Variation in nitrogen deposition and available soil nitrogen in a forest–grassland ecotone in Canada

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Abstract

Regional variation in nitrogen (N) deposition increases plant productivity and decreases species diversity, but landscape- or local-scale influences on N deposition are less well-known. Using ion-exchange resin, we measured variation of N deposition and soil N availability within Elk Island National Park in the ecotone between grassland and boreal forest in western Canada. The park receives regionally high amounts of atmospheric N deposition (22 kg ha^{-1} yr^{-1}). N deposition was on average higher ton clay-rich luvisols than on brunisols, and areas burned 1 – 15 years previously received more atmospheric N than unburned sites. We suggest that the effects of previous fires and soil type on deposition rate act through differences in canopy structure. The magnitude of these effects varied with the presence of ungulate grazers (bison, moose, elk) and vegetation type (forest, shrubland, grassland). Available soil N (ammonium and nitrate) was higher in burned than unburned sites in the absence of grazing, suggesting an effect of deposition. On grazed sites, differences between fire treatments were small, presumably because the removal of biomass by grazers reduced the effect of fire. Aspen invades native grassland in this region, and our results suggest that fire without grazing might reinforce the expansion of forest into grassland facilitated by N deposition.

Keywords

Introduction

High rates of nitrogen deposition (> 15 g N m^{-2} yr^{-1}) have been linked to the eutrophication and acidification of forest soil (Jefferies & Maron 1997; Fenn et al. 1998; Bobbink et al. 1998). While the composition of the tree layer in

5 forests is rarely changed by deposition, understorey vegetation may change dramatically due to eutrophication or acidification and different competitive regimes (Falkengren-Grerup 1989; van Dobben et al. 1999). Similar changes in grasslands and heaths have also been reported (Bobbink et al. 1998). Deposition to the soil in forests is typically measured as throughfall

10 precipitation 1.5 m above the soil. Little is known about the variability of deposition to the soil with complex vegetation structure where soils, grazers, and fire produce a mixture of grassland, shrubland, and forest with varying vegetation height and canopy density.

The physical structure of the vegetation affects rates of local deposition.

15 Taller vegetation and canopy edges increase the rate of deposition to the ecosystem (Beier & Gundersen 1989; Weathers et al. 2001) by filtering the air and reducing wind speed. Vegetation structure can be altered by fire, grazing, storm damage, pests, and other disturbances. For example, infrequent fire increases the number of stems of woody plants (Romo et al.

20 1993; Peterson & Reich 2001; Vilà et al. 2001) and grasses (Hulbert 1969). Low to moderate densities of ungulates tend to increase the variation in height in browsed stands compared to unbrowsed stands (Danell et al. 2003). Intense grazing reduces the height of herbaceous vegetation (Díaz et al. 1992). It is not known, however, how much and for how long strucutural

25 changes affect deposition rates.

Local rates of deposition and cycling of N between canopy and soil may also be increased by the volatilization of ammonia from faeces (Risser &

Parton 1982; Nason et al. 1988) and release of N from the soil from nitrification and denitrification (Lemke et al. 1998). Volatilization from livestock waste is the largest source for regional ammonium deposition in the U.S.A. and Europe (Tanner 1990). Thus, grazers can increase N losses

5   from grasslands due to volatilization (Risser & Parton 1982). N loss by volatilization from faeces corresponds to at least one third of N inputs in mixed-grass prairie (Woodmansee 1979; Frank & Groffman 1998).

Soils are also a source of gaseous N forms that may contribute to deposition. Soils with a high N content often have high nitrification and

10   denitrification rates (Aber 1992). A small portion of soil nitrate is converted by denitrification to gaseous N_2O (nitrous oxide), NO (nitric oxide), and N_2 and released to the atmosphere. N_2O emissions contribute about 1 percent to subcanopy N deposition in N-limited temperate forests (Oura et al. 2001). NO emissions are thought to be of similar magnitude as N_2O (Matson 1997).

15   In the boreal region, N_2O production increases with the clay (poorer drainage) and water content of the soil (Lemke et al. 1998; Corre et al. 1999) and increases in the order forest, pasture/meadow, fertilized arable land (Corre et al. 1999; Groffman et al. 2000).

Higher rates of N deposition are linked to higher soil N availability

20   (Kazada & Katzensteiner 1993; Köchy & Wilson 2001). The stength of this link varies with soil type and soil N content due to their influence on mineralization and denitrification (Lovett & Rueth 1999; Lemke et al. 1998). The effect of deposition on soil N further differs among tree species (Lovett & Rueth 1999). Fire often initially increases mineral soil-N because consumers

25   of soil N are damaged by the fire and because organic N in litter or biomass is mineralized (Wan et al. 2001). In grassland, tiller density of burnt over grasses is higher (Hulbert 1969) which entails higher stemflow volume and higher N input to the soil (Seastedt 1985). Biomass and soil N, however, are

usually reduced by fire because more N is lost through combustion of organic matter than is returned by deposition and fixation (Wan et al. 2001).

