GRASS-TREE INTERACTIONS
IN WESTERN CANADA

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Abstract

Forest expansion into prairie is generally thought to result from reduced bison browsing on trees and elimination of tree-destroying fires. In addition, forest expansion may be accelerated by deposition of mineral nitrogen (N) from the atmosphere, because additional N should allow trees to overtop grasses faster.

I measured N deposition with ion-exchange resin for 2 yr in 6 national parks in western Canada. Parks in densely populated regions with intense industrialization or farming received significantly more N than parks in sparsely populated regions. Rates of N deposition were significantly and positively correlated with forest expansion. Forest expansion increased the total amount of N in the ecosystem. ^{15}N analysis suggested that increased N deposition was anthropogenic.

Forest expansion likely occurs through interactions between individual plants. I tested the effect of water availability on standing crop of invading shrubs and of grasses in invaded prairie in a removal experiment. Total standing crop decreased only when water availability was as low as in drought years. Low water availability appeared to affect shrubs more strongly than grasses. Above-average water supply had no effect on standing crop.

I tested two herbicides for selective removal of grasses (seth-oxydim) and the selective removal of shrubs (metsulfuron) in rangeland. Both herbicides reduced target plant standing crop without damaging the other growth form. Higher concentrations of metsulfuron were necessary

to remove parts of a clonal shrub than to remove a complete clone.

I examined with a reciprocal removal experiment whether the competitive effect of invading woody species on invaded grasses and on resources (light, N, water) is related to plant mass or to growth form. Shrubs had generally similar or larger absolute effects on grasses and resources than grasses had on shrubs or on resources. The larger effects were attributable to shrub mass because grasses consistently had larger per-gram effects (effect size/standing crop). The experiment supported the hypothesis that higher N supply to woody plants would enable them to outcompete grasses in the absence of grazing and fire.

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1.INTRODUCTION

1.1.   THE FOREST-GRASSLAND ECOTONE

The ecotone between boreal forest and temperate grassland is characterized by a gradient from continuous forest to increasingly smaller forest islands and an antiparallel gradient of continuous grassland to increasingly smaller grassland islands. This type of landscape is called forest steppe (Walter 1984) or parkland (Bird 1930).

The Canadian aspen parkland region has been moving southwards during the last century (Maini 1960, Archibold & Wilson 1980) because aspen groves (*Populus tremuloides*) and snowberry brush (*Symphoricarpos occidentalis*) expand and displace mixed-grass prairie. The invasion of woody species into prairie has parallels in many other temperate forest-grassland ecotones in North America (Walter 1935, Buell & Facey 1960, Jeffrey 1961, Blackburn & Tueller 1970, Bragg & Hulbert 1976, Petranka & McPherson 1979, Arno & Gruell 1986, Archer et al. 1988), South America (Ellenberg 1962, Facelli & León 1986), Europe (Rejmánek & Rosén 1992), Asia (Tkachenko & Genov, 1992, Backéus 1992), Africa (Scholes & Archer 1997) and Oceania (Fensham & Kirkpatrick 1992).

1.2. CONTINENTAL-SCALE CONTROL OF THE FOREST-GRASSLAND ECOTONE

The factors that control the position and movement of the forest-grassland ecotone vary with scale (Wardle 1985, Woodward & Williams 1987, Cornelius et al. 1991, Vetaas 1992). On the continental scale, climate restricts the geographical region in which a species can live either directly, caused by constraints on physiology, or indirectly, through constraints on mutualists or resources (Walter 1986, Archer 1994).

The expansion of forest in North America has occurred not only recently (Archibold & Wilson 1980), but seems to have started about 7500 B.P. as a response to the global cooling trend of the latest ice-age cycle (Ritchie 1976, Pielou 1991, Neilson 1993, Wang et al. 1993). Lower summer temperatures reduced evapotranspiration and improved the water balance. This may have increased tree seedling survival (Petersen & Petersen 1992) and decreased drought mortality (Pallardy & Kozlowski 1981), thus increasing the chance of establishment (Neilson 1986, Barton 1993).

More recent forest expansion in North America appears to coincide with the arrival of European settlers. Their control of fire and bison herds have therefore been suggested as causes for the expansion of forest (Bird 1961, Blackburn & Tueller 1970, Campbell et al. 1994, Archer 1996).

Before the arrival of European settlers, prairie fires presumably occurred every 2 to 10 years (Rundel 1981, Wright & Bailey 1982),

either naturally by lightning or intentionally set by native people to attract game to the resprouting burned grass (Nelson & England 1971, Pyne 1986) or for slash-and-burn agriculture (Hodge 1965). Fire frequency increased as more European hunters, traders, and settlers arrived because the chances of camp fires escaping increased (Nelson & England 1971). In fact, 1835 to 1860 was a period with more frequent fires (Nelson & England 1971). Steam-powered trains also were are significant cause of accidental fires (Nelson & England 1971). Fires damage woody species more than grasses (Blackburn & Tueller 1970, Svedarsky et al. 1986) because shrubs and trees have most of their biomass aboveground, whereas grasses have most of their biomass belowground. Settlers extinguished wild fires because farmsteads were endangered (Wright & Bailey 1982, Pyne 1986). Without fire, shrubs and trees grow unchecked (Svedarsky et al. 1986). However, aspen (*Populus tremuloides*), the most aggressive invader of the northern prairies, vigorously produces tillers after light or moderate fires (Bork et al. 1997) so that the net effect of fire on forest expansion depends on fire frequency and intensity (Cole & Taylor 1995, Bork et al. 1997).

Before the arrival of Europeans, bison were abundant in North America (Allen 1967, Rodney 1969). Where the intensity of ungulate grazing was reduced, shrubs and trees invaded the pastures (Glendening 1952, Svedarsky & Buckley 1975, Wright & Bailey 1982). Consequently, the extirpation of bison has been suggested as a cause for forest expansion (Campbell et al. 1994). However, established trees are little affected by browsing (Potter & Krenetsky 1967, Petersen & Petersen 1992). Inten-

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sive grazing can even promote shrub growth by reducing the competitive ability of grasses, destroying the grass cover, or dispersal of seeds (Buffington & Herbel 1965, Van Auken & Bush 1989, Harrington 1991, Milchunas & Lauenroth 1993). In the northern Great Plains, naturally growing trees are restricted to moist depressions. Bison, however, prefer to browse grasslands on upland locations (Morgan 1980, Hudson & Frank 1987, Bork et al. 1997) and used the northern Great Plains only during the summer (Morgan 1980). Thus, bison on their summer range presumably did not browse trees frequently, but intense browsing in combination with fire is necessary to reduces tree abudance strongly (Bork et al. 1997). Bison on their winter range in the forest surrounding the northern Great Plains (Morgan 1980) may have had a larger effect on local aspen abundance because of the higher browsing intensity.

A third large-scale factor that may have contributed to forest expansion has emerged more recently. Pollution has increased the concentration of nitrogenous compounds in the atmosphere which has a fertilizing effect on vegetation and may have accelerated the expansion of forests. The amount of mineral nitrogen in the atmosphere has dramatically increased since the end of the last century due to the increase of fossil fuel combustion in vehicles and in industrial processes, especially electrical power generation (Skeffington & Wilson 1988, Ellis et al. 1990, Vitousek et al. 1997). Thus, nitrate oxide emissions in the U.S.A. increased sevenfold from 1900 to 1980. Total deposition of inorganic nitrogen forms from the atmosphere now contribute 31-40 kg N ha^{-1} yr^{-1} in industrialized areas of Europe and North America (van Breemen &

van Dijk 1988, Lindberg et al. 1986, Fenn & Bytnerowicz 1993). Some models estimate total deposition in western Europe to be even higher, ranging from 56 to 197 kg N ha^{-1} yr^{-1} (Diederen & Duyzer 1988 in Pearson & Stewart 1993). The higher estimates are due to the inclusion of certain forms of deposited nitrogen that are rarely measured because the available methods are insufficient.

As a result of "fertilization" by atmospheric N deposition, plant production increases and species that require more nitrogen (for example, trees and fast-growing weed-type species) may replace species typical of nitrogen-poor habitats (Ellenberg 1988, Gundersen 1991). Very high rates of N deposition, however, are toxic and may reduce plant growth (Rowland et al. 1985, Pearson & Stewart 1993). Although N deposition is low in prairie (2-5 kg N ha^{-1} yr^{-1}, estimate of "wet" + "dry" deposition to inert surfaces based on data from the Canadian Precipitation Monitoring Network 1990-1993, Linsey et al. 1987, and Lovett & Lindberg 1993), toxic effects from fertilization in grasslands also occur at a lower level (23 kg N ha^{-1} yr^{-1}, Hyder et al. 1975) than in forests (>400 kg N ha^{-1} yr^{-1}, Kenk & Fischer 1988).

I compared the deposition pattern of atmospheric mineral nitrogen in western Canada with rates of tree invasion (chapter 2) to explore whether deposition contributes to tree invasion in the northern prairies.

The increase of CO_2 in the atmosphere also coincides with forest expansion in grasslands. Higher CO_2 concentrations should favour plants with C_3 photosynthesis. This would explain the displacement of C_4

species dominated grasslands in the tropics and SW-U.S.A. by C_3 trees. There are, however, many counter-arguments. No wide-spread replacement of C_4 grasses by C_3 grasses in grasslands has been reported, C_3 trees also displace C_3 grasses, and C_4 species at current CO_2 concentrations still have higher photosynthetic rates than C_3 plants (Archer et al. 1995). Furthermore, higher annual temperatures and drier soil conditions, a consequence of rising CO_2 concentrations due to the greenhouse effect, would probably counteract any gains in competitiveness that C_3 plants would have under high (660 ppm) CO_2 concentrations (Nie et al. 1992). There is also evidence that a gradual increase of CO_2 concentrations would have smaller effects on C and N sequestration than predicted by experiments in which CO_2 concentrations are increased in one step (Luo & Reynolds 1999).

1.3. INDIVIDUAL-SCALE CONTROL OF TREE-GRASS INTERACTION

Climate and atmospheric deposition patterns set a limit for tree or shrub establishment at the continental scale. Competition, the mechanism by which invasion occurs, however, works at the scale of the individual (Walter 1986).

Competition is a frequent and widespread mechanism in arid grasslands (Fowler 1986) and is working at a wide range of productivity (Wilson 1991, Reader et al. 1993). Low-productivity of temperate grasslands is correlated with lower availability of water, lower net nitrogen

mineralization rate, and higher mean annual temperature compared to temperate forests (Walter 1984). Light is not very important in restricting growth in the prairie ecosystem. This is indicated by the low density of the grass canopy compared to forb or tree canopies. Also, total grass biomass under artificial shades was not significantly reduced over unshaded controls (Tilman 1990), but responses of individual species may vary (Van Auken et al. 1992).

Experiments indicate that nitrogen, not water is generally the limiting belowground resource in temperate grassland. Thus, aboveground biomass increases when prairie is fertilized with mineral nitrogen (DiTommaso & Aarssen 1989, Tilman 1990). Addition of other nutrients (Ca, K, Mg, P, S, trace metals) or water over eight years had no consistent significant effect on aboveground biomass (Tilman 1990). Water had a significant effect only in a year with a major drought (Tilman 1990).

Grasslands are dominated by graminoids, a life form with a high root:shoot mass ratio (Caldwell & Richards 1986, Wilson 1988b, Wilson 1993a). This high R:S ratio reflects the higher annual productivity of grass roots over shoots (Milchunas & Lauenroth 1993), suggesting that plants allocate more internal resources to roots because belowground resources (nitrogen, water) are more growth limiting than aboveground resources (light) (Wilson 1988b, Heal et al. 1989, Ingestad & Ågren 1991). Prairie shrubs often grow in depressions where, averaged over time, soil moisture is likely higher than on elevated ground. The higher soil moisture might benefit shrubs with a lower R:S ratio than grasses.

I tested the effect of water on grass and shrub productivity

(chapter 3) under water availability comparable to precipitation in drought, average, and wet years. I hypothesized that only extreme low availability would have a significant effect on productivity and would affect shrubs stronger than grasses.

The invasion of woody plants into grassland is concerning range managers because the fodder value of the rangeland is decreasing. Most invading woody species are clonal (snowberry/*Symphoricarpos*, aspen/ *Populus*, wolfwillow/*Elaeagnus*). The attempt to remove these invaders mechanically is usually frustrating. Herbicides appear to be more suc-cessful (Bowes & Spurr 1996), but may also damage desirable plants. However, these shrubs are the desired plants in, e.g., prairie shelter belts and herbicides against competing grasses may improve shrub estab-lishment. Accompanying a removal experiment to separate the competitive effects of grasses and shrubs on each other, I tested the efficiency of two herbicides, one selective against forbs and one selective against grasses (chapter 4).

Plant communities work like cybernetic systems, which means that communities are maintained by negative feedbacks and changed by positive feedbacks (Mauersberger & Straškraba 1987, Oksanen 1988, Wedin & Tilman 1990, Hobbie 1992, Agnew et al. 1993, Høgg et al. 1994, Vinton & Burke 1995, van der Putten 1997, Mills & Bever 1998). Taller plants, e.g., trees, often replace shorter plants, e.g. grasses, by a positive feed-back loop. In communities with low nutrient supply, plants generally compete for nutrients. The nutrient pool increases over time due to rock mineralization, N-fixation or atmospheric deposition (Vitousek & Walker

1987). Nutrients become less limiting and growth forms with a low competitive ability for soil resources increase their growth rate (Tilman & Wedin 1991, Reynolds & Pacala 1993, Loreau 1998). These growth forms are often tall, have a high competitive ability for light and shade out lower growth forms (Tilman 1990). Thus, plants with a high competitive ability for light have changed the prevalent form of competition in the community from nutrient to light competition.

Taller plants usually also have more mass than lower plants. More mass is related to higher nutrient uptake. Are shrubs and trees invading prairie because they have more mass or is it their tall growth form that allows woody species to displace grasses?

I compared the competitive effects (the ability to withstand the competition of neighbour plants) between shrubs and grasses based on their mass (Goldberg 1990) (chapter 5). I hypothesized that shrubs have larger absolute competitive effects on grasses and resources but smaller per-gram effects than grasses.

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 fertiliza-
tion 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. Atmos-
pheric N deposition, measured with ion-exchange resin, was highest in
four parks in a region with agro-industrial land-use (moderately popu-
lated, 5-100 inhabitants/km^2) and lowest in parks in a mostly forested
region with minimal agro-industrial land-use (sparsely populated, <5
inhabitants/km^2). 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 vari-
ation 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 availa-
bility compared to the effect of soil type, fire history, grazing, or
vegetation type. I measured N mass and natural abundance of ^{15}N in vege-
tation and soil in two parks: Elk Island in the agro-industrial region,

receiving 22.1 kg N ha^{-1} yr^{-1}, and Jasper in the forested region,

receiving 7.77 kg N ha^{-1} yr^{-1}. 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. δ^{15}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^{-1} yr^{-1}, 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^{-1} yr^{-1}) 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 eco-systems. Therefore, I measured N deposition and available soil N in six national parks in western Canada in a 1000×1000 km^2 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 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). NH_4-N emissions in western Canada are low (Environment Canada 1998), representing <5% of NO_x-N emissions (Environment Canada 1996). Vehicle exhausts contain isotopically light N (negative δ^{15}N value), whereas fuel combustion in boilers produces isotopically heavy N (positive δ^{15}N value) (Heaton 1990). Therefore, the δ^{15}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 δ^{15}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}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.

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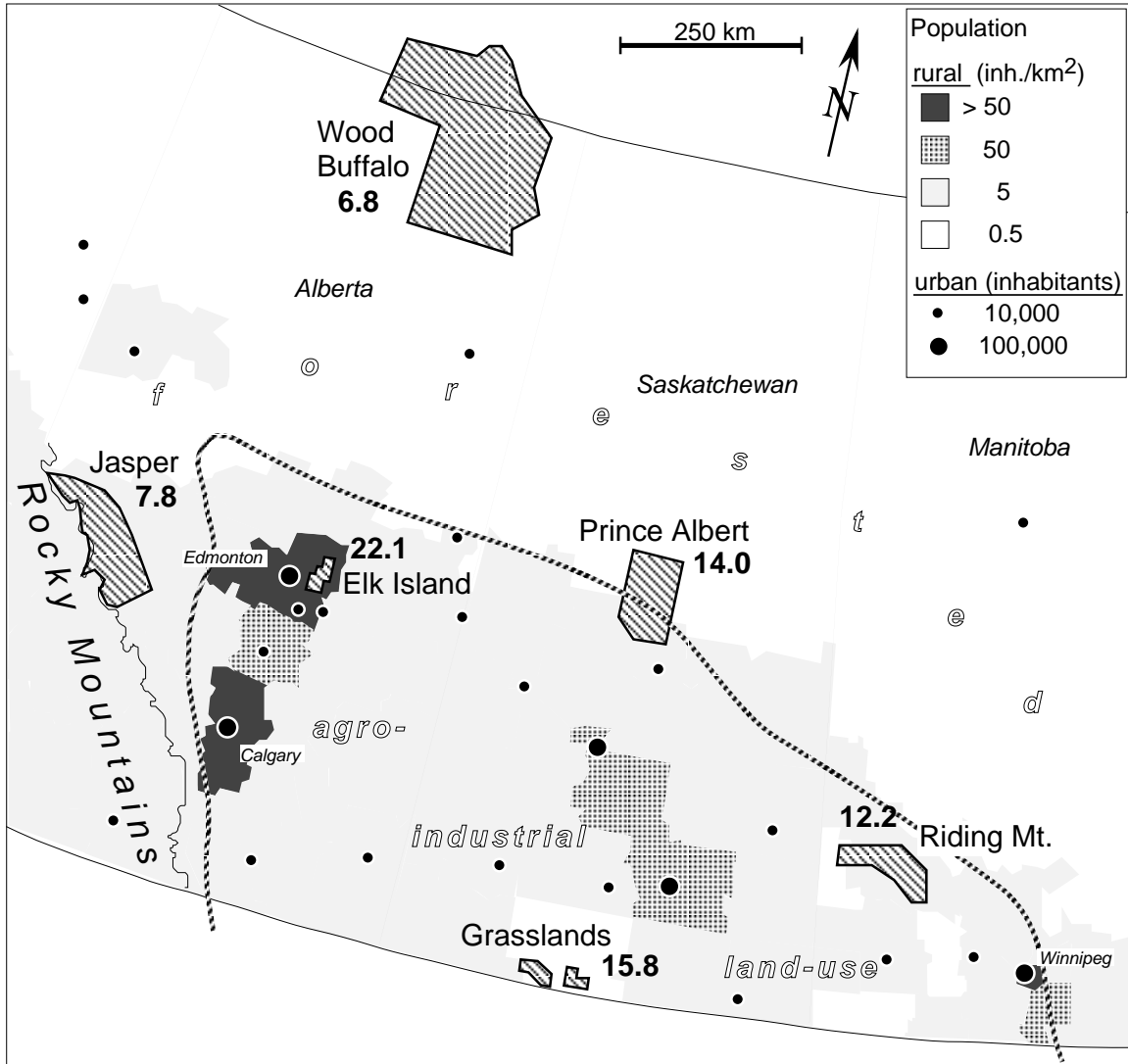
FIG. 2.1. Location of sites (national parks), N deposition rate (kg N ha^{-1} yr^{-1}), population density, and regional land-use. Population density is based on electoral boundaries. Elk Island National Park is enlarged 200%. The hatched line indicates the border between the agro-industrial and the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

2.3.   METHODS

2.3.1. <u>Study sites</u>

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. Grass-
lands 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 Is-
land, however, is dominated by *Poa pratensis* and *Calamagrostos canaden-
sis*.

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

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

Park	agro-industrial region				forested region	
	<u>Elk Island</u>	<u>Grasslands</u>	<u>Prince Albert</u>	<u>Riding Mt.</u>	<u>Jasper</u>	<u>Wood Buffalo</u>
Geography						
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_x emissions (kg NO2 ha^{-1} yr^{-1}) (1)	>5000	50-500	0-500	500-2000	0-50	0-50
Climate (2)						
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 113°11'W	49°22'N 107°53'W	53°55'N 106°05'W	50°39'N 99°56'W	52°53'N 118°04'W	60°01'N 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

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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
Trend in climate change *						
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
Dominant forest species †	aspen (4)	aspen	aspen-spruce	aspen-spruce (7)	spruce-aspen (8)	aspen (9)
Dominant grassland type	Poa pratensis-Calamagrostis canadensis	mixed-grass prairie (5)	Festuca scabrella prairie (6)	Festuca scabrella prairie (11)	Koeleria-Artemisia-Linum grassland (8)	northern prairie (9, 12)
Dominant soil type (10)	Gray Luvisol	Brown Chernozemic Brown Solonetzic	Gray Luvisol	Black Chernozemic	Regosol	Gley-, Fibri-, Bruni-, Cryosols
Resin bag location						
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

(2) Environment Canada 1993

(3) Walter & Lieth 1967

(4) Soper 1951, Bork et al. 1997

(5) Coupland 1950

(6) Carbyn 1971

(7) Dickson 1909

(8) Holland & Coen 1982

(9) Raup 1935

(10) NAS 1974

(11) Blood 1966a,b

(12) Schwarz & Wein 1997

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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 parti-cles, 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 inte-grate 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^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 cations. Thus, the total ion-

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exchange capacity of each bag was 3 mmol (3300 mmol m^{-2}). The amounts of cations and anions in soil leachate and throughfall of temperate forests range from 16 to 1028 mmol m^{-2} yr^{-1} (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

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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 $TiCl_3$. 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 ($N_{extracted} = 0.6902 \cdot \ln(N_{added}+1)$, $R^2 = 0.85$, $n = 204$). 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 kg N ha^{-1} yr^{-1}). Results for soil bags were divided by resin volume and length of sampling period and expressed as kg N ha^{-1} 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.

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I assumed that surface bags with an equivalent of ≥100 kg N ha^{-1} yr^{-1} (108 out of 1016 bags) and soil bags with an equivalent of ≥1000 kg N ha^{-1} 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 α = 0.01) and normal (Shapiro-Wilks test at α = 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. δ^{15}N and N in vegetation and soil at Elk Island and Jasper

Field sampling.— I measured δ^{15}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 km × 2 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_3-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}N and N using a continuous-flow mass spectrometer (Europa, Crewe, U.K.) at the Department of Soil Science, University of Saskatchewan. $\delta^{15}N$ values are expressed in reference to the ^{15}N concentration of standard atmospheric

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

Species	Regression equation	R^2
	stem mass	
Symphoricarpos occidentalis	$0.48285d^2 - 1.92303d + 3.62547$	0.89
Shepherdia canadensis	$0.37792d^2 - 3.84917$	0.96
Corylus cornuta	$0.40064d^2 - 2.13860d + 4.73454$	0.90
Elaeagnus commutata	$0.01774d^3 + 0.00798d^2 + 0.39961d - 1.2522$	0.97
Rosa acicularis	$0.17882d^2 - 0.54081$	0.82
	leaf mass	
Symphoricarpos occidentalis	$6.925 \cdot 10^{-4}\,d^4 + 1.46048$	0.44
Shepherdia canadensis	$0.02196d^2 + 0.43914d - 1.65041$	0.89
Corylus cornuta	$0.05952d^2 - 0.91247$	0.64
Elaeagnus commutata	$0.03891d^2 + 0.2386$	0.80
Rosa acicularis	$0.08036d^2 - 0.16055$	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 compart-
ment mass and dividing the sum by the total mass of the pooled compart-

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

Statistical analyses.— I compared $\delta^{15}N$ 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. $\delta^{15}N$ data were homoscedastic and normal. Two $\delta^{15}N$ 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 ≥ 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 (YYYY-MM)	Nominal altitude (feet)	Focal length (inches)	Scanning resolution (dpi)	Pixels	Scale
Elk Island, 53°43'07"N 112°47'47"W, 730 m.a.s.l., 4.73 km²									
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
Grasslands, 49°12'17"N 106°41'55"W, 900 m.a.s.l., 4.93 km²									
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
Jasper, 53°04'01"N 118°06'00", 1000 m.a.s.l., 3.47 km²									
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/1 "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

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Table continued from preceeding page

Index Map	Colour	Roll	Frame	Date (YYYY-MM)	Nominal altitude (feet)	Lens diameter (inches)	Scanning resolution (dpi)	Pixels	Scale
Prince Albert, 53°36'04"N 106°30'42"W, 490 m a.s.l., 3.89 km²									
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
		A17935	19						
73G "c"	b/w	A17936	113	1962-10	7800	6	180	1843200	10295
73G "e"	b/w	A20417	150	1968-05	9820	6	252	1428140	16374
73G "k"	b/w	A24402	182	1976-05	27000	6	720	1291186	49202
73G "o"	b/w	A27572	125	1990-05	32300	6	792	1058490	59775
Riding Mountain, 50°56'02"N 100°54'25"W, 520 m a.s.l., 2.14 km²									
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
Wood Buffalo, 59°08'00"N 112°25'00W, 250 m a.s.l., 3.46 km²									
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^2 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

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(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

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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 × 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
α = 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 × park and year × season × 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 kg N ha^{-1} yr^{-1}); in spring 1996, it had the lowest of
all parks (1.1 kg N ha^{-1} 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, high-
est in spring or early summer and declined during the growth period. N
availability in spring was exceptionally high in 1996 in Prince Albert
(1533 kg N ha^{-1} yr^{-1}).
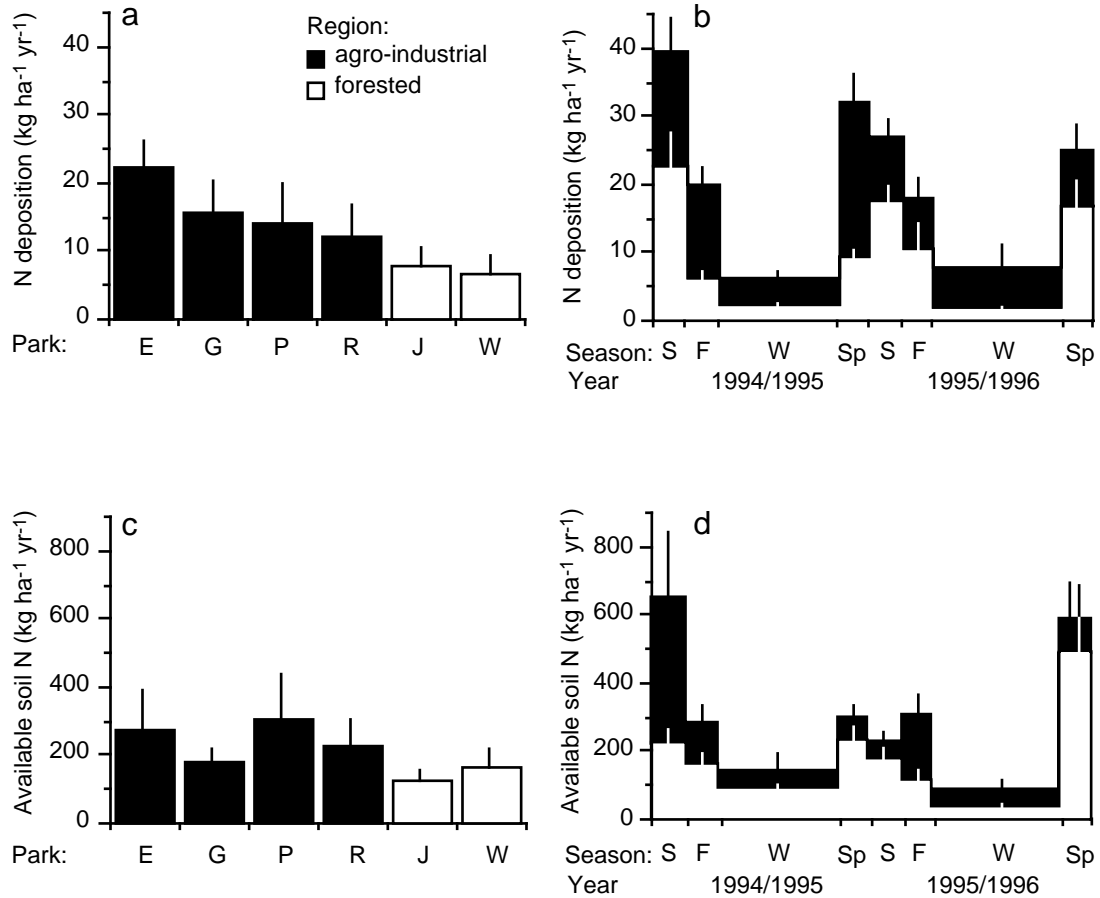
FIG. 2.2. Deposition of atmospheric N (a, b) and available soil N (c, d) in six western Canadian national parks (E: Elk Island, G: Grasslands, J: Jasper, P: Prince Albert, R: Riding Mountain, W: Wood Buffalo) in the agro-industrial (more densely populated) and the forested (sparsely populated) region 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 ± 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 uni-variate (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	P	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
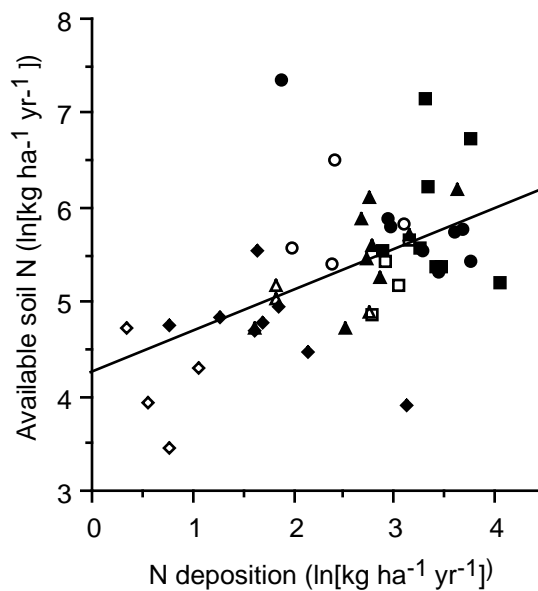
FIG. 2.3. Relationship between available soil N and N deposition in six western Canadian national parks, four in the agro-industrial region (more densely populated, black symbols) and two in the forested region (sparsely populated, white symbols), measured for two years in four seasons (summer [mid-June – August]: □, ■; fall [August – October]: △, ▲; winter [October – May]: ◇, ◆; spring [May – mid-June]: ○, ●). 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. <u>Atmospheric deposition and available soil nitrogen — Elk Island</u>

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 × 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 × 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 × fire × 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 × fire × vegetation interaction, $F_{2,424}$ = 4.14, P = 0.02). None of these inter-actions contributed >6% to the accounted-for-variation, and thus prob-ably 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 kg N ha^{-1} 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.
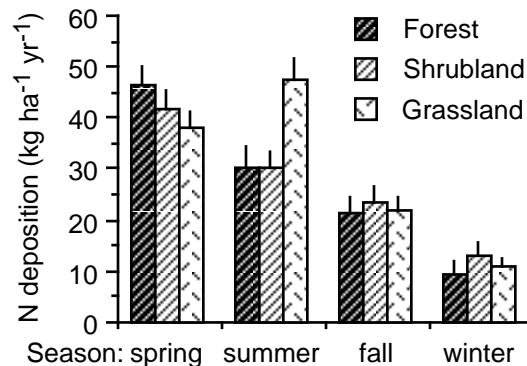
FIG. 2.4. Deposition of atmospheric N in Elk Island National Park, western Canada. Spring: May — mid-June, summer: mid-June — August, fall: August — October, winter: October — May. Bars represent means (+ SE) of two years (n = 18-25).

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

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

* This combination does not exist at Elk Island.

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

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

* This combination does not exist at Elk Island.

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

δ^{15}N values in vegetation and soil tended to be lower in Elk

Island (22.1 kg ha^{-1} yr^{-1} N deposition) than in Jasper (7.8 kg ha^{-1} yr^{-1}

N deposition). The difference between δ^{15}N values was significant,

however, only for some compartment - vegetation type combinations (Fig.

2.5; park × compartment[vegetation type] interaction: $F_{17,241}$ = 3.32, P

< 0.0001). δ^{15}N values of stems, leaves, and litter in forest were sig-

nificantly lower in Elk Island than in Jasper, whereas δ^{15}N values of

aboveground mass in shrubland and grassland did not differ between the

parks (Fig. 2.5; park × vegetation type interaction: $F_{2,54}$ = ~~12.0~~, P <

0.0001). Roots tended to have higher δ^{15}N values than other tissues and

δ^{15}N values of soil were higher than δ^{15}N values of tissues. δ^{15}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 δ^{15}N values are presumably due to the presence of N-

fxing shrubs. In summary, δ^{15}N values of aboveground tissues (including

litter) tended to be lower in Elk Island than in Jasper and the differ-

ence 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 ($F_{1,54}$ = ~~6.27~~, P =
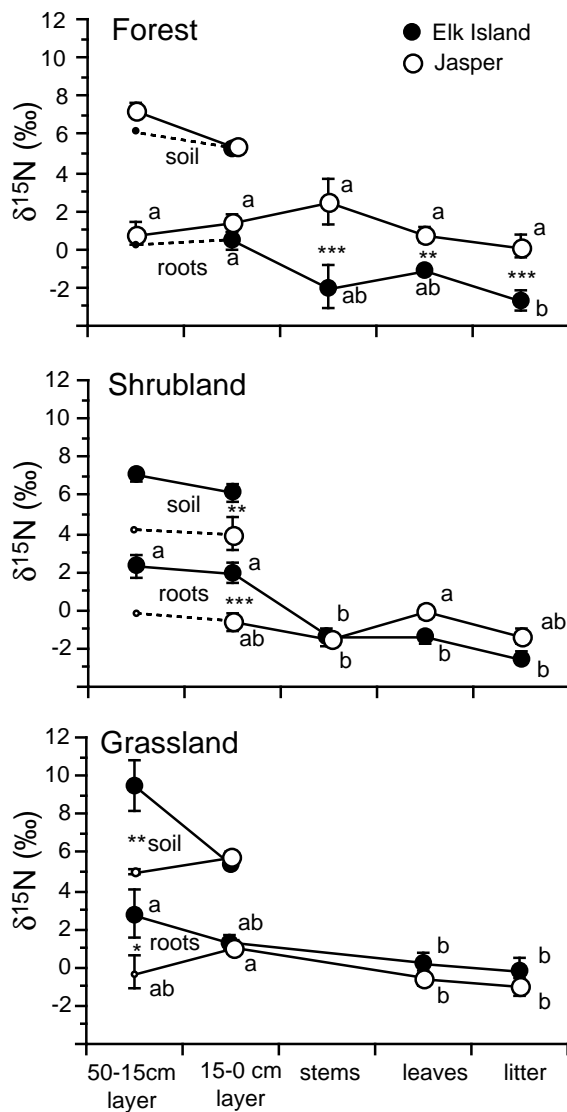
FIG. 2.5. $\delta^{15}N$ values of vegetation and soil compartments in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means ± SE, n = 6-10; small circles denote $n \le 3$). Compartments within a park that share the same letter are not significantly different (Tukey-Kramer test, α = 0.05). Significant differences between parks within a compart-ment are marked with asterisks between the circles (a-priori contrasts, *: $P \le 0.05$, **: $P \le 0.01$, ***: $P \le 0.001$).
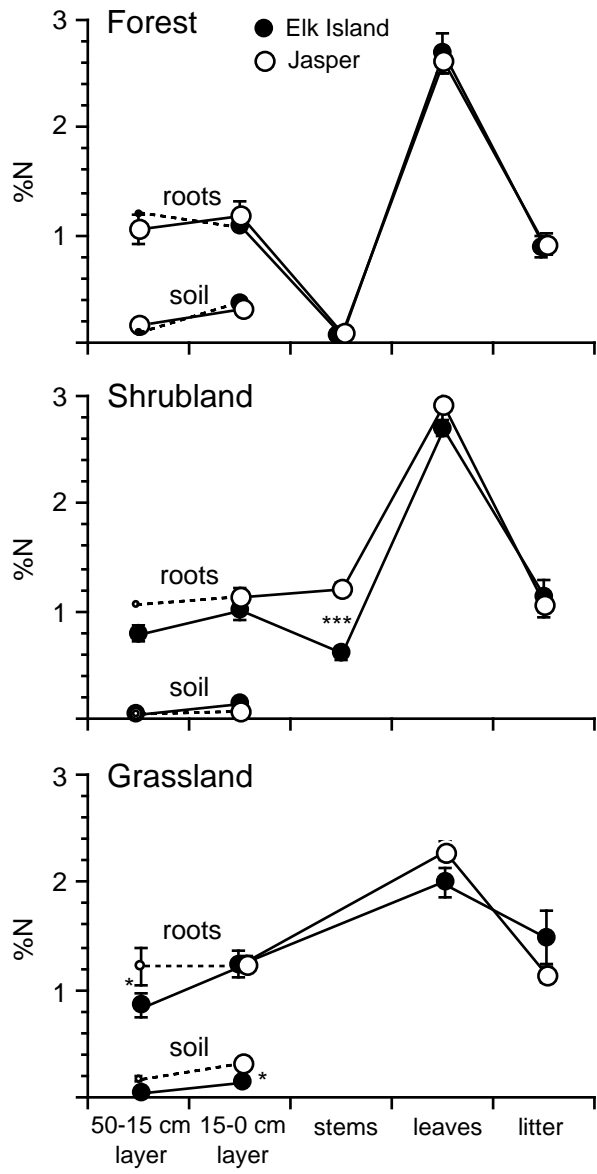
FIG. 2.6. Concentration of N in vegetation and soil compartments in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means ± SE, n = 6-10; small circles denote n ≤3). Significant differences between parks within a compartment are marked with asterisks between the circles (a-priori contrasts, *: P ≤ 0.05, ***: P ≤ 0.001).

0.01), among vegetation types ($F_{2,54}$ = 3.23, P = 0.04), among soil and vegetation compartments ($F_{17,243}$ = 167, P < 0.0001), and with the inter-action 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 signifi-cantly 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 × 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 × 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
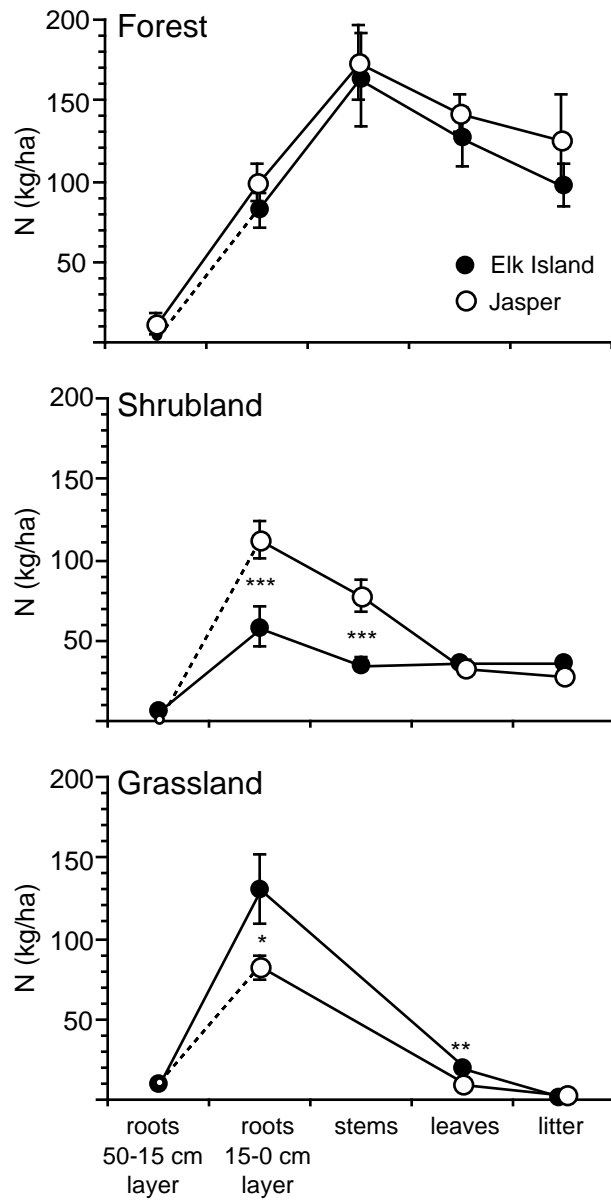
Fig. 2.7. Amount of N in vegetation in a park with high (Elk Island, ●) and low (Jasper, ○) N deposition (means ± SE, n = 6-10; small circles denote n ≤ 3). Significant differences between parks within a compartment are marked with asterisks between the circles (a-priori contrasts, *: P ≤ 0.05, **: P ≤ 0.01, ***: P ≤ 0.001).

equality of slopes among all parks: $F_{5,22}$ ~~= 9.33, P < 0.0001).~~ I exam-

ined 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 expan-

sion (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-
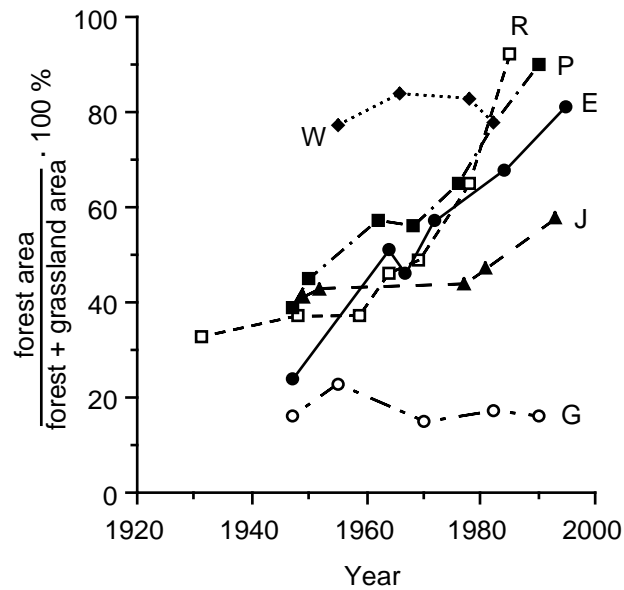
Fig. 2.8. Forest expansion in six western Canadian national parks

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).
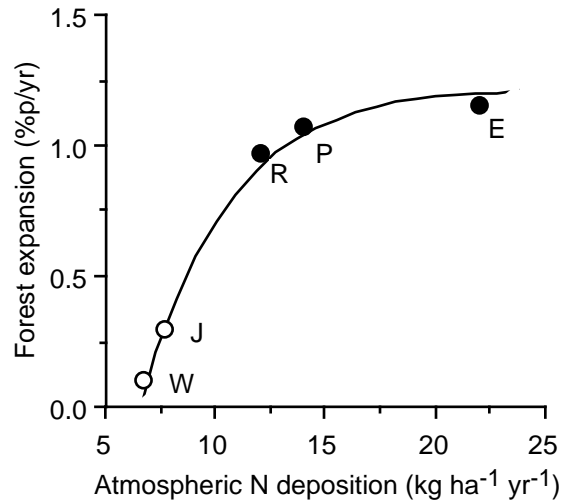
FIG. 2.9. Relationship between rate of forest expansion (percentage-points forest area per year, %p/yr) and atmospheric N deposition in five western Canadian national parks. Three parks (E: Elk Island, P: Prince Albert, R: Riding Mountain) were in the agro-industrial (more densely populated) region (black 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).
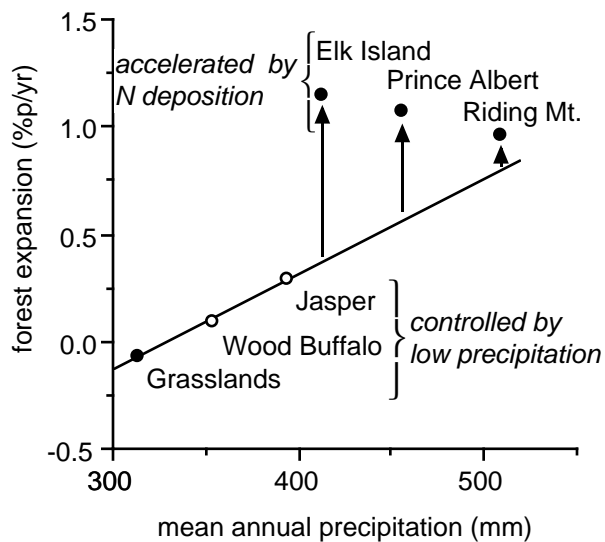
FIG. 2.10. Relationship between rate of forest expansion (percentage-

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.

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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).

	Jasper			Elk Island		
year:	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_x-N ha^{-1} yr^{-1} compared to 10^{-7} kg NO_x-N ha^{-1} yr^{-1} in northern Alberta (population <1 inhabitant/km^2) (Environment Canada 1996). The largest sources of NO_x 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_x-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_x 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^{-1} yr^{-1} in the forested region to 11.0 kg N ha^{-1} yr^{-1} 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 kg ha^{-1} 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

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(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. <u>N deposition and availability — Elk Island</u>

N deposition and soil N availability within Elk Island varied

most clearly with season. Remaining variation with grazing, fire, vege-

tation 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 varia-

tion 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. δ^{15}N and N in vegetation and soil at Elk Island and Jasper

Vegetation in Elk Island had generally lower δ^{15}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 δ^{15}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 δ^{15}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}N-depleted motor vehicle exhausts (Heaton 1990) that emitted 43% of all 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 NO_x pollution from motorways in Switzerland (Ammann et al. 1999). The conclusion that car exhausts have caused the decrease of δ^{15}N values in western Canada is based on the assumption that the ^{15}N signal is more or less undiluted by atmospheric processes. More research about

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

In forest and shrubland, δ^{15}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 δ^{15}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}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}N-depleted N as the δ^{15}N values of stems is much lower than that of roots. The difference between shrubland stems in Elk Island and Jasper, how-ever, is obscured because low δ^{15}N values of Jasper shrubland soil (Fig. 2.5), caused by N-fixing shrubs, presumably decreased δ^{15}N values in the whole plant (Nômmik et al. 1994).

In grassland, δ^{15}N values of leaves and litter were as high in Elk Island as in Jasper (Fig. 2.5). δ^{15}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).

