

## 2. NITROGEN DEPOSITION AND FOREST EXPANSION IN WESTERN CANADA

### 2.1. ABSTRACT

Forest expansion into arid cold-temperate grassland due to fire control or elimination of bison herds may be accelerated by fertilization from atmospheric nitrogen (N) deposition. I measured N deposition and available soil N over 2 yr in six national parks in western Canada. The parks varied in distance from sources of anthropogenic N. Atmospheric N deposition, measured with ion-exchange resin, was highest in four parks in a region with agro-industrial land-use (moderately populated, 5-100 inhabitants/km<sup>2</sup>) and lowest in parks in a mostly forested region with minimal agro-industrial land-use (sparsely populated, <5 inhabitants/km<sup>2</sup>). Similarly, available soil N, also measured with ion-exchange resin, was highest in parks in the agro-industrial region and lowest in parks in the forested region. Available soil N increased significantly with N deposition across parks. I measured the local variation of N deposition and availability at 84 locations within Elk Island, a park in the agro-industrial region. Seasonality had the strongest effect on local variation of N deposition and soil N availability compared to the effect of soil type, fire history, grazing, or vegetation type. I measured N mass and natural abundance of <sup>15</sup>N in vegetation and soil in two parks: Elk Island in the agro-industrial region,

receiving 22.1 kg N ha<sup>-1</sup> yr<sup>-1</sup>, and Jasper in the forested region, receiving 7.77 kg N ha<sup>-1</sup> yr<sup>-1</sup>. Mass of N in vegetation per area increased by 74% in Elk Island, but only by 26% in Jasper during the past five decades, due to forest expansion into grassland.  $\delta^{15}\text{N}$  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. I determined the rate of forest expansion in partially forested parks from aerial photographs and found a strong positive relationship ( $R^2 = 0.99$ ) with N deposition. The strong relationships between N deposition, available soil N, N mass in vegetation, and forest expansion suggest that even comparatively low rates of anthropogenic N deposition accumulate over time in moderately populated regions and contribute to changes in ecosystem structure.

## 2.2. INTRODUCTION

High amounts of anthropogenic nitrogen (N) compounds deposited from the atmosphere (20 - 50 kg N ha<sup>-1</sup> yr<sup>-1</sup>, Jefferies & Maron 1997) have changed vegetation in western Europe and mid-eastern North America (e.g., Ellenberg 1988). The change of vegetation in less exposed regions (<2 kg N ha<sup>-1</sup> yr<sup>-1</sup>) is usually attributed to other factors, e.g., fire control, removal of grazers, and climate change (Hastings & Turner 1965, Bragg & Hulbert 1976, Archer et al. 1988). It has become clear, however, that even moderately increased N deposition rates affect ecosystem

function and reduce or alleviate N limitation of growth (Vitousek et al. 1997).

High amounts of deposited N are correlated with the increase of tall species in nutrient-poor grassland (Ellenberg 1988, Bobbink et al. 1988), heathland (Berendse 1994a), and of forest understorey species (Hofmann et al. 1990). Increase of forest species typical of N-rich, acidic sites have also been reported (Tyler 1987, Ellenberg 1988, Bobbink et al. 1992). Trees in exposed forests first showed accelerated growth, but later the damaging effects of acidification and nutrient imbalances caused by N deposition prevailed (Nihlgård 1985, Hofmann et al. 1990, Dise & Wright 1995, for exceptions see Wittig et al. 1985, Nilsson et al. 1988, Becker et al. 1992).

Effects of N deposition on ecosystems have mostly been studied on a small regional scale or in regions of high deposition (e.g., Ulrich et al. 1979, Potter et al. 1991, Aber et al. 1993, Magill et al. 1997, but see Johnson & Lindberg 1992). N deposition, however, varies on a continental scale (Grennfelt & Hultberg 1986, NADP 1994, 1995, 1996) and long-term low-level deposition may also have significant effects on ecosystems. Therefore, I measured N deposition and available soil N in six national parks in western Canada in a 1000 × 1000 km<sup>2</sup> area where the average density of industry and population is comparatively low.

N deposition may also vary locally due to volatilization of ammonia from faeces (Risser & Parton 1982, Nason et al. 1988) and due to the capture of gases and particles containing N by tall vegetation (Binkley 1995). I also tested whether N deposition or soil N availabili-

ty varies locally with factors that may control biological N emissions or affect N availability, i.e., soil type, fire regime, bovine grazing, and vegetation type.

Anthropogenic  $\text{NO}_x$  deposition in western Canada has three main sources: vehicle exhaust (50%), industrial processes (29%) -especially in the petrochemical sector-, and industrial fuel combustion (21%) mostly for heat and power generation (Environment Canada 1996).  $\text{NH}_4\text{-N}$  emissions in western Canada are low (Environment Canada 1998), representing <5% of  $\text{NO}_x\text{-N}$  emissions (Environment Canada 1996). Vehicle exhausts contain isotopically light N (negative  $\delta^{15}\text{N}$  value), whereas fuel combustion in boilers produces isotopically heavy N (positive  $\delta^{15}\text{N}$  value) (Heaton 1990). Therefore, the  $\delta^{15}\text{N}$  value of deposited N should tend to be negative. Some deposited N is taken up by the canopy and incorporated into the biomass (Brumme et al. 1992, Lumme 1994). I compared the  $\delta^{15}\text{N}$  values of vegetation in a park with high deposition with that in a park with low deposition to explore whether the origin of anthropogenic N deposition can be deduced from the  $^{15}\text{N}$  signal.

Fertilization by atmospheric deposition could accelerate tree growth more than grass growth (Kellman 1989, Wilson 1998) and may have contributed to the expansion of forest into grassland in the northern Great Plains during the past century (Archibold & Wilson 1980). The forest expansion has created concern for vegetation management in national parks in the forest-prairie transition zone (Fig. 2.1, Vetsch 1987, Bork et al. 1997, Schwarz & Wein 1997). I have tested whether long-term deposition is correlated with forest expansion.

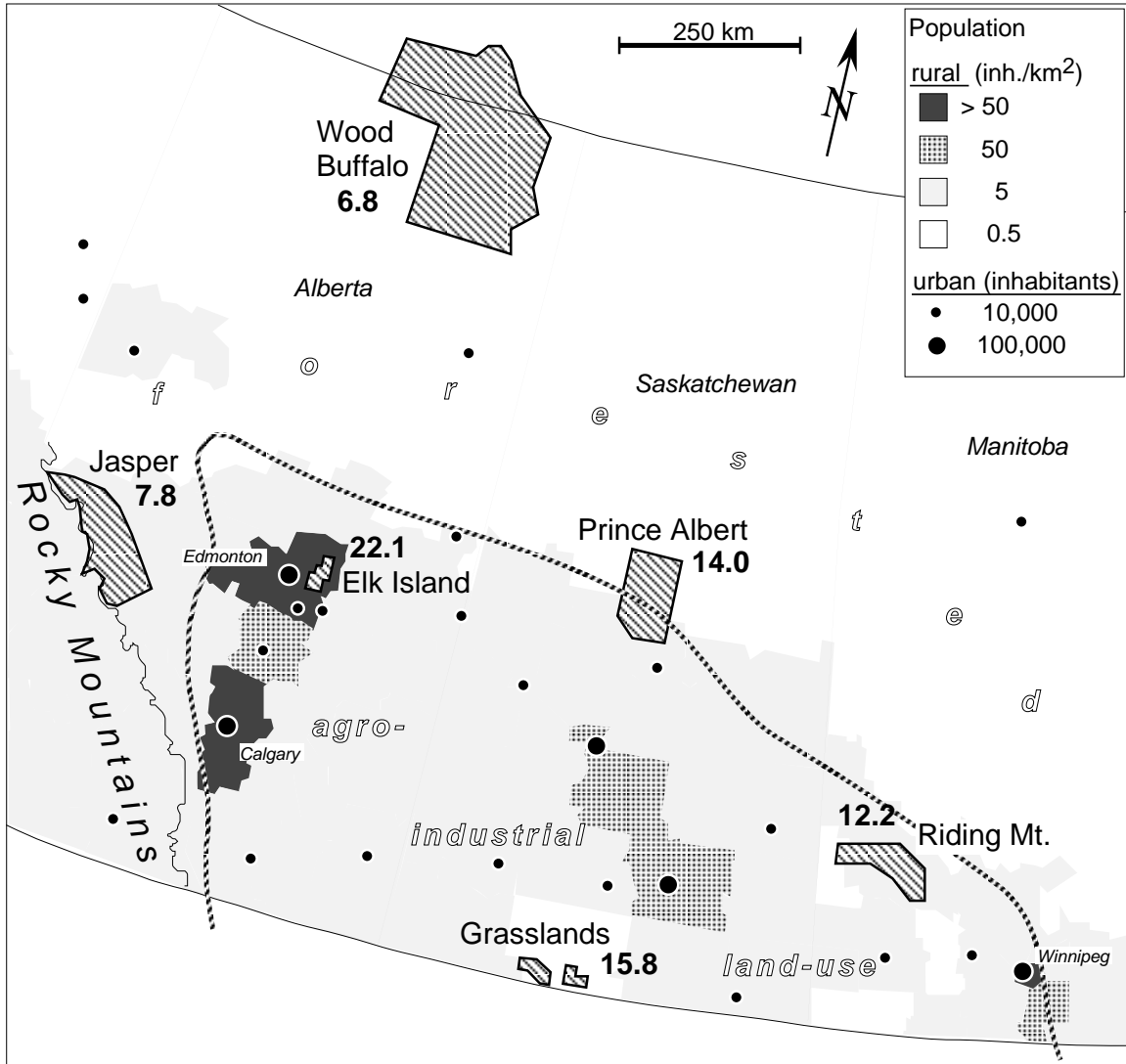


FIG. 2.1. Location of sites (national parks), N deposition rate (kg N ha<sup>-1</sup> yr<sup>-1</sup>), population density, and regional land-use. Population density is based on electoral boundaries. Elk Island National Park is enlarged 200%. The hatched line indicates the border between the agro-industrial and the forested region.

## 2.3. METHODS

### 2.3.1. Study sites

I measured atmospheric nitrogen deposition and available soil N in six national parks in western Canada (Fig. 2.1). Four parks (Elk Island, Grasslands, Prince Albert, Riding Mountain) were in the prairie and aspen parkland vegetation zone, a more densely populated region with agro-industrial land-use and higher than natural deposition. I call this the "agro-industrial region". Two parks (Jasper and Wood Buffalo) were in an area dominated by montane or boreal old-growth forest, a sparsely populated region with minimal land-use. I call this the "forested region". Jasper and Wood Buffalo both include grassland (Raup 1935, Holland & Coen 1982). The geography, climate, vegetation, and soils of the parks are described in Table 2.1. In all parks the invasive woody species is aspen (*Populus tremuloides*), a clonal tree, and in variable abundance the clonal shrubs *Symphoricarpos occidentalis*, *Shepherdia canadensis*, *Corylus cornuta*, *Elaeagnus commutata*, and *Rosa* spp. Grasslands in the parks are of mixed-prairie or fescue-prairie type (Coupland 1950, Blood 1966b, Carbyn 1971) with *Stipa* spp., *Festuca scabrella*, *Koeleria cristata*, *Agropyron* spp., and *Poa* spp. Grassland in Elk Island, however, is dominated by *Poa pratensis* and *Calamagrostos canadensis*.