Semi-arid grasslands are being invaded by shrubs and trees in many parts of the world (Facelli & Léon 1986; Fensham & Kirkpatrick 1992; Van

5   Auken 2000). The start of expansion of forest in prairie in North America coincided in time with the extirpation of bison and elimination of wild fires after the settlement of Europeans. Grazing and fire limit stand growth only after certain levels of intensity and frequency. In addition, moisture and nutrient limitations and competition between woody and herbaceous plants

10 may contribute to forest expansion (Kellman & Miyanishi 1982; Brown et al. 1998; Davis et al. 1998; Köchy & Wilson 2000). In the ecotone between boreal forest and semi-arid grassland, climate and competition are presumably more important as controls of tree invasion than are fire and grazing (Archer 1994). Deposition of atmospheric N may be expected to

15 increase the competitive ability of woody species and accelerate forest invasion at the northern edge of the prairie (Köchy & Wilson 2001).

The deposition of N to natural ecosystems often changes understorey composition and favours growth of trees and shrubs. The variability of N deposition with vegetation type or other factors that affect vegetation

20 structure is largely unknown. We tested whether N deposition varies locally with factors that affect deposition rates or soil N availability, namely soil type, fire regime, bovine grazing, and vegetation type.

Methods

Study sites

25 Elk Island National Park (53°31'-47'N,112°46'-58'W, 42 km NE of Edmonton, Alberta, western Canada) lies in aspen parkland, at an ecotone between mixed-grass prairie in the South and boreal forest in the North. The park has occupied 196 km^2 since 1947. It was established in 1906 on forest reserve

land when it was dominated by "scrubby prairie". Today, the park is covered by aspen forest (*Populus tremuloides*) with little remnant grassland (Fig. 1). Grassland is dominated by *Poa pratensis* L. and *Calamagrostis canadensis* (Michx.) Beauv. Fire guards established in 1910 protected Elk Island from

5   larger fires. Since 1979, vegetation in parts of Elk Island has been managed by selected prescribed burns. Brunisols and luvisols are two common soil types in Elk Island (Crown 1977). Brunisols are more sandy and better drained than luvisols. In luvisols, the eluviation of clay from upper layers forms a less permeable layer with higher clay content below. Most of the

10   park is grazed by high densities of bison (*Bison bison* L.), moose (*Alces alces* L.), elk (*Cervus elaphus* L.), and deer (*Odocoileus* spp.) (Cairns & Telfer 1980). July mean temperature in Edmonton is 16.9 °C, January mean temperature is -13.8 °C, and mean annual precipitation is 445 mm.
Fig. 1 approximately here

15

Atmospheric deposition and available soil nitrogen

   Resin bags.—   We measured N deposition and available soil N with ion-exchange resin bags (Köchy & Wilson 2001). Resin bags, in a manner

20   similar to leaves but different from meteorological instruments, capture mineral N (NO_3^-, NO_2^-, NH_4^+) through adsorption and absorption (Lindberg et al. 1986). Dust deposited on the resin bags is presumably washed into the resin with percolating rain. Similarly, gaseous inorganic N compounds (NO_2, NH_3) might react with the water contained in moist resin and form ions that

25   can attach to the resin. Resin bags presumably also collect N deposited as coarse particles that contribute considerably to dry deposition (Shachak & Lovett 1998). We do not expect that resin bags designed to collect N deposition that are placed on the ground take up N from the soil because there is no capillary connection; bags were placed in stainless steel cages

(see below). 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.

5   1994).

The variability of resin bag measurements is on average 57% (coefficient of variation) for deposition and 67% for soil N availability. This was estimated from nine to ten bags in each of eight consecutive seasons. The bags were distributed in similar soil and open grassland vegetation along a transect of

10   6 km in Grasslands National Park, 600 km SE of Elk Island National Park (Köchy & Wilson 2001).

Each resin bag ($\approx$9 cm^2) contained 2 cm^3 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^3 for anions and

15   cations. Thus, the total ion-exchange capacity of each bag was 3 mmol (3300 mmol m^{-2}). 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 (Köchy & Wilson 2001). We did not treat resin against microbial colonization because the effect of

20   microbes on N capture is much smaller than the amount of N in soil solution or deposition (Giblin et al. 1994). Before use, bags were washed in 2 mol/L NaCl and rinsed in double-distilled water to remove dyes and background N from the resin.

25   *Field sampling.*—We installed resin bags for measuring N deposition at ground level. We placed these surface bags in canopy gaps $\geq$4 m from the edge of forest canopy and $\geq$1 m from shrubs (horizontal distance) to reduce the effect of canopy leaching on N deposition measurements (Lindberg et al. 1986; Potter et al. 1991). The bags were protected from animal disturbance

by flat stainless steel cages (10 cm × 10 cm × 0.5 cm, 2-mm-mesh) fixed to the ground with stainless steel pins. We measured available soil N with resin bags buried about 10 cm deep in intact vegetation. Bags for measuring N deposition and soil available N were deployed in pairs separated by < 20 m.