δ^{15}N values of soil were always higher than those of tissues (Fig. 2.5). This reflects isotopic fractionation processes during decom-position, nitrification, denitrification, ammonia volatilization, and leaching of depleted nitrate (Handley & Raven 1992). The increase of δ^{15}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}N-depleted litter to the soil surface (Nadelhoffer & Fry 1994). Higher δ^{15}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 occured 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 grass-land 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 (Högbom & 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 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 presribed 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 ≈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

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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.

Aross ~~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^{-1} yr^{-1} 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

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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. <u>Conclusions</u>

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.

3. WATER AVAILABILITY AND COMPETITION

IN THE NORTHERN GREAT PLAINS

3.1.   ABSTRACT

I examined the response of grass and shrub standing crop to water availability in a natural, arid grassland in the northern Great Plains, Canada. Water availability was manipulated during the hot season (late June-early September) by excluding rain and supplying water at levels corresponding to precipitation amounts in dry, wet, and average years. Competition between grasses and shrubs was manipulated by removing grasses or shrubs with a herbicide. Low water supply significantly reduced total standing crop when grasses and shrubs interacted but not in the absence of competition. The general effect of water supply on standing crop was small, suggesting that water limitation during a single hot season was of little importance for vegetation structure. The effect of water supply did not differ between open prairie and within shrub clones, suggesting that similar mechanisms operate in both habitats.

3.2.   INTRODUCTION

Temperate grasslands are thought to be mostly controlled by

precipitation or water availability (Walter 1984, Lauenroth & Sala 1992, Paruelo et al. 1993, Briggs & Knapp 1995). However, herbaceous vegetation in oak savanna in Minnesota was limited by water in only one out of eight years which was a major drought year (Tilman 1990) and there is little evidence that water availability affects competition between prairie plants (Fowler 1986, Wilson 1988a). Thus, water availability may have strong effects on competition only in years with very high or low precipitation. Furthermore, competition in temperate grasslands may also be little affected by water availability because the ecosystem is dominated by one growth form and therefore species responses may be similar (Taub & Goldberg 1996).

Prairie grasses and prairie shrubs differ strongly in growth form. Grasses with their high root:shoot mass ratio should be better competitors for soil water than woody species with their low R:S ratio (Tilman 1988). Shrubs, on the other hand, often have deeper roots than grasses and therefore may be less affected by grass competition for soil water (Sala et al. 1989). Therefore, shrubs and grasses should differ strongly in their response to water availability. Still, even woody plants and grasses appear to differ in their response only in years of extreme low or high precipitation (Cable 1969, Golluscio et al. 1998).

The most abundant shrub in the northern Great Plains, snowberry, *Symphoricarpos occidentalis*, grows in dense clones. Clones appear to be denser in depressions or on north-facing slopes, suggesting that snowberry is responding to water availability (Pelton 1953). Due to shading, evaporation inside clones may be lower and water supply may have a

smaller effect on competition than outside, allowing the shrubs to displace grasses. Higher soil moisture also accelerates N mineralization (Myers et al. 1982) and may therefore increase competitiveness of shrubs.

I examined the response of prairie vegetation to water availability by comparing the standing crop of grasses and shrubs at three levels of water supply. I hypothesized that low water supply would decrease the standing crop of shrubs more than that of grasses, whereas high water supply would increase the standing crop of shrubs more than that of grasses. I also hypothesized that when grasses and shrubs grow together the amount of water available to each growth form would be lower. Therefore, low water supply should affect grasses and shrubs more strongly when they grow together than when they grow without the other growth form. Finally, I tested whether the responses of grasses and shrubs vary with habitat.

3.3.   METHODS

The experiment was carried out in mixed-grass prairie (Coupland 1950) dominated by *Stipa* spp., *Agropyron subsecundum*, *Bouteloua gracilis*, *Koeleria gracilis*, and *Poa* spp. in the northern Great Plains, 120 km south of Regina, Saskatchewan, Canada (104°38'W, 49°18'N). The prairie at this site includes *Symphoricarpos occidentalis* (snowberry) clones (95% snowberry cover inside the clone) with a sparse undergrowth

of grasses and sedges. I refer to these clones as brush habitat, in contrast to the prairie habitat outside the clones where young snowberry stems have 10-20% cover. Soils are dark-brown solonetzic on clayey loam.

I applied two factors (water supply and growth-form removal) with three levels each in a factorial design to plots in each habitat. Nine plots were randomly located within the brush habitat and nine plots were randomly located in the prairie habitat. Brush and prairie plots (40 cm diameter) were established when the soil had thawed in May 1995 by trenching 10-15 cm deep to confine roots within plots. Roots of *Symphoricarpos* and of grasses were concentrated in the upper 15 cm of the soil (*personal observation*). Root uptake of most species at our site is greatest at 0-15 cm depth (Johnson 1960). The plot perimeter was lined with 1.5 mm thick, 10 cm deep plastic (lawn edging). All prairie plots contained snowberry stems and all brush plots contained grass.

To test the effect of water supply on shrub and grass growth I manipulated water supply in plots from June 22 to September 9, 1995 by excluding rain and watering by hand. Rain was excluded from all plots

water supply rate	month			
	June	July	August	September
low	25	35	22	34
average	72	61	42	36
high	117	114	53	61

Table 3.1. Monthly water supply rates (L/m^2) in the three water supply treatments.

with clear plastic tents (93% PAR penetration). The tents had a triangular base and one open side to allow air circulation. The closed tent sides faced the dominant wind directions on rainy days (SE, NW; Environment Canada 1986-1994). There were three water supply rates: low, average and high (Table 3.1). The monthly amount of water was related to monthly precipitation at Regina during the 1958 - 1994 period (Environment Canada 1958-1994). The low water supply of a month was calculated as the mean precipitation of the same month of the five driest years. The average water supply of a month was calculated as the mean precipitation of the same month of all years. The high water supply of a month was calculated as the mean precipitation of the same month of the five wettest years. The plots were watered three times per month with one third of the monthly rate.

To determine the response of grasses and shrubs to water supply, I applied three removal treatments (intact vegetation, shrubs removed, or grasses removed). Shrubs and grasses were removed by carefully painting a fast decaying herbicide (glyphosate, RoundUp) with a sponge or paint brush on shrub or grass leaves on 28 May (2.5% dilution), and again on 6 June, 1995 (3.0% dilution).

One plot was randomly assigned to each water supply rate × removal combination, resulting in nine plots per habitat or 18 plots per site. Sites were c. 100 m^2, comprising bush and prairie habitat. The experiment was replicated at 10 sites for a total of 180 plots.

In each plot I determined standing crop of grasses and shrubs non-destructively during 5-16 June and 9-23 September, 1995. Grass

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standing crop was determined with a point-frequency counting frame (Mueller-Dombois & Ellenberg 1974). The number of pins (2.5 mm diameter, spacing 2 × 6 cm) intersecting with leaves of grasses or herbs were multiplied with a regression equation ($\sqrt{m}$ = 2.089 intersections/pin + 0.6976, R^2 = 0.608, n = 38) to calculate grass mass (m). The regression equation was based on using the frame on one 30 × 30 cm^2 patch in the prairie and brush habitat at each site (total 20 patches) on 18 June and 15 September, 1995. Two patches were eliminated from the regression because they were outliers causing a negative intercept. Grasses and herbs in the patches were cut 1 cm above the ground, dried at 105°C until mass was constant, and weighed.

Shrub standing crop was determined by measuring the diameter of all shrub stems in all prairie and brush plots and applying a regression equation. I measured the diameter at the thinnest portion within 3-4 cm height with calipers (accuracy 0.01 mm). The regression (m = 0.3174d^2 - 0.7097d + 0.4458, R^2 = 0.984) was based on the diameter (d(mm)) and aboveground mass (m(g)) of 20 shrubs harvested outside the plots on 18 June, 1995. Shrubs were cut 1 cm above the ground, dried at 105°C until mass was constant, and weighed. Diameters measured in September were generally smaller than those measured in June, presumably because I measured the diameter at the visually thinnest stem portion within 3-4 cm height in June but measured at actually thinner portions of the stem within 3-4 cm height in September. As a result, growth rates were apparently negative and I present only results based on September measurements.

The design of the experiment was block-factorial with site as a random factor and habitat, water supply and growth-form removal as fixed factors. Variation in standing crop (sum of grass and shrub) was examined with analysis of variance (ANOVA). To increase homogeneity of variances and normality, mass was ln-transformed. All ANOVAs were calculated with JMP for Macintosh 3.2.1 (SAS Institute 1997). Total rather than grass and shrub standing crop was used in ANOVA, because shrub and grass standing crop in intact plots were measured in the same plots and were therefore not independent.

3.4.   RESULTS

Standing crop varied with habitat and removal treatment in a foreseeable way due to the much higher physical density of woody shrubs than herbaceous grasses. Thus, standing crop, across all other treatments, was significantly higher in brush than in prairie (Fig. 3.1; $F_{1,9}$ = 24.5, P = 0.0008). Total standing crop in intact vegetation was higher than in grass-removal plots which was higher than in shrub-removal plots (Fig. 3.1; $F_{2,18}$ = 59.6, P < 0.0001). A significant habitat × removal interaction (Fig. 3.1; $F_{2,18}$ = 103, P < 0.0001) revealed that total standing crop in shrub-removal plots was higher in prairie than in brush, whereas total standing crop in grass-removal plots and in intact vegetation was higher in brush than in prairie. In both habitats, grass mass in shrub removal treatments was significantly less than in

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intact vegetation (t-tests, $P < 0.05$). This difference, however, was present already in June. Water availability had no significant main or interaction effect on total standing crop.

Grasses and shrubs in removal plots showed leaf damages that may have been caused by dryness due to high evaporation or by herbicide drift. Therefore, to detect an effect of water supply on total standing crop, I restricted the data set to plots with intact vegetation. The ANOVA showed that water supply had a significant effect on standing crop (Fig. 3.2; $F_{2,18} = 5.07$, $P = 0.02$). Standing crop at high water supply was not significantly different from that at average water supply, which, however, was significantly higher than that at low water supply
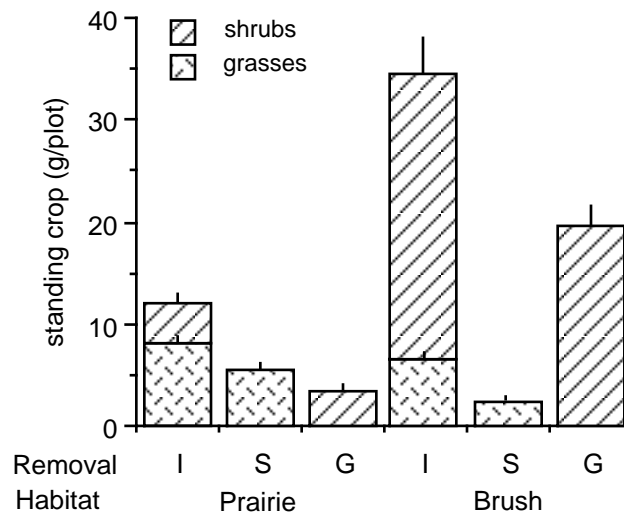
FIG. 3.1.   Effect of habitat and growth-form removal on standing crop of grasses and shrubs. I: intact vegetation, none removed, S: shrubs removed, G: grasses removed. Bars indicate means (across water supply treatments) + 1 SE ($n = 9$).

(simple contrast: t = 2.45, P = 0.02). As for the complete data set, standing crop was significantly higher in brush than in prairie ($F_{1,9}$ = 43.2, P = 0.0001). There was no significant water supply × habitat interaction (P = 0.14).

I tested with the restricted data set whether grasses and shrubs differed in their response to water supply by separating grass and shrub mass and adding growth form as an additional fixed, completely factorial effect to the ANOVA. The effect of water supply across all other treatments was no longer significant (P = 0.06) and did not interact with any other factor. As for the complete data set, standing crop, across removal and water supply treatments was significantly higher in brush than in prairie ($F_{1,9}$ = 64.1, P < 0.0001, Fig. 3.1: Removal: "I" treat-
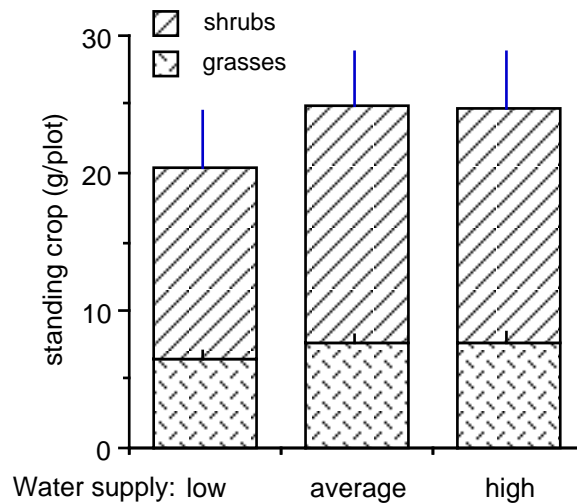
FIG. 3.2.   Effect of water supply on standing crop of grasses and shrubs in intact vegetation (no-removal treatment). Bars indicate means (across habitats) + 1 SE (n = 20).

ments). A significant habitat × growth form interaction ($F_{1,9}$ = 78.3, P < 0.0001), however, showed that grass standing crop did not differ significantly between habitats, whereas shrub standing crop was significantly lower in prairie than in brush (simple contrasts: t = 11.1, P < 0.0001; Fig. 3.1: Removal: "I" treatments).

3.5. DISCUSSION

Low water supply significantly reduced total standing crop (Fig. 3.2), but only in intact vegetation. This was mainly due to lower shrub production (Fig. 3.2), presumably because snowberry with its broad, thin leaves is more susceptible to drought than the prairie grasses with their coarse, narrow leaves. In addition, roots of grasses and snowberry are concentrated in the upper soil layers (Johnson 1960, George & McKell 1978) so that plants of both growth forms would directly compete for the available water. This is similar to the grass-shrub interaction in a West African humid savanna (Le Roux et al. 1995) where grasses and shrubs compete for the same water. In other grasslands, shrubs take up water from deeper soil layers than grasses do and therefore woody plants in those grasslands are less affected by low water supply (Knoop & Walker 1985, Weltzin & McPherson 1997, Golluscio et al. 1998).

High water supply in my experiment did not significantly increase total standing crop (Fig. 3.1), perhaps because shrub growth at average and high water supply is more limited by nitrogen than by water.

This is supported by very low N availability under grass-shrub vegetation at one site where N availability was measured by resin extraction (chapter 5.3.3) to explore the method's sensitivity for competition experiments. Water supply in shrub and grass removal plots may have had no significant effect on standing crop because available water and nitrogen were not growth-limiting in the absence of competitors. Total standing crop may also have varied little with water supply because plant growth, especially growth of woody plant, may be strongly influenced by moisture conditions in the preceeding year (Bailey & Wroe 1974) or by moisture very early in the growing season, i.e., before the application of my treatments. It may also be necessary that water deficits accumulate over several years before there is a measurable effect on shrub or grass growth. For example, several years of below-average precipitation on the northern Great Plains during the 1930s severely reduced basal cover of the dominant grass species (Albertson & Tomanek 1965). The general effect of water on plant growth may also have been small because growth was mostly completed before the application of the water treatments. Snowberry is reported to end growth in mid-June (Kirby & Ransom-Nelson 1987). The dominant prairie grasses in the region flower in mid-June to early July (*personal observation*, Johnson 1960). This suggests that although the dry season in the northern Great Plains is in July and August (Walter & Lieth 1967) the effect of water availability on growth may be stronger during the time of peak growth in spring.

Woody and grass transplants showed little response to water availability also in other competition experiments at the same location,

at a location 200 km W and at a location 400 km N of my sites in the same year (J. D. Bakker and D. A. Peltzer, pers. comm.). In these experiments, water availability was also manipulated with rain shelters and controlled water supply. The congruence of results suggests that water is rarely a growth-limiting resource in the northern Great Plains. This is in line with long-term results in an oak savanna in Minnesota where water was growth-limiting in only one out of eight years (Tilman 1990).

Standing crop did not vary with the interaction of water supply and habitat, suggesting that habitat-related variables like soil structure or litter cover had little effect on water availability. This might indicate that the correlation of shrub density with depressions and north-facing slopes may not be linked to consistently higher soil moisture but to flushes of higher soil moisture, e.g. in spring, whereas during the rest of the year, N is the limiting resource (Seastedt & Knapp 1993).

Typically, shrubs and grasses compete for resources, and shrub removal increases grass growth (Scholes & Archer 1997, Li & Wilson 1998, Wilson 1998, chapter 5). Shrub removal in this experiment, however, did not increase grass growth. This may be due to herbicide drift or due to shrubs outside the plots growing roots into the plots.

In conclusion, only very low water supply had a significant effect on grass-shrub interaction in temperate grassland and reduced total standing crop. This suggests that water becomes only rarely a growth-limiting resource for both grasses and shrubs in the northern Great Plains in the later part of the growing period.

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4. THE SELECTIVE EFFECT OF METSULFURON AND SETHOXYDIM ON SHRUBS, GRASSES AND SEDGES

4.1.   ABSTRACT

I tested two herbicides for selective control of established perennial dicots (mostly shrubs) and monocots (grasses and sedges) in native prairie. Metsulfuron applied in four pulses (total 0.2325 kg a.i. ha^{-1}) reduced aboveground dicot mass from 559 to 53 g/m^2 and increased monocot mass from 56 to 87 g/m^2. Sethoxydim applied in three pulses (total 10.433 kg a.i. ha^{-1}) reduced aboveground monocot mass from 40 to 17 g/m^2 without affecting dicot mass. Remaining monocots consisted mostly of sedges (*Carex* sp.). The herbicides were highly selective but high amounts were needed to control established vegetation.

4.2.   INTRODUCTION

Selective herbicides are useful when desired and undesired plants grow closely together, e.g., for the removal of established shrubs from pasture without damaging the grass sward (Bowes & Spurr 1996), for the removal of grasses from prairie shelter belts (L. Als-pach, P.F.R.A., pers. comm.) or for tree plantations to reduce competi-tion from grasses (Woods et al. 1992). Selective herbicides are a good

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alternative when undesirable plants would colonize soil disturbed by mechanical removal (Fairbank et al. 1990, Richardson et al. 1990). High selectivity of herbicides is also advantageous where spray drift might affect natural vegetation or non-target crops (chapter 3, p. 67).

Metsulfuron is a post-emergence systemic herbicide developed for control of herbaceous broadleaf weeds in grain crops (Ahrens 1994). It can be taken up by both roots and leaves and has been used successfully to eliminate several woody species in grassland (Derr 1989, McDaniel et al. 1991, Bowes & Spurr 1996). However, control of woody species in un-disturbed vegetation (Derr 1989, McDaniel et al. 1991) may require more metsulfuron than what is necessary in recently disturbed vegetation (Bowes & Spurr 1996). As a consequence, more metsulfuron may have a more deleterious impact on established grasses.

Sethoxydim is a post-emergence contact and systemic herbicide developed for control of grasses in broadleaf crops such as canola, flax, and legumes (Ahrens 1994). It is taken up primarily through the foliage. The effect of sethoxydim on woody species has not been studied so far.

I examined the effectiveness of metsulfuron and sethoxydim for selective control of dicots (mostly shrubs) and monocots (grasses and sedges) in undisturbed mixed-grass prairie.

4.3.   METHODS

The study was conducted 120 km south of Regina, Saskatchewan, Canada (49°20'N, 104°40'W), in natural mixed-grass prairie (Coupland 1950, Looman 1980). I applied two treatments of herbicide (applied vs control) in factorial combination with two treatments of target growth form (shrubs vs grasses) to four plots in each of two habitats. Habitat was either mixed-grass prairie (*Stipa comata*, *Bouteloua gracilis*, *Agropyron* spp.) with sparse growth of snowberry (*Symphoricarpos occidentalis*, 5-15% cover) or snowberry brush (95% cover) with grasses and sedges (5-10% cover) underneath the canopy. The plots (2 m × 2 m) were established in the first week of May 1996 by trenching to a depth of 15 cm to confine roots within plots. In each habitat, one plot was treated with metsulfuron to kill dicots (i.e., snowberry), one plot was treated with sethoxydim to kill perennial monocots (i.e., grasses and sedges), and two plots received no herbicide (one as a control for dicots and one as a control for monocots). The experimental design was completely replicated at five sites within a 1 km^2-area. Thus, my experiment was a blocked-factorial design with the three factors herbicide, growth form, and habitat and blocked on sites. Plots were randomly assigned to herbicide × target growth form combinations within each habitat.

I used 7.5 g a.i./ha of metsulfuron methyl (*Ally*, DuPont, Canada) on May 27, and 75 g a.i./ha on June 11, June 26, and July 20, 1996 to kill dicots. I used 0.497 kg a.i./ha of sethoxydim (*Poast*, BASF, Canada) on June 15, and 4.968 kg a.i./ha on June 26 and July 20, 1996 to

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kill perennial monocots. Since I was mostly interested in the effect of sethoxydim on perennials, I used 45.6 g a.i./ha of clethodim (*Select*, Rhône-Poulenc, Canada) on May 27 to kill annual monocots so their biomass would not be included with the perennials' after harvest in the fall. Metsulfuron and sethoxydim concentrations were increased after the first application because the initial concentrations appeared to be ineffective based on visual inspection 2-3 wk after application. Herbicide treatments were repeated until mortality was >90%, resulting in three applications of sethoxydim and four applications of metsulfuron.

Metsulfuron was mixed with 1.5 m^3 water/ha and applied uniformly with a 12-L backpack sprayer from above the bush canopy. Snowberry forms a dense canopy above the monocots, therefore, clethodim and sethoxydim were applied underneath the bush canopy. To ensure uniform coverage I mixed clethodim and sethoxydim with 7.5 m^3 water/ha. All herbicides were mixed with a surfactant (sodium hexametaphosphate) at 2 g/L and blue food colouring to control spray coverage.

Standing crop of the target growth form and the remaining vegetation (non-targets) within each plot was harvested from one 0.15 m × 1.0 m subplot, 1 m from a plot edge during August 28-29, 1996 and dried at 75° C to constant mass.

I determined the effect of each herbicide on standing crop of targets with an analysis of variance for blocked-factorial designs (Lorenzen & Anderson 1993). Factors were site (random effect), habitat, herbicide, and growth form (fixed effects). To determine the effect of each herbicide on the remaining vegetation I used remaining standing crop as dependent variable.

4.4. RESULTS

Averaged over habitats, metsulfuron significantly reduced dicot standing crop to 9% of that in control plots (Fig. 4.1a), but sethoxydim did not significantly reduce monocot standing crop (Fig. 4.1b, herbicide × growth form interaction: $F_{1,4}$ = 9.57, P = 0.04). The habitat × herbicide and habitat × herbicide × growth form interactions were not significant, suggesting that the herbicides had similar effects in both prairie and brush habitat. Shrub removal significantly increased the standing crop of grasses (Fig. 4.1a; a-priori means contrasts: t = 4.85, P = 0.02), but the removal of grasses had no effect on the stand-
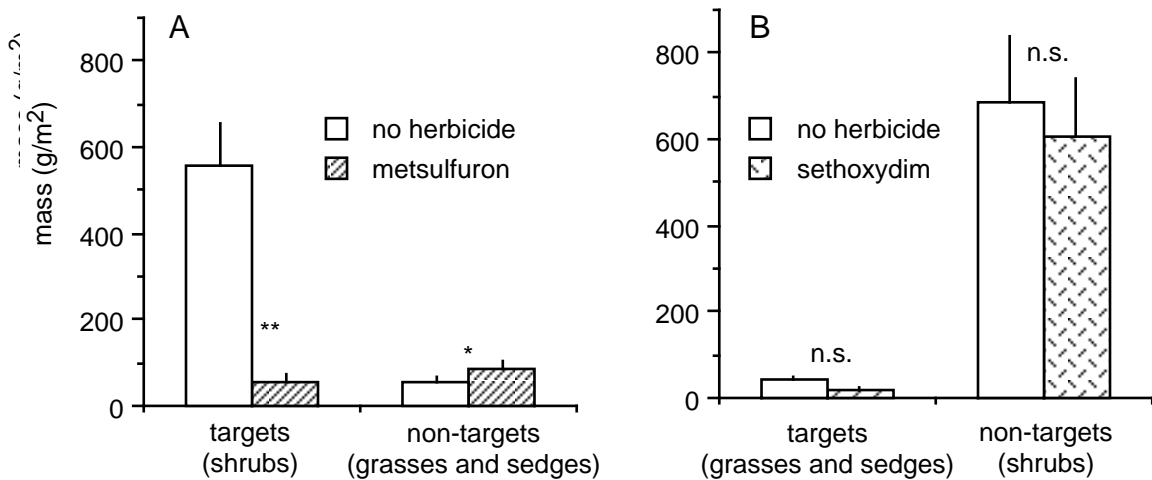
FIG. 4.1. Effect of metsulfuron (a) and sethoxydim (b) on standing crop of target and non-target growth forms. Bars represent means averaged over habitat treatments and sites, error bars indicate 1 SE (n = 10). Asterisks show significant differences between sprayed and unsprayed treatments (a-priori means contrasts, n.s.: P > 0.05, *: $P \leq$ 0.05, **: $P \leq$ 0.01).

ing crop of shrubs (Fig. 4.1b), resulting in a significant herbicide ×
growth form interaction ($F_{1,4}$ = 24.4, P = 0.008).

4.5.   DISCUSSION

Both herbicides were selective in the sense that they tended to
reduce the mass of the target growth form without reducing the mass of
non-target growth forms (Fig. 4.1). The amounts of herbicides required
to achieve this level of control, however, were up to 30 times higher
than recommended doses and much higher than the amount used by Bowes &
Spurr (1995) to achieve 100% mortality in similar vegetation and the
same geographical region. The large difference between Bowes & Spurr's
and my experiment is consistent with high variability of metsulfuron
potency in bioassays on *Brassica rapa* (Streibig et al. 1995). Higher
doses of metsulfuron may be required to control shrubs in undisturbed
vegetation (Derr 1989, McDaniel et al. 1991, Bowes & Spurr 1996). Timing
of application seems important for degree of shrub control, but differs
among species (Derr 1989, McDaniel et al. 1991). I started spraying as
soon as shrub leaves expanded, which may have been too early. Shrubs
consisted mostly of snowberry, a clonal plant with tillers connected by
an extensive rhizome system (Pelton 1953). Sprayed snowberry tillers may
have obtained resources through roots below 15 cm soil depth from un-
damaged tillers outside the plot. Therefore it may be more effective to
apply treatments to the whole clone.

Monocots were not significantly reduced by sethoxydim even though I applied 21 times the recommended dose (Fig. 4.1b). About 90% of the remaining plant mass were sedges (*Carex* spp.). The abundance of sedges appeared to have increased after the herbicide application from initially 10-15% cover in prairie. The effect of sethoxydim on sedges could not be quantified because sedges were not sampled separately from grasses. The high selectivity of sethoxydim in favour of sedges could be applied to stop invasion of exotic grasses into northern natural sedge communities (Wein et al. 1992).

The removal of shrubs increased monocot mass (Fig. 4.1a). The enhanced growth of grasses after shrub control is likely due to reduced competition for nitrogen and light (Harrington & Johns 1990, McDaniel et al. 1991, Van Auken et al. 1992, Wilson 1993b, chapter 5). The reduction of grass standing crop to 42% of its initial mass, however, did not affect shrub mass (Fig. 4.1b, see Felker et al. 1984, Aerts et al. 1991, Woods et al. 1992). This may indicate that shrubs in my experiment were little affected by grass competition.

The low impact of sethoxydim and metsulfuron on non-target growth forms make these herbicides suitable for selective control where mechanical damage or soil disturbance should be avoided. However, the amount of herbicide needed for effective control may vary strongly among locations and years, and treatments may have to be applied to the whole shrub clone.

5. COMPETITIVE EFFECTS OF INVADING SHRUBS AND INVADED GRASSES IN THE NORTHERN GREAT PLAINS

5.1.   ABSTRACT

Differences in competitive effects among species may be related both to differences in mass and differences in growth forms. I tested whether the competitive effect of invading woody species on invaded grasses and on resources was related to mass or growth form. I conducted the experiment in mixed-grass prairie in western Canada for two years. I measured the effect of woody species on grasses as the increase of aboveground net primary productivity (ANPP) of grasses when shrubs (*Symphoricarpos occidentalis*) were removed. I measured the effect of grasses on woody species as the increase of shrub ANPP when grasses were removed. In prairie where shrub invasion was recent and shrub abundance low, shrubs suppressed grasses as much as grasses suppressed shrubs, even though shrubs had 6 times more standing crop. Shrubs reduced available soil nitrogen more strongly than grasses did, but shrubs and grasses did not differ in their effects on light or soil water. In brush, however, where shrub invasion has continued for a longer time and shrub standing crop was 37 times grass standing crop, shrubs suppressed grasses strongly, whereas grasses did not suppress shrubs. Thus, as invasion progressed, the interaction between shrubs and grasses changed from symmetric to asymmetric. On a per-gram basis, however, shrubs had

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smaller effects on light attenuation, nitrogen uptake, and water uptake
than grasses, suggesting that the competitive effect of invading shrubs
is related mostly to shrub size. In spite of their smaller per-gram
effects on resources, woody stems allow shrubs to accumulate more mass
and height, and to eventually displace grasses in spite of the grasses'
greater per-gram effects on resources.

5.2.   INTRODUCTION

The invasion of native grasslands by woody species is a global
pattern, occurring not only in subtropical savannas (Scholes & Archer
1997) but also in temperate steppes (Blackburn & Tueller 1970, Archibold
& Wilson 1980, van Auken & Bush 1989, Fuller & Anderson 1993, Knight et
al. 1994). Elimination of undesirable woody species from, for example,
pastures is often difficult or unsuccessful (e.g., Niering & Goodwin
1974, Bragg & Hulbert 1976, Svedarsky et al. 1986, Archer 1989, Rich-
ardson et al. 1990, Harrington & Johns 1990, Bock & Bock 1992, Brown
1995, Bowes & Spurr 1996, chapter 4), showing that our knowledge about
tree-grass interactions is still insufficient.

In both grasslands and forests, competition occurs across a wide
range of productivity (Wilson 1991, Reader et al. 1993, Wilson 1998).
Competition generally shifts from belowground to aboveground as produc-
tivity increases and the aboveground resource (light) becomes more
limiting than the belowground resources (water and nutrients) (Wilson

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1993a,b, Wilson & Tilman 1993, 1995). Consequently, the invasion of woody species into grasslands may be related to changes in the relative availabilities of above- and belowground resources.

Competition between plants is the product of effects on and responses to their neighbours, generally through resources (Goldberg 1990). Competitive responses (the extent to which plants are suppressed by neighbours) differ little between trees and grasses (Wilson 1998). Competitive effects (the extent to which plants suppress their neighbours) generally increase with plant size (Grace 1985, Goldberg & Landa 1991) and are often larger in more productive communities (Grace 1993, Wilson 1999). Thus, trees may replace grasses because trees can accumulate more mass.

Competition for aboveground resources (light) is fundamentally different from competition for belowground resources (nutrients and water) because light is supplied along one spatial dimension, whereas soil resources are generally replenished along three spatial dimensions (Reynolds & Pacala 1993, Huisman & Weissing 1994, Schwinning & Weiner 1998). Therefore, specific allocation patterns enable growth forms to compete better either for light or for soil resources (Tilman 1990). For example, the tall stature of trees allows them to preempt light and their woody tissue makes them more nitrogen-efficient. Grasses with their fibrous roots, however, may be expected to take up more available soil resources (Caldwell & Richards 1986). Thus, trees may replace grasses not only because trees have more mass, but also because their allocation pattern allows them to preempt light and use less nutrients.

Calculating per-gram competitive effects (competitive effect divided by biomass) permits the separation of the effect of size and the effect of growth form on competitive effects (Goldberg 1990). Contrasting growth forms should have similar per-gram effects if competitive effects are only related to mass. Variation in per-gram effects would suggest that growth form contributes to competitive effects. Thus, grasses are expected to have larger per-gram effects on soil resources because of their long fibrous roots, whereas trees are expected to have larger per-gram effects on light because of their tall stature.

Per-gram effects do not seem to differ among species with a similar growth form or among seedlings of different herbaceous growth forms (Goldberg 1987, Goldberg & Fleetwood 1987, Peart 1989, Rösch et al. 1997). However, a native summer annual had larger per-root length effects than introduced winter annuals (Gordon & Rice 1993), established trees had larger per-gram effects than shrubs (Harrington & Johns 1990), and *Quercus* seedlings had larger per-gram shoot effects than grass seedlings (Welker et al. 1991). Thus, allocation patterns seem to contribute to competitive ability when the competitors are sufficiently different. This suggests that seedlings of woody species have initially little competitive advantage over grasses. As woody species increase in mass and height, however, they should become more competitive due to mass and growth form.

I explored the contributions of mass and growth form to competitive effects by comparing the effects of shrubs and grasses on each other and on three important resources, light, nitrogen (N), and water.

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Second, I examined whether competitive effects change during invasion by comparing the competitive effects between shrub stands with high and low stem density.

5.3.   METHODS

5.3.1. Location, design and site preparation

The experiment was conducted in the northern Great Plains (49°18'N, 104°38'W), 120 km south of Regina, Saskatchewan, Canada, in natural mixed-grass prairie (Coupland 1950, Looman 1980) in 1996 and 1997. I worked at the edge of snowberry stands (*Symphoricarpos occidentalis*). Inside the stands that I refer to as "brush" was dense snowberry (40-70 cm tall) with a sparse grass understorey (grass canopy at 10-30 cm height). Grasses in brush were mostly *Stipa viridula*, *S. curtiseta*, and *Agropyron subsecundum*. Outside the stands were sparse snowberry stems (10-30 cm tall) scattered in grassland (canopy at 10-30 cm height) that I refer to as "prairie". Prairie was dominated by *Stipa* spp. (including *S. comata*), *Agropyron subsecundum*, *Bouteoua gracilis*, *Koeleria gracilis*, and *Poa* spp.

In these two habitats, I applied four removal treatments to plots. Removal treatments were I: intact vegetation, i.e., no vegetation removed; S: shrubs removed (including forb removal); G: grasses removed (includes sedge removal); and SG: both shrubs and grasses removed ("cleared plot"). Forbs and sedges had very low abundance at my sites.

No other growth forms occurred. There were two intact-vegetation plots in each habitat, one serving as a reference for grasses and a second as an independent reference for shrubs. Thus, there were five plots in each habitat. Differences between vegetation and resources among plots allowed me to separate the effects of shrubs and grasses on each other and on resources.

The plots, 2 m × 2 m, were established in the first week of May 1996 by trenching to a depth of 15 cm to isolate roots within plots. Trenching was repeated in May 1997 to cut newly grown roots. Plots were randomly assigned to treatment combinations within each habitat. The experiment was completely replicated at five sites within a 1-km^2 area.

I used herbicides to remove shrubs and grasses. I used 7.5 g/ha of metsulfuron (*Ally*, DuPont, Canada) on May 27 and 75 g/ha on June 11, June 26 and July 20, 1996 and May 30 and July 3, 1997 to kill shrubs and forbs (Ahrens 1994, Bowes & Spurr 1995, 1996). I used 190 mL/ha cleth-odim (*Select*, Rhône-Poulenc, Canada) on May 27, 1996 and May 9, 1997 to kill annual grasses. I used 2.7 L/ha sethoxydim (*Poast*, BASF, Canada) on June 15 and 27 L/ha sethoxydim on June 26 and July 20, 1996 and May 9 and 30, 1997 to kill perennial grasses (Ahrens 1994). I carefully applied 3.6 g/L glyphosate (*RoundUp*, Monsanto, Canada) locally on June 2, 1997 to kill sedge patches. Sethoxydim and metsulfuron concentrations were increased after the first application because the initial concen-tration appeared to have been ineffective on visual inspection after 3 wk. Herbicide treatments were repeated until mortality was close to 100%. Dead plants remained in place and continued to cast shade.

Metsulfuron was added to ≈0.15 L/m^2 water and clethodim and sethoxydim were added to ≈0.75 L/m^2 water. A surfactant (Na-hexameta-phosphate, 2 g/L) and blue food colouring were added to the mixtures. I applied the mixtures with a 12-L backpack sprayer. In prairie, herbicides were applied uniformly from above the vegetation canopy. In brush, snowberry forms a dense canopy above the grasses and therefore, metsulfuron was applied from above the brush canopy, whereas clethodim and sethoxydim were applied below the brush canopy. We did not add any water to intact plots, because the amounts of water applied with the herbicides to plots was negligeably small compared to rainfall.

5.3.2. Effects of shrubs and grasses on each other

I assessed the effect of one growth form (neighbour growth form) on the other (target growth form) by comparing the aboveground net primary production (ANPP) of the target growth form in intact vegetation with the ANPP of the target growth form in vegetation where the neighbour growth form had been removed.

I assessed the per-gram effect of growth forms on each other by calculating regressions of target growth form ANPP on standing crop of the neighbour growth form. Grass was considered as a target growth form in one intact-vegetation plot and in the shrub-removal plot in each habitat at each site. Shrubs were considered as a target growth form in the other intact-vegetation plot and in the grass-removal plot in each habitat at each site.

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I measured grass ANPP in plots with grasses as target growth form as the mass of current-year culms and blades with green bases plus current year's litter. Grass litter remains attached for ≈0.5 yr (Sims & Coupland 1979). I measured shrub ANPP in plots with shrubs as target growth form as the total mass of current-year shoots (herbaceous stems and twigs with their attached leaves) plus shrub litter from litter traps. Ignoring the radial growth of older stems resulted in <5% under-estimation of actual stem mass (calculated from Table 2.2).

I measured grass standing crop in each plot as the mass of culms and blades with green bases. I measured shrub standing crop in each plot as the total mass of live shoots (woody stems + herbaceous stems with their attached leaves).

Shoots and litter were harvested during August 28-29, 1996 and September 4-8, 1997. Grass shoots, shrub shoots and grass litter were harvested from one 1 m × 15 cm strip in each plot. The strip was ≥0.5 m from the plot edge. In early spring, loose grass litter in each plot with grasses as target growth form (one half of the intact-vegetation plots and all shrub-removal plots) had been removed by hand. I did not wish to disturb the plots by tearing out attached litter, so I spray-painted the remaining attached litter. Painted litter was removed after harvest so that only litter produced during the current growing season was collected. Shrub litter was collected in three litter traps (10 cm diameter, 5 cm deep) per plot in each plot with shrubs as target growth form (one half of the intact-vegetation plots and all grass-removal plots) during the growing season each year. After sorting, shoots and

litter were dried at 70°C to constant mass and weighed. A hailstorm on August 28, 1997 removed almost all shrub leaves and many twigs. There-fore, I separated the material in the traps into leaves, current-year stems and older stems, calculated their respective mass per 0.15 m^2 and added the result to the mass measured in the strips.

5.3.3. <u>Effects of grasses and shrubs on resources</u>

I tested whether growth form effects on resources differed between habitats by comparing resource levels in each removal treatment. I assessed the per-gram effect of each growth form on resources by com-paring the ratios of resource consumption:standing crop. I considered three resources: light, available soil nitrogen, and soil water.

I measured light with a 40-cm integrating photosynthetic photon flux (PPF) probe (Sunfleck Ceptometer, Decagon Devices, Pullman, Wash-ington, U.S.A.) 1-3 cm above the soil surface perpendicular from all plot edges and above the canopy on July 18 and August 24, 1996 and July 14, 1997, within two hours of solar noon on a cloudless day. Light meas-urements in 1996 did not differ significantly between July and August. Therefore, I analyzed in greater detail only 1996 data from August and restricted light measurements in 1997 to one date. In 1996 I also meas-ured light at the top of the grass foliage canopy (≈ 30 cm above ground). Again, measurements were similar in both months and only August data is presented. On 1996-08-24, maximum PPD was 1434 μmol photons m^{-2}

s^{-1} and on 1997-07-14, maximum PPD was 1723 µmol photons m^{-2} s^{-1}. I cal-culated light penetration for each plot as the mean of the four PPD measurements divided by the PPD above the canopy · 100%. Light attenua-tion by vegetation was taken as an index of light consumption and calcu-lated as 100% - light penetration.

In each plot I collected mineral N with ion-exchange resin bags (3 cm × 3 cm), each containing 2 cm^3 dry mixed-bed (anionic and cat-ionic) 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 cations (Binkley & Hart 1989). Thus, the total ion-exchange capacity of each bag was 3 mmol (3.3 mol/m^2). Amounts of cations and anions in soil leachate and throughfall of temperate forests range from 16 to 1028 mmol m^{-2} yr^{-1} (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 the measure-ment 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.

Bags were inserted 10 cm into the soil on May 22, 1996 and May 2, 1997 and removed on August 27, 1996 and August 28, 1997. The amount of N collected by the resin was assessed by removing the resin from air-dried retrieved bags and extracting the resin in 30 mL 2 mol/L NaCl ·

0.1 mol/L HCl (Giblin et al. 1994) for 1 h. Nitrate in the extract was converted to ammonium by reduction with $TiCl_3$ and ammonium was converted to ammonia by increasing the pH of the solution with 10 mol/L NaOH. The concentration of N in the extract was then measured using an ion-selective electrode (Orion, Boston, Massachusetts, U.S.A.). I added known amounts of nitrate and ammonia to unused bags to determine an extraction rate ($N_{extracted}$ (mol/L) = 0.9618 N_{added} (mol/L) + 0.0071, R^2 = 0.92, n = 48). I calculated actual N uptake of bags used in the field by applying the extraction rate equation to amounts of extracted N (Köchy & Wilson 1997).

I calculated net N uptake in each vegetated plot in each habitat and site as [N on resin in the cleared plot] - [N on resin in each vegetated plot]. Results did not change qualitatively when uptake was standardized, i.e., divided by the resource level in cleared plots.

I measured soil water from three soil cores (2 cm diameter, 10 cm deep) per plot on May 27, July 18-20 and August 27, 1996 and on May 29, June 23, July 14, and September 8, 1997. Soil from the three cores was mixed and a ≈40 cm^3 soil subsample was dried at 70°C to constant mass and weighed. Soil water is expressed as g water/g dry soil · 100%. The largest differences of soil water among plots were measured in late August 1996 and mid July 1997. Therefore, I restricted statistical comparisons and calculation of net water uptake to these dates.

I calculated net water uptake in each vegetated plot in each habitat and site as [% water in the cleared plot] - [% water in each vegetated plot]. Results did not change qualitatively when uptake was

standardized, i.e., divided by the resource level in cleared plots.

5.3.4 <u>Statistics</u>

I examined the effectiveness of the removal treatments by com-
paring separately for grass and shrub standing crop the four removal
treatments (I, S, G, SG) among each other and between habitats and years
with analysis of variance (ANOVA) for block-factorial designs. Standing
crop of both growth forms differed most strongly among removal treat-
ments in the second year (1997, Fig. 5.1, p. 95). For all data I per-
formed statistical tests separately for each year and as well as for
both years, where year was treated as an additional factorial effect in
ANOVAs and analyses of covariance (ANCOVAs). The trends of the results
were similar in each case, therefore I present results only from the
second year.

In order to test whether neighbour removal affected target ANPP
I considered four of the removal treatments (the two intact-vegetation
treatments, the shrub-removal treatment and the grass-removal treatment)
as two orthogonal factors with two levels each. One factor was target
growth form (shrubs or grasses) and the other factor was neighbour
removal (intact vegetation or the other, neighbour growth form removed).
Thus, the combination shrub target growth form - intact vegetation was
represented by one intact-vegetation plot, the combination shrub target
growth form - neighbours removed was represented by a grass removal

plot, the combination grass target growth form - intact vegetation was represented by the other intact-vegetation plot and the combination grass target growth form - neighbours removed was represented by a shrub removal plot. This arrangement allowed me to compare with an ANOVA for a block-factorial design the ANPP of shrubs in intact vegetation with the ANPP of shrubs without neighbours and the ANPP of grasses in intact vegetation with the ANPP of grasses without neighbours.

I tested whether grasses and shrubs differed in their per-gram effects on each other by regressing grass ANPP on shrub standing crop and shrub ANPP on grass standing crop using ln-transformed data. Analyses of covariance had shown that regressions did not differ significantly between habitats.

I compared the effect of the four removal treatments (I, S, G, SG) on light penetration, available soil N and soil water between habitats with ANOVA for block-factorial designs. When there was a significant habitat × removal interaction, I determined which removal treatments differed between habitats by making four orthogonal contrasts (one for each removal treatment). Then I tested for each habitat which removal treatments differed from each other by using the simple or linear contrasts described in Table 5.1. When there was a significant removal treatment effect, but no significant habitat × removal interaction, I compared removal treatments across habitats using the same contrasts (Table 5.1). Since these contrasts were planned comparisons, I used a significance level of $\alpha = 0.05$ for each comparison.

I compared light attenuation, N uptake, and water uptake per

Table 5.1. A-priori comparisons using contrasts to answer specific
  questions when the effect of removal treatments or the habitat ×
  removal treatment interaction was significant. Treatments combined for
  linear contrasts are bracketed. Removal treatments: I: intact vegeta-
  tion, S: shrubs removed, G: grasses removed, SG: shrubs and grasses
  removed.

Contrast	Question
① (I, S, G) vs SG	Does vegetation affect resource levels at all? Yes ⇒ ②
② (S, G) vs I	Does removing a growth form affect resource levels in intact vegetation? Yes ⇒ ③
③ S vs G	Do grasses and shrubs have similar effects on resource levels ? Yes ⇒ ④⑤
④ S vs I	Do shrubs affect resource levels in intact vegetation?
⑤ G vs I	Do grasses affect resource levels in intact vegetation?

gram biomass among intact vegetation, grasses, and shrubs and between

habitats. I calculated per-gram consumption for each plot as resource

consumption divided by plot standing crop. I then compared the per-gram

consumption among intact vegetation (no removal), shrubs (grass re-

moval), and grasses (shrub removal) with an ANOVA for block-factorial

design and using planned comparisons analogous to tests 3-5 in Table

5.1.

I also calculated the per-gram effects as resource consumption divided by target standing crop, i.e., instead of using plot standing crop I used shrub standing crop for shrub consumption and grass standing crop for grass consumption. These results did not differ qualitatively from the ones based on plot standing crop. Therefore, I present only results based on plot standing crop.