Elk Island vegetation is managed by prescribed burns and is grazed by high densities of bison (*Bison bison*), moose (*Alces alces*), deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) (Cairns & Telfer

TABLE 2.1. Description of sites: six national parks in western Canada.

| Park   | agro-industrial region              |                              |                                     | forested region                     |  |                         |
|--|-------------------------------------|------------------------------|-------------------------------------|-------------------------------------|--|-------------------------|
|  | Elk Island                          | Grasslands                   | Prince Albert                       | Riding Mt.                          | Jasper                                       | Wood Buffalo            |
| <b>Geography</b>   |                                     |                              |                                     |                                     |  |                         |
| Latitude (N) range   | 53° 31' -47'                        | 49° 00' -13'                 | 53° 35' -54° 20'                    | 50° 30' -51° 01'                    | 52° 08' -53° 29'                             | 58° 10' -60° 30'        |
| Longitude (W) range  | 112° 46' -58'                       | 107° 12' -44'                | 106° 00' -45'                       | 99° 31' -101° 06'                   | 116° 47' -119° 32'                           | 111° 30' -115° 30'      |
| Mean elevation (m)   | 750                                 | 800                          | 650                                 | 650                                 | 1000   | 500                     |
| NO <sub>x</sub> emissions<br>(kg NO <sub>2</sub> ha <sup>-1</sup> yr <sup>-1</sup> ) (1) | >5000                               | 50-500                       | 0-500                               | 500-2000                            | 0-50   | 0-50                    |
| <b>Climate (2)</b>   |                                     |                              |                                     |                                     |  |                         |
| Climate type (3)   | arid, temperate-boreal, continental | arid, temperate, continental | arid, temperate-boreal, continental | arid, temperate-boreal, continental | montane within temperate-boreal, continental | boreal, continental     |
| Meteorological station   | Ft. Saskatchewan                    | Val Marie                    | Waskesiu Lake                       | Wasagaming                          | Jasper                                       | Fort Smith              |
| Location   | 53° 43' N<br>113° 11' W             | 49° 22' N<br>107° 53' W      | 53° 55' N<br>106° 05' W             | 50° 39' N<br>99° 56' W              | 52° 53' N<br>118° 04' W                      | 60° 01' N<br>111° 57' W |
| Elevation a.s.l. (m)   | 620                                 | 808                          | 532                                 | 626                                 | 1061   | 203                     |
| Annual precipitation (mm)  | 412.2                               | 312.5                        | 455.7                               | 508                                 | 393.7  | 352.9                   |
| Annual mean temperature (°C)   | 2.6                                 | 3.5                          | 0.3                                 | 0                                   | 3.1  | -3                      |

Table continued on following page

Table 2.1 continued from preceding page

| Park   | agro-industrial region                                 |                                   |                                      | forested region                       |   |                                 |
|--|--|-----------------------------------|--------------------------------------|---------------------------------------|---|---------------------------------|
|  | Elk Island   | Grasslands                        | Prince Albert                        | Riding Mt.                            | Jasper  | Wood Buffalo                    |
| <b>Trend in climate change *</b>                 |  |                                   |                                      |                                       |   |                                 |
| Long-term change in annual precipitation (mm/yr) | 0.45   | -0.398                            | 0.077                                | 0.777                                 | -0.817  | 1.291                           |
| Long-term change in annual temperature (°C/yr)   | 0.038  | 0.032                             | 0.015                                | 0.026                                 | 0.027   | 0.038                           |
| <b>Dominant forest species †</b>                 | aspen (4)  | aspen                             | aspen-spruce                         | aspen-spruce (7)                      | spruce-aspen (8)                              | aspen (9)                       |
| <b>Dominant grassland type</b>                   | <i>Poa pratensis</i> - <i>Calamagrostis canadensis</i> | mixed-grass prairie (5)           | <i>Festuca scabrella</i> prairie (6) | <i>Festuca scabrella</i> prairie (11) | <i>Koeleria-Artemisia-Linum</i> grassland (8) | northern prairie (9, 12)        |
| <b>Dominant soil type (10)</b>                   | Gray Luvisol   | Brown Chernozemic Brown Solonchic | Gray Luvisol                         | Black Chernozemic                     | Regosol                                       | Gley-, Fibri-, Bruni-, Cryosols |
| <b>Resin bag location</b>                        |  |                                   |                                      |                                       |   |                                 |
| Road surface                                     | gravel †   | gravel                            | paved                                | paved                                 | gravel  | gravel                          |
| Peak vehicle density (July-August), estimated    | 20/d †   | 3/d                               | 200/d                                | 200/d                                 | 1/d   | 30/d                            |

\* at closest meteorological station with continuous records for c. 1940-1990.

† "aspen" = *Populus tremuloides*, "spruce" = *Picea glauca*

‡ only for grassland, shrubland, and forest on ungrazed-unburned brunisol; other locations were remote from roads

(1) Environment Canada 1996

(5) Coupland 1950

(9) Raup 1935

(2) Environment Canada 1993

(6) Carbyn 1971

(10) NAS 1974

(3) Walter & Lieth 1967

(7) Dickson 1909

(11) Blood 1966a,b

(4) Soper 1951, Bork et al. 1997

(8) Holland & Coen 1982

(12) Schwarz & Wein 1997



1980). The other parks are unmanaged, save for the suppression of fires.

### 2.3.2. Atmospheric deposition and available soil nitrogen

*Resin bags.*— I measured N deposition and available soil N with ion-exchange resin bags (Lindberg et al. 1986, Binkley & Hart 1989, van Dam 1990). Measurements of N deposition using resin bags may be more relevant to plants than measures of precipitation and estimates of dry deposition because resin, like leaves, is not inert and collects dry deposition and throughfall (Lindberg et al. 1986). Non-inert surfaces can capture more N through adsorption and absorption (Davidson & Wu 1990). Resin bags also presumably collect N deposited as coarse particles, a form of N deposition that is not measured by most other methods, but which contributes considerably to dry deposition due to their higher N concentration and amount (Lovett & Lindberg 1993, Shachak & Lovett 1998). 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 made out of nylon stockings were 3 cm × 3 cm, each containing 2 cm<sup>3</sup> dry mixed-bed (anionic and cationic) ion-exchange resin (AG 501-X8, BioRad, Hercules, California, U. S. A.) with an ion-exchange capacity of 1.5 mmol/cm<sup>3</sup> for anions and cations. Thus, the total ion-

exchange capacity of each bag was 3 mmol (3300 mmol m<sup>-2</sup>). The amounts of cations and anions in soil leachate and throughfall of temperate forests range from 16 to 1028 mmol m<sup>-2</sup> yr<sup>-1</sup> (Pastor & Bockheim 1984, Johnson & Lindberg 1992, Boxman et al. 1994). Therefore, the amount of resin was sufficient to take up all ions contained in atmospheric deposition or soil solution during each measurement period without becoming saturated. I did not treat resin against microbial attack because the effect of microbes on N capture is much smaller than the amount of N in soil solution or deposition (Binkley 1984, Giblin et al. 1994). Bags were washed in 2 mol/L NaCl and rinsed in double-distilled water to remove dyes and background N from the resin.

*Field sampling.*— I collected N deposited from the atmosphere with resin bags in flat stainless steel cages (10 cm × 10 cm × 0.5 cm, 2-mm-mesh) that I fixed to the ground with stainless steel pins. Cages were designed to reduce disturbance from animals. I 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, van Dam 1990, Potter et al. 1991). I measured available soil N with resin bags buried about 10 cm deep under undisturbed vegetation (aspen or spruce forest in all parks except Grasslands). Each soil bag was <20 m from a surface bag.

Ten pairs of surface and soil bags were distributed at 1-2 km intervals along roadsides with little traffic in all parks except Elk Island (Table 2.1). The surface bags were installed c. 10 m from the

road across the road ditch, which was usually at a slightly higher elevation than the road. Traffic in all parks peaks during a few weeks in July-August (Table 2.1). During the rest of the year, traffic is negligible except in Riding Mountain, where probably 40 vehicles/d pass through. The usually little traffic on the park roads has presumably only a small effect on N deposition in the parks. In Elk Island, I deployed 132 pairs of bags throughout the park to additionally examine within-park effects of soil types, grazing, burning and vegetation type. I measured N deposition and available soil N in combinations of two soil types (luvisol and brunisol), two ungulate grazing regimes (grazed and ungrazed), two fire regimes (burned and unburned within the previous 15 years), and three vegetation types (forest, shrubland, and grassland). Burned ungrazed forest, shrubland, and grassland on brunisol did not occur in Elk Island, so that a total of 21 treatment combinations was examined. I deployed four pairs of bags for each treatment combination. Usually, the four pairs were installed within <200 m of each other at one site, but resin bags for grazed, unburned brunisol combinations and for ungrazed, unburned forest on brunisol were installed in two sets of two pairs at separate sites. Sites were spread across the park according to availability of suitable locations.

I sampled N for two years in summer, fall, winter, and spring. 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. I retrieved bags when I set out the next set of bags, the last set during 3-10 July 1996. Bags that I could not retrieve in spring because

they were covered by snow or ice were retrieved in summer. The additional time was included in my calculations.

*Laboratory analyses.*— I stored retrieved bags individually in sterile plastic bags at 4°C for up to 13 months. Then I let the resin bags air-dry, protected from dust for 2 d. I removed the resin from the nylon bags and extracted the resin in 30 ml of 2 mol/L KCl for 60 min (Binkley & Hart 1989). The solution was frozen until analysis. Then, nitrate in the solution was converted to ammonium by reduction with  $\text{TiCl}_3$ . All ammonium in the solution, ammonium from converted nitrate and that which was collected by the resin as ammonium, 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, U.S.A.). Thus, nitrate and ammonia were not measured separately. I added known amounts of nitrate and ammonia ranging from 0.05 to 5 mmol/L to unused bags to determine an extraction rate ( $N_{\text{extracted}} = 0.6902 \cdot \ln(N_{\text{added}}+1)$ ,  $R^2 = 0.85$ ,  $n = 204$ ). The range of 0.05 to 5 mol/L covered N concentrations found in precipitation, throughfall, and soil leachate in Wisconsin (Pastor & Bockheim 1984) and represented all but the most extreme concentrations in my resin bags used in the field. I determined the amount of N collected by resin in the field by using this equation.

*Statistical analyses.*— Results for surface bags were divided by mean bag area and length of sampling period to calculate daily deposi-

tion rate (expressed as  $\text{kg N ha}^{-1} \text{ yr}^{-1}$ ). Results for soil bags were divided by resin volume and length of sampling period and expressed as  $\text{kg N ha}^{-1} \text{ yr}^{-1}$  for a 10-cm-thick soil layer. I compared daily rates of deposited N and available soil N among parks using a univariate analysis of variance (ANOVA, Lorenzen & Anderson 1993) with year as a random factor and season and region, i.e., agro-industrial vs. forested, as fixed factors. Parks were nested as a random factor within region and crossed with the other factors. My design is an extension of a repeated-measures design. In accordance with Looney & Stanley's (1989) recommendation, I also used multivariate analysis of variance (MANOVA) to compare rates of all eight sampling periods. I used a sum matrix to determine the overall effects of land-use and park, and a compound contrast matrix to separate the interaction effects of season and year with region and park. I report significance when the  $F$  statistic in either ANOVA or MANOVA (Pillai-Bartlett Trace) was significant at  $\alpha/2 = 0.025$  (Looney & Stanley 1989). For comparisons among parks, I used only data from ungrazed forest vegetation in Elk Island because the grazed areas in Elk Island appeared to be more heavily grazed than those in other parks. I determined the relationship between available soil N and N deposition, using regression based on the means of each park for each sampling period.

I examined daily rates of deposited N and available soil N within Elk Island using a univariate ANOVA with year as a random factor, and season, soil type, grazing, fire, and vegetation type as fixed factors. I was unable to also analyze the data with MANOVA because too many samples were lost due to bison disturbance.