5   We deployed 132 pairs of bags throughout the park to examine the effects of soil type, grazing, burning and vegetation type. We 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

10   vegetation types (forest, shrubland, and grassland). Burned, ungrazed vegetation types on brunisol did not occur in Elk Island, so that a total of 21 treatment combinations was examined. We deployed four pairs of bags for each treatment combination. Usually, the four pairs were installed within <100 m of each other at one site, but resin bags for the grazed, unburned

15   brunisol treatment and the ungrazed, unburned forest on brunisols were installed in two sets of two pairs at separate sites. Sites were spread across the park according to availability of suitable locations (Fig. 1). Deposition and soil N were sampled during four seasons for two years (June 1994 – 1996). Resin bags retrieved from the field were extracted with 2 M acidified

20   NaCl and the total N content of the extracted solution converted to ammonia and measured with an ion-selective electrode (Köchy & Wilson 2001). We determined the extraction rate from resin bags with known amounts of ammonium and nitrate ($N_{extracted} = 0.69 \cdot \ln (N + 1)$, $R^2 = 0.85$, $n = 204$, for 0.05 – 5 mmol N/L) to calculate the amount of N collected by resin in the

25   field.

Data analysis.– One hundred and three above-surface and 26 below-surface bags contained N equivalent to >100 kg ha^{-1} yr^{-1}. This high rate is typical of deposition in industrialized regions or close to industrial animal

husbandry barns. We assume that these samples may have been contaminated by urine or faeces and excluded these data from analyses. Fifty-two above-surface and forty-nine below-surface bags were destroyed by animals or lost. Although this left 517 above-surface and 597 below-

5   surface bags, there were no above-surface data for one season of five treatments (brunisol: burned, grazed grassland; luvisol: burned grazed grassland and forest, unburned grazed grassland [both years], and unburned, ungrazed shrubland and forest) and no below-surface data for one season of two treatments (brunisol: unburned, grazed grassland; luvisol:

10   burned, grazed grassland). For each remaining treatment we calculated the average amount of N (expressed as g/m^2 for deposition and μg/cm^3 for soil N) retained by the resin in each season. We summed the seasonal averages to calculate annual rates of N deposition and N availability. N availability in the ungrazed burned forest site on luvisol was 0.97 μg cm^{-3} yr^{-1} in the first

15   year, whereas values for all other sites were < 0.63. This outlier was excluded because it was due to a recent fire after which vegetation and therefore N uptake had not yet fully reestablished. We compared annual rates among treatments with ANOVA. Mean squares were calculated with JMP 3.2.1 (SAS Institute 1997) and *F* and *P* values with Excel 4.0 (Microsoft

20   1992). Before analysis, we log-transformed the data because Brown-Forsythe tests indicated that the treatment variances were not homogeneous. Sampling year was considered a random effect and crossed factorially with all treatment effects. Since the experimental design was not completely factorial and data were not complete, we used partially factorial

25   ANOVAs. We removed from the full-factorial ANOVAs all 4-way interactions and the soil type × fire regime × grazing interaction to increase the degrees of freedom. For deposition we also removed all other 3-way interactions. In a second step, we pooled all interactions that were not significant at *P*= 0.2 with the residual error term (Underwood 1997). Treatment means were

compared post-hoc with the Student-Newman-Keuls-test (Underwood 1997).

Results

Deposition

5   Averaged across all other treatments, vegetation on luvisols received more deposition (2.4 ± 1.0 g·m^2, mean $\pm$ SD, $n = 17$) than vegetation on brunisols (2.0 ± 0.6 g·m^2, $n = 16$; see Table 1 for ANOVA statistics). The magnitude of this effect varied with grazing, fire regime, and vegetation type. The difference between soil types was significant in ungrazed but not in grazed

10   vegetation (Fig. 2A, Table 1, soil × grazing). Ungrazed sites on luvisol comprised no burned sites. When the analysis was restricted to unburned sites, there were no significant differences among treatments. For fire regimes, comparison of means revealed no significant differences between soil types (Fig. 2C, Table 1, soil × fire). Burned brunisol sites did not include

15   ungrazed sites. When we restricted the analysis to grazed sites, deposition in burned sites on luvisols were slightly but not significantly lower than on brunisols. Differences in deposition between soil types did not differ with vegetation types despite a significant soil × vegetation interaction (Fig. 2D, Table 1, soil × vegetation). The interaction arose because N deposition was

20   very similar among vegetation types on luvisol, but increased with vegetation stature on brunisol.

\# Fig. 2 approximately here \#

N deposition in burned sites was generally higher than in unburned sites, but there was no significant main effect of fire. Fire regime interacted with

25   grazing, soil type (explained above), and vegetation type. In grazed vegetation, burned sites received more deposition than unburned sites, whereas the difference was not significant in ungrazed vegetation (Fig. 2B, Table 1, fire × grazing). Burned ungrazed vegetation did not include

brunisols. When we restricted the analysis to luvisols, the differences between fire treatments were both significant. Burned shrubland had higher deposition rates than unburned shrubland, but in forest and grassland, rates did not differ between fire regimes (Fig. 2E, Table 1, fire × vegetation).

5   Deposition to vegetation averaged across all treatments was significantly higher in the first year (2.4 ± 0.6 g·m^2, mean ± SD, n = 16) than in the second year (2.0 ± 1.0 g·m^2, n = 19; Table 1). In addition, a significant year × grazing interaction (Table 1) indicated that ungrazed vegetation received more deposition than grazed vegetation in the first year, but in the second year the

10   relation was reversed.

Soil nitrogen

    Soil N was on average higher in burned (0.28 ± 0.11 μg cm^{-3} yr^{-1}, mean ± SD, n = 16) than unburned sites (0.26 ± 0.14, n = 23; see Table 1 for ANOVA

15   statistics), but also varied significantly in interaction with grazing (Fig. 3A, Table 1) and in interaction with soil type (Fig. 3B, Table 1). When vegetation had not been grazed, soil on burned sites had more N than on unburned sites (Fig. 3A). In contrast, when vegetation had been grazed, burned sites tended to have more available N, but not significantly so. Since burned,

20   ungrazed sites were restricted to luvisols, the interaction may have been due to the unbalanced design. When the analysis was restricted to luvisols, the interaction and trends remained. Burned sites on brunisol had more available N than unburned sites (Fig. 3B), whereas on luvisols, N availability did not differ between fire regimes. Burned sites on brunisol included only

25   grazed sites. When we restricted the analysis to grazed sites, fire regime had no effect on N availability in brunisols. Therefore, we assume that the soil type × fire regime interaction was an artifact caused by the unbalanced design.

Fig. 3 approximately here

Soil N varied with vegetation type as a main effect (Fig. 3D, Table 1) with N availability decreasing in the order grassland, forest, shrubland. A three-way interaction among fire regime, grazing treatment, and vegetation type

5 (Fig. 3C, Table 1) indicated that the magnitude of differences between fire and grazing treatments varied with vegetation type. When we restricted the analysis to luvisols, the pattern for ungrazed sites remained the same but the three-way interaction was not significant. Finally, an interaction between soil type and vegetation type (Fig. 3E, Table 1) indicated that the ranking of N

10 availability among vegetation types was not consistent between soil types. On luvisols, N availability was highest in grassland and similar in forest and shrubs, whereas on brunisols all vegetation types had similar N availability.

Discussion

Deposition

15 N deposition in Elk Island National Park averaged 2.1 g N m^{-2} yr^{-1} on ungrazed, unburned sites. The high rate of deposition in Elk Island, near Edmonton, is presumably due to high emissions from vehicles, industry, and power generation. The background rate of deposition, measured in parks upwind and remote from large cities, is one third of that in Elk Island National

20 Park (Köchy & Wilson 2001).

Direct effect of soil type.— N deposition was generally higher on luvisols (more clayey, moister) than on brunisols (less clayey, drier) (Fig. 2A,C,D). We cannot reject the possibility that the difference is due to the lack of one set of treatment combinations. The consistent trend in three interactions

25 suggests, however, that the difference in deposition between soil types is not an artifact. Both nitrification and denitrification can release NO (nitric oxide) and N_2O (nitrous oxide) from the soil. NO is transformed aboveground to

NO_2 (nitrogen dioxide) of which 50% is estimated to be taken up by the canopy (Matson 1997). N_2O may also be taken up by leaves (Grundmann et al. 1993). The rates of N_2O and NO emissions are usually similar in an ecosystem (IFIA & FAO 2001). Since NO is difficult to measure, N_2O is used

5   as an indicator. NO_x released from the soil may be intercepted by the foliage, assimilated, and increase the organic N content of throughfall (Piirainen et al. 1998). N_2O emissions increase with soil moisture (Corre et al. 1999; Mohn et al. 2000) and clay content (Lemke et al. 1998). They are ten times higher from clayey soil than from sandy soil in aspen forest in Saskatchewan

10   (Corre et al. 1999) where vegetation and climate are similar to those in Elk Island. The difference in emissions of 0.003 g N_2O-N m^{-2} yr^{-1}, however, cannot explain the difference observed in Elk Island (0.8 g m^{-2} yr^{-1}, Fig. 2D). Emissions from luvisol and brunisol in Elk Island could be higher because of higher deposition rates in Elk Island (2.1 g m^{-2} yr^{-1}) than in southern

15   Saskatchewan (1.5 g m^{-2} yr^{-1}, Köchy & Wilson 2001). Emissions on the order of 0.7 g m^{-2} yr^{-1}, however, have only been observed in a eutrophied forest receiving 3 g N m^{-2} yr^{-1} (Rennenberg et al. 1998). Therefore, we conclude that variation in gaseous N emissions from the soil is not a major contributor to difference in deposition rates between soil types.

20

   Interaction effects with soil type.— The interactions of soil type with grazing, fire, and vegetation type (Fig. 2A,C,D) suggest that aboveground properties of the vegetation affected deposition rates. Deposition rate is increased by canopy surface roughness, canopy edges (relative height), and

25   leaf surface (Beier & Gundersen 1989; Weathers et al. 2001). Thus, deposition at ground level tended to increase as vegetation height decreased on brunisols (Fig. 2D). On luvisols, deposition in forests and shrubland was similar to that in grassland, suggesting that tree and shrub canopies were more open and less effective in retaining deposited N.

Woody canopies may be thinned by browsers. Ungulates decrease shrub height and reduce tree density in Elk Island by $2/3$ (Bork et al. 1997), especially on drier sites, where bison prefer to graze and which have brunisols. Reduced woody density would increase deposition at ground

5 level on brunisols (Fig. 2A). Deposition rates on luvisols would not increase much in the presence of ungulates if we retain our assumption that canopies on luvisols are more open in general. Deposition to burned sites tended to be higher on both brunisols and luvisols (Fig. 2C), suggesting that fire reduces canopies similarly on both soil types, presumably because the effect

10 of fire varies with topographic position independent of soil moisture at Elk Island (Bork et al. 1997). Fire also increases stem density of woody (Peterson & Reich 2001; Vilà et al. 2001) which could increase deposition by increasing wind resistance (Marton 1956) or increasing interception because of increased stem surface (Harrison et al. 2000). Stem density,

15 however, decreases again over time since fire (Bailey et al. 1990; Harrell et al. 2001) and did not differ between burned and unburned grazed sites in Elk Island (Bork et al. 1997).

Effect of fire and grazing.— Fire and grazing together significantly

20 increased deposition rates (Fig. 2B). This is likely due to reduced tree density and shrub height (Bork et al. 1997). Although fire in grazed areas also increases shrub density (Bork et al. 1997), this may not have affected deposition rates because shrub leaf mass is reduced by burning (Bork et al. 1997). The effect of previous burning (averaged across grazing regimes)

25 was strongest in shrubland and significantly increased deposition rates (Fig. 2E). We assume that the simultaneous decrease of tree density, shrub height and leaf mass significantly opened up the canopy which is also indicated by higher grass mass after fire (Bork et al. 1997). The canopy openness presumably reduced deposition interception and increased deposition at

ground level. Clearly, the invoked mechanisms to explain the observed pattern of deposition remain to be tested.

Soil nitrogen

5   *Direct and interaction effects of fire.—* N availability in soil was on average higher in sites that had burned between one and 15 years previously (Fig. 3A–C). Burning increases N availability for three to five years (Wan et al. 2001) because N in ash is mineralized faster than litter N, because reduced vegetation cover takes up less N, and because insolation of bare soil

10   accelerates mineralization. In unburned vegetation, N availability of grazed sites was higher than in ungrazed sites (Fig. 3A) because ungulates increase mineralization by transforming organic N into inorganic N contained in their faeces. Fire also increased N availability compared to that in ungrazed, unburned vegetation (Fig. 3A), presumably because grazing

15   reduces the litter layer similar to fire (Knapp & Seastedt 1986), but fire did not further increase N availability in grazed sites. N availability in burned and grazed sites even tended to be lower than either grazed or burned sites (Fig. 3A), especially in forests (Fig. 3C), possibly reflecting higher N uptake by vegetation for producing new suckers, stems, and branches to compensate

20   for lost biomass (Petersen & Petersen 1992). In ungrazed sites, the positive effect of fire increased with herbaceous cover (Fig. 3C). We assume that N mineralization in all vegetation types was limited by litter and that limitation was strongest in grassland (Knapp & Seastedt 1986). Therefore, grassland benefited most from litter removal. In shrubland, available N may have been

25   higher in burned than unburned sites (Fig. 3C) not only due to fire effects on litter but also because of higher deposition(Fig. 2E). In forest, fire may have had a smaller effect because *Populus* might reduce fire severity because of its high moisture content (Campbell & Campbell 2000).

Effects of vegetation.— Available soil N was higher in forests than in shrubland (Fig. 3D). This was presumably due to higher N input with litter in forests. Total N in forest litter is 10 g/m^2 but only 4 g/m^2 in shrubland (Köchy & Wilson 2001). Decomposition rates are probably similar in both habitats

5   since litter quality estimated by N concentration in forest (0.9%) and shrub litter (1.1%) is similar (Köchy 1999). In brunisols, N availability in grassland was intermediate between forest and shrubland, but in luvisols, N availability was highest in grassland (Fig. 3E). Total N in grass litter is low (0.1 g/m^2), but decomposition could be faster because of slightly higher quality (1.2% N)

10   and photodegradation in open areas (Zlotin & Khodashova 1980; Köchy & Wilson 1997). In luvisols, N availability may have been higher in grassland (Fig. 3E) because these soils are typical of moister conditions that enhance N availability and movement of nitrate in the soil.

15   We found significant differences in deposition rates and soil N availability among treatments despite unintentionally small sample sizes in some treatments and an unbalanced design. Studies including all treatment combinations and using more replicates might detect more interesting differences. Additional studies could also establish whether the detected

20   pattern is more general and might apply to other regions.

Conclusions

Previous burning increased deposition to vegetation (Fig. 2B, c, E) and presumably increased available soil N in ungrazed vegetation (Fig. 3A). In

25   contrast, in grazed vegetation the contribution of deposition to soil N availability was low because the presence of ungulates affects both deposition rates (through vegetation structure) and N cycling.

Köchy & Wilson (2001) showed that the rate of expansion of forest (mostly clonal aspen) into prairie is correlated with the rate of N deposition. They

suggested that aspen allocate the extra N to produce new stems and increase in area. Prescribed fires have been proposed as a check of forest invasion (Bailey et al. 1990). Our results, however, suggest that this measure may be counterproductive when fire frequency is low and the area is

5   ungrazed. After burning, N availability in grassland is high, giving woody species a competitive advantage for establishment (Köchy & Wilson 2000). This would be reinforced by higher deposition rates to low woody plants (*i.e.* young trees or shrubs). Simultaneous grazing by ungulates would balance the interaction of fire and deposition and keep the forest open (Bork et al.

10   1997).

These interactions and feedbacks, especially those between fire and grazing, should also be kept in mind in the management of other parks or forests in the region. Prince Albert National Park (500 km E of Edmonton, deposition rate 1.4 g N m^{-2} yr^{-1}) and Riding Mountain National Park (1000

15   km E of Edmonton, 1.2 g N m^{-2} yr^{-1}) also experience higher than natural rates of deposition (Köchy & Wilson 2001) but are not grazed by bison. There, we would expect that fires are not sufficient to maintain grasslands. We encourage studies exploring the quantitative relationships and mechanisms producing the observed patterns. This would allow to make

20   more specific recommendations for forest and landscape management.

Tables

Table 1. Details of ANOVA for significant effects. Top: treatment effects on deposition rate, bottom: effects on available soil N.

Effect on deposition	F	$df_{nominator}$	P
soil type	18.9	1	0.0003
soil type × grazing	23.0	1	0.001
soil type × fire regime	11.4	1	0.003
soil type × vegetation type	5.43	2	0.01
fire regime × grazing	22.9	1	0.0001
fire regime × vegetation type	4.77	2	0.02
year	15.0	1	0.001
year × grazing	4.79	1	0.04
$df_{denominator}$		20	

5

Effect on soil N availability	F	$df_{nominator}$	P
fire regime	5.06	1	0.04
fire regime × grazing	15.8	1	0.001
fire regime × soil type	4.50	1	0.05
vegetation type	4.71	2	0.02
fire × grazing × vegetation type	3.69	2	0.048
soil × vegetation type	5.38	2	0.02
$df_{denominator}$		16	

Figure captions

Fig. 1. Map of Elk Island National Park showing the distribution of land cover, major soil types, fires 1979–1995, and approximate locations of grazed and ungrazed sampling sites.

5   Fig. 2. Atmospheric nitrogen deposition rates in aspen parkland (means ± SD and sample size). Means with different letters are significantly different (SNK-test). Fig. 2c is a rearrangement of Fig. 2C to facilitate comparisons. Exclamation marks indicate means that comprise only grazed, unburned luvisols and may be biased.

10   Fig. 3. Available soil N in aspen parkland (means ± SD and sample size). Means with different letters are significantly different (SNK-test on ln-transformed data). Exclamation marks indicate means that comprise only grazed, unburned luvisols and may be biased.
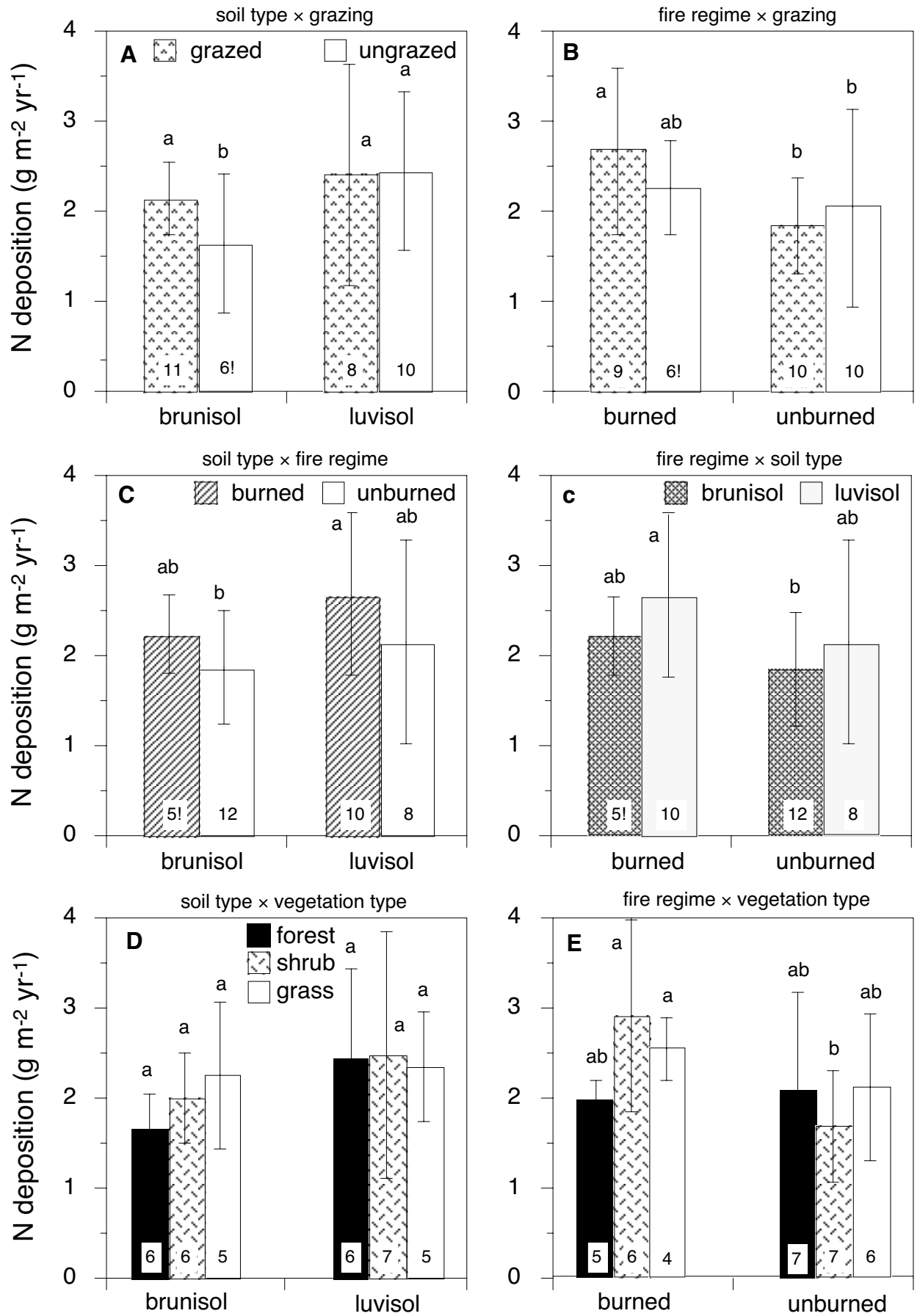
Elk Island National Park

Vegetation
- grassland
- shrubland
- forest

Soil type
- // luvisols
- \\ brunisols

Fire history
- ≡ 1993-1995
- ||| 1989-1992
- | | 1984-1988
- ─ 1979-1983

Grazing/ Sites
- ⬢ ungrazed
- ⬡ grazed
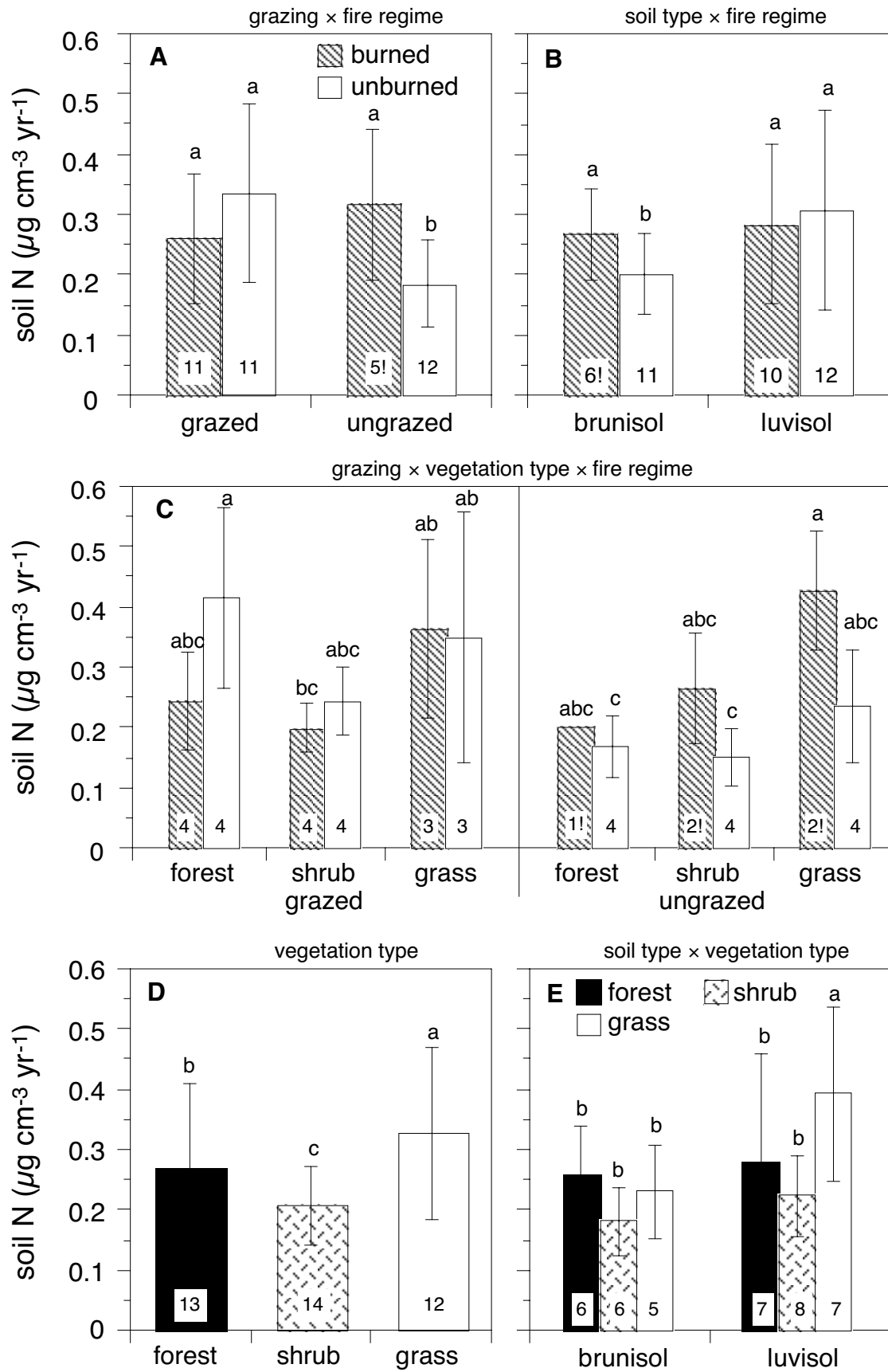
0   1.25   2.5   5   7.5   10
Kilometers