My experiment was completely factorial because all possible treatment combinations occurred. The results were therefore analyzed with ANOVAs for blocked-factorial designs with sites as random effect blocks (Lorenzen & Anderson 1993). Habitat and removal treatments were fixed effects. The habitat treatments were considered randomized within each site. All removal treatments, including target growth form × neighbour-removal treatments were randomized within each habitat. The main or interaction effects of habitat and removal treatment and the main or interaction effects of habitat, target growth form, and neighbour-removal treatments were tested with their interaction effect with site as the error term in ANOVA (Lorenzen & Anderson 1993). My design is sometimes also called a blocked factorial split-plot design where the main plots are habitats and the split-plots are removal treatments or target growth form × neighbour-removal treatments (Snedecor & Cochran 1989).

Standing crop, ANPP, and light attenuation data were ln-transformed and available soil N data were square-root transformed to meet assumptions of homoscedasticity and normality. All statistics were calculated with JMP for Macintosh (version 3.2.1, SAS Institute 1997).

5.4.   RESULTS

5.4.1. Treatment effects on standing crop

Herbicide application caused significant variation of shrub and grass standing crop among removal treatments, across habitats and years (Fig. 5.1; grasses: $F_{3,12}$ = 73.4, P < 0.0001; shrubs: $F_{3,12}$ = 107, P < 0.0001). Herbicides significantly reduced shrub abundance in shrub-removal plots (Fig. 5.1; S vs I: t = 11.7, P < 0.0001) and grass abundance in grass-removal plots (Fig. 5.1; G vs I: t = 6.25, P < 0.0001). Herbicides did not reduce the abundance of the remaining growth form (grass standing crop: S vs I: t = 4.25, P(one-tailed) = 0.9994; shrub standing crop: G vs I: t = 0.187, P(one-tailed) = 0.6). Herbicides significantly reduced shrub and grass standing crop in cleared plots (SG) over any other removal treatment (Fig. 5.1; simple means comparisons, SG vs I, S, G: shrubs: all $P \leq 0.02$, grasses: all $P \leq 0.001$). Thus, the removal treatments had the desired effects.

Shrub standing crop across removal treatments and years was significantly higher in brush than in prairie ($F_{1,4}$ = 11.7, P = 0.03), whereas grass standing crop was significantly higher in prairie than in brush (Fig. 5.1; $F_{1,4}$ = 29.6, P = 0.006).

Shrub and grass standing crop, across habitats and removal treatments, were each significantly higher in the first than in the second year (shrubs: $F_{1,4}$ = 24.6, P < 0.0001; grasses: $F_{1,4}$ = 348, P < 0.0001). Differences among removal treatments tended to be larger in the

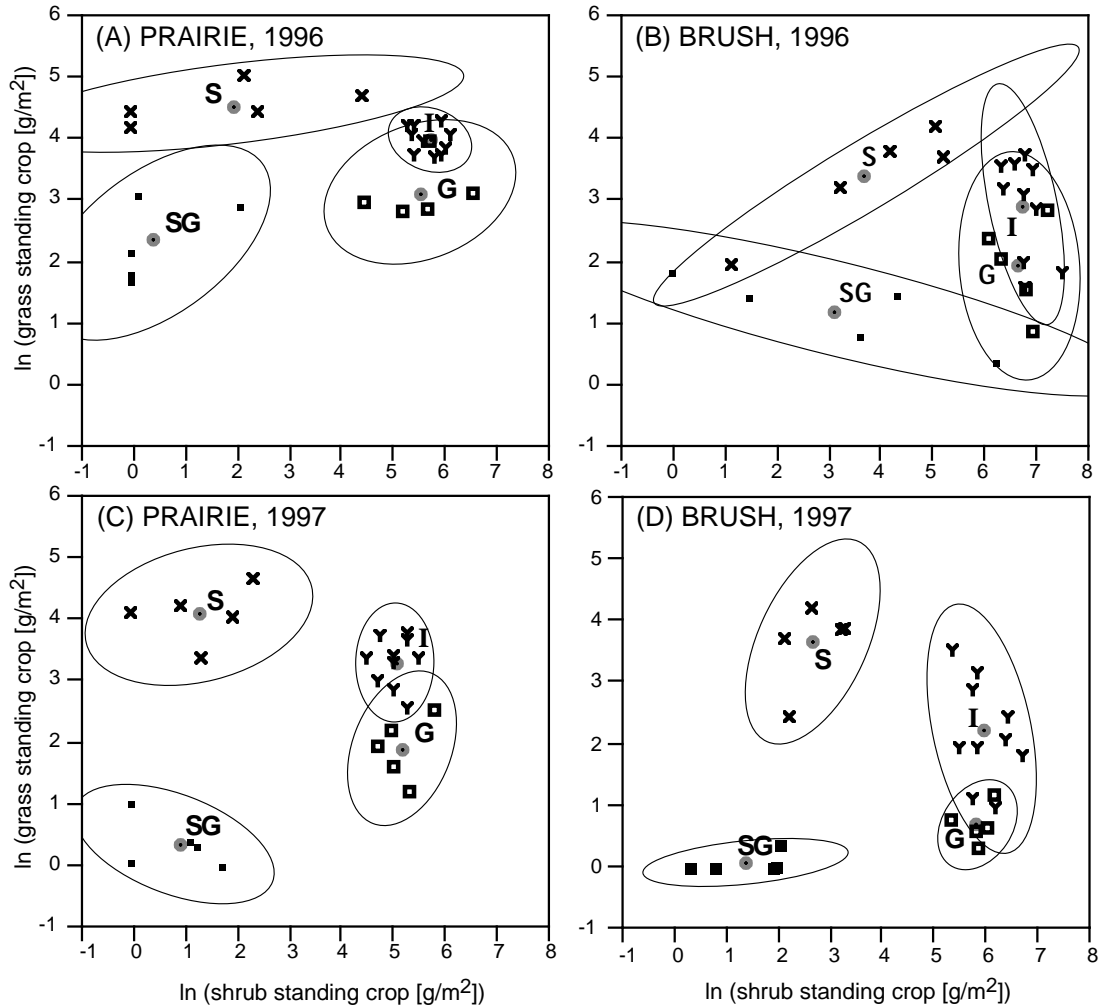FIG. 5.1. Effectiveness of four growth form removal treatments (I, S, G, SG), based on standing crop in two habitats (prairie, brush) over two years. I (**Y**): grasses and shrubs at natural abundance, S (×): shrubs removed; G (□): grasses removed; SG (■): shrubs and grasses removed. Grey dots indicate the mean for each treatment. Ellipses represent the 95%-confidence area (bivariate normal density) for each group mean.

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second year, but the removal treatment × year interaction was signifi-
cant only for grasses (Fig. 5.1; $F_{3,12}$ = 4.94, P = 0.02). For the sake
of clarity and brevity I report further results only for the second year
(1997).

5.4.2   Effects of shrubs and grasses on each other

In general, shrubs had significantly higher aboveground net
primary productivity (ANPP) than grasses (Fig. 5.2; $F_{1,4}$ = 22.0, P =
0.009). Across neighbour-removal treatments, shrub ANPP in prairie was
lower than in brush, but not significantly. Grass ANPP in prairie was
significantly higher than in brush (Fig. 5.2; habitat × target growth
form interaction: $F_{1,4}$ = 23.7, P = 0.008; prairie vs brush: shrubs: t =
2.87, P = 0.06; grasses: t = 4.02, P = 0.03). Habitat had no signifi-
cant main effect on ANPP (P = 0.6).

Removing the neighbour growth form generally increased ANPP of
the target growth form (Fig. 5.2; $F_{1,12}$ = 85.5, P = 0.0008). A signifi-
cant interaction among habitat, remaining growth form and neighbour
removal treatments (Fig. 5.2; $F_{1,4}$ = 20.4, P = 0.01) allowed me to com-
pare means of shrub and grass ANPP between intact vegetation and vegeta-
tion where one growth form had been removed, in both prairie and brush.
Shrub removal significantly increased grass ANPP in both habitats
(prairie: t = 8.15, P = 0.001; brush: t = 13.6, P = 0.0002); grass
removal significantly increased shrub ANPP in prairie (t = 4.16, P =

0.01) but not in brush (t = 0.54, P = 0.6). Across habitats, shrub

removal significantly increased grass ANPP but grass removal did not

increase shrub ANPP (removal × remaining growth form interaction: $F_{1,4}$ =

11.5, P = 0.03; means comparisons: shrubs: t = 1.31, P = 0.3; grasses:

t = 6.11, P = 0.009).
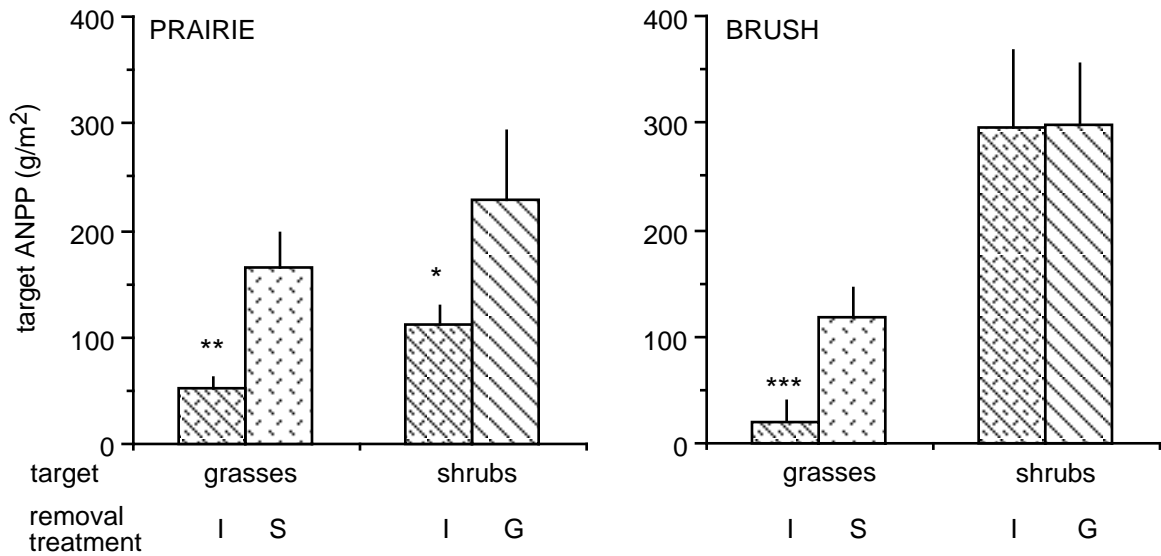
FIG. 5.2. Effect of removal and habitat treatments on aboveground net
primary productivity (ANPP) of either shrubs or grasses (targets). I:
intact grass-shrub vegetation; G: grasses removed; S: shrubs removed.
Bars represent means of five sites + SE. Significant differences
between removal treatments for each growth form in each habitat are
indicated by asterisks (simple linear contrasts on log-transformed data;
*: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$).

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ANPP of both growth forms decreased as standing crop of the con-
trasting growth form increased (Fig. 5.3; grasses: $F_{1,18}$ = 15.7, P =
0.001; shrubs: $F_{1,18}$ = 7.39, P = 0.01). The regression slopes did not
differ significantly from each other, i.e., the regression lines can be
assumed to be parallel with a common slope of -0.38 (Zar 1996). The
intercept of the shrub regression was significantly higher than that of
the grass regression (comparison of regression elevations, Zar 1996).
Back-transformation of the log-log regressions results in grass ANPP =
262 · shrub standing crop$^{-0.38}$ and shrub ANPP = 361 · grass standing
crop$^{-0.38}$, suggesting that grass standing crop had a 361/262 = 1.4 times
larger per-gram effect than shrub standing crop.
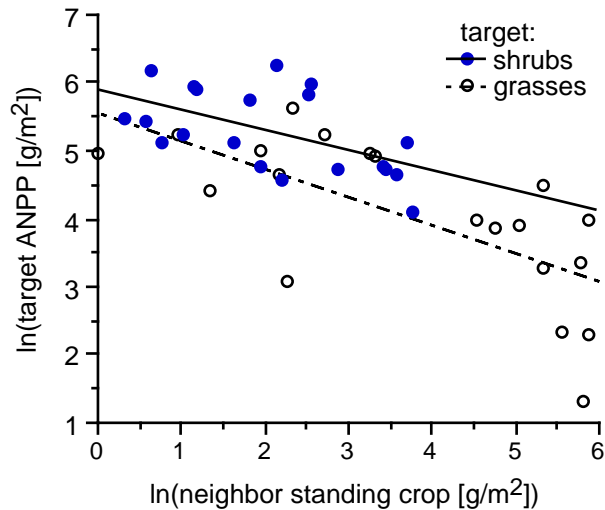
FIG. 5.3. Aboveground net primary productivity (ANPP) of targets
(grasses and shrubs) as a function of the standing crop of the con-
trasting growth form. Grasses: R^2 = 0.47, ln(y) = 5.57 − 0.411 ln(x),
shrubs: R^2 = 0.29, ln(y) = 5.89 − 0.294 ln(x).

5.4.3. Effects of shrubs and grasses on resources

Light penetration to the grass canopy (Fig. 5.4a) was signifi-cantly higher in prairie than in brush ($F_{1,4}$ = 104, P = 0.0004). Shrub removal significantly increased light penetration to the grass canopy (t = 7.82, P < 0.0001), whereas grass removal did not increase light penetration to that level (removal effect: $F_{3,12}$ = 38.7, P < 0.0001). A significant habitat × removal interaction ($F_{3,12}$ = 5.62, P = 0.005) occurred because shrubs had a stronger effect on light in brush than in prairie. Light penetration in cleared plots was <100% because of remaining dead stems and litter in the plots.

Light penetration to the ground (Fig. 5.4b), across removal treatments, was significantly higher in prairie than in brush ($F_{1,4}$ = 65.2, P = 0.001) and, across habitats, varied significantly among removal treatments ($F_{3,12}$ = 188, P < 0.0001). A significant interaction between habitat and removal treatment ($F_{3,12}$ = 3.72, P = 0.04) allowed me to compare means of light penetration among removal treatments separ-ately for each habitat. In both habitats, shrub and grass removal increased light penetration similarly (prairie: t = 2.59, P = 0.03; brush: t = 5.47, P = 0.0002).

Available soil N (Fig. 5.4c), across habitats, varied signifi-cantly with removal treatment ($F_{3,12}$ = 88.4, P < 0.0001). Shrub removal significantly increased available soil N (t = 4.89, P = 0.0004), but grass removal did not. Although trends among removal treatments did not differ significantly between prairie and brush (P = 0.2), a significant
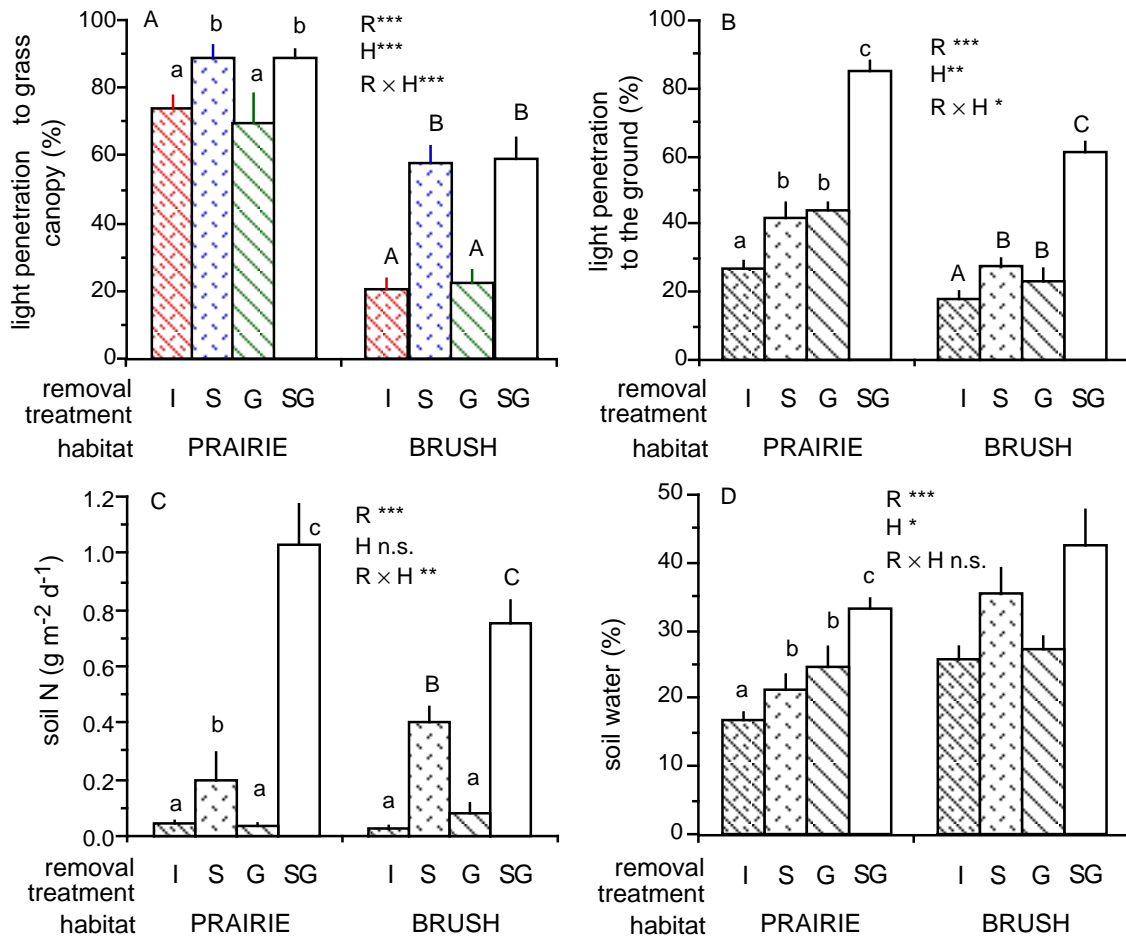
FIG. 5.4. Effect of removal treatment (R) and habitat (H) on light penetration to the grass canopy (c. 30 cm above ground) (a), to the ground (1-3 cm above soil surface) (b), available soil nitrogen (10 cm depth) (c) and soil water (0-10 cm) (d). Removal treatments: I: intact shrub-grass vegetation; S: shrubs removed; G: grasses removed; SG: shrubs and grasses removed. Bars represent means + SE (I: n = 10; S, G, SG: n = 5). For each resource, removal treatments that differ significantly from each other are marked with different letters above the bars of the prairie treatment. If R × H was significant, significantly different removal treatments within a habitat are indicated in both habitats; removal treatments that differ significantly between habitats are indicated by uppercase letters in the brush treatment. Results of ANOVA: n.s.: $P > 0.05$, *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.

interaction between habitat and removal treatments (Fig. 5.4c; $F_{3,12}$ = 6.74, P = 0.007) revealed that available soil N in vegetation without shrubs was lower in prairie than in brush (t = 3.71, P = 0.004), whereas available N in cleared plots (SG) was higher in prairie than in brush (t = 2.22, P = 0.048). On the other hand, available soil N in vegetation without grasses (G) and in intact vegetation (I) did not differ significantly between habitats (P > 0.3).

Soil water (Fig. 5.4d), across removal treatments, was significantly lower in prairie than in brush ($F_{1,4}$ = 21.0, P = 0.01) and, across habitats, varied significantly among removal treatments ($F_{3,12}$ = 23.3, P < 0.0001). Soil water was significantly lower in intact vegetation than in vegetation where one growth form had been removed (t = 3.63, P = 0.003) but did not differ between shrub and grass removal (t = 1.08, P = 0.3). There was no significant habitat × removal treatment interaction (P = 0.1).

5.4.4. Per-gram effects on resources

Light attenuation (100% - light penetration in each plot) per gram standing crop (Fig. 5.5a), across habitats, varied significantly among removal treatments ($F_{2,8}$ = 66.3, P < 0.0001). A significant interaction between habitat and removal treatments ($F_{2,8}$ = 9.92, P = 0.007) allowed me to compare means among removal treatments separately for each habitat. Remaining grasses attenuated significantly more light
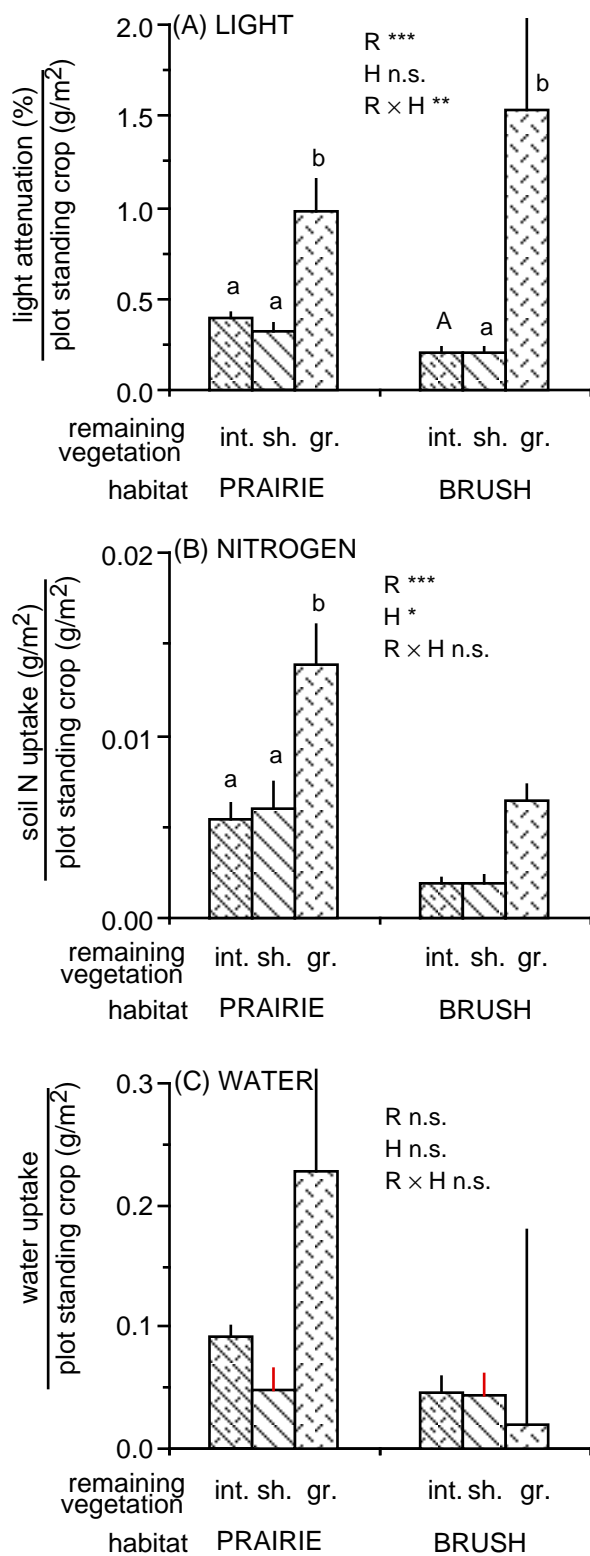
FIG. 5.5. Differences among remaining vegetation (R) and habitats (H) in light attenuation (a), soil N uptake (b) and water uptake (c) per gram standing crop. int.: intact grass-shrub vegetation; sh.: shrub vegetation (grasses removed); gr.: grass vegetation (shrubs removed). Light attenuation = 100% - light penetration (Fig. 5.4b). Soil N uptake = SOIL N in SG plots - SOIL N in I, S or G plots (Fig. 5.4c). Water uptake = SOIL MOISTURE (%) in SG plots - SOIL MOISTURE (%) in I, S or G plots (Fig. 5.4d). Bars represent means + SE (int.: $n = 10$; sh., gr.: $n = 5$). For each resource, remaining-vegetation treatments that differ significantly from each other are marked with different letters above the bars of the prairie treatment. If R × H was significant, significantly different remaining-vegetation treatments within a habitat are indicated in both habitats; remaining-vegetation treatments that differ significantly between habitats are indicated by uppercase letters in the brush treatment. Results of ANOVA: *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.