I assumed that surface bags with an equivalent of  $\geq 100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (108 out of 1016 bags) and soil bags with an equivalent of  $\geq 1000 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (28 out of 998 bags) had been contaminated and excluded them from analyses, as this level is unexpected. When data were not homoscedastic (modified Levene [Brown-Forsythe] test at  $\alpha = 0.01$ ) and normal (Shapiro-Wilks test at  $\alpha = 0.05$ ). I ln-transformed them so that the assumptions for ANOVA were met. Mean squares were calculated with JMP 3.2 (SAS Institute 1996) and  $F$  and  $P$  values with Excel 4.0 (Microsoft 1992) according to Lorenzen & Anderson (1993) because SAS Institute calculates  $F$  values assuming a particular covariance structure (Ayres & Thomas 1990). I pooled non-significant effect terms ( $P \geq 0.20$ ) with the error term (Lorenzen & Anderson 1993) when effects with zero degrees of freedom occurred in the model due to missing data.

### 2.3.3. $\delta^{15}\text{N}$ and N in vegetation and soil at Elk Island and Jasper

*Field sampling.*— I measured  $\delta^{15}\text{N}$  and N concentrations in vegetation and soil in one park with high deposition (Elk Island) and one with low deposition (Jasper) to study the effect of N deposition on N accumulation in the vegetation. In both parks we selected sites that included portions of forest, shrubland, and grassland. Sites in Elk Island were within an area of  $1 \text{ km} \times 2 \text{ km}$  southeast of the Moss Trail on eluviated eutric brunisol intermixed with orthic gray luvisol on hummocky, ridged terrain (Crown 1976; Canadian System of Soil Classifi-

cation). The grazed, old-growth aspen forest (*Populus tremuloides*) had a patchy shrub understorey of *Corylus cornuta* (49% of stems) and *Rosa* spp. (32%). Shrubland consisted of exclusively *Corylus*. Grassland was dominated by tall grasses. Sites at Jasper were within a stretch of 10 km in the Athabasca River valley between Pyramid Lake and Jasper Lake on well-drained cumulic regosols on older, higher river banks (Holland & Coen 1982; Canadian System of Soil Classification). The old-growth poplar-white spruce forest (*Populus tremuloides*-*P. balsamifera*-*Picea glauca*) had a sparse shrub understorey of mostly *Rosa acicularis* (49%) and *Symphoricarpos occidentalis* (37%). Shrubland consisted of exclusively *Shepherdia canadensis*, a shrub associated with N-fixing actinomycetes. Grassland was dominated by short grasses with C<sub>3</sub>-type photosynthesis. In both parks, sites for vegetation measurements were within the area of sites used to measure deposition and soil N.

In both parks I took samples of each of the following vegetation and soil compartments: 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. The 0-15 cm soil layer represents the main rooting depth. Each compartment (if present) was sampled in 10 forest, 10 shrubland, and 10 grassland plots. Trees were sampled in 10 m × 10 m plots, shrubs in one 1 m × 2 m subplot centered within a tree plot, and herbs and litter in one 0.1 m × 1 m sub-subplot centered within a subplot. Root and soil mass were sampled in each 0.1 m × 1 m sub-subplot with a 2-cm diameter soil corer at 0-15 cm and 15-50 cm depth. Three soil cores were taken from each sub-subplot and depth and mixed. In

some plots rocks prevented us from taking soil and root samples from the 15-50 cm soil layer.

I 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 in Petersen & Petersen (1992). I determined shrub stem and leaf mass by measuring basal stem diameter and calculating mass according to regression equations. The equations for *Symphoricarpos occidentalis*, *Shepherdia canadensis*, and *Corylus cornuta* were established from 30 shrubs per species growing just outside the plots (Table 2.2). Equations for wolfwillow (*Elaeagnus commutata*) and rose (*Rosa acicularis*) were established from 30 shrubs per species growing in natural prairie near Regina, Saskatchewan (Table 2.2). The regression equation for wild red raspberry (*Rubus idaeus*) was taken from Brown (1976).

*Laboratory analyses.*— Biomass and soil samples were dried to constant mass at 70°C and weighed. I took randomly selected subsamples of all vegetation compartments of each plot for analysis of tissue N 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 m × 1 m sub-subplots, and ten subsamples of soil and roots. Subsamples for each compartment in each plot were pooled, ground, and analyzed for  $^{15}\text{N}$  and N using a continuous-flow mass spectrometer (Europa, Crewe, U.K.) at the Department of Soil Science, University of Saskatchewan.  $\delta^{15}\text{N}$  values are expressed in reference to the  $^{15}\text{N}$  concentration of standard atmospheric



TABLE 2.2. Regression equations to calculate shrub mass (g) from diameter at ground ( $d$  [mm]) for species without previously published equations.

| Species                            | Regression equation                           | $R^2$ |
|------------------------------------|---|-------|
| <u>stem mass</u>                   |   |       |
| <i>Symphoricarpos occidentalis</i> | $0.48285d^2 - 1.92303d + 3.62547$             | 0.89  |
| <i>Shepherdia canadensis</i>       | $0.37792d^2 - 3.84917$                        | 0.96  |
| <i>Corylus cornuta</i>             | $0.40064d^2 - 2.13860d + 4.73454$             | 0.90  |
| <i>Elaeagnus commutata</i>         | $0.01774d^3 + 0.00798d^2 + 0.39961d - 1.2522$ | 0.97  |
| <i>Rosa acicularis</i>             | $0.17882d^2 - 0.54081$                        | 0.82  |
| <u>leaf mass</u>                   |   |       |
| <i>Symphoricarpos occidentalis</i> | $6.925 \cdot 10^{-4} d^4 + 1.46048$           | 0.44  |
| <i>Shepherdia canadensis</i>       | $0.02196d^2 + 0.43914d - 1.65041$             | 0.89  |
| <i>Corylus cornuta</i>             | $0.05952d^2 - 0.91247$                        | 0.64  |
| <i>Elaeagnus commutata</i>         | $0.03891d^2 + 0.2386$                         | 0.80  |
| <i>Rosa acicularis</i>             | $0.08036d^2 - 0.16055$                        | 0.65  |

dinitrogen ( $N_2$ ) with a  $^{15}N:^{14}N$  ratio of ~~0.36637%~~ (Hoefs 1987) as

$$\delta^{15}N = \frac{[^{15}N:^{14}N] \text{ in sample} - [^{15}N:^{14}N] \text{ in standard}}{[^{15}N:^{14}N] \text{ in standard}} \cdot 1000\%$$

I calculated average  $\delta^{15}N$  values and N concentrations for stems (incorporating stems of trees and shrubs) and for leaves (incorporating leaves of trees, shrubs, and herbs and herbaceous stems) by multiplying the  $\delta^{15}N$  value and the N concentration of each compartment with compartment mass and dividing the sum by the total mass of the pooled compart-

ments. This is equivalent to first calculating the average  $^{15}\text{N}/^{14}\text{N}$  ratio across compartments and then converting it to  $\delta^{15}\text{N}$ .

*Statistical analyses.*— I compared  $\delta^{15}\text{N}$  values, N concentrations and N mass (N concentration · biomass) between parks and among vegetation types and compartments with an ANOVA, 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 nested as a random factor within park × vegetation type.  $\delta^{15}\text{N}$  data were homoscedastic and normal. Two  $\delta^{15}\text{N}$  values were excluded from analysis because they were extremely high (>100%), suggesting that they were artifacts. N concentration data did not meet assumptions for ANOVA. I did not find any transformation that would make the data homoscedastic and normal. Therefore, I used an arcsine-square-root transformation, because it reduced heteroscedasticity most. N mass data were ln-transformed to achieve homoscedasticity and normality. I excluded N mass data for the lower roots layer from analysis because of small sample size in some treatment groups caused by rocky soil.

#### 2.3.4. Forest expansion

I calculated forest expansion in all parks from sequences of  $\geq 4$  aerial photographs from 1930 to 1995 (National Air Photo Library, Ottawa, Canada) (for details of photographs see Table 2.3). For each

TABLE 2.3. Details of air photographs used to calculate forest expansion. For each park, the geographic location, elevation, and area of the scanned region is indicated. Area and scale were calculated from topographic maps. b/w: black-white, IR: infrared.

| Index Map  | Colour | Roll   | Frame   | Date<br>(YYYY-MM) | Nominal<br>altitude<br>(feet) | Focal<br>length<br>(inches) | Scanning<br>resolution<br>(dpi) | Pixels  | Scale |
|--|--------|--------|---------|-------------------|-------------------------------|-----------------------------|---------------------------------|---------|-------|
| <u>Elk Island, 53°43'07"N 112°47'47"W, 730 m a.s.l., 4.73 km<sup>2</sup></u> |        |        |         |                   |                               |                             |                                 |         |       |
| 83H NE "a"   | b/w    | A11057 | 26      | 1947              | 10420                         | 6                           | 216                             | 1254688 | 16511 |
| 83H "c"  | b/w    | A18562 | 35      | 1964              | 10120                         | 6                           | 180                             | 1001052 | 15404 |
| 83H "e"  | b/w    | A19927 | 126     | 1967              | 10100                         | 6                           | 180                             | 1134966 | 14467 |
| 83H "l"  | b/w    | A22893 | 123     | 1972              | 8400                          | 6                           | 144                             | 1086048 | 11831 |
| 83H "q"  | b/w    | A26592 | 14      | 1984-09           | 22400                         | 6                           | 504                             | 1194732 | 39481 |
| 83H "l"  | b/w    | A28181 | 98      | 1995-05           | 31500                         | 6                           | 720                             | 1159340 | 57256 |
| <u>Grasslands, 49°12'17"N 106°41'55"W, 900 m a.s.l., 4.93 km<sup>2</sup></u> |        |        |         |                   |                               |                             |                                 |         |       |
| 72G SE "b"   | b/w    | A11243 | 62      | 1947              | 10000                         | 6                           | 180                             | 844066  | 15775 |
| 72G "b"  | b/w    | A15123 | 26      | 1955              | 18000                         | 6                           | 360                             | 1099104 | 28732 |
| 72G "d"  | b/w    | A21760 | 38      | 1970              | 25300                         | 3.5                         | 1008                            | 1048586 | 76457 |
| 72G "a"  | IR     | A31307 | 181     | 1982              | 9250                          | 6                           | 144                             | 851857  | 12189 |
| 72G "h"  | b/w    | A27596 | 55      | 1990              | 22800                         | 6                           | 504                             | 1090915 | 39244 |
| <u>Jasper, 53°04'01"N 118°06'00", 1000 m a.s.l., 3.47 km<sup>2</sup></u>     |        |        |         |                   |                               |                             |                                 |         |       |
| 83E "a"  | b/w    | A12790 | 54-55   | 1949              | 20000                         | 6                           | 504                             | 772156  | 42064 |
| 83 SW "c"  | b/w    | A16083 | 106-107 | 1952              | 9500                          | 6                           | 180                             | 791350  | 14839 |
| 83E "b"  | b/w    | A19662 | 163     | 1966              | 30000                         | 6                           | 864                             | 843094  | 69009 |
| 83E "g"  | b/w    | A24742 | 42      | 1977              | 34000                         | 6                           | 864                             | 678600  | 76920 |
| 83E/l "a"  | b/w    | A25817 | 55      | 1981-08           | 8500                          | 6                           | 180                             | 1056270 | 12844 |
| 83E "i"  | b/w    | A27994 | 13      | 1993-10           | 33000                         | 6                           | 864                             | 689449  | 76312 |

