11 GREAT PