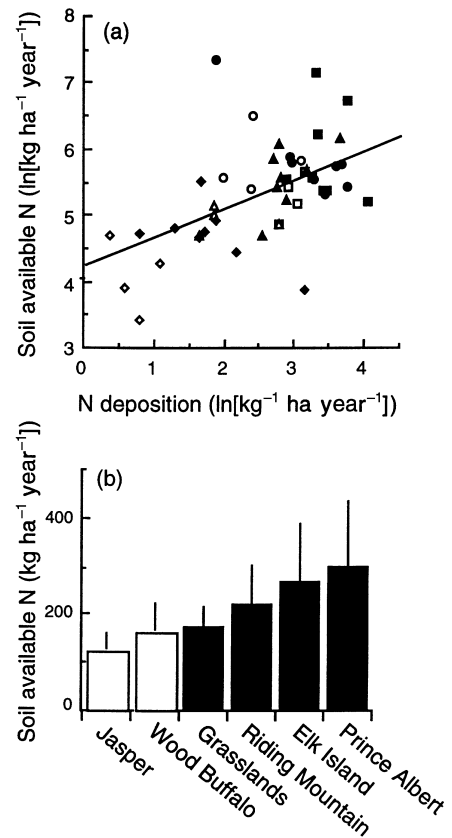


Fig. 2 (a) The relationship between soil available N and N deposition in six parks in four seasons, averaged over 2 years. Open symbols represent low-deposition parks (Jasper and Wood Buffalo, Fig. 1) and filled symbols high-deposition parks (all others). Summer, fall, winter and spring measurements are represented by squares, triangles, diamonds and circles, respectively. Soil available N increased significantly with N deposition. (b) Soil available N (mean \pm SE) in six parks averaged over 2 years. Filled bars represent high-deposition parks.

Riding Mountain and Grasslands, in densely populated regions, and lowest in Jasper and Wood Buffalo, in less densely populated regions (Fig. 1). Deposition also varied significantly among seasons (Table 2) and was generally lowest in winter (Fig. 2a, diamonds) and highest in summer (Fig. 2a, squares).

Soil available N did not vary significantly among parks (Table 2) but varied highly significantly with the interaction between years and parks, suggesting that

Table 2 ANOVA tables for N deposition and available soil N in six parks over four seasons in each of 2 years. **P* \leq 0.05, ***P* \leq 0.01, ****P* \leq 0.001

Effect	d.f.	N deposition		Soil N	
		MS	<i>F</i>	MS	<i>F</i>
Park	5	6.630	13.69**	0.745	0.91
Year	1	0.713	2.43	0.164	1.55
Park \times year	5	0.484	1.65	0.823	7.72***
Season	3	32.328	824.27***	3.490	4.38
Park \times season	15	1.291	2.18	0.432	1.92
Year \times season	3	0.039	0.13	0.797	7.48***
Park \times year \times season	15	0.592	2.01*	0.225	2.11**
Residual	407	0.294		0.106	

any difference among parks varied between years. Means contrasts for each year showed that the four parks with the highest rates of N deposition (Fig. 1) had significantly higher soil available N than did the two parks with the lowest deposition rates (Fig. 2b; year 1: $t = 2.85$, $P = 0.01$; year 2: $t = 3.72$, $P = 0.002$).

Soil available N increased significantly with N deposition (Fig. 2a: $R^2 = 0.29$, $F_{1,46} = 18.5$, $P < 0.0001$). The goodness of fit (R^2) increased to 0.39 when an exceptionally high level of N availability in spring 1996 in Prince Albert was excluded.

^{15}N AND N MASS AT HIGH AND LOW N DEPOSITION

$\delta^{15}\text{N}$ values in forest shoots (stems, leaves and litter) were significantly lower in Elk Island (receiving high rates of N deposition, Fig. 1) than in Jasper (receiving low rates), suggesting that N in forest tissue at Elk Island tended to be anthropogenic in origin. The difference between parks was significant only for forest shoots (Fig. 3; means contrasts, park \times compartment [vegetation type] interaction: $F_{17,241} = 3.32$, $P < 0.0001$). Thus, the difference between parks occurred only in the above-ground tissues of the tallest vegetation type.