Table continued on following page

Table continued from preceeding page

| Index Map   | Colour | Roll    | Frame   | Date<br>(YYYY-MM) | Nominal<br>altitude<br>(feet) | Lens<br>diameter<br>(inches) | Scanning<br>resolution<br>(dpi) | Pixels  | Scale |
|---|--------|---------|---------|-------------------|-------------------------------|------------------------------|---------------------------------|---------|-------|
| <u>Prince Albert, 53°36'04"N 106°30'42"W, 490 m a.s.l., 3.89 km<sup>2</sup></u>   |        |         |         |                   |                               |                              |                                 |         |       |
| 73G "a"   | b/w    | A11058  | 369-370 | 1947-07           | 9920                          | 6                            | 216                             | 989768  | 16859 |
| 73G NE "b"  | b/w    | A12906  | 167-169 | 1950-09           | 9680                          | 6                            | 252                             | 1322880 | 17013 |
| 73G "c"   | b/w    | A17935  | 19      | 1962-10           | 7800                          | 6                            | 180                             | 1843200 | 10295 |
| 73G "e"   | b/w    | A17936  | 113     | 1968-05           | 9820                          | 6                            | 252                             | 1428140 | 16374 |
| 73G "k"   | b/w    | A20417  | 150     | 1968-05           | 9820                          | 6                            | 252                             | 1428140 | 16374 |
| 73G "o"   | b/w    | A24402  | 182     | 1976-05           | 27000                         | 6                            | 720                             | 1291186 | 49202 |
| 73G "o"   | b/w    | A27572  | 125     | 1990-05           | 32300                         | 6                            | 792                             | 1058490 | 59775 |
| <u>Riding Mountain, 50°56'02"N 100°54'25"W, 520 m a.s.l., 2.14 km<sup>2</sup></u> |        |         |         |                   |                               |                              |                                 |         |       |
| 62K NE "a"  | b/w    | A4332   | 28      | 1931-09           | 10000                         | 8                            | 252                             | 1315608 | 12653 |
| 62K NE "b"  | b/w    | A11576  | 79      | 1948-10           | 9420                          | 6                            | 252                             | 1149168 | 13539 |
| 62JKNO "d"  | b/w    | A16846  | 178     | 1959              | 10020                         | 6                            | 288                             | 1315404 | 14462 |
| 62K "d"   | b/w    | A18654  | 35      | 1964              | 9700                          | 6                            | 252                             | 1038284 | 14243 |
| 62K "i"   | b/w    | A20372  | 28      | 1969              | 10020                         | 6                            | 288                             | 1269730 | 14720 |
| 62K "a"   | colour | A31179  | 182     | 1978-05           | 8000                          | 6                            | 216                             | 1341760 | 10740 |
| 62K "n"   | b/w    | A26662  | 43      | 1985-05           | 30000                         | 6                            | 972                             | 1211820 | 50853 |
| <u>Wood Buffalo, 59°08'00"N 112°25'00"W, 250 m a.s.l., 3.46 km<sup>2</sup></u>    |        |         |         |                   |                               |                              |                                 |         |       |
| 84 NE "b"   | b/w    | A15163  | 50      | 1955              | 20000                         | 6                            | 506                             | 1212904 | 32738 |
| 84P "b"   | b/w    | VRR2678 | 608-610 | 1966-06           | 6850                          | 6                            | 180                             | 1396577 | 11179 |
| 84P "e"   | b/w    | A24868  | 25-26   | 1978-05           | 5850                          | 6                            | 144                             | 1421849 | 8987  |
| 84P "f"   | b/w    | A26005  | 165-165 | 1982-06           | 5800                          | 6                            | 144                             | 1406087 | 8943  |

park I selected one area of 2-5 km<sup>2</sup> that included contiguous areas of grassland and forest. I chose sites that I had visited or for which vegetation descriptions had been published (Raup 1935, Blood 1966b, Carbyn 1971, Holland & Coen 1982) to ensure that the grasslands were mainly of prairie type and not wetlands. The photographs were digitized and the resolution chosen so that the same geographical area within each park was covered by approximately 1000 × 1000 pixels (Table 2.3). The images were analyzed by density-slicing (Frey & Curtin 1997), i.e., shades of gray were manually assigned to either forest or grassland and the number of pixels of each vegetation type counted. I calculated the increase of percentage forest area over time, e.g., if the forest area was 25% of the total area in 1930 and 65% of the total area in 1990, the increase was 40 percentage points (%p) over a period of 60 years, an expansion rate of 40 %p/60 yr = 0.67 %p/yr. The rates were calculated by fitting linear regressions to percent forest area over time in each park. I tested with analysis of covariance whether the slopes differed among each other. Since not all slopes were equal I compared the slopes pairwise with a Tukey-Kramer test ( $\alpha = 0.05$ ; Zar 1996) and pooled equal slopes (Zar 1996).

I tested whether forest expansion rates could be described by linear or non-linear regression on annual N deposition, mean annual precipitation, long-term change of annual precipitation, or long-term change of mean annual temperature. The long-term rate of change of annual precipitation and of mean annual temperature was calculated from annual precipitation and mean annual temperature data for 1942 - 1992

(Environment Canada, Ottawa, Canada) and expressed as mm/yr and °C/yr. I used records from Edmonton-Municipal Airport, Regina Airport, Prince Albert Airport and Dauphin Airport to calculate the rate of precipitation and temperature change in Elk Island, Grasslands, Prince Albert, and Riding Mountain because records of closer stations were not available for the whole period.

I compared the increase of N in biomass (above- and belowground) across vegetation types on the landscape scale between Jasper and Elk Island. I calculated the amount of N in forest mass by multiplying the percentage of forest (as calculated from the earliest and most recent air photographs) with the amount of N measured in forest vegetation (section 2.3.3, Fig. 2.7). I calculated the amount of N in grassland in the same way. By using 1996 measurements of N mass to calculate historic N mass, I was assuming that the amount of N per area within a vegetation type did not change over time. This assumption is justified because N deposition had no significant effect on N mass in forests (section 2.3.3). N on the landscape scale was then calculated by adding N mass in forest and prairie. I did not test the increase of N mass for statistical significance, because the calculations were based on means.

## 2.4. RESULTS

### 2.4.1. Atmospheric deposition and available soil N - among-park comparisons

Deposition rates in parks in the agro-industrial region were

significantly higher than those in the forested region (Figs. 2.1, 2.2, Table 2.4). The difference was smaller during the second year (Fig. 2.2b), causing a significant year  $\times$  region interaction (Table 2.4). This was confirmed by separate univariate ANOVAs for each year (year 1:  $F_{1,4} = 79.2$ ,  $P = 0.0009$ ; year 2:  $F_{1,4} = 7.52$ ,  $P = 0.05$ , Bonferroni-adjusted  $\alpha = 0.025$ ).

Deposition rates were highest in Elk Island and lowest in Wood Buffalo (Fig. 2.2a). Deposition rates in the agro-industrial region showed a geographical pattern with high rates near Edmonton, declining southeastwards (Fig. 2.1).

Deposition rates varied significantly among seasons (Table 2.4). Rates were generally lowest in winter and highest in summer (Fig. 2.2b). The seasonal pattern also varied significantly among parks and between years (season  $\times$  park and year  $\times$  season  $\times$  park interactions, Table 2.4), with Elk Island and Grasslands receiving their highest daily N input in spring and other parks in summer. Prince Albert showed the largest seasonal variation: in summer 1994 it had the highest deposition rate of all parks ( $58.0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ); in spring 1996, it had the lowest of all parks ( $1.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ).

Soil N availability was also significantly higher in parks in the agro-industrial region than in the forested region (Fig. 2.2, Table 2.5). Seasonal variation was significant (Table 2.5) and similar to that of deposition (Fig. 2.2d). Rates of available N were, on average, highest in spring or early summer and declined during the growth period. N availability in spring was exceptionally high in 1996 in Prince Albert ( $1533 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ).

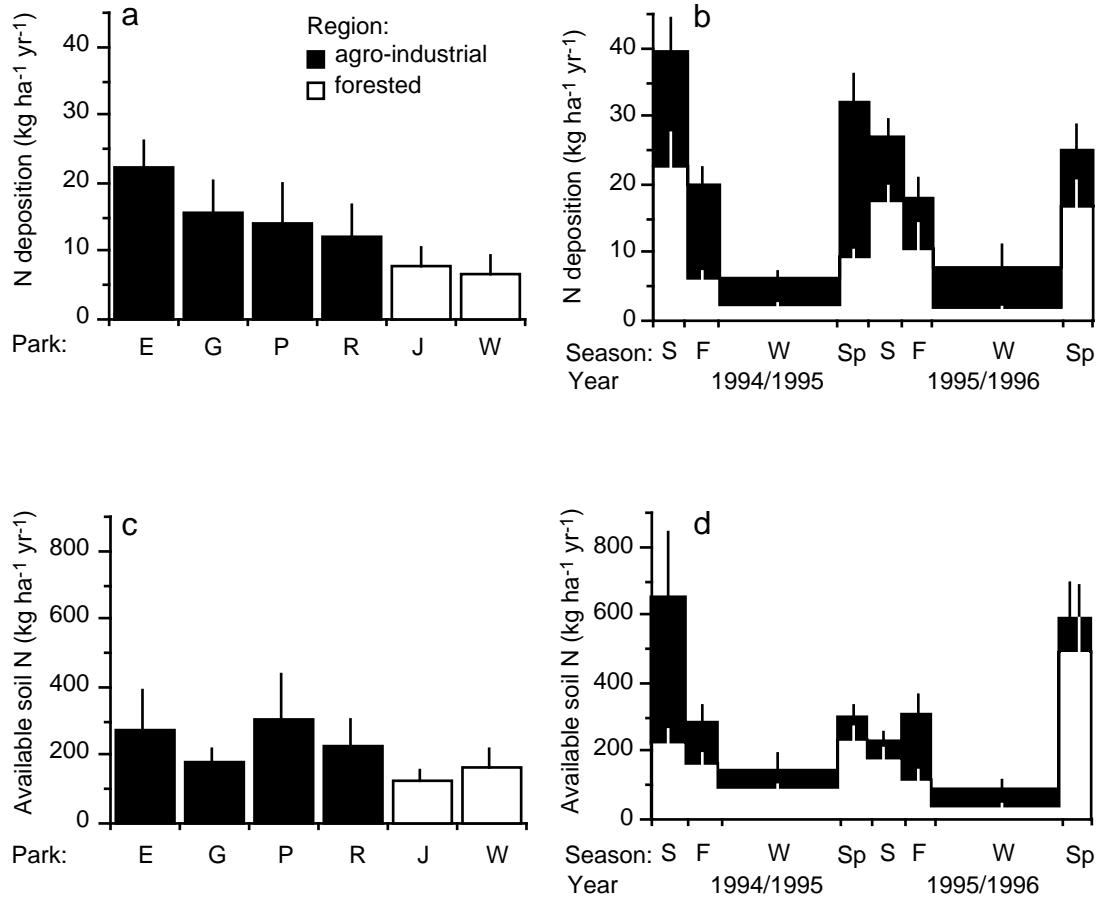


FIG. 2.2. Deposition of atmospheric N (a, b) and available soil N (c, d) in six western Canadian national parks (E: Elk Island, G: Grasslands, J: Jasper, P: Prince Albert, R: Riding Mountain, W: Wood Buffalo) in the agro-industrial (more densely populated) and the forested (sparsely populated) region measured for two years in four seasons (S: summer [mid-June - August], F: fall [August - October], W: winter [October - May], Sp: spring [May - mid-June]). Bars represent means  $\pm$  SE (a, c:  $n = 751$  days; b, d:  $n = 42$  [agro-industrial region],  $n = 20$  [forested region]).