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per gram standing crop than remaining shrubs (prairie: t = 5.92, P = 0.0004, brush: t = 9.73, P < 0.0001) or than intact vegetation (prairie: t = 5.28, P = 0.0007, brush: t = 11.6, P < 0.0001) in each habitat. In contrast, remaining shrubs did not differ significantly in their light attenuation from intact vegetation in either habitat (P > 0.15). Intact vegetation attenuated significantly more light per gram standing crop in prairie than in brush (t = 5.04, P = 0.001). Similarly, remaining shrubs tended to attenuate more light per gram standing crop in prairie than in brush (P < 0.10). In contrast, remaining grasses tended to attenuate more light per gram standing crop in brush than in prairie (P < 0.10). Habitat had no significant main effect on per-gram light attenuation (P = 0.2).

N uptake (available soil N in cleared plots minus available soil N in I, S, or G treatments) per gram standing crop (Fig. 5.5b), across removal treatments, was significantly higher in prairie than in brush ($F_{1,4}$ = 13.1, P = 0.02) and, across habitats, varied significantly with removal treatments ($F_{2,8}$ = 63.0, P < 0.0001). There was, however, no significant habitat × removal treatment interaction (P = 0.065), therefore, I compared removal treatments across both habitats. Remaining grasses consumed significantly more available N per gram standing crop than remaining shrubs (t = 8.86, P < 0.0001) or than intact vegetation (t = 10.7, P < 0.0001). Remaining shrubs did not differ significantly in their N uptake from intact vegetation (P = 0.6).

Soil water uptake (% water in cleared plots minus % water in I, G, or S plots) did not vary significantly with either habitat or removal

treatments or the interaction between these two factors (Fig. 5.5c; all $P > 0.2$).

5.5.   DISCUSSION

5.5.1. Effects of grasses and shrubs on each other

In prairie, shrub removal increased grass ANPP threefold, and grass removal increased shrub ANPP twofold (Fig. 5.2). Thus, in prairie, both shrubs and grasses were suppressed by the other growth form. The suppression of shrubs by grasses is surprising because shrub standing crop in prairie was six times higher than grass standing crop (Fig. 5.1 c). Thus, in prairie undergoing shrub expansion, grasses and shrubs had more or less symmetric effects. Symmetry emerged even though shrubs had much more standing crop than grasses, implying that grasses had a higher per-gram effect on shrubs than shrubs had on grasses.

In brush, shrub removal increased grass ANPP sixfold (Fig. 5.2), suggesting that shrubs strongly suppressed grasses. This was not surprising since shrubs had 37 times more standing crop than grasses (Fig. 5.1d). In contrast, grass removal in brush had no effect on shrub ANPP (Fig. 5.2), that is, grasses had a per-gram effect approaching zero. Since shrubs had a per-gram effect greater than zero, shrubs had a larger per-gram effect on grasses than grasses had on shrubs. This is the opposite of what I observed in prairie. Thus, competition between shrubs and grasses in brush was highly asymmetric.

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My results suggest that the interaction between grasses and shrubs is symmetric during early stages of shrub expansion but becomes asymmetric when expansion has continued for a longer time and shrub mass has accumulated. The shift from symmetric to asymmetric competition may reflect a shift from competition for soil resources in prairie to competition for light in brush (Weiner 1990, Wilson & Tilman 1991, Wilson 1993b).

5.5.2. <u>Effects of shrubs and grasses on resources</u>

Light penetration in intact vegetation was significantly higher in prairie than in brush (Fig. 5.4a,b). In both habitats, shrub removal increased light penetration to the ground as much as did grass removal (Fig. 5.4b). This shows that, in both habitats, shrub and grass canopies reduced light to a similar degree even though shrub leaves are flat and wide, whereas grass leaves are erect and linear. However, shrubs in brush were taller than grasses and light at the grass canopy level (Fig. 5.4a) and beneath (Fig. 5.4b) was presumably below the light saturation point of open-prairie grass species. Grasses did not pre-empt light available to shrubs because grasses are of similar height or smaller than shrubs in both habitats. Therefore, regardless of the similar effects of shrubs and grasses on light penetration, shrubs pre-empt light because of their size.

Available N in intact vegetation did not differ significantly between prairie and brush (Fig. 5.4c: removal I). In contrast, available N is frequently higher under woody plants than under grasses (Petranka & McPherson 1979, Miles 1985, Brady 1990, Jackson et al. 1990, Zak et al. 1990, Callaway et al. 1991, McPherson et al. 1991, Wesser & Armbruster 1991, Wilson 1993a, Belsky 1994, Vieira et al. 1994, Wilson & Kleb 1996). The differences in our region are typically small, however, and are not always significant (Li & Wilson 1998). Available N in plots from which all vegetation had been removed (Fig. 5.4c: SG removal) was significantly higher in prairie than under brush. This may reflect higher levels of organic matter and higher rates of mineralization under prairie than forest (Dormaar & Lutwick 1966, Bettany et al. 1973, Severson & Arneman 1973, Schlesinger 1991). In both prairie and brush, shrub removal significantly increased available soil N, whereas grass removal did not (Fig. 5.4c). This might simply reflect the mass difference between the two growth forms (Fig. 5.1).

Soil water was significantly lower in prairie than brush (Fig. 5.4d), as typically occurs in comparisons of grasses and woody plants (Petranka & McPherson 1979, Miles 1985, Zak et al. 1990, Jackson et al. 1990, Brady 1990, Callaway et al. 1991, McPherson et al. 1991, Wesser & Armbruster 1991, Belsky 1994, Vieira et al. 1994, Köchy & Wilson 1997). In my system, higher soil moisture probably reflects the lower topographic position of brush. Soil is also moister under woody vegetation than prairie at the same level (Wilson & Kleb 1996), suggesting that brush increases soil moisture, either through snow trapping (Timoney et

al. 1993), hydraulic lift (Caldwell et al. 1998), or reduced evapotran-

spiration (Selleck & Schuppert 1957, Mitchell et al. 1993). Soil water

had similar effects in both habitats but varied among the four removal

treatments (Fig. 5.4d). The increase of soil water, however, did not

differ between shrub and grass removal (Fig. 5.4d).

Resources differed in the extent to which they were reduced by

grasses or shrubs. Available N was much greater in plots from which all

vegetation had been removed than in plots from which only one growth

form had been removed. This suggests that the remaining growth form in

each plot took up N that would otherwise have been consumed by the

removed growth form, and that each exerted strong demand for N (Welker

et al. 1991). For water, the available amount is the difference between

the water remaining in intact-vegetation plots and in plots from which

both growth forms had been removed, because the water taken up by intact

vegetation may be close to the maximum that can be extracted by vegeta-

tion. Based on this, each growth form took up equal or more than half

the available water (Fig. 5.4d), suggesting that, as for N, the water

uptake by the remaining growth form in each plot compensated for the

removal of the other growth form. In contrast to N, the demand for water

by grasses was stronger in prairie than in brush, presumably because

grass mass in brush was very low. Water uptake may be overestimated,

however, because in plots with both growth forms removed, less water may

have been intercepted by the remaining stems, therefore less water may

have evaporated and more water may have entered the soil. In prairie,

shrubs and grasses were equally tall and light levels (≈1000 μmol

photons m^{-2} s^{-1} at grass canopy) were sufficient for maximum photosynthesis of both shrubs and grasses, except for the C$_4$ grass *Bouteloua gracilis*. This suggests that for C$_3$ species, light competition in prairie was low. In brush, the taller shrubs were still light saturated, but open-prairie grasses under the shrub canopy may experience suboptimal photosynthesis ($\approx$300 μmol photons m^{-2} s^{-1}). In summary, the contrasting responses of resources to vegetation removal suggest that competition in prairie was strongest for N, whereas in brush it was strongest for light.

Current models of grass-shrub interactions in temperate grasslands emphasize competition for water (e.g., Sala et al. 1997, Weltzin & McPherson 1997), even though in temperate grasslands the balance of rainfall and evapotranspiration is high (Walter 1984), so that N limits productivity more often than water (Tilman 1990, Wilson & Shay 1990, Peltzer et al. 1998).

Comparisons of the resource reductions by shrubs and grasses in neighbour-removal plots suggest that the decreases were not a simple function of standing crop. Specifically, shrubs had 3-9 times more standing crop than grasses (Fig. 5.1c,d), but attenuated as much light and took up equal amounts of water (Fig. 5.4a,b,d). Furthermore, the very high mass of shrubs relative to grasses did not correspond to the smaller differences between them in N uptake (Fig. 5.4c). Therefore, differences between shrub and grass effects on resources suggest that the growth forms differed in their per-gram effects on resources.

5.5.3. <u>Per-gram effects on resources</u>

Grasses attenuated significantly more light per gram of mass than did shrubs (Fig. 5.5a). This was because shrubs and grasses reduced light to a similar degree (Fig. 5.4b), but shrubs had more standing crop than grasses (Fig. 5.1) because of their woody stems. Grasses also took up significantly more N per gram of mass than did shrubs (Fig. 5.5b). Similar results as for N were found for water in prairie (Fig. 5.5c), although the results were not significant.

On a per-gram basis, grasses not only attenuated more light and took up more N than did shrubs but also more than did intact vegetation (Fig. 5.5a,b). This may simply reflect the large amounts of shrub mass removed (Fig. 5.1c,d) which made resources available for uptake, but it also suggests that grasses are physiologically able to take up far more resources in pure stands than they are able to when growing with shrubs.

The high resource uptake efficiency of grasses relative to shrubs may be caused by differences in allocation patterns. Grass standing crop consists only of photosynthetic leaves, whereas shrub standing crop also includes unproductive stems. Therefore, grasses can allocate photosynthates completely to resource uptake, that is, to producing new roots and leaves, whereas shrubs must allocate a portion of the photosynthates to the building and maintenance of stems. *Symphoricarpos* leaf mass is ≈16% of standing crop (based on data used for Table 2.1). If resource uptake is divided by photosynthetic tissue mass, shrubs have higher or equal per-gram uptake than grasses. Similarly, the leaf-area

to root-length ratio of forbs was larger than that of a grass in a chalk grassland (Mortimer 1992). High rates of N uptake per standing crop in grasses may also reflect the high root:shoot mass ratio of grasses (6:1, Caldwell & Richards 1986, Wilson 1993a) relative to woody vegetation (1:1 to 1:3, George & McKell 1978, Wilson 1993a). However, adding root mass to aboveground mass assuming a root:shoot ratio of 6:1 for grasses and 1:1 for shrubs still leaves grasses with higher per-gram effects than shrubs.

My study is probably the first to show that per-gram effects at the population level differ between growth forms but that the relative size of per-gram effects is similar across habitats. In my study, per-gram effects of established shrubs on resources were smaller than those of established grasses. In contrast, tree seedlings had higher per-gram shoot effects than grass seedlings on available soil N (Welker et al. 1991). This may be because the tree seedlings had lower mass and a higher root:shoot ratio than the grasses.

Within the same growth form or in pot experiments, per-gram effects tend to be similar (Goldberg 1987, Goldberg & Fleetwood 1987, Peart 1989, Rösch et al. 1997), but a field removal experiment showed that established trees had twice the per-gram effect than established shrubs on herbaceous vegetation (Harrington & Johns 1990) and a native summer annual had larger per-root-length effects than introduced winter annuals on soil water potential (Gordon & Rice 1993).

5.5.4. <u>Grass-shrub competition</u>

Grasses generally consumed more resources per gram standing crop
(Fig. 5.5), but grasses in brush were strongly suppressed by shrubs
(Fig. 5.2). This suggests that shrubs were better competitors when their
standing crop was large enough to balance the higher per-gram resource
consumption of grasses, that is, when shrub mass was about 3-8 times
that of grass mass (Fig. 5.5). In fact, based on the regressions of
target ANPP on neighbour standing crop (Fig. 5.3), shrubs had a 1.4
times larger per-gram effect than grasses on target growth forms, or,
1.4 times more grass mass than shrub mass is needed to reduce target
ANPP by one unit, at which point the grass-shrub interaction would be
symmetric.

What is the contribution of grass to the exclusion of woody
species from prairies? The responses of resources to growth-form removal
suggest that, of the three most likely to be competed for by grasses and
shrubs, N was in much higher demand in prairie than either water or
light (Fig. 5.4). Thus, the ability to compete for N should be an impor-
tant determinant of success in my system. Grasses had very high N uptake
per gram of mass, relative to shrubs (Fig. 5.5), because of their high
root:shoot ratios and absence of woody tissues. Thus, at equal masses,
and especially in the case of young woody plants establishing among
grasses, grasses may be superior competitors. The situation changes,
however, as shrub mass increases. In prairie undergoing invasion, where
shrub mass is six times that of grass (Fig. 5.1c), competition between

the growth forms is symmetric. In established brush where shrub mass is 37 times that of grass (Fig. 5.1d), competition is asymmetric because of the large mass of shrubs relative to grasses. Shrubs grow taller and shift competition from soil resources to light (King 1990, Wilson 1993a,b). This is similar to the shifts in interaction between trees and grasses in a subtropical savanna where oak seedlings initially escape root competition by grasses, then compete for water, and finally escape root competition as the oak roots extend beyond the grass rooting layer (Weltzin & McPherson 1997).

Shrub invasion can be described as a positive feedback loop (Wilson 1998). Individual shrubs that have become established in prairie have a small effect on resources because they are low and cannot pre-empt light and because they have small standing crop so that they acquire little N. Prairie grasses may be adapted to N limitation, but when the shrubs have grown tall enough to shade the grasses the reduc-tion of light may severely reduce grass production (Wilson 1993a,b, Li & Wilson 1998). The effect of shrub shading may particularly affect C_4 grasses which tend to have a higher light compensation point than shrubs (Larcher 1984). The effect of grasses on shrub production appears to decrease as the shrubs grow denser. Once woody species have emerged from the grass canopy, their growth rate increases dramatically (Hill et al. 1995). In dense brush, grasses no longer have any effect on shrub pro-duction (Fig. 5.1; Li & Wilson 1998).

The interaction of shrubs and grasses would be affected by fac-tors that reduce or increase biomass of one growth form more than the

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other, or that would increase or reduce one of the main resources. Thus, wild fires, bison browsing, cattle grazing, N deposition from the atmosphere, droughts, and wet periods have different effects on shrubs and grasses and, in interaction or alone, may re-set the balance between shrubs and grasses (Archer 1996, Wilson 1998, chapter 2).

6. CONCLUSIONS

Invasion of trees and shrubs into prairie has created concern among naturalists, nature reserve managers, and range managers (Bork et al. 1997). The cause for invasion has been sought in changed disturbance patterns following the colonization by European settlers. The reduction of grassland fires and elimination of large bison herds supposedly removed factors that used to control tree growth (Blackburn & Tueller 1970, Bragg et al. 1993, Campbell et al. 1994). The evidence, however, is equivocal (Potter & Krenetsky 1967, Franklin et al. 1971, Fensham & Kirkpatrick 1992, Milchunas & Lauenroth 1993).

Forest may also expand into prairie because of fertilization by anthropogenic mineral nitrogen deposited from the atmosphere. This factor has been overlooked so far. I found that N deposition in western Canada increased along a gradient of population density and industrialization (Fig. 2.1). Thus, deposition in Wood Buffalo, in a remote area of the boreal forest region, was 7 kg ha^{-1} yr^{-1}, whereas deposition in Elk Island, 40 km downwind of the city of Edmonton (metropolitan population: 750,000), was 22 kg ha^{-1} yr^{-1}. These deposition rates are similar to those measured in even more industrialized areas of North America and Europe (Jefferies & Maron 1997). The numbers, however, are not directly comparable, because the resin I used measures other deposition components than common meteorological methods. Nonetheless, my results show that deposition in the more densely populated northern Great Plains is up to three times higher than what can be considered natural. The large

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amounts of NO$_x$ from car exhausts (Environment Canada 1996) and the ^{15}N

composition of exposed litter, leaves and stems in forests in Elk Island

(Fig. 2.5) suggest that pollution by traffic is a major source of N de-

position.

The fertilizing effect of nitrogen can be expected to affect the

N-limited forests and grasslands in the study region. Higher rates of N

deposition were positively correlated with higher availability of N in

the soil. Greater availability of N would increase the growth of tall

growth forms, particularly the growth of shrubs and trees that can store

more nitrogen in their tissue (Fig. 2.7). Although I did not find a

higher concentration of N in Elk Island vegetation than in Jasper (Fig.

2.6), I found that the rate of deposition was positively correlated with

the rate of forest expansion (Fig. 2.9) and that the total N storage in

the vegetation increased with increasing relative forest area (Table

2.7). So far, reports and studies of deposition effects on vegetation

were concerned with N cycling within the same ecosystem (Fenn et al.

1998). My study appears to be the first to describe a significant

terrestrial vegetation change in North America due to anthropogenic N

deposition.

Thus, the line of evidence suggests that N from car exhausts is

distributed through the air, fertilizing natural vegetation, which

shifts the proportion of forest to grassland area in favour of the for-

est. The shift from prairie to forest on the continental scale is

presumably a result of competition on the scale of individual plants.

Competition between individual plants in prairie is usually between grasses. Superior competitors are those grasses that reduce the most limiting resource to a level that decreases the growth of the inferior competitors (Tilman & Wedin 1991). The most limiting resource in prairie is usually nitrogen and rarely water (Tilman 1990, Tilman & Wedin 1991). This agrees with my finding that fertilization by N deposition is correlated with the invasion of woody species.

Shrubs in prairie are often more abundant in depressions where soil moisture may be higher than on level ground (Pelton 1953). This might indicate that soil moisture increases the competitive ability of shrubs, perhaps because water increases the N mineralization (Myers et al. 1982). I found, however, that water availability had generally little effect on grass and shrub vegetation (Fig. 3.1). Similarly, grasses and shrubs had little effect on water availability (Fig. 5.4d). Grass and shrub growth was only reduced by extremely low water supply when the two growth forms grew together (Fig. 3.2). In contrast, grasses and shrubs strongly reduced available soil N and apparently competed strongly for it (Figs. 5.2, 5.4c).

Shrubs have more mass and a taller growth form than grasses. Higher mass conveys higher competitive ability for soil resources (Goldberg 1990) because it is correlated with longer or more roots with a larger root surface (Caldwell & Richards 1986). However, shrubs have most of their biomass aboveground, making them inferior competitors for belowground resources but superior competitors for light (Tilman 1990). The higher mass of shrubs may allow them to sequester more belowground

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resources despite their low root:shoot mass ratio. The role of mass for competitive ability can be assessed by comparing the competitive effects in relation to plant mass (Goldberg 1990).

Competitive effects of grasses and shrubs were not equivalent. In prairie, six times more shrub than grass mass was necessary to reduce the other growth form's standing crop to the same extent (Fig. 5.2). In other words, the per-gram competitive effect of shrubs was one sixth that of grasses. Similarly, the per-gram competitive effect of shrubs on available soil N was about one half that of grasses (Fig. 5.5). Thus, experimental evidence strongly indicates that grasses are the superior competitors in prairie. Ranks of per-gram competitive effects did not differ between prairie and brush habitat, indicating that shrub domi-nance is not tied to a specific habitat (Fig. 5.5). Fertilization by atmospheric N deposition will therefore reduce the competitive advantage of grasses and shift the competitive relation between shrubs and grasses in favour of the shrubs.

I propose the mechanism depicted in Fig. 6.1 as a model for the displacement of grasses by shrubs. N fertilization will increase the standing crop of shrubs (represented by its C content). Due to their growth form, a portion of the production is invested into stems that gradually elevate the shrub canopy above the grasses. The shrub canopy reduces the light that is available to the grasses (Fig. 5.4a) which reduces grass growth. When the shrub canopy has become as dense as in brush, the growth of grasses growing underneath is strongly reduced (Fig. 5.2). The presence of grass in brush no longer affects shrub

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standing crop even though the per-gram effect of grasses on available

soil N remains larger than the per-gram effect of shrubs (Fig. 5.5). A

similar mechanism, although with reversed roles, has been described for

heathlands in the Netherlands. There, deposition allows a tall grass to

overtop and shade out a dwarf shrub (Berendse 1994a).

The positive feedback between shrubs and grasses at the scale of

the individual plant apparently produced a shift from grassland to

forest at the continental scale. The co-ordinated pattern at the larger

scale presumably emerged because anthropogenic N deposition covers a
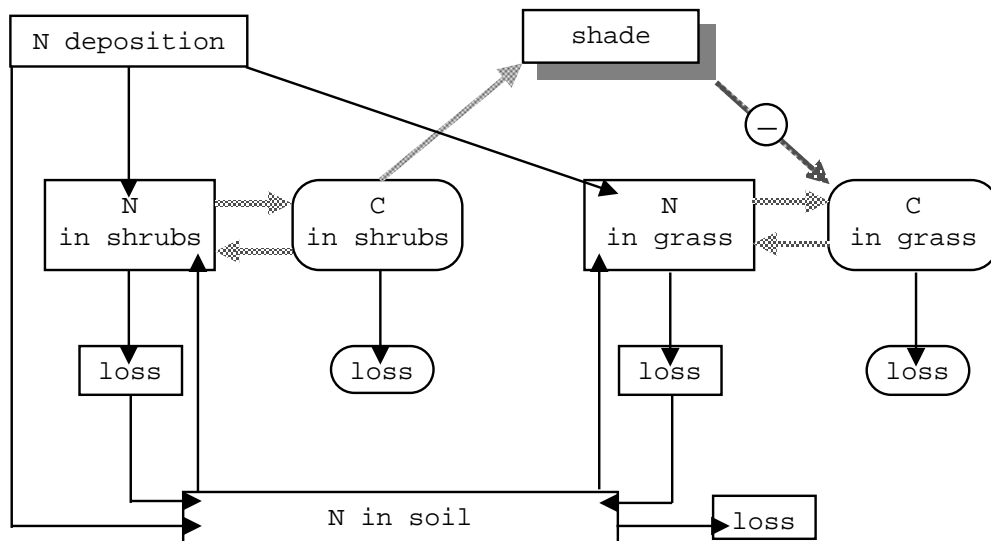
FIG. 6.1.   Mechanistical model of shrub-grass interactions in prairie

at the scale of individuals when N is the most growth-limiting resource.

"Loss" is in relation to the plants, not the ecosystem. Thus, it in-

cludes herbivory, decomposition, volatilization, burning, etc. Black

arrows indicate mass flows, light arrows causal, positive relations.