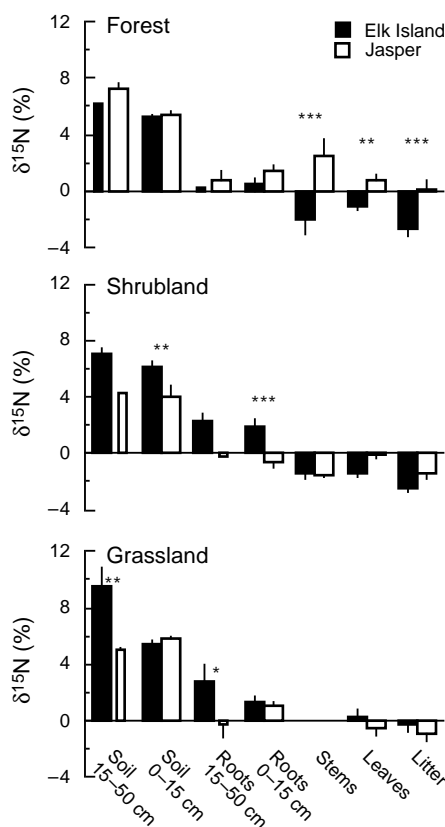


Fig. 3 $\delta^{15}\text{N}$ values in vegetation and soil compartments in a park with high (Elk Island, solid bars) and low (Jasper, open bars) N deposition (means \pm SE, $n = 6-10$; narrow bars denote $n \leq 3$ due to stony soil). Significant differences between parks within a compartment are marked with asterisks (*a-priori* contrasts, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

In contrast to the results for forest shoots, roots and soils in shrubland and prairie showed the opposite pattern, with higher $\delta^{15}\text{N}$ values in Jasper than Elk Island (Fig. 3). $\delta^{15}\text{N}$ values of soil were higher than $\delta^{15}\text{N}$ values of tissues, and roots tended to have higher $\delta^{15}\text{N}$ values than other tissues (Fig. 3).

Tissue N concentration did not differ significantly between parks for any compartment or habitat, except stems in shrubland (0.6% and 1.2% in Elk Island and Jasper, respectively).

The mass of N in vegetation increased along a successional gradient from prairie to forest (Fig. 4; vegetation type effect: $F_{2,54} = 210$, $P < 0.0001$), with an increasing proportion of N stored in above-ground tissues (compartment effect: $F_{8,144} = 68.42$, $P < 0.0001$). N mass (kg ha^{-1}) in forests did not differ significantly between Elk Island and Jasper. In shrubland, N mass of shallow roots and stems was significantly higher in Jasper than in Elk Island. In grassland, N mass of shallow roots and leaves was significantly higher in Elk Island than in Jasper, due to twice as much biomass in Elk Island for these compartments (Fig. 4; means contrasts, park \times compartment [vegetation type] interaction: $F_{8,144} = 4.94$, $P < 0.0001$).

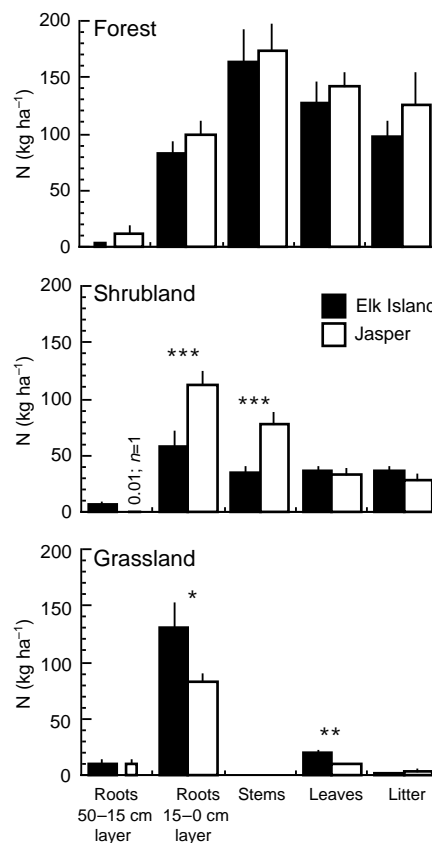


Fig. 4 Mass of N in vegetation in a park with high (Elk Island, solid bars) and low (Jasper, open bars) N deposition (means \pm SE, $n = 6-10$; narrow bars denote $n \leq 3$). Significant differences between parks within a compartment are marked with asterisks (*a-priori* contrasts, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$).

FOREST EXPANSION

Relative forest area ((forested area/total area) · 100%; total area = forest + grassland area) increased significantly over time in Elk Island, Prince Albert and Riding Mountain but not in Jasper, Wood Buffalo and Grasslands (Fig. 5, ANCOVA testing equality of slopes among all parks: $F_{5,21} = 7.45$, $P < 0.001$).