TABLE 2.4. N deposition in six national parks in western Canada during two years examined with univariate (ANOVA) and multivariate (MANOVA) analysis of variance. Four parks were in the agro-industrial and two in the forested region. "Year" and "Park" were considered random effects. Overall significance is assumed when  $P < \alpha/2$  in either ANOVA or MANOVA (\*:  $P \leq 0.025$ , \*\*:  $P \leq 0.005$ , \*\*\*:  $P \leq 0.0005$ ).

| Effect                       | ANOVA   |       |         | MANOVA         |        |        | overall significance |            |
|------------------------------|---------|-------|---------|----------------|--------|--------|----------------------|------------|
|                              | MS      | F     | df      | Pillai's Trace | F      | df     |                      | P          |
| Year                         | 0.37467 | 0.53  | 1, 4    | 0.5060         | 0.0326 | 1.18   | 1, 35                | 0.2846     |
| Season                       | 78.0659 | 36.35 | 3, 12   | 0.0023         | 0.9130 | 115.39 | 3, 33                | 0.0001 *** |
| Year × Season                | 0.25848 | 0.08  | 3, 12   | 0.9694         | 0.0960 | 1.17   | 3, 33                | 0.3368     |
| Region                       | 60.1903 | 12.77 | 1, 1.9  | 0.1737         | 0.4174 | 25.07  | 1, 35                | 0.0001 *** |
| Year × Region                | 3.21784 | 4.57  | 1, 4    | 0.0992         | 0.2342 | 10.71  | 1, 35                | 0.0024 **  |
| Season × Region              | 1.35046 | 0.59  | 3, 6.84 | 0.6445         | 0.2200 | 3.10   | 3, 33                | 0.0399     |
| Year × Season × Region       | 0.40519 | 0.31  | 3, 12   | 0.8209         | 0.0517 | 0.60   | 3, 33                | 0.6194     |
| Park[Region]                 | 2.20083 | 3.13  | 4, 4    | 0.1476         | 0.0997 | 0.97   | 4, 35                | 0.4366     |
| Year × Park[Region]          | 0.70357 | 1.20  | 4, 405  | 0.3111         | 0.1680 | 1.77   | 4, 35                | 0.1575     |
| Season × Park[Region]        | 3.21458 | 2.42  | 12, 12  | 0.0695         | 1.0806 | 4.93   | 12, 105              | 0.0001 *** |
| Year × Season × Park[Region] | 1.32571 | 2.26  | 12, 405 | 0.0090         | 0.6098 | 2.23   | 12, 105              | 0.0150 *   |
| Residual error               | 0.58727 |       | 405     |                |        |        |                      |            |

TABLE 2.5. Available soil N in six national parks in western Canada during two years examined with univariate (ANOVA) and multivariate (MANOVA) analysis of variance. Four parks were in the agro-industrial and two in a the forested region. "Year" and "Park" were considered random effects. Overall significance is assumed when  $P \leq \alpha/2$  in either ANOVA or MANOVA (\*:  $P \leq 0.025$ , \*\*:  $P \leq 0.005$ , \*\*\*:  $P \leq 0.0005$ ).

| Effect                       | ANOVA   |       |         | MANOVA |                |       | overall significance |        |     |
|------------------------------|---------|-------|---------|--------|----------------|-------|----------------------|--------|-----|
|                              | MS      | F     | df      | P      | Pillai's Trace | F     |                      | df     | P   |
| Year                         | 4.24049 | 0.93  | 1, 4    | 0.389  | 0.2415         | 9.23  | 1, 29                | 0.005  | **  |
| Season                       | 41.151  | 9.49  | 3, 4.26 | 0.0272 | 0.6249         | 14.99 | 3, 27                | 0.0001 | *** |
| Year × Season                | 3.38146 | 1.46  | 3, 12   | 0.2744 | 0.2029         | 2.29  | 3, 27                | 0.1008 |     |
| Region                       | 25.1558 | 24.58 | 1, 4.46 | 0.0077 | 0.3834         | 18.04 | 1, 29                | 0.0002 | *** |
| Year × Region                | 0.34677 | 0.08  | 1, 4    | 0.7961 | 0.0036         | 0.1   | 1, 29                | 0.7496 |     |
| Season × Region              | 0.38036 | 0.27  | 3, 3    | 0.8465 | 0.0144         | 0.13  | 3, 27                | 0.9407 |     |
| Year × Season × Region       | 0.46815 | 0.34  | 3, 12   | 0.7941 | 0.2138         | 2.45  | 3, 27                | 0.0855 |     |
| Park[Region]                 | 0.67649 | 0.15  | 4, 403  | 0.9541 | 0.1906         | 1.71  | 4, 29                | 0.1753 |     |
| Year × Park[Region]          | 4.54873 | 6.45  | 4, 403  | 0.0001 | 0.5076         | 7.47  | 4, 29                | 0.0003 | *** |
| Season × Park[Region]        | 2.31453 | 1.7   | 12, 403 | 0.1853 | 1.0514         | 2.25  | 12, 87               | 0.0591 |     |
| Year × Season × Park[Region] | 1.36123 | 1.93  | 12, 403 | 0.0295 | 0.7031         | 2.22  | 12, 87               | 0.0172 | *   |
| Residual error               | 0.705   |       | 403     |        |                |       |                      |        |     |

Available soil N increased significantly with deposited N (Fig. 2.3;  $R^2 = 0.29$ ,  $F_{1,46} = 18.5$ ,  $P < 0.0001$ ). The goodness of fit ( $R^2$ ) increased to 0.39 when the exceptionally high N availability in spring 1996 in Prince Albert was excluded. The regression shows a clustering of points according to season, because both N deposition and available soil N were strongly seasonal (Figs. 2.2b, d). Across all sample dates, i.e., independent of season, mean daily available soil N also increased with

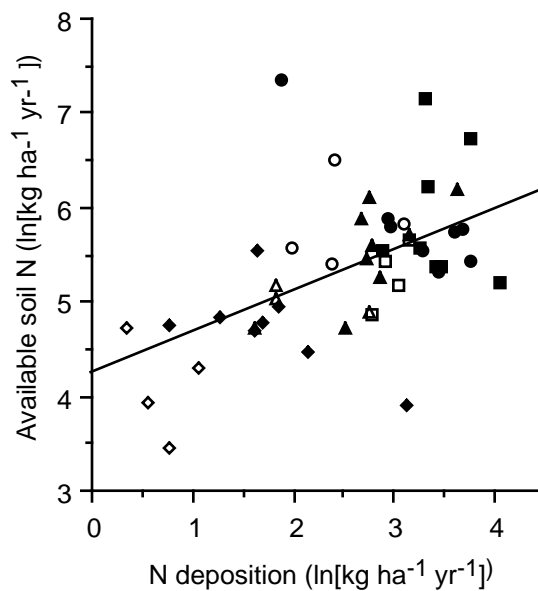


FIG. 2.3. Relationship between available soil N and N deposition in six western Canadian national parks, four in the agro-industrial region (more densely populated, black symbols) and two in the forested region (sparsely populated, white symbols), measured for two years in four seasons (summer [mid-June - August]:  $\square$ ,  $\blacksquare$ ; fall [August - October]:  $\triangle$ ,  $\blacktriangle$ ; winter [October - May]:  $\diamond$ ,  $\blacklozenge$ ; spring [May - mid-June]:  $\circ$ ,  $\bullet$ ). Symbols represent means of 10 samples. The significant regression for all points is  $y = 4.249 + 0.437x$  ( $R^2 = 0.29$ ).

mean daily deposition, but not significantly ( $R^2 = 0.48$ ,  $F_{1,4} = 3.76$ ,  $P = 0.12$ ).

#### 2.4.2. Atmospheric deposition and available soil nitrogen – Elk Island

Within Elk Island, deposition rates varied most strongly with season ( $F_{3,3} = 39.62$ ,  $P = 0.0065$ ) which explained 45% of the accounted-for-variation in N deposition (calculated by dividing the effect sum of square by the sum of all effect sum of squares). Deposition, averaged over all other treatments, was highest in spring and declined during the growth period (Fig. 2.4). In grassland vegetation, however, the peak of N deposition was in early summer (Fig. 2.4), causing a significant season  $\times$  vegetation effect ( $F_{6,424} = 4.63$ ,  $P = 0.0001$ ). Further, deposition in unburned sites (averaged over grazing treatments and soil types) was similar in forests and grassland and was higher there than in shrubland. In burned sites the order was reversed: shrubland  $>$  grassland  $>$  forest (Table 2.6; fire  $\times$  vegetation interaction,  $F_{2,424} = 6.41$ ,  $P = 0.002$ ). Brunisol sites received more atmospheric N than luvisol sites, except in burned grassland (Table 2.6; soil  $\times$  fire  $\times$  vegetation interaction,  $F_{2,424} = 3.11$ ,  $P = 0.05$ ) and grazed sites received more atmospheric N than ungrazed sites except in unburned forest (Table 2.6; grazing  $\times$  fire  $\times$  vegetation interaction,  $F_{2,424} = 4.14$ ,  $P = 0.02$ ). None of these interactions contributed  $>6\%$  to the accounted-for-variation, and thus probably have little importance.

Available soil N (Table 2.7) did not vary significantly with the main effects of soil type, fire, grazing or vegetation type, but the effects of these treatments did interact significantly with season or year in two- to fourway interactions. None of the interactions explained more than 6% of the accounted-for variation. Part of the variation was caused by high N availability ( $4460 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) in one ungrazed forest site on luvisol one month after a prescribed fire. Two months later at the same site, soil N was no longer unusually high. There also was a tendency for grazed sites in interaction with other treatments to have higher N availability than ungrazed sites. Available soil N was not significantly correlated with deposited N within Elk Island.

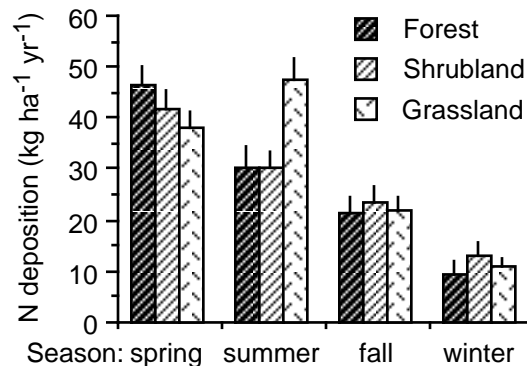


FIG. 2.4. Deposition of atmospheric N in Elk Island National Park, western Canada. Spring: May – mid-June, summer: mid-June – August, fall: August – October, winter: October – May. Bars represent means (+ SE) of two years ( $n = 18-25$ ).

TABLE 2.6. Rate of N deposition ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ) at Elk Island National Park (mean  $\pm$  SE,  $n = 751$  days).

| Treatment |          |            | Vegetation     |                |                 |
|-----------|----------|------------|----------------|----------------|-----------------|
| Soil      | Fire     | Grazing    | Forest         | Shrubland      | Grassland       |
| Brunisol  | unburned | ungrazed   | $14.7 \pm 5.5$ | $15.7 \pm 6.4$ | $18.0 \pm 5.9$  |
|           |          | grazed     | $15.8 \pm 6.3$ | $22.2 \pm 7.6$ | $23.7 \pm 7.6$  |
|           | burned   | ungrazed * | —              | —              | —               |
|           |          | grazed     | $18.8 \pm 7.8$ | $22.0 \pm 6.7$ | $32.7 \pm 10.3$ |
| Luvisol   | unburned | ungrazed   | $32.1 \pm 7.5$ | $17.4 \pm 5.4$ | $21.5 \pm 8.0$  |
|           |          | grazed     | $19.1 \pm 6.6$ | $10.6 \pm 3.1$ | $19.6 \pm 3.3$  |
|           | burned   | ungrazed   | $19.2 \pm 8.3$ | $24.5 \pm 5.7$ | $23.9 \pm 6.0$  |
|           |          | grazed     | $21.1 \pm 7.8$ | $41.2 \pm 7.2$ | $23.1 \pm 7.4$  |

\* This combination does not exist at Elk Island.