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large area with little spatial variation. N deposition might co-ordinate the competition feedback loops across a large area like the time signal co-ordinates radio-controlled clocks. In more general terms, N deposition could be described as a synchronized large-scale disturbance (Begon et al. 1990, Veblen et al. 1992). The similar responses of vegetation to the disturbance across a large area suggests that the shrub-grass feedback is an abundant mechanism at the northern edge of the prairie.

Continuously increasing N emissions will cause more vegetation changes in North America and the unintentional opportunity to study the feedback mechanism of vegetation change.

7. LITERATURE CITED

Aber, J. D. 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. Trends in Ecology and Evolution 7:220-224.

Aber, J. D., A. Magill, R. Boone, J. M. Melillo, P. Steudler, and R. Bowden. 1993. Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. Ecological Applications 3:156-166.

Aber, J. D., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. Ecological Modelling 101:61-78.

Aerts, R., R. G. A. Boot, and P. J. M. van der Aart. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. Oecologia 87:551-559.

Agnew, A. D. Q., J. B. Wilson, and M. T. Sykes. 1993. A vegetation switch as the cause of a forest/mire ecotone in New Zealand. Journal of Vegetation Science 4:273-278.

Ahrens, W. H. (ed.). 1994. Herbicide Handbook. Weed Science Society of America, Champagne, Illinois, U.S.A.

Albertson, F. W., and G. W. Tomanek. 1965. Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. Ecology 46:714-720.

Allen, D. L. 1967. The life of prairie and plains. MacGraw-Hill, New York, New York, U.S.A.

Ammann, M., R. Siegwolf, F. Pichlmayer, M. Suter, M. Saurer, and C. Brunold. 1999. Estimating the uptake of traffic-derived NO_2 from ^{15}N abundance in Norway spruce needles. Oecologia 118:124-131.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Naturalist 134:545-561.

———. 1994. Regulation of ecosystem structure and function: climatic versus non-climatic factors. Pages 245-255 in J. Griffiths (ed.). Handbook of agricultural meteorology. Oxford University Press, Oxford, U.K.

———. 1996. Assessing and interpreting grass-woody plant dynamics.

Pages 101-134 in: J. Hodgson and A. W. Illius. The ecology and
management of grazing systems. CAB International, Wallingford, U.K.

Archer, S., Ch. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic
succession in a subtropical savanna: conversion of grassland to thorn
woodland. Ecological Monographs 58:111-127.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanisms of
shrubland expansion: land use, climate or CO_2?. Climate Change 29:91-
99.

Archibold, O. W., and M. R. Wilson. 1980. The natural vegetation of
Saskatchewan prior to agricultural settlement. Canadian Journal of
Botany 58:2031-2042.

Arno, S. F., and G. E. Gruell. 1986. Douglas-fir encroachment into
mountain grassland in southwestern Montana. Journal of Range Manage-
ment 39:272-276.

Ayres, M. P., and D. L. Thomas. 1990. Alternative formulations of the
mixed-model ANOVA applied to quantitative genetics. Evolution 44:221-
226.

Backéus, I. 1992. Distribution and vegetation dynamics of humid savan-
nas in Africa and Asia. Journal of Vegetation Science 3:345-356.

Bailey, A. W., and R. A. Wroe. 1974. Aspen invasion in a portion of
the Alberta parklands. Journal of Range Management 27:263-266.

Barton, A. M. 1993. Factors controlling plant distributions: drought,
competition, and fire in montane pines in Arizona. Ecological Mono-
graphs 63:367-397.

Becker, M., M. Bonneau, and F. Le Tacon. 1992. Long-term vegetation
changes in an *Abies alba* forest: natural development compared with
response to fertilization. Journal of Vegetation Science 3:467-474.

Begon, M., J. L. Harper, and C. R. Townsend 1990. Ecology:
Individuals, Populations and Communities. Blackwell, Boston, U.S.A.

Belsky, A. J. 1994. Influences of trees on savanna productivity: tests
of shade, nutrients, and tree-grass competition. Ecology 75:922-931.

Berendse, F. 1994a. Competition between plant populations at low and
high nutrient supplies. Oikos 71:253-260.

——. 1994b. Litter decomposability - a neglected component of plant

fitness. Journal of Ecology 82:187-190.

Berger, R. P., and R. K. Baydack. 1992. Effects of aspen succession on sharp-tailed grouse, *Tympanuchus phasianellus*, in the Interlake region of Manitoba. Canadian Field-Naturalist 106:185-191.

Bert, D., S. W. Leavitt, and J.-L.Dupouey. 1997. Variations of wood δ^{13}C and water-use efficiency of *Abies alba* during the last century. Ecology 78:1588-1596.

Bettany, J. R., J. W. B. Stewart, and E. H. Halstead. 1973. Sulfur fractions and carbon, nitrogen and sulfur relationships in grassland forest and associated transitional soils. Soil Science Society of America Proceedings 37:915-918.

Binkley, D. 1984. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Science Society of America Journal 48:1181-1184.

———. 1995. The influence of tree species on forest soils: processes and patterns. Pages 1-33 in D. J. Mead, and I. S. Cornforth, editors. Proceedings of the Trees and Soil Workshop, Lincoln University 28 February - 2 March 1994. Lincoln University Press, Canterbury, New Zealand. Agronomy Society of New Zealand Special Publication 10.

Binkley, D., and S. C. Hart. 1989. The components of nitrogen availability assessments in forest soils. Advances in Soil Science 10:57-112.

Bird, R. D. 1930. Biotic communities of the aspen parkland of central Canada. Ecology 11:356-442.

———. 1961. Ecology of the aspen parkland of Western Canada. Publication 1066. Research Branch, Canada Department of Agriculture, Ottawa, Canada.

Blackburn, W. H., and P. T. Tueller. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51:841-848.

Blood, D. A. 1966a. Range relationships of elk and cattle in Riding Mountain National Park, Manitoba. Wildlife Management Bulletin, Series 1/19. Canada Department of Northern Affairs and Department of Northern Affairs and National Resources, Natural and Historic Resour-

ces Branch, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Blood, D. A. 1966b. The *Festuca scabrella* association in Riding Mountain National Park, Manitoba. Canadian Field Naturalist 80:24-32.

Bobbink, R., L. Bik, and J. H. Willems. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. Acta Botanica Neerlandica 37:231-242.

Bobbink, R., G. Heil, and M. Raessen. 1990. Atmospheric deposition and canopy exchange in heathland ecosystems. Dutch Priority Programme on Acidification, report project 119.

Bobbink, R., D. Boxman, E. Fremstad, G. Heil, A. Houdijk, and J. Roelofs. 1992. Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna. Pages 111-161 in P. Grennfelt, and E. Thörnelöf, editors. Critical Loads for Nitrogen - report from a workshop held at Lökeberg, Sweden, 6-10 April 1992. Nord 1992/41. Nordic Council of Ministers, Copenhagen, Denmark.

Bock, J.H., and C.E. Bock. 1992. Vegetation responses to wildfire in native versus exotic Arizona grassland. Journal of Vegetation Science 3:439-446.

Bork, E. W., R. J. Hudson, and A. W. Bailey. 1997. *Populus* forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. Canadian Journal of Botany 75:1518-1526.

Bowes, G. G., and D. T. Spurr. 1995. Improved forage production following western snowberry (*Symphoricarpos occidentlis* Hook.) control with metsulfuron methyl. Canadian Journal of Plant Science 75:935-940.

Bowes, G. G., and D. T. Spurr. 1996. Control of aspen poplar, balsam poplar, prickly rose and western snowberry with metsulfuron-methyl. Canadian Journal of Plant Science 76:885-889.

Boxman, A. W., H. F. G. van Dijk, and J. G. M. Roelofs. 1994. Soil and vegetation responses to decreased atmospheric nitrogen and sulphur inputs into a Scots pine stands in the Netherlands. Forest Ecology and Management 68:39-45.

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Boyce, R. L., A. J. Friedland, C. P. Chamberlain, and S. R. Poulson. 1996. Direct canopy nitrogen uptake from ^{15}N-labeled wet deposition by mature red spruce. Canadian Journal of Forest Research 26:1539-1547.

Brady, N. C. 1990. The nature and properties of soils. MacMillan, New York, New York, U.S.A.

Bragg, T. B., and L. C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-23.

Bragg, W. K., A. K. Knapp, and J. M. Briggs 1993. Comparative water relations of seedling and adult *Quercus* species during gallery forest expansion in tallgrass prairie. Forest Ecology and Management 56:29-41.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany 82:1024-1030.

Brown, D. 1995. The impact of species introduced to control tree invasion on the vegetation of an electrical utility right-of-way. Canadian Journal of Botany 73:1217-1228.

Brown, J. K. 1976. Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research 6:153-158.

Brumme, R., U. Leimcke, and E. Matzner. 1992. Interception and uptake of NH_4 and NO_3 from wet deposition by above-ground parts of young beech (*Fagus silvatica* L.) trees. Plant and Soil 142:273-279.

Buell, F. M. and J. E. Cantlow. 1951. A study of two forest stands in Minnesota with an interpretation of the prairie-forest margin. Ecology 32:294-316.

Buell, F. M., and V. Facey. 1960. Forest-prairie transition west of Hasca park, Minnesota. Bulletin of the Torrey Botanical Club 87:46-58.

Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland range. Ecological Monographs 35:139-164.

Cable, D. R. 1969. Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extrac-

tion. Ecology 50:27-38.

Cairns, A. L., and E. S. Telfer. 1980. Habitat use by 4 sympatric ungulates in boreal mixedwood forest. Journal of Wildlife Management 44:849-857.

Caldwell, M. M., and H. J. Richards. 1986. Competing root systems: morphology and models of absorption. Pages 251-273 in T. J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, U. K.

Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113:151-161.

Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of Quercus douglasii on understory productivity in central California. Ecology 72:1484-1499.

Campbell, C., I. D. Campbell, C. B. Blyth, and J. H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360-362.

Carbyn, L. N. 1971. Description of the *Festuca scabrella* association in Prince Albert National Park, Saskatchewan. Canadian Field Naturalist 85:25-29.

Cole, K. L., and R. S. Taylor. 1995. Past and current trends of change in a dune prairie/oak savanna reconstructed through a multiple-scale history. Journal of Vegetation Science 6:399-410.

Cornelius, J. M., P. R. Kemp, J. A. Ludwig, and G. L. Cunningham. 1991. The distribution of vascular plant species and guilds in space and time along a desert gradient. Journal of Vegetation Science 2:59-72.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. Ecological Monographs 20:271-315.

Crown, P. H. [c. 1976]. Soil survey of Elk Island National Park Alberta. Alberta Institute of Pedology, [Edmonton]. Alberta Institute of Pedology (Series) S-77-38, Alberta Soil Survey Report no. 38.

Davidson, C. I., and Y.-L. Wu. 1990. Dry deposition of particles and vapors. Pages 103-216 in S. E. Lindberg, A. L. Page, and S. A. Norton, editors. Acid Precipitation (Advances in Environmental

Science). Vol. 3. Sources, Deposition, and Canopy Interactions. Springer, New York, New York, U.S.A.

Derr, J. F. 1989. Multiflora rose (*Rosa multiflora*) control with metsulfuron. Weed Technology 3:381-384.

Dickson, J. R. 1909. The Riding Mountain Forest Reserve. Department of the Interior, Ottawa, Ontario, Canada. Forestry Branch-Bulletin 6.

Diederen, H. S. M. A., and J. H. Duyzer. 1988. Ammonia from emission to deposition. Summary report for Commission of the European Communities and Dutch Ministry of Housing, Planning and Environment. University of Utrecht, Utrecht, The Netherlands .

Dise, N. B., and R. F. Wright. 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. Forest Ecology and Management 71:153-161.

DiTommaso, A., and L. W. Aarssen. 1989. Resource manipulations in natural vegetation: a review. Vegetatio 84:9-29.

Dormaar, J. F., and L. E. Lutwick. 1966. A biosequence of soils of the rough fescue prairie-poplar transition in southwestern Alberta. Canadian Journal of Earth Sciences 3:457-471.

Eckstein, R. L., and P. S. Karlsson. 1997. Above-ground growth and nutrient use by plants in a subarctic environment: effects of habitat, life-form and species. Oikos 79:311-324.

Eilers, G., R. Brumme, and E. Matzner. 1992. Above ground N-uptake from wet deposition by Norway spruce (*Picea abies* Karst.). Forest Ecology and Management 51:239-249.

Ellenberg jr., H. 1988. Floristic changes due to nitrogen deposition in Central Europe. Pages 375-383 in Nilsson and P. Grennfelt, editors. Critical Loads of Sulphur and Nitrogen. Report from a workshop held at Skokloster, Sweden, 19-24 March 1988. Miljørapport 1988:15. Nordic Council of Ministers.

Ellenberg, H. 1962. Wald in der Pampa Argentiniens? Veröffentlichungen des Geobotanischen Instituts der ETH, Stiftung Rübel 37:39-56.

Ellis, E. C., R. E. Erbes, and J. K. Grott. 1990. Abatement of atmospheric emissions in North America: Progress to date and promise for the future. Pages 285-322 in S. E. Lindberg, A. L. Page, and S. A.

Norton, editors. Acid Precipitation. Advances in Environmental
   Science. Vol. 3. Sources, Deposition, and Canopy Interactions.
   Springer, New York, New York, U.S.A.

Environment Canada. 1958-1994. Monthly meteorological summaries
   [Regina]. Regina, Saskatchewan, Canada.

———. 1993. Canadian climate normals 1960-1990 [V. 2] Prairie prov-
   inces. Atmospheric Environment Service, Ottawa.

———. 1996. Canadian emissions inventory of criteria air contaminants
   (1990). Reports EPS 5/AP/7E.

———. 1998. National pollutant release inventory 1996: Summary report.
   Environment Canada, Hull, Québec, Canada.

Facelli, J. M., and R. J. C. León. 1986. El establicimiento espontáneo
   de árboles en la Pampa: Un enfoque experimental. Phytocoenologia
   14:263-274.

Fairbank, L. G., R. Cousens, A. M. Mortimer, and R. G. R. Smith. 1990.
   Effects of soil type on crop yield-weed density relationships between
   winter wheat and Bromus sterilis. Journal of Applied Ecology 27:308-
   318.

Felker, P., D. Smith, R. L. Bingham, and I. Reyes. 1984. Evaluation of
   herbicides for use in transplanting Leucaena leucocephala and *Proso-
   pis alba* on semi-arid lands without irrigation. Forest Science
   30:747-755.

Fenn, M. E., and A. Bytnerowicz. 1993. Dry deposition of nitrogen and
   sulfur to ponderosa and jeffrey pine in the San Bernadina National
   Forest in Southern California. Environmental Pollution 81:277-285.

Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Brown, B. T. Bormann, D. W.
   Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemyer
   1998. Nitrogen excess in North American ecosystems: predisposing
   factors, ecosystem responses, and management strategies. Ecological
   Applications 8:706-733.

Fensham, R. J., and J. B. Kirkpatrick. 1992. The eucalypt forest-
   grassland/grassy woodland boundary in central Tasmania. Australian
   Journal of Botany 40:123-138.

Fowler, N. 1986. The role of competition in plant communities in arid

and semiarid regions. Annual Review of Ecology and Systematics 17:89-110.

Franklin, J. F., H. Moir, G. W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research 3:215-224.

Frey, T. C., and Ch. G. Curtin. 1997. A low-tech technique for aerial photograph analysis. Bulletin of the Ecological Society of America 78:203-204.

Fuller, L. G., and D. W. Anderson. 1993. Changes in soil properties following forest invasion of black soils of the Aspen Parkland. Canadian Journal Soil Science 73:613-627.

Gebauer, G., and P. Dietrich. 1993. Nitrogen isotope ratios in different compartments of a mixed stand of spruce, larch and beech trees and of understorey vegetation including fungi. Isotopenpraxis 29:35-44.

George, M. R., and C. M. McKell. 1978. Distribution of food reserves in snowberry (*Symphoricarpus oreophilus*). Journal of Range Management 31:101-104.

Giblin, A. E., J. A. Laundre, K. J. Nadelhoffer, and G. R. Shaver. 1994. Measuring nutrient availability in arctic soils using ion exchange resins: A field test. Soil Science Society of America Journal 58:1154-1162.

Glendening, G. E. 1952. Some quantitaitve data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. Ecology 33:319-328.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211-1223.

————. 1990. Components of resource competition in plant communities. Pages 27-49 in J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, San Diego, California, U.S.A.

Goldberg, D. E., and L. Fleetwood. 1987. Competitive effect and response in four annual plants. Journal of Ecology 75:1131-1143.

Goldberg, D. E., and K. Landa. 1991. Competitive effect and response:

hierarchies and correlated traits in the early stages of competition. Journal of Ecology 79:1013-1030.

Golluscio, R. A., O. E. Sala, and W. K. Lauenroth. 1998. Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. Oecologia 115:17-25.

Gordon, D. R., and K. J. Rice. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. Ecology 74:68-82.

Grace, J. B. 1985. Juvenile vs. adult competitive abilities in plants: size-dependence in cattails (*Typha*). Ecology 66:1630-1638.

————. 1993. The effects of habitat productivity on competition intensity. Trends in Ecology and Evolution 8:229-230.

Graham, M. 1923. Canada's wild buffalo: Observations in the Wood Buffalo Park: with an appendix: A reconnaissance in the home of the wood buffalo by F. V. Seibert, B.A.Sc., D. L.S., M. E.I.C. Ottawa, Ontario, Canada Department of the Interior, North West Territories and Yukon Branch.

Grennfelt, P., and H. Hultberg. 1986. Effects of nitrogen deposition on the acidification of terrestrial and aquatic ecosystems. Water, Air, and Soil Pollution 30:945-963.

Gundersen, P. 1991. Nitrogen deposition and the forest nitrogen cycle: role of denitrification. Forest Ecology and Management 44:15-28.

Handley, L. L., and J. A. Raven. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. Plant, Cell and Environment 15:965-985.

Harrington, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. Ecology 72:1138-1149.

Harrington, G. N. and G. G. Johns 1990. Herbaceous biomass in a *Eucalyptus* savanna woodland after removing trees and/or shrubs. Journal of Applied Ecology 27:775-787.

Hastings, J. R., and R. M. Turner. 1965. The Changing Mile: an Ecological Study of Vegetation Change with Time in the Lower Mile of an Arid and Semi-Arid Region. University of Arizona Press, Tucson,

Arizona, USA.

Haugland, E. 1993. Competition between an established grass sward and seedlings of *Rumex longifolius* DC. and *Taraxacum officinale* (Web.) Marss. Norwegian Journal of Agricultural Sciences 7:409-420.

Heal, O. W., T. V. Callaghan, K. Chapman. 1989. Can population and process ecology be combined to understand nutrient cycling? Pages 205-216 in M. Clarholm and L. Bergström, editors. Ecology of arable Land: Perspectives and Challenges. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Heaton, T. H. E. 1990. $^{15}N/^{14}N$ ratios of NO_x from vehicle engines and coal-fired power stations. Tellus 42B:304-307.

Heil, G. W., J. A. Werger, W. DeMol, D. van Dam, and B. Heijne. 1988. Capture of atmospheric ammonium by grassland canopies. Science 239:764-765.

Hill, J. D., C. D. Canham, and D. M. Wood. 1995. Patterns and causes of resistance to tree invasion in rights-of-way. Ecological Applications 5:459-470.

Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology and Evolution 10:336-339.

Hodge, F. W. (ed.). 1965. Handbook of American Indians North of Mexico. Rowman and Littlefield, New York, New York, U.S.A.

Hoefs, J. 1987. Stable isotope geochemistry. Springer, Berlin, Germany.

Hofmann, G., D. Heinsdorf, and H.-H. Krauß. 1990. Wirkung atmogener Stickstoffeinträge auf Produktivität und Stabilität von Kiefern-Forstökosystemen. Beiträge für die Forstwirtschaft 24:59-73.

Högbom, L., and P. Högberg. 1991. Nitrate nutrition of *Deschampsia flexuosa* (L.) Trin. in relation to nitrogen deposition in Sweden. Oecologia 87:488-494.

Høgg, E. H., N. Malmer, and B. Wallén. 1994. Microsite and regional variation in the potential decay rate of *Sphagnum magellanicum* in south Swedish raised bogs. Ecography 17:50-59.

Holland, W. D., and G. M. Coen (eds.). 1982. Ecological (biophysical)

land classification of Banff and Jasper National Parks. Alberta
Institute of Pedology Publication SS-82-44.

Hudson, R. J., and S. Frank 1987. Foraging ecology of bison in aspen
boreal habitats. Journal of Range Management 40:71-75.

Huisman, J., and F. J. Weissing. 1994. Light-limited growth and compe-
tition for light in well-mixed aquatic environments: An elementary
model. Ecology 75:507-520.

Hunt, H. W., E. R. Ingham, D. C. Coleman, E. T. Elliott, and C. P. P.
Reid. 1988. Nitrogen limitation of production and decomposition in
prairie, mountain meadow, and pine forest. Ecology 69:1009-1016.

Hyder, D. N., R. E. Bement, E. E. Remmenga, and D. F. Hervey. 1975.
Ecological responses of native plants and guidelines for management
of shortgras prairie. US Department of Agriculture, Agricultural
Research Service, Technical Bulletin 1503.

Ingestad, T., and G. I. Ågren. 1991. The influence of plant nutrition
on biomass allocation. Ecological Applications 1:168-174.

Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W.Bartolome.
1990. Influence of tree canopies on grassland productivity and
nitrogen dynamics in deciduous oak savanna. Agriculture, Ecosystem
and Environment 32:89-105.

Jefferies, R. L., and J. L. Maron. 1997. The embarassment of riches:
atmospheric deposition of nitrogen and community and ecosystem
processes. Trends in Ecology and Evolution 12:74-78.

Jeffrey, W. W. 1961. A prairie to forest succession in Wood Buffalo
Park, Alberta. Ecology 42:442-444.

Johnson, D. W., and S. E. Lindberg (eds.). 1992. Atmospheric deposi-
tion and forest nutrient cycling. A synthesis of the Integrated
Forest Study. Springer, New York, New York, U.S.A. Ecological Studies
91.

Johnson, R. E. 1960. Rooting characteristics of prairie species in
Saskatchewan. PhD thesis, University of Sasktachewan, Saskatoon,
Saskatchewan, Canada.

Kazada, M., and K. Katzensteiner. 1993. Factors influencing the soil

solution chemistry in Norway spruce stands in the Bohemian Forest, Austria. Agriculture Ecosystems and Environment 47:135-145.

Kellman, M. 1989. Mineral nutrient dynamics during savanna–forest transformation in Central America. Pages 137-151 in J. Proctor, editor. Mineral nutrients in tropical forest and savanna systems. Blackwell, Oxford, U.K.

Kellman, M., and A. Carty. 1986. Magnitude of nutrient influxes from atmospheric sources to a Central American *Pinus caribea* woodland. Journal of Applied Ecology 23:211-226.

Kenk, G., and H. Fischer. 1988. Evidence from nitrogen fertilisation in the forests of Germany. Environmental Pollution 54:199-218.

King, D. A. 1990. The adaptive significance of tree height. American Naturalist 135:89-828.

Kirby, D. R., and T. A. Ransom-Nelson. 1987. Western snowberry community structure in south-central North-Dakota. Prairie Naturalist 19:65-67.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662-668.