Fig.
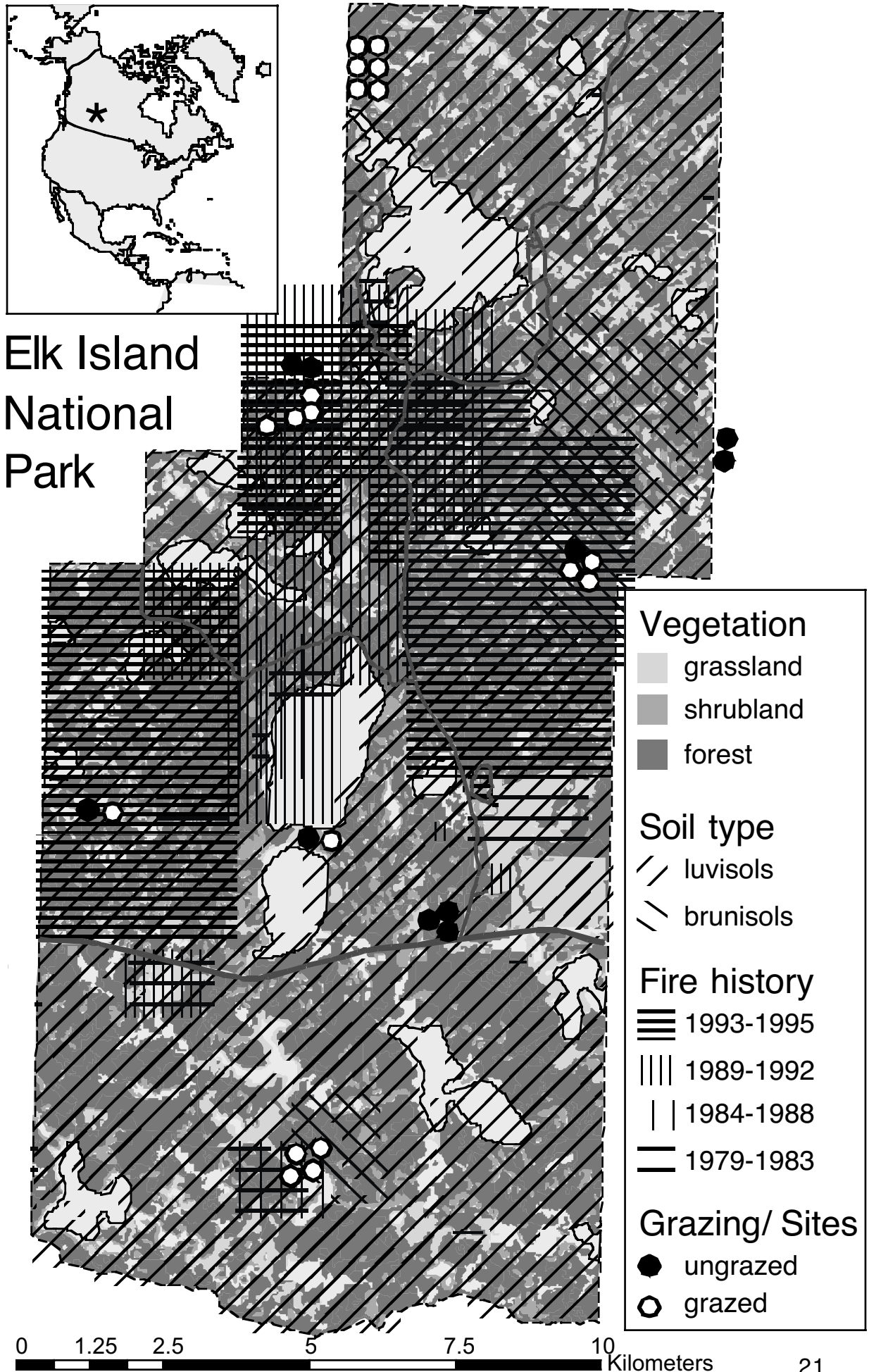
Fig. 2

Fig. 3

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