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 grass-land 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-

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 cer-
tain 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 deposi-
tion 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 Precipita-
tion 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 nitro-
gen 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

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(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.