TABLE 2.7. Availability of soil N ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ) at Elk Island National Park (mean  $\pm$  SE,  $n = 751$  days).

| Treatment |          |            | Vegetation    |              |               |
|-----------|----------|------------|---------------|--------------|---------------|
| Soil      | Fire     | Grazing    | Forest        | Shrubland    | Grassland     |
| Brunisol  | unburned | ungrazed   | $184 \pm 45$  | $128 \pm 39$ | $171 \pm 65$  |
|           |          | grazed     | $293 \pm 90$  | $201 \pm 39$ | $163 \pm 42$  |
|           | burned   | ungrazed * | —             | —            | —             |
|           |          | grazed     | $287 \pm 60$  | $218 \pm 66$ | $289 \pm 34$  |
| Luvisol   | unburned | ungrazed   | $150 \pm 32$  | $168 \pm 43$ | $297 \pm 78$  |
|           |          | grazed     | $538 \pm 239$ | $287 \pm 71$ | $399 \pm 195$ |
|           | burned   | ungrazed   | $578 \pm 443$ | $262 \pm 42$ | $425 \pm 161$ |
|           |          | grazed     | $183 \pm 53$  | $179 \pm 52$ | $349 \pm 102$ |

\* This combination does not exist at Elk Island.

#### 2.4.3. $\delta^{15}\text{N}$ and N in vegetation and soil at Elk Island and Jasper

$\delta^{15}\text{N}$  values in vegetation and soil tended to be lower in Elk Island (22.1 kg ha<sup>-1</sup> yr<sup>-1</sup> N deposition) than in Jasper (7.8 kg ha<sup>-1</sup> yr<sup>-1</sup> N deposition). The difference between  $\delta^{15}\text{N}$  values was significant, however, only for some compartment - vegetation type combinations (Fig. 2.5; park  $\times$  compartment[vegetation type] interaction:  $F_{17,241} = 3.32$ ,  $P < 0.0001$ ).  $\delta^{15}\text{N}$  values of stems, leaves, and litter in forest were significantly lower in Elk Island than in Jasper, whereas  $\delta^{15}\text{N}$  values of aboveground mass in shrubland and grassland did not differ between the parks (Fig. 2.5; park  $\times$  vegetation type interaction:  $F_{2,54} = \del{12.07},  $P < 0.0001$ ). Roots tended to have higher  $\delta^{15}\text{N}$  values than other tissues and  $\delta^{15}\text{N}$  values of soil were higher than  $\delta^{15}\text{N}$  values of tissues.  $\delta^{15}\text{N}$  values of roots and soils were significantly lower in Jasper than in Elk Island in the upper layer in shrubland and the lower layer in grassland. In shrubland, lower  $\delta^{15}\text{N}$  values are presumably due to the presence of N-fixing shrubs. In summary,  $\delta^{15}\text{N}$  values of aboveground tissues (including litter) tended to be lower in Elk Island than in Jasper and the difference increased with vegetation height.$

N concentration of compartments (Fig. 2.6) varied little, suggesting that the statistically significant differences have little biological meaning. N concentrations in stems in Jasper shrubland were higher than those in Elk Island because shrubland in Jasper consisted of N-fixing *Shepherdia*, whereas shrubs in Elk Island were not N-fixing. N concentration varied significantly between parks ( $F_{1,54} = \del{6.27},  $P =$$

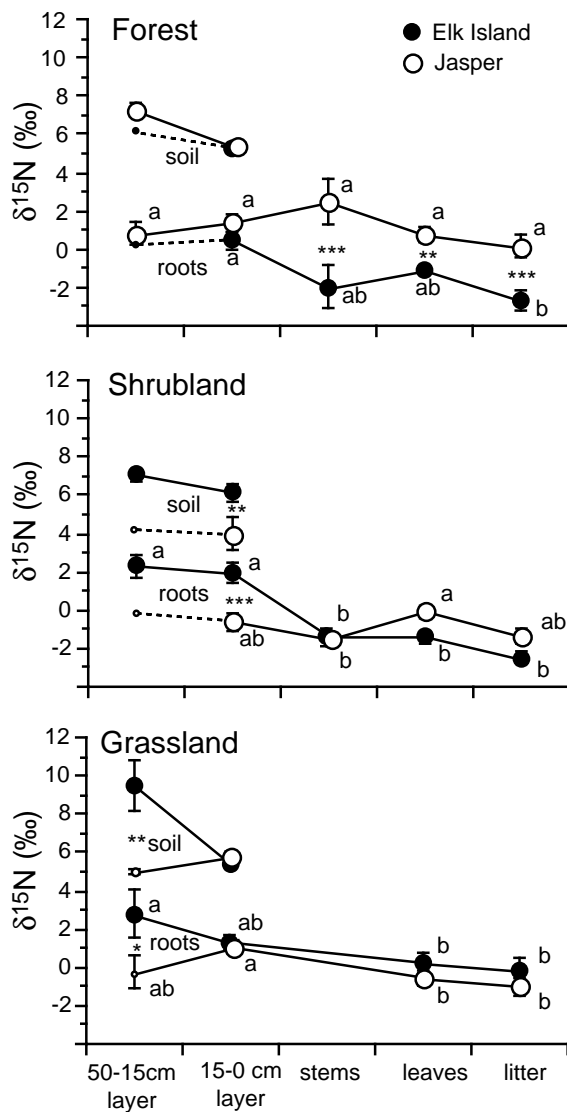


FIG. 2.5.  $\delta^{15}\text{N}$  values of vegetation and soil compartments in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means  $\pm$  SE,  $n = 6-10$ ; small circles denote  $n \leq 3$ ). Compartments within a park that share the same letter are not significantly different (Tukey-Kramer test,  $\alpha = 0.05$ ). Significant differences between parks within a compartment are marked with asterisks between the circles (a-priori contrasts, \*:  $P \leq 0.05$ , \*\*:  $P \leq 0.01$ , \*\*\*:  $P \leq 0.001$ ).



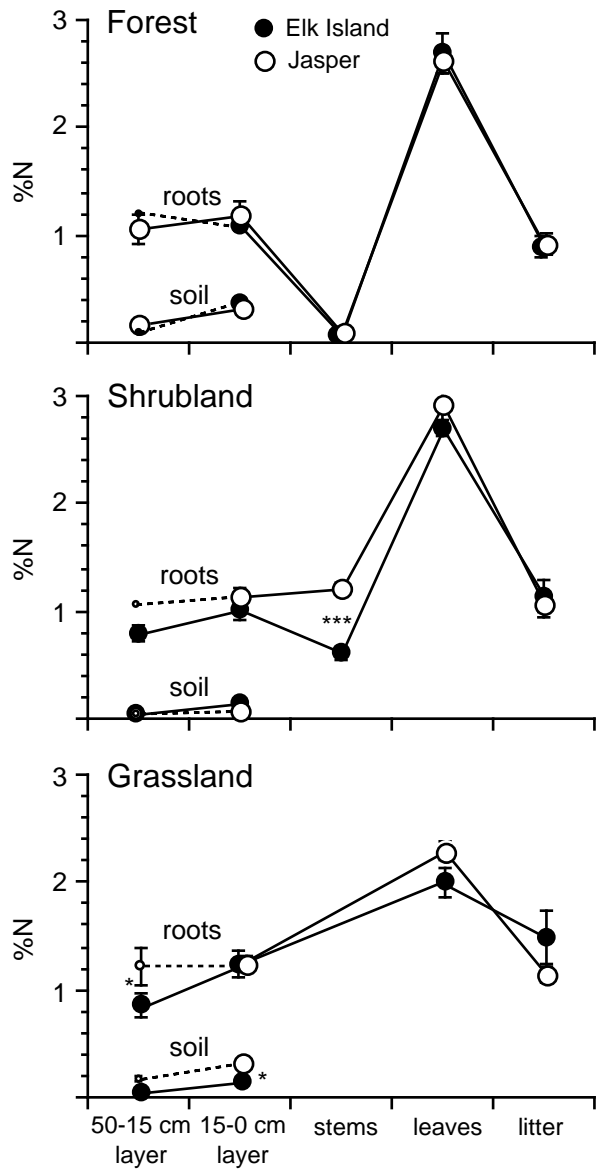


FIG. 2.6. Concentration of N in vegetation and soil compartments in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means  $\pm$  SE,  $n = 6-10$ ; small circles denote  $n \leq 3$ ). Significant differences between parks within a compartment are marked with asterisks between the circles (a-priori contrasts, \*:  $P \leq 0.05$ , \*\*\*:  $P \leq 0.001$ ).

~~0.01~~), among vegetation types ( $F_{2,54} = \del{3.23},  $P = \del{0.04}), among soil and vegetation compartments ( $F_{17,243} = \del{167},  $P < 0.0001$ ), and with the interaction of parks and compartments ( $F_{17,243} = 2.69$ ,  $P = 0.0004$ ). However, means contrasts of compartments between parks were almost all non-significant.$$$

N mass averaged over all compartments did not differ significantly between Elk Island and Jasper except for shrubland where N mass in Jasper was significantly higher than in Elk Island likely due to the presence of N-fixing shrubs (Fig. 2.7; park  $\times$  vegetation interaction:  $F_{2,54} = 5.27$ ,  $P = 0.008$ ). Total N mass increased along a successional gradient from prairie to forest (Fig. 2.7; vegetation type effect:  $F_{2,54} = 210$ ,  $P < 0.0001$ ) with an increasingly higher proportion of N stored in aboveground compartments (Fig. 2.7; compartment effect:  $F_{8,144} = 68.42$ ,  $P < 0.0001$ ). Significant differences between Elk Island and Jasper in N mass of the upper root layer in shrubland and grassland and leaves in grassland caused a significant park  $\times$  compartment interaction (Fig. 2.7;  $F_{8,144} = 4.94$ ,  $P < 0.0001$ ).

#### 2.4.4. Forest expansion

Relative forest area (forest area/(forest area + grassland area) \* 100%) increased significantly in Elk Island, Prince Albert, and Riding Mountain (pooled slope: 1.1 %p/yr [percentage points per year], Fig. 2.8) but not in Jasper, Wood Buffalo, and Grasslands (ANCOVA testing

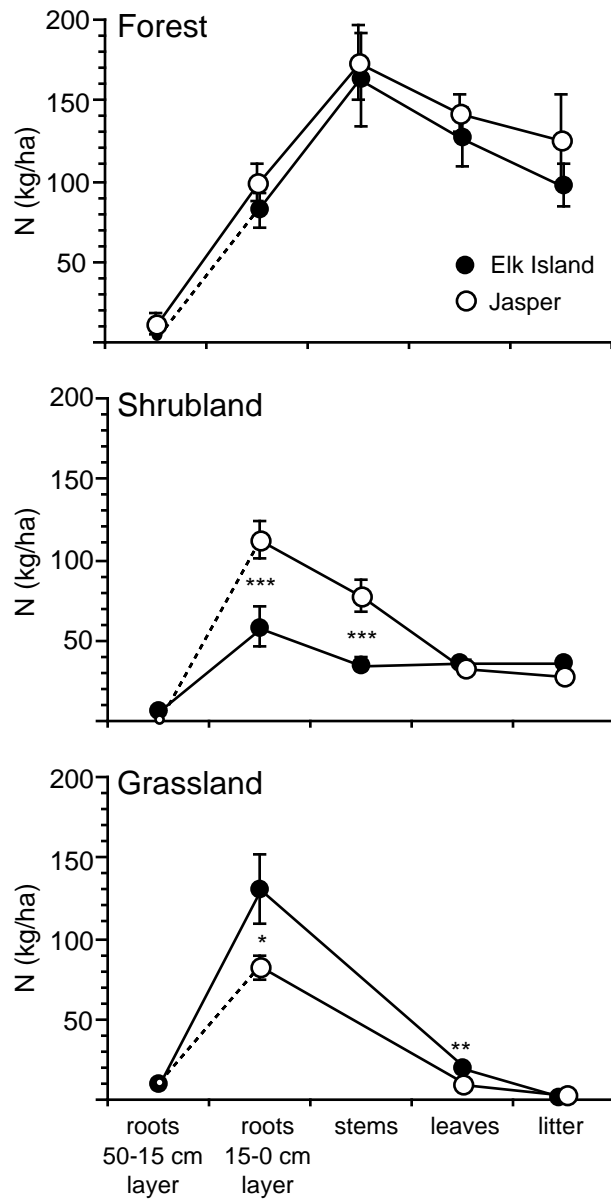


Fig. 2.7. Amount of N in vegetation in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means  $\pm$  SE,  $n = 6-10$ ; small circles denote  $n \leq 3$ ). Significant differences between parks within a compartment are marked with asterisks between the circles (a-priori contrasts, \*:  $P \leq 0.05$ , \*\*:  $P \leq 0.01$ , \*\*\*:  $P \leq 0.001$ ).