The rate of forest expansion (E) in all parks increased significantly with mean annual precipitation (P ; $E = -2.00066 + 0.00638P$; $R^2 = 0.69$, $F_{1,4} = 8.80$, $P = 0.04$) but two lines of evidence suggest that N deposition also affects forest expansion. First, removing two parks with the highest rates of N deposition (Elk Island and Prince Albert) from the regression greatly improved the correlation between expansion and precipitation ($R^2 = 0.99$). This suggests that, in the absence of N deposition, forest expansion would be closely related to precipitation alone. Secondly, multiple regression of forest expansion using both annual precipitation and deposition as predictor variables ($R^2 = 0.91$, $F_{2,3} = 15.1$, $P = 0.03$) was much stronger than using precipitation alone.

Forest expansion did not vary with mean annual temperature, long-term change of mean annual temperature or long-term change of annual precipitation.

Forest expansion increased significantly with N deposition for the five parks dominated by woody vegetation ($E = -9.15 + 10.3/(1 + e^{-0.31D})$, $R^2 = 0.99$, $F_{1,2} = 611$, $P = 0.002$, excluding Grasslands National Park lying far south of the forest, Fig. 1).

No historical data are available for N deposition comparable with those for forest expansion, but the pattern of human population growth over the period reflects the pattern of forest expansion in the parks with the highest deposition rates (Fig. 5).

Forest area in Jasper, which received low rates of N deposition, increased from 41% to 53% during 1949–

93 (Fig. 5). Using N content data (Fig. 4) we calculated that this increase in forest area represents an increase in ecosystem N from 289 to 365 kg ha⁻¹, or 26%. Forest area in Elk Island, which received high rates of N deposition, increased from 24% to 81% during 1947–95 (Fig. 5). This represents an increase in ecosystem N from 235 to 410 kg ha⁻¹, or 74%. Both increases are likely to be underestimates because they do not include the probable accumulation of N within each vegetation type over time, but this possible underestimation does not influence the difference found between parks.

Discussion

Parks close to cities and in relatively densely populated regions experienced high rates of N deposition (Fig. 1), soil available N (Fig. 2) and forest expansion (Fig. 5). The low values of $\delta^{15}\text{N}$ in forest biomass in Elk Island (Fig. 3) suggest that the deposited N was anthropogenic in origin (Heaton 1990).

Our results for regional pattern of high N deposition in populated regions (Fig. 1) was similar to that for North America as a whole, where high rates of atmospheric N deposition occur in and downwind of industrialized areas of the north-eastern United States and southern Canada (Johnson & Lindberg 1992; NADP 1996). The highest rate of N deposition occurred in Elk Island, the park closest to a metropolitan area (Fig. 1). The high rate was presumably due to N emissions from Edmonton (population 840 000), which produces 37–168 kg NO_x-N ha⁻¹ year⁻¹ compared with < 0.1 kg NO_x-N ha⁻¹ year⁻¹ produced in northern Alberta (population < 1 inhabitants/km²) (Cheng 1994).

Elevated deposition rates in Grasslands, Prince Albert and Riding Mountain (Fig. 1) may be caused by the prevailing westerly and north-westerly winds carrying N particles from sources in Edmonton and Calgary (population 750 000) and from oil refineries on the Alberta-Saskatchewan border west of Prince Albert (Fig. 1). High deposition rates east of Alberta may also be associated with fertilizer application in the surrounding agricultural regions. This would be consistent with the high deposition rates we observed during early summer (when farmers apply fertilizer) and the low rates observed in winter (Fig. 2a). Official statistics, however, assume that no measurable amounts of NO_x are released from applied fertilizer (Environment Canada 1998).

Our N deposition rates, measured with ion-exchange resin, correspond with those measured by a combination of methods in similar regions (Lovett & Lindberg 1993). Assuming that wet deposition is about half of total deposition (Lovett & Lindberg 1993), wet deposition in our study ranged from 5.1 kg N ha⁻¹ year⁻¹ in low-deposition parks to 11.0 kg N ha⁻¹ year⁻¹ in high-deposition parks. These values are similar to those measured at other low-deposition sites (Lovett & Lindberg 1993) but are considerably greater than wet deposition measured by meteorological stations in the