Knight, C. L., J. M. Briggs, and M. D. Nellis. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. Landscape Ecology 9:117-000.

Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. Journal of Ecology 73:235-253.

Köchy, M., and S. D. Wilson. 1997. Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78:732-739.

Larcher, W. 1984. Ökologie der Pflanzen auf physiologischer Grundlage. UTB 232. Ulmer, Stuttgart, Germany.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397-403.

Le Roux, X., T. Bariac, and A. Mariotti. 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. Oecologia 104:147-155.

Legge, A. H. 1988. Present and potential effects of acidic and acidi-
  fying air pollutants on Alberta's environment - critical point I -
  Summary Report. Acid deposition research program and University of
  Calgary. Kananaskis Centre for Environmental Research, Alberta,
  Canada.

Li, X., and S. D. Wilson. 1998. Facilitation among woody plants estab-
  lishing in an old field. Ecology 79:2694-2705.

Lindberg, S. E., G. M. Lovett, D. D. Richter, and D. W. Johnson. 1986.
  Atmospheric deposition and canopy interactions of major ions in a
  forest. Science 231:141-145.

Linsey, G. A., D. W. Schindler, and M. P. Stainton. 1987. Atmospheric
  deposition of nutrients and major ions at the Experimental Lakes Area
  in northwestern Ontario. Canadian Journal of Fisheries and Aquatic
  Sciences 44 (Sppl. 1):206-214.

Looman, J. 1980. The vegetation of the Canadian prairie provinces II.
  The grasslands. Part I. Phytocoenologia 8:153-190.

Looney, S. W., and W. B. Stanley. 1989. Exploratory repeated measures
  analysis for two or more groups. American Statistician 43:220-225.

Loreau, M. 1998. Ecosystem development explained by competition within
  and between material cycles. Proceedings of the Royal Society of
  London B 265:33-38.

Lorenzen, Th. J., and V. L. Anderson. 1993. Design of experiments: a
  no-name approach. Dekker, New York, New York, U.S.A.

Lovett, G. M. 1994. Atmospheric deposition of nutrients and pollutants
  in North America: an ecological perspective. Ecological Applications
  4:629-650.

Lovett, G. M., and S. E Lindberg. 1993. Atmospheric deposition and
  canopy interactions of nitrogen in forests. Canadian Journal of
  Forest Research 23:1603-1616.

Lumme, I. 1994. Nitrogen uptake of Norway spruce (*Picea abies* Karst.)
  seedlings from simulated wet deposition. Forest Ecology and Manage-
  ment 63:87-96.

Luo, Y., and J. F. Reynolds. 1999. Validity of extrapolating field CO_2

experiments to predict carbon sequestration in natural ecosystems. Ecology 80:568-1583.

Macko, S. A., and N. E. Ostrom. 1994. Pollution studies using stable isotopes. Pages 45-62 in K. Lajtha, and R. Michener, editors. Stable isotopes in ecology and environmental science. Blackwell, Oxford, UK.

Magill, A. H., J. D. Aber, J. J. Hendricks, R. D. Bowden, J. M. Melillo, and P. A Steudler. 1997. Biogeochemical response of forest ecosystems to simulated chronic nitrogen deposition. Ecological Applications 7:402-415.

Maini, J. S. 1960. Invasion of grassland by *Populus tremuloides* in the Northern Great Plains. Diss. University of Saskatchewan, Saskatoon, Canada.

Mauersberger, P., and M. Straškraba. 1987. Two approaches to generalized ecosystem modelling: thermodynamic and cybernetic. Ecological Modelling 39:161-169.

McDaniel, K. C., D. L. Anderson, and J. F. Balliette. 1991. Wyoming big sagebrush control with metsulfuron and 2,4-D in northern New Mexico. Journal of Range Management 44:623-627.

McKone, M. J., and C. M. Lively. 1993. Statistical analysis of expriments conducted at multiple sites. Oikos 67:184-186.

McPherson, G. R., G. A. Rasmussen, D. B. Wester, and R. A. Masters. 1991. Vegetation and soil zonation associated with *Juniperus pinchotii* Sudw. trees. Great Basin Naturalist 51:316-324.

Microsoft. 1992. Excel 4.0. Microsoft Corporation, Delaware, U.S.A.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Miles, J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. Journal of Soil Science 36:571-584.

Mills, K. E., and J. D. Bever. 1998. Maintenance of diversity within plant communities: soil pathogens as agents of negative feedback. Ecology 79:1595-1601.

Mitchell, R. J., B. R. Zutter, T. H. Green, M. A. Perry, D. H. Gjerstad, and G. R. Glover. 1993. Spatial and temporal variation in competitive effects on soil moisture and pine response. Ecological Applications 3:167-174.

Morecroft, M. D., E. K. Sellers, and J. A. Lee. 1994. An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands. Journal of Ecology 82:475-483.

Morgan, R. G. 1980. Bison movement patterns on the Canadian Plains: an ecological analysis. Plains Anthropology 25:143-159.

Mortimer, S. R. 1992. Root length/leaf area ratios of chalk grassland perennials and their importance for competitive interactions. Journal of Vegetation Science 3:665-672.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley, New York, New York, U.S.A.

Myers, R. J. K., C. A. Campbell, and K. L. Weier 1982. Quantitative relationship between net nitrogen mineralization and moisture content of soils. Canadian Journal of Soil Science 62:111-124.

Myrick, R. H., and K. M. Hunt. 1998. Air quality monitoring in Alberta: 1996 summary report. Air Issues and Monitoring Branch, Alberta Environmental Protection, Edmonton, Alberta, Canada.

Nadelhoffer, K. J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 23-44 in K. Lajtha and R. Michener, editors. Stable isotopes in ecology and environmental science. Blackwell, Boston, Massachusetts, U.S.A.

NADP (National Atmospheric Deposition Program). 1994. NADP/NTN Annual data summary. Precipitation Chemistry in the United States. 1993. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, U.S.A.

———. 1995. NADP/NTN Annual data summary. Precipitation Chemistry in the United States. 1994. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado, U.S.A.

———. 1996. NADP/NTN Annual data summary. Precipitation Chemistry in the United States. 1995. Natural Resource Ecology Laboratory, Colo-

rado State University, Fort Collins, Colorado, U.S.A.

NAS. 1974. The National Atlas of Canada. MacMillan, Toronto, Ontario, Canada.

Nason, G. E., D. J. Pluth, and W. B. McGill. 1988. Volatilization and foliar recapture of ammonia following spring and fall application of nitrogen-15 urea to a Douglas-fir ecosystem. Soil Science Society of America Journal 52:821-828.

Neilson, R. P. 1986. High-resolution climatic analysis and southwest biogeography. Science 232:27-34.

————. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. Ecological Applications 3:385-395.

Nelson J. G., and R. E. England. 1971. Some comments on the causes nd effects of fire in the northern grasslands area of Canada and the nearby United States, ca. 1750-1900. Canadian Geographer 15:295-306.

Nie, D., M. B. Kirkham, L. K. Ballou, D. J. Lawlor, and E. T. Kanemasu. 1992. Changes in prairie vegetation under elevated carbon dioxide levels and two soil moisture regimes. Journal of Vegetation Science 3:673-678.

Niering, W. A., and R. H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: arresting 'succession' on rights-of-way and pastureland. Ecology 55:784-795.

Nihlgård, B. 1985. The ammonium hypothesis - an additional explanation to the forest dieback in Europe. Ambio 14:2-8.

Nilsson, S. I., M. Berdén, and B. Popovic. 1988. Experimental work related to nitrogen deposition, nitrification and soil acidification - a case study. Environmental Pollution 54:233-248.

Nômmik, H., D. J. Pluth, K. Larsson, and M. K. Mahendrappa. 1994. Isotopic fractionation accompanying fertilizer nitrogen transformation in soil and trees of a Scots Pine ecosystem. Plant and Soil 58:169-182.

Oksanen, L. 1988. Ecosystem organization: mutualism or cybernetics or plain Darwinian struggle for existence? American Naturalist 131:424-444.

Pallardy, S. G., and T. T. Kozlowski. 1981. Water relations of *Popu-*

lus clones. Ecology 62:159-169.

Paruelo, J. M., M. R. Aguiar, R. A. Golluscio, R. J. C. Leon, and G.
Pujol. 1993. Environmental controls of NDVI dynamics in Patagonia
based on NOAA-AVHRR satellite data. Journal of Vegetation Science
4:425-428.

Pastor, J., and J. G. Bockheim. 1984. Distribution and cycling of
nutrients in an aspen-mixed-hardwood-spodosol ecosystem in Northern
Wisconsin. Ecology 65:339-353.

Pearson, J., and G. R Stewart. 1993. The deposition of atmospheric
ammonia and its effects on plants. New Phytologist 125:283-305.

Peart, D. P. 1989. Species interactions in a successional grassland.
II. Colonization of vegetated sites. Journal of Ecology 77:252-266.

Pelton, J. 1953. Studies on the life-history of *Symphoricarpos occi-
dentalis* Hook. in Minnesota. Ecological Monographs 23:17-39.

Peltzer, D., S. D. Wilson, and A. K. Gerry. 1998. Competition inten-
sity along a productivity gradient in a low-diversity grassland.
American Naturalist 151:465-476.

Petersen, E. B., and N. M. Petersen. 1992. Ecology, management, and
use of aspen and balsam poplar in the prairie provinces, Canada.
Minister of Supply and Services Canada. Ottawa, Ontario, Canada.

Petranka, J. W., and J. K. McPherson. 1979. The role of *Rhus copal-
lina* in the dynamics of the forest-prairie ecotone in north-central
Oklahoma. Ecology 60:956-965.

Pielou, E. C. 1991. After the ice age: the return of life to glaciated
North America. University of Chicago Press, Chicago, Illinois, U.S.A.

Potter, L. D, and J. C. Krenetsky 1967. Plant succession with released
grazing on New Mexico rangelands. Journal of Range Management 20:145-
151.

Potter, Ch. S., H. L. Ragsdale, and W. T. Swank. 1991. Atmospheric
deposition and foliar leaching in a regenerating southern Appalachian
forest canopy. Journal of Ecology 79:97-115.

Pyne, S. J. 1986. "These conflagrated prairies". A cultural fire
history of the grasslands. Proceedings of the Ninth North-American

Prairie Conference:131-137.

Raby, S. 1966. Prairie fires in the north-west. Saskatchewan History 19:81-99.

Raup, H. M. 1935. Botanical investigations in Wood Buffalo Park. Department of Mines, Ottawa, Ontario, Canada. National Museum of Canada, Biological Series, No. 20, Bulletin No. 74.

Reader, R. J., A. Jalili, J. P. Grime, R. E. Spencer, and N. Matthews. 1993. A comparative study of plasticity in seedling rooting depth in drying soil. Journal of Ecology 81:543-550.

Redmann, R. E. 1975. Production ecology of grassland plant communities in western North Dakota. Ecological Monographs 45:83-106.

Rejmánek, M., and E. Rosén. 1992. Cycles of heterogeneity during succession: a premature generalization? Ecology 73:2329-2331.

Reynolds, H. L., and S. W. Pacala. 1993. An analytical treatment of root-to-shoot ratio and plant competition for soil nutrient and light. American Naturalist 141:51-70.

Richardson, D. M., R. M. Cowling, and D. C. Le Maitre. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. Journal of Vegetation Science 1:629-642.

Risser, P. G., and W. J. Parton. 1982. Ecosystem analysis of the tall-grass prairie: nitrogen cycle. Ecology 63:1342-1351.

Ritchie, J. C. 1976. The late-quaternary vegetational history of the western interior of Canada. Canadian Journal of Botany 54:1793-1818.

Rode, M. W. 1993. Leaf-nutrient accumulation and turnover at three stages of succession from heathland to forest. Journal of Vegetation Science 4:263-268.

Rodney, W. 1969. Kootenay Brown: his life and times 1839-1916. Gray's, Sidney, B.C., Canada.

Rösch, H., M. W. van Rooyen, and G. K. Theron. 1997. Competitive effect and response of ten Namaqualand ephemeral plant species at two nutrient levels. South African Journal of Botany 63:210-215.

Rowland, A., A. J. S. Murray, and A. R. Wellburn. 1985. Oxides of nitrogen and their impact upon vegetation. Reviews on Environmental

Health 5:295-343.

Rundel, P. W. 1981. Fire as an ecological factor. Pages 501-538 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler. Physiological Plant Ecology I, Responses to the physical environment. Encyclopedia of Plant Physiology Vol. 12 A. Springer, Berlin, Germany.

Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81:501-505.

Sala, O. E., W. K. Lauenroth, and R. A. Golluscio. 1997. Plant functional types in temperate semi-arid regions. Pages 217-233 in T. M. Smith, and H. H. Shugart, editors. Plant functional types. Cambridge University Press, Cambridge.

SAS Institute. 1996. JMP 3.2. SAS Institute, Inc., Cary, North Carolina, U.S.A.

————. 1997. JMP 3.2.1. SAS Institute, Inc., Cary, North Carolina, U.S.A.

Schlesinger, W. H. 1991. Biogeochemistry: an analysis of global change. Academic Press, London, U.K.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517-544.

Schwarz, A. G., and R. W. Wein. 1997. Threatened dry grasslands in the continental boreal forests of Wood Buffalo National Park. Canadian Journal of Botany 75:1363-1370.

Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447-455.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability acros multiple time scales – the Transient Maxima Hypothesis. American Naturalist 141:621-633.

Selleck, G. W., and K. Schuppert, K. 1957. Some aspects of microclimate in a pine forest and in an adjacent prairie. Ecology 38:650-653.

Severson, R. C., and H. F. Arneman. 1973. Soil characteristics of the forest-prairie ecotone in north-western Minnesota. Soil Science Society of America Proceedings 37:593-599.

Shachak, M., and G. M. Lovett. 1998. Atmospheric deposition to a
    desert ecosystem and its implications for management. Ecological
    Applications 8:455-463.

Sims, P. L., and R. T. Coupland. 1979. Producers. Pages 49-72 in R. T.
    Coupland, editor. Grassland ecosystems of the world: analysis of
    grasslands and their uses. Cambridge University Press, Cambridge,
    U.K.

Skeffington, R. A., and E. J. Wilson. 1988. Excess nitrogen deposi-
    tion: Issues for consideration. Environmental Pollution 54:159-184.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical methods. Univer-
    sity of Iowa Press, Ames, Iowa, U.S.A.

Soper, J. D. 1951. The mammals of Elk Island National Park, Alberta,
    Canada. Department of Resources and Development, National Parks
    Branch, Canadian Wildlife Service, Ottawa, Ontario, Canada. Wildlife
    Management Bulletin 1-3.

Stock, H. D., and O. A. M. Lewis. 1986. Soil nitrogen and the role of
    fire as a mineralizing agent in a South African coastal fynbos
    system. Journal of Ecology 74:317-328.

Streibig, J. C., A. Walker, A. M. Blair, and 17 other co-authors. 1995.
    Variability of bioassays with metsulfuron-methyl in soil. Weed
    Research 35:215-224.

Svedarsky, W. D., and Ph. E. Buckley. 1975. Some interactions of fire,
    prairie and aspen in Northwestern Minnesota. Pages 115-121 in M. K.
    Wali, editor. Prairie: A multiple View. University of North Dakota
    Press, Grand Forks, North Dakota, U.S.A.

Svedarsky, W. D., Ph. E. Buckley, and T. A. Feiro. 1986. The effect of
    13 years of annual burning on an aspen-prairie ecotone in north-
    western Minnesota. Pages 118-122 in Proceedings of the Ninth North-
    American Prairie Conference.

Taub, D. R., and D. Goldberg. 1996. Root system topology of plants
    from habitats differing in soil resource availability. Functional
    Ecology 10:258-264.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and

lignin as predictors of litter decay rates: a microcosm test. Ecology
70:97-104.

Tilman, D. 1988. Plant strategies and the dynamics and structure of
plant communities. Princeton University Press, Princeton, New Jersey,
U.S.A.

―――. 1990. Constraints and tradeoffs: toward a predictive theory of
competition and succession. Oikos 58:3-15.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition
between successional grasses. Ecology 72:1038-1049.

Timoney, K. P., La Roi, G. H., and M. R. T. Dale. 1993. Subarctic
forest-tundra vegetation gradients: the sigmoid wave hypothesis.
Journal of Vegetation Science 4:387-394.

Tkachenko, V. S., and A. P. Genov. 1992. Ecological and genetic series
of vegetation of the nature reserve "Kamennye Mogily" (Donetsk
Oblast). Ukrayins'kyi Botanichnyi Zhurnal 49:19-24.

Tyler, G. 1987. Probable effects of soil acidification and nitrogen
deposition on the floristic composition of oak (*Quercus robur* L.)
forest. Flora 179:165-170.

Ulrich, B., R. Mayer, and P. K. Khanna. 1979. Deposition von Luftve-
runreinigungen und ihre Auswirkungen in Waldökosystemen im Solling.
Schriften aus der Forstlichen Fakultät der Universität Göttingen und
der Niedersächsischen Forstlichen Versuchsanstalt. Sauerländer,
Frankfurt a. M., Germany.

Van Auken, O. W., and J. K. Bush. 1989. *Prosopis glandulosa* growth:
influence of nutrients and simluated grazing of *Bouteloua curtipen-
dula*. Ecology 70:512-516.

Van Auken, O. W., J. K. Bush, and D. D. Diamond. 1992. The role of
light and nutrients in determining dominance of *Paspalum plicatulum*
Michx. and *Schizachyrium scoparium* (Michx.) Nash, two C-4 grasses.
Bulletin of the Torrey Botanical Club 119:401-406.

van Breemen, N., and H. F. G. van Dijk. 1988. Ecosystem effects of
atmospheric deposition of nitrogen in The Netherlands. Environmental
Pollution 54:249-274.

van Dam, D. 1990. Atmospheric deposition and nutrient cycling in chalk grassland. PhD thesis. University of Utrecht, The Netherlands.

van der Putten, W. H. 1997. Plant-soil feedback as a selective force. Trends in Ecology and Evolution 12:169-170.

van Vuuren, M. M., and L. J. van der Eerden. 1992. Effects of three rates of atmospheric nitrogen deposition enriched with ^{15}N on litter decomposition in a heathland. Soil Biology and Biochemistry 24:527-532.

Veblen, Th. T., Th. Kitzberger, and A. Lara 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. Journal of Vegetation Science 3:507-520.

Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science 3:337-344.

Vetsch, J. L. 1987. The implications of CO_2 induced climatic change for Prince Albert National Park, Saskatchewan. M. A. thesis, University of Waterloo, Canada.

Vieira, I. C. G., C. Uhl, and D. Nepstad. 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazônia. Vegetatio 115:91-99.

Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecology 76:1116-1133.

Vitousek, P. M., and L. R. Walker. 1987. Colonization, succession and resource availability: ecosystem-level interactions. Pages 207-223 in A. J. Gray, A. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell, Oxford, U.K.

———. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59:247-265.

Vitousek, P. M., P. A. Matson, and K. Van Cleve. 1989. Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. Pages 161-171 in M. Clarholm and L. Bergström, editors. Ecology of arable Land: Perspectives and Challenges. Kluwer

Academic, Dordrecht, The Netherlands.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7:737-750.

Walter, H. 1935. Ist die Prärie von Natur aus baumlos? Geographische Zeitschrift 41:16-26.

———. 1984. Vegetation und Klimazonen: Grundriß der globalen Ökologie. UTB 14. Ulmer, Stuttgart, Germany. (= Walter, H. 1985. Vegetation of the earth and ecological systems of the geo-biosphere. Springer, Berlin, Germany.)

———. 1986. Allgemeine Geobotanik. UTB 284. Ulmer, Stuttgart, Germany.

Walter, H., and H. Lieth. 1967. Klimadiagramm-Weltatlas. Fischer, Jena, Germany.

Wang, Y., T. E. Cerling, and W. R. Effland. 1993. Stable isotope ratios of soil carbonate and soil organic matter as indicators of forest invasion of prairie near Ames, Iowa. Oecologia 95:365-369.

Wardle, P. 1985. New Zealand timberlines. 3. A synthesis. New Zealand Journal of Botany 23:263-271.

Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84:433-441.

Wein, R. W., G. Wein, S. Bahret, and W. J. Cody. 1992. Northward invading non-native vascular plants in and adjacent to Wood Buffalo National Park, Canada. Canadian Field-Naturalist 106:216-224.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecology and Evolution 5:360-364.

Welker, J. M., D. R. Gordon, and K. J. Rice 1991. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. Oecologia 87:459-466.

Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, U.S.A. Oecologia 112:156-164.

Wesser, S. D., and W. S. Armbruster. 1991. Species distribution con-

trols across a forest-steppe transition: a causal model and experimental test. Ecological Monographs 61:323-342.

Wilson, J. B. 1988a. Shoot competition and root competition. Journal of Applied Ecology 25:279-296.

————. 1988b. A review of evidence on the control of root:shoot ratio, in relation to models. Annals of Botany 61:433-449.

Wilson, S. D. 1991. Variation in competition in eucalypt forests: the importance of standardization in pattern analysis. Journal of Vegetation Science 2:577-586.

————. 1993a. Belowground competition in forest and prairie. Oikos 68:146-150.

————. 1993b. Belowground competition and nitrogen availability in alpine heath and grassland. Journal of Ecology 81:445-451.

————. 1998. Competition between grasses and woody plants. Pages 231-254 in G. P. Cheplick, editor. Population ecology of grasses. Cambridge University Press, Cambridge, U.K.

————. 1999. Plant interactions during secondary succession. In L. Walker, editor. Disturbed ecosystems of the world. Elsevier, The Netherlands. In Print.

Wilson, S. D., and H. R. Kleb. 1996. The influence of prairie and forest vegetation on soil moisture and available nitrogen. American Midland Naturalist 136:222-231.

Wilson, S. D., and J. M. Shay. 1990. Competition, fire and nutrients in a mixed-grass prairie. Ecology 71:1959-1967.

Wilson, S. D., and D. Tilman. 1991. Components of plant competition along a productivity gradient. Ecology 72:1050-1065.

————. 1993. Plant competition in relation to disturbance, fertility and resource availability. Ecology 74:599-611.

————. 1995. Competitive responses of eight old-field plant species in four environments. Ecology 76:1169-1180.

Wittig, R., H.-J. Ballach, and C. J. Brandt. 1985. Increase of number of acid indicators in the herb layer of the millet grass-beech forest of the Westphalian Bight. Angewandte Botanik 59:219-232.

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Woods, P. V., E. K. S. Nambiar, and P. J. Smethurst. 1992. Effect of annual weeds on water and nitrogen availability to *Pinus radiata* trees in a young plantation. Forest Ecology Management 48:145-163.

Woodward, F. I., and B. G. Williams. 1987. Climate and plant distribution at global and local scales. Vegetatio 69:189-197.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology - United States and southern Canada. Wiley, New York, New York, U.S.A.

Zak, D. R., D. F. Grigal, S. Gleeson, and D. Tilman. 1990 Carbon and nitrogen cycling during old-field succession: constraints on plant and microbial biomass. Biogeochemistry 11:111-129.

Zar, J. H. 1996. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey, U.S.A.