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 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 deposition.

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 forest. 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 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 dominance 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 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

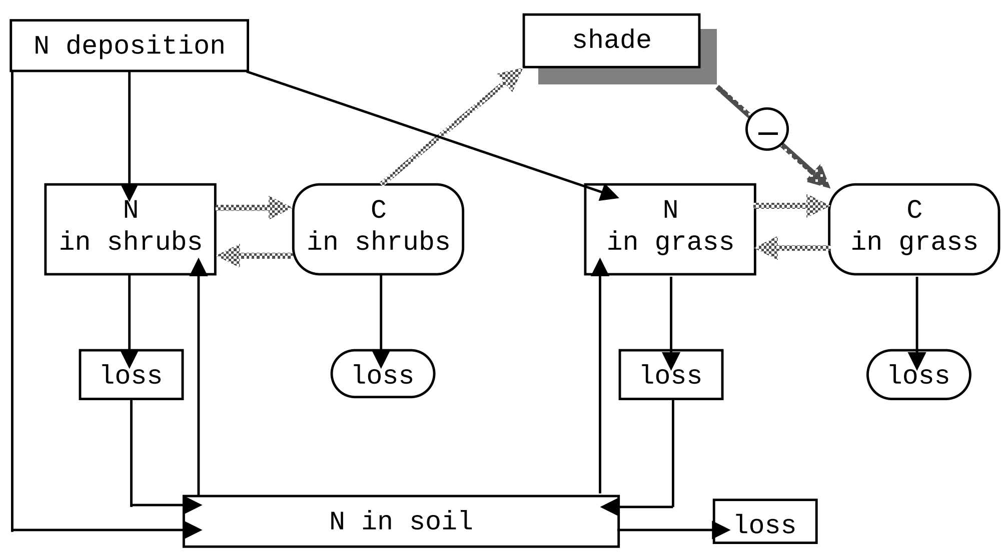

FIG. 6.1. Mechanistical model of shrub-grass interactions in prairie at the scale of individuals when N is the most growth-limiting resource. "Loss" is in relation to the plants, not the ecosystem. Thus, it includes herbivory, decomposition, volatilization, burning, etc. Black arrows indicate mass flows, light arrows causal, positive relations.

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.