equality of slopes among all parks:  $F_{5,22} = 9.33, P < 0.0001$ ). I examined the relationship between the rate of forest expansion and the rate of N deposition for parks on or north of the present forest-prairie transition belt (i.e., all except Grasslands). The rate of forest expansion ( $E$ ) increased significantly with deposition ( $D$ ) (Fig. 2.9;  $E = -9.15 + 10.34/(1+e^{-0.31D})$ ,  $R^2 = 0.99$ ,  $F_{1,2} = 611$ ,  $P = 0.002$ ). Forest expansion in the five parks was not significantly related with mean annual precipitation (Fig. 2.10), long-term change of annual precipita-

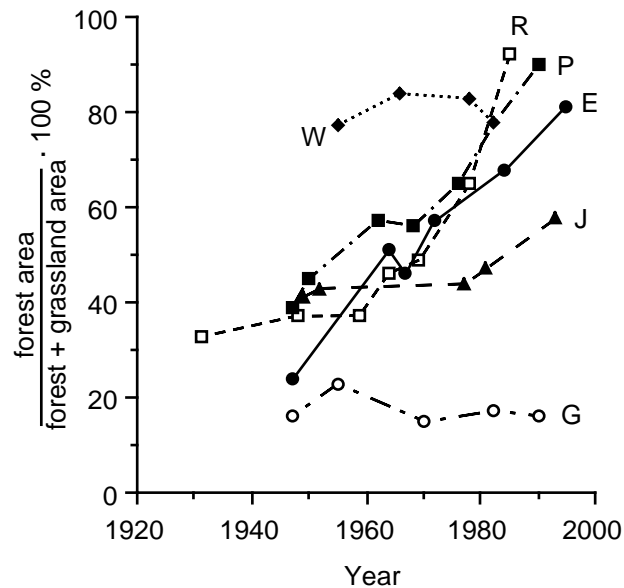


Fig. 2.8. Forest expansion in six western Canadian national parks determined by digital analysis (density-slicing) of aerial photographs. Four parks (E: Elk Island, G: Grasslands, P: Prince Albert, R: Riding Mountain) were in the agro-industrial (more densely populated) region receiving high rates of N deposition and two parks (J: Jasper, W: Wood Buffalo) were in the forested (sparsely populated) region receiving low rates of N deposition.

tion, or long-term change of mean annual temperature.

N in biomass across vegetation types increased by 26% from 1949 (289 kg/ha) to 1993 (365 kg/ha) in Jasper and by 74% from 1947 (235 kg/ha) to 1995 (410 kg/ha) in Elk Island (Table 2.8).

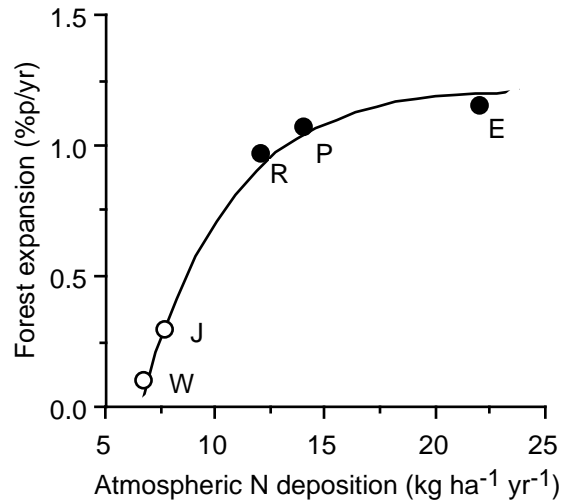


FIG. 2.9. Relationship between rate of forest expansion (percentage-points forest area per year, %p/yr) and atmospheric N deposition in five western Canadian national parks. Three parks (E: Elk Island, P: Prince Albert, R: Riding Mountain) were in the agro-industrial (more densely populated) region (black symbols) and two parks (J: Jasper, W: Wood Buffalo) were in the mostly forested (sparsely populated) region (white symbols). The line represents the logistic regression  $y = -9.15 + 10.34/(1+e^{-0.31x})$  ( $R^2 = 0.99$ ).

## 2.5. DISCUSSION

### 2.5.1. Atmospheric deposition – among-park comparisons

Atmospheric deposition of N in western Canada was higher in the densely populated agro-industrial region than in the sparsely populated, forested region (Figs. 2.1, 2.2), reflecting higher N emissions from industry and transportation in the agro-industrial region (Environment Canada 1996). This pattern was similar to that of the whole continent, where high rates of atmospheric N deposition have been measured in and downwind of industrialized areas of the northeastern United States and southern Canada (Johnson & Lindberg 1992, NADP 1994, 1995, 1996).

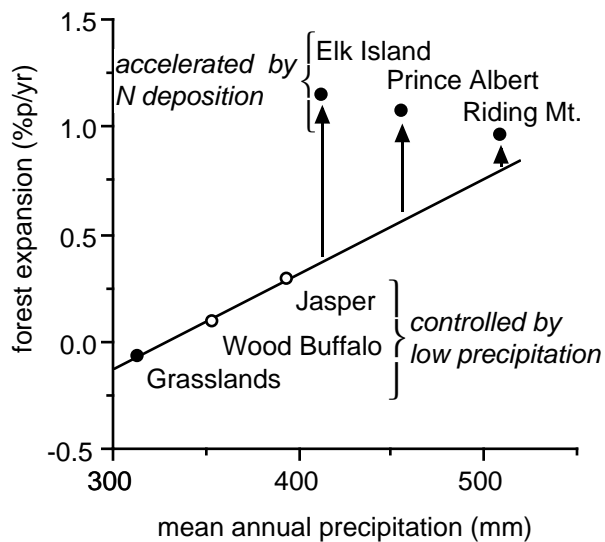


FIG. 2.10. Relationship between rate of forest expansion (percentage-points forest area per year, %p/yr) and annual precipitation in six western Canadian national parks. Four parks (black symbols) are exposed to high N deposition, two parks (white symbols) to low N deposition.

TABLE 2.8. Amount of N in biomass (above- and belowground) in two national parks in western Canada based on N concentration and mass measurements in 1996 (Fig. 2.7) and air photo interpretation (Fig. 2.8).

| year:                   | Jasper |      |      | Elk Island |      |      |
|-------------------------|--------|------|------|------------|------|------|
|                         | 1949   | 1993 | 1996 | 1947       | 1995 | 1996 |
| forest                  |        |      |      |            |      |      |
| area (%)                | 41     | 58   | —    | 24         | 81   | —    |
| amount of N (kg/ha)     | —      | —    | 553  | —          | —    | 469  |
| grassland               |        |      |      |            |      |      |
| area (%)                | 59     | 42   | —    | 76         | 19   | —    |
| amount of N (kg/ha)     | —      | —    | 105  | —          | —    | 161  |
| grassland + forest      |        |      |      |            |      |      |
| area (%)                | 100    | 100  |      | 100        | 100  |      |
| calculated amount of N  | 289    | 365  |      | 235        | 410  |      |
| increase in amount of N |        | 26%  |      |            | 74%  |      |

The highest rate of N deposition was observed in Elk Island, the park closest to a metropolitan area (Figs. 2.1, 2.2a). The high rate was presumably due to N emissions from Edmonton (population 840,000) which produces 37-168 kg NO<sub>x</sub>-N ha<sup>-1</sup> yr<sup>-1</sup> compared to 10<sup>-7</sup> kg NO<sub>x</sub>-N ha<sup>-1</sup> yr<sup>-1</sup> in northern Alberta (population <1 inhabitant/km<sup>2</sup>) (Environment Canada 1996). The largest sources of NO<sub>x</sub> in and around Edmonton are power plants, petroleum industry, furnaces, and traffic exhausts (Legge 1988). Industrial ammonium emissions in Alberta are low (Environment Canada

1998), constituting <5% of NO<sub>x</sub>-N emissions. Non-industrial anthropogenic sources (hog and chicken farms, liquid fertilizer application) are presumably even smaller, but no official statistics are available. Ammonia concentrations in the air are usually below the detection limit (Myrick & Hunt 1998).

Elevated deposition rates in Grasslands, Riding Mountain, and Prince Albert (Figs. 2.1, 2.2a) may be caused by the prevailing westerly and northwesterly 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. 2.1). 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 I observed during early summer (when farmers apply fertilizer) and the low rates observed in winter (Figs. 2.2b, d). Official statistics, however, assume that no measurable amounts of NO<sub>x</sub> are released from applied fertilizer (Environment Canada 1996).

My N deposition rates, measured with ion-exchange resin, correspond with those measured by a combination of methods in similar regions in the Integrated Forest Study (IFS, Lovett & Lindberg 1993). Assuming that wet deposition is about  $\frac{1}{2}$  of total deposition (Lovett & Lindberg 1993), wet deposition in my study ranged from 5.1 kg N ha<sup>-1</sup> yr<sup>-1</sup> in the forested region to 11.0 kg N ha<sup>-1</sup> yr<sup>-1</sup> in the agro-industrial region. These values are similar to those measured at low-deposition sites in the IFS, but are considerably greater than wet deposition measurements by meteorological stations in the northern Great Plains (NADP 1994,



1995, 1996, CAPMoN: M. Shaw, *pers. comm.*). Higher deposition rates in my study and in the IFS are presumably caused by the presence of surrounding vegetation from which rain drops can re-insert dry-deposited particles into the boundary layer (Lovett 1994). Higher rates may also result from the capture of coarse dry particles that had higher N concentration than fine dry particles (Shachak & Lovett 1998). Coarse dry particles are not included in common meteorological measurements. Capillary water may have transported mineral N from the soil or litter to the resin bags. However, this contributed only marginally to my higher deposition rate measurements, because I found that resin bags take up more N from deposition than from N conversion processes in the soil or the litter layer (Köchy & Wilson 1997).

#### 2.5.2. Available soil nitrogen – among-park comparisons

Prince Albert and Elk Island had the highest rates of available soil N among parks in the agro-industrial region (Fig. 2.2c). The seasonal pattern of soil N availability was similar to that for deposition rates (Fig. 2.2b, d). Most remarkable was the high soil N availability in Prince Albert in spring in 1996 ( $1540 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ). Spring rates in other parks were either low or comparable to rates in other seasons, suggesting that the high N availability in Prince Albert was exceptional.

Available soil N increased with deposited N across all parks

(Fig. 2.3), presumably because most of the deposited N enters the soil by stemflow and throughfall (Eilers et al. 1992). A positive correlation between soil N and N deposition was also observed in an Austrian spruce forest (Kazada & Katzensteiner 1993). N added to N-limited ecosystems, such as natural forests or grasslands, is retained almost completely (Kenk & Fischer 1988, Aber et al. 1993). Therefore, N deposition may improve mineralization in the soil (Morecroft et al. 1994) and contribute to accelerated N cycling in these ecosystems.