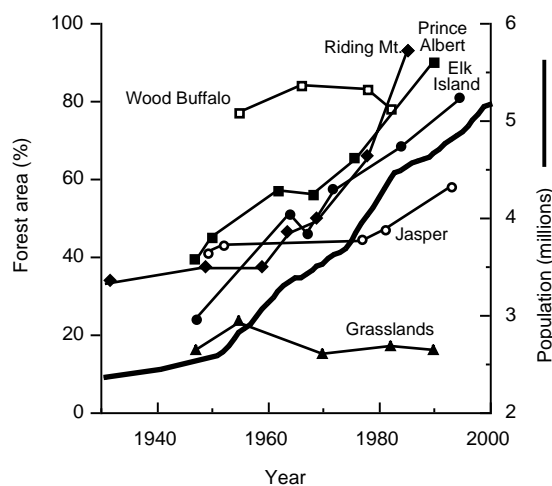


Fig. 5 Proportion of forest area in aerial photographs as a function of year in six parks. Black symbols = high-deposition parks; white symbols = low-deposition parks; thick line = human population in the provinces of Alberta, Saskatchewan and Manitoba.

northern Great Plains in 1993 ($1.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$, NADP 1996; $1.3\text{--}3.0 \text{ kg N ha}^{-1} \text{ year}^{-1}$, Canadian Air Pollution Monitoring Network, M. Shaw, personal communication). Higher deposition rates in our study and in that by Lovett & Lindberg (1993) are presumably caused by coarse dry particles that tend to have higher N concentrations than fine dry particles (Shachak & Lovett 1998), and by the presence of surrounding vegetation which captures N-bearing particles (Lovett 1994). Coarse dry particles are not included in common meteorological measurements. It is also possible that the movement of capillary water may have transported mineral N from the soil or litter to the resin bags. We found, however, that surface resin bags take up more N from deposition than from litter N mineralization (Köchy & Wilson 1997), making capillary transport unlikely to contribute to N collected by surface resin bags.

Two parks with high rates of deposition (Prince Albert and Elk Island, Fig. 1) also had the highest rates of available soil N (Fig. 2b). Available soil N increased with deposited N across all parks (Fig. 2a), presumably because much of the deposited N enters the soil by stemflow, throughfall and, eventually, litter decomposition. A positive correlation between soil N and N deposition was also observed in forests in Austria and the north-eastern USA (Kazada & Katzensteiner 1993; Lovett & Rueth 1999). N added to N-limited ecosystems, such as natural forests or grasslands, is retained almost completely (Aber *et al.* 1993). Therefore, N deposition may increase mineralization in the soil (Morecroft *et al.* 1994) and contribute to accelerated N cycling in these ecosystems.

Forest vegetation had significantly lower $\delta^{15}\text{N}$ values in Elk Island than in Jasper, suggesting that some of the N accumulated by the Elk Island ecosystem was anthropogenic (Heaton 1990; Ammann *et al.* 1999). The difference was strongest for stems, leaves and litter in forests (Fig. 3), presumably because they were more exposed to deposition and had a larger receptor surface than shrubland or grassland vegetation (Kellman & Carty 1986) and thus assimilated deposited N with little isotopic fractionation. Further, wood accumulates N over time and therefore may present a clearer signal than other tissues (Gebauer & Dietrich 1993). The difference of $\delta^{15}\text{N}$ values in stems, leaves and litter between Elk Island and Jasper ranged between 2% and 4% in forest (Fig. 3), a difference in the same range as that measured along a gradient of NO_x pollution from motorways in Switzerland (Ammann *et al.* 1999). We suggest that this difference could originate from ^{15}N -depleted motor vehicle exhausts (Heaton 1990) that accounted for 32% of all NO_x in Alberta in 1995 (Environment Canada 1998), assuming that the ^{15}N signal is more or less unchanged by atmospheric processes. However, the lower ^{15}N values in vegetation in Elk Island could also be explained by fractionation during faster N cycling due to higher N inputs (Högberg 1997): fractionation during mineralization

would result in mineral N depleted in ^{15}N entering soil solution and being incorporated into shoots, leaving recalcitrant N rich in ^{15}N in the soil. Although the mechanism remains to be elucidated, either pathway links lower ^{15}N in shoot tissues to increased N deposition.

$\delta^{15}\text{N}$ values of soil were always higher than those of tissues and increased with soil depth (Fig. 3), reflecting repeated microbial nitrification and mineralization during the downward movement of organic and inorganic N compounds, and uptake of ^{15}N -depleted mineral N from the soil (Högberg 1997). Thus, the significantly higher $\delta^{15}\text{N}$ values in the soil and roots in Elk Island shrubland and grassland compared with that in Jasper (Fig. 3) might indicate higher rates of isotopic fractionation caused by higher rates of decomposition due to the higher N deposition and availability in Elk Island (Handley & Raven 1992).

For parks within aspen parkland or boreal forest (all but Grasslands), forests in high-deposition parks expanded 10 times faster than forests in low-deposition parks (Fig. 5). Because forest ecosystems contained more N than grassland (Fig. 4), the increase in forest area represents large increases in the amount of N stored in ecosystems with high N deposition. The average expansion rate of forest in high-deposition parks was $1\% \text{ year}^{-1}$ (Fig. 5). This is in line with previous measurements of expansion rates of aspen into grassland in western Canada, of between $0.5\% \text{ year}^{-1}$ and $5\% \text{ year}^{-1}$ (Maini & Coupland 1964; Bailey & Wroe 1974).

Forest expansion in five parks within aspen parkland or boreal forest (all but Grasslands) was closely related to rates of N deposition (Fig. 5), suggesting that forest expansion may be accelerated by N deposition. Clearly, a larger survey, the inclusion of historical N deposition data and experimental evidence is needed to rigorously test this hypothesis. Our results do show, however, that the hypothesis cannot be simply dismissed. N fertilization by deposition may mostly benefit woody species that invade grassland and reduce available soil N more strongly than grasses (Köchy & Wilson 2000). Woody species may be especially favoured because the annual peak of atmospheric N deposition coincides with the period of most rapid growth in late spring and early summer (Fig. 2a, square symbols). Fast-growing species also tend to produce N-rich litter that decomposes quickly (Aerts & Chapin 2000). In our study, however, N deposition did not increase N concentrations in litter (Fig. 4), perhaps because additional N was used to produce more tissue with the same concentration, or because the dominant tree, *P. tremuloides*, relocates most N before leaf abscission (Taylor *et al.* 1989). Trees are further favoured by deposition because their stature reduces aerodynamic and boundary layer resistances to deposition relative to grasses (Kellman & Carty 1986; Binkley 1995). Thus, trees may increase deposition rates, resulting in a self-maintaining positive feedback (Kellman & Carty 1986; Wilson 1998).

Tissue N concentrations differed little between parks receiving high (Elk Island) and low (Jasper) rates of N deposition, suggesting that the deposited N that was assimilated by leaves was allocated to new growth and is reflected by forest expansion (Fig. 5). The slightly but significantly higher concentration of N in shrubland stems in Jasper (Fig. 4) was probably related to the dominance of the shrub *Shepherdia*, a symbiont with N-fixing bacteria. In contrast, N deposition in other areas leads to increased tissue N concentration (Vitousek *et al.* 1997). The conditions under which N deposition leads to either increased tissue nutrient concentration or successional changes in community composition remain to be determined.

In Grasslands National Park, forests did not expand despite high N deposition (Fig. 5). This park lies outside the forest biome (Fig. 1), with its forests consisting of *P. tremuloides* restricted to the bottoms of a few river valleys. *P. tremuloides* has no particular adaptation to tolerate water deficits, therefore forest expansion in this location may be more limited by moisture than by nitrogen.

Forest expansion has also been attributed to a decrease in mean annual temperature and changes in weather patterns (Buell & Cantlon 1951; Bailey & Wroe 1974) but we found no significant correlation with long-term temperature trends or variation in annual precipitation. Across all parks, forest expansion increased significantly with annual precipitation, but the correlation was strengthened by adding the effect of N deposition.

Historical records of N deposition are not available but forest expansion in parks near the treeline and receiving high rates of N deposition reflects the increase in the human population over the same period (Fig. 5). Population size is probably an underestimate of N deposition, since the per-capita rate of fossil-fuel consumption is likely to have increased over the study period.

The expansion of forest into temperate grassland has also been attributed to decreases in the frequency and importance of fires and bison (Bork *et al.* 1997; Schwarz & Wein 1997), but experiments have shown *Populus* to be very resistant to both of these disturbances (Wilson 1998). Further, the low pre-historical concentrations of charcoal in lake sediments suggest that fires were not important for excluding trees from the Great Plains (Hickman & Schweger 1996). Future studies should aim at determining the relative contributions of fire, herbivory and N deposition to forest expansion. Our study shows a strong relationship between N deposition and forest expansion and suggests that even relatively low levels of N deposition in sparsely populated regions can have profound effects on ecosystems.

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