#### 2.5.3. N deposition and availability – Elk Island

N deposition and soil N availability within Elk Island varied most clearly with season. Remaining variation with grazing, fire, vegetation type, and soil type was large compared to the treatment means and inconsistent (Fig. 2.4, Tables 2.6, 2.7). Local variation in deposition may have been caused, for example, by ammonia released from ungulate urine deposits (Redman 1975, Nason et al. 1988) or by vegetation height and density (Heil et al. 1988, van Dam 1990, Binkley 1995). Local variation in available soil N may be due to breakdown of organic matter from recent fires, patchy urine and faeces deposits, higher uptake of N by grazed plants to compensate for losses by grazing (Risser & Parton 1982, Stock & Lewis 1986), and interception of deposited N by litter on the ground (Knapp & Seastedt 1986, Köchy & Wilson 1997). Thus, N deposition was not reflected in soil N availability within Elk Island, probably

because the spatial variation of N deposition within Elk Island was large.

#### 2.5.4. $\delta^{15}\text{N}$ and N in vegetation and soil at Elk Island and Jasper

Vegetation in Elk Island had generally lower  $\delta^{15}\text{N}$  values than vegetation in Jasper. The difference was strongest for stems, leaves, and litter in forests (Fig. 2.5), presumably because they were more exposed to deposition and had a larger receptor surface than shrubland or grassland vegetation (Boyce et al. 1996). Lower  $\delta^{15}\text{N}$  values in Jasper shrubland soil and roots than those in Elk Island are presumably due to the presence of N-fixing shrubs. It is unclear, however, why the difference was not observed in stems, leaves, and litter in shrubland.

The difference of  $\delta^{15}\text{N}$  values of stems, leaves, and litter between Elk Island and Jasper ranges between 2% and 4% in forest. I suggest that this difference could be due to increased anthropogenic deposition in Elk Island (Macko & Ostrom 1994) originating mostly from  $^{15}\text{N}$ -depleted motor vehicle exhausts (Heaton 1990) that emitted 43% of all  $\text{NO}_x$  in Alberta in 1990 (Environment Canada 1996). The difference between the two parks is in the same range as that measured along a gradient of  $\text{NO}_x$  pollution from motorways in Switzerland (Ammann et al. 1999). The conclusion that car exhausts have caused the decrease of  $\delta^{15}\text{N}$  values in western Canada is based on the assumption that the  $^{15}\text{N}$  signal is more or less undiluted by atmospheric processes. More research about

how the  $^{15}\text{N}$  signal changes from source to plant tissue is required to make more confident statements.

In forest and shrubland,  $\delta^{15}\text{N}$  values of stems, leaves and litter were lower in Elk Island than in Jasper (Fig. 2.5). Stems in forest showed the largest difference between the parks. (Observe that  $\delta^{15}\text{N}$  values of roots in forest are similar in both parks, suggesting that differences were mostly due to aboveground uptake, cf. Boyce et al. 1996). Wood accumulated  $^{15}\text{N}$ -depleted N over time and therefore may present a clearer signal than other tissues (see Gebauer & Dietrich 1993). Stems in Elk Island shrubland also show the accumulation of  $^{15}\text{N}$ -depleted N as the  $\delta^{15}\text{N}$  values of stems is much lower than that of roots. The difference between shrubland stems in Elk Island and Jasper, however, is obscured because low  $\delta^{15}\text{N}$  values of Jasper shrubland soil (Fig. 2.5), caused by N-fixing shrubs, presumably decreased  $\delta^{15}\text{N}$  values in the whole plant (Nõmmik et al. 1994).

In grassland,  $\delta^{15}\text{N}$  values of leaves and litter were as high in Elk Island as in Jasper (Fig. 2.5).  $\delta^{15}\text{N}$  values in Elk Island grassland may not have been increased by deposition because of the high stemflow in grassland (van Dam 1990). Deposition to grassland may also have been reduced by filtration by surrounding forests (Bobbink et al. 1990).

$\delta^{15}\text{N}$  values of soil were always higher than those of tissues (Fig. 2.5). This reflects isotopic fractionation processes during decomposition, nitrification, denitrification, ammonia volatilization, and leaching of depleted nitrate (Handley & Raven 1992). The increase of  $\delta^{15}\text{N}$  values with soil depth (Fig. 2.5) has been attributed to repeated

microbial nitrification and mineralization during the downward movement of organic and inorganic N compounds and the input of  $^{15}\text{N}$ -depleted litter to the soil surface (Nadelhoffer & Fry 1994). Higher  $\delta^{15}\text{N}$  values in soil in Elk Island grassland and shrubland might indicate higher rates of decomposition, mineralization and N loss, possibly due to the higher availability of N (Hunt et al. 1988).

A small amount of deposited N is assimilated by leaves (van Vuuren & van der Eerden 1992, Brumme et al. 1992, Lumme 1994), but in my study, N deposition at Elk Island may have been too small to increase N concentrations in leaves and litter significantly (Fig. 2.6). The higher N concentration of shrubland stems in Jasper occurred because the shrubs were associated with N-fixing bacteria.

#### 2.5.5. Forest expansion

Forests in high-deposition parks expanded ten times faster (Fig. 2.9) and, by increasing in area, accumulated more nitrogen (Table 2.8) than forests in low-deposition parks. Woody species that invade grassland reduce available soil N more strongly than grasses (chapter 5) and may benefit most from N fertilization by deposition. The fertilization may lead to accelerated N cycling (Högberg & Högberg 1991, Berendse 1994b), increase water-use efficiency of the woody invaders (Bert et al. 1997), decrease competition for N, and increase competition for light (Haugland 1993, Reynolds & Pacala 1993). This may favour fast growing,

weedy species and tall, woody species (Tilman 1988, Vitousek et al. 1989, Wilson & Tilman 1995). Fast-growing 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, and because the highest deposition locally was found in grassland vegetation (Fig. 2.4). Fast-growing species also often produce N-rich litter that decomposes quickly (Vitousek & Walker 1989, Berendse 1994b, Eckstein & Karlsson 1997). In my study, N deposition did not increase N concentrations in litter (Fig. 2.6), perhaps because the dominant tree, *Populus tremuloides*, relocates most N before leaf abscission (Taylor et al. 1989). Trees are further favoured by deposition because their tall growth form allows them to scour air for nutrients more effectively than grasses (Kellman & Carty 1986, Binkley 1995) and thus increase deposition rates which results in a self-maintaining positive feedback (Vetaas 1992, Wilson 1998, chapter 6). Higher water-use efficiency of trees induced by increased deposition (Bert et al. 1997) may enable them to invade temperate grasslands restricted to dry, coarsely textured soils. However, the high initial proportion of forest in Wood Buffalo Park (Fig. 2.9) may indicate that substantial woody biomass can exist in areas with low deposition and that forest expansion is not controlled by N deposition. This argument, however, is much weakened by the fact that in four parks with similar initial proportion of forest, expansion rates were strongly correlated with the deposition rate (Fig. 2.9).

The forest expansion curves of Elk Island, Prince Albert, and Riding Mountain, have a similar shape. Apart from having a general in-

creasing trend, there is slower or reversed expansion around 1970. This dip is also apparent in the other parks and coincides with lower annual temperatures in the same time frame. Lower temperatures may have slowed forest expansion. In contrast, an even stronger dip in annual temperature around 1950 did not appear to have reduced expansion. Forest expansion in Riding Mountain was slow between 1931 and 1959. This could be related to the time needed for the gradient of high atmospheric  $\text{NO}_x$  concentrations to extend from the Edmonton-Calgary area to the park. It is unlikely that different fire histories in the parks would be correlated with forest invasion, because it was standard park policy to protect the forest and to suppress or extinguish wild fires. Elk Island is using prescribed burns, but also has the highest forest expansion rate.

Wood Buffalo with an initial woody cover in 1955 of 77% stands out among the parks. One could argue that its rate of forest expansion was low because its forest was not capable of much additional expansion. However, the description of the general area in c. 1920 (Graham 1923) and the site in 1930 (Raup 1935) that was covered by air photographs suggests that dry grassland used to be more abundant before 1955. More recent observations also indicate that expansion is still continuing (Schwarz & Wein 1997). Forest has decreased grassland area in the park from  $\approx 85$  ha in 1928 to 3 ha in 1982 (Schwarz & Wein 1997). Thus, forest expansion in Wood Buffalo was not constrained.

In Grasslands National Park, forests did not expand despite high N deposition (Fig. 2.8). This park lies outside the forest biome, with its forests consisting of *Populus tremuloides* restricted to a few river

valleys. *Populus tremuloides* has no particular adaptation to tolerate water deficits, therefore, forest expansion in Grasslands may be more limited by moisture than by nitrogen.

Across ~~all~~ parks, forest expansion was not related to annual precipitation. It was, however, related to precipitation in the three parks with annual precipitation <420 mm (Fig. 2.10). Above this threshold, forest expansion seemed to be more related to N deposition rates (Fig. 2.10). The inclusion of more sites with a wider range of N deposition and annual precipitation could clarify whether there is an interaction between annual precipitation and deposition.

My study suggests that anthropogenic N deposition could be a factor contributing to forest expansion in more densely populated areas (Fig. 2.9) whose role has been overlooked so far. Forest expansion has been attributed to an decrease in mean annual temperature (Buell & Cantlow 1951, Vetsch 1987) and changes in weather patterns (Bailey & Wroe 1974), but I found no significant correlation with long-term temperature increase or with annual precipitation. Expansion of woody species and forest clumps in arid grasslands used to be checked by recurrent wild fires and browsing by bison on the trees and shrubs (Bird 1961, Archer 1996, Bork et al. 1997). Aspen, however, the main tree invader in cool-temperate arid grasslands, increases with fire frequency up to a certain point (Cole & Taylor 1995) because of its rapid regeneration from roots, but decreases under an annual fire regime (Svedarsky et al. 1986). Aspen is eliminated only by intense fires followed by intense browsing (Bork et al. 1997). The elimination of wild fires and bi-



son may be a precondition for forest expansion in grassland. My study suggests that N deposition is accelerating forest expansion. Future studies should aim at determining the relative contributions of fire, herbivory, and fertilization by N deposition.

The average expansion rate of forest in high-deposition parks was 1 %p/yr [percentage-points forest area per yr] (Fig. 2.9). This is in line with earlier estimates and measurements of expansion rates of between 0.5 %p/yr and 5 %p/yr, with higher rates closer to more densely populated areas (Maini 1960, Bailey & Wroe 1974, Vetsch 1987, Berger & Baydack 1992) where rates of N deposition are higher. Forest expansion may not have increased linearly with deposition but leveled out at about 15 kg N ha<sup>-1</sup> yr<sup>-1</sup> for various reasons. (1) The forest at Elk Island may have reached a point of N saturation where N losses equal N inputs (Aber 1992). (2) The rate of nitrogen cycling in the system may be at its maximum under current climatic conditions. (3) There may be a time lag between increases of N deposition and forest expansion (Aber et al. 1997), or (4) intensive browsing by ungulates may have slowed forest growth (Campbell et al. 1994). Forest expansion was probably not greatly limited by availability of germination sites because the dominant tree, *Populus tremuloides*, spreads easily by suckers.

The addition of N to ecosystems through deposition should result in an increase of N in biomass (Rode 1993). I found that the additional N has been stored mostly in the increased area of forest (Table 2.8) with a concomitant decrease in grassland area, supporting my hypothesis that N deposition may have caused a shift in vegetation types. The

additional N generally did not increase the N concentration within individual vegetation types (Fig. 2.6) or produce more biomass of the same vegetation type per area (Fig. 2.7).

#### 2.5.6. Conclusions

N deposition in the agro-industrial region was >2 times higher than in the forested region. The N that was added to the ecosystems apparently resulted in higher soil N availability, which appears to have contributed to the expansion of forest into grassland and higher N mass in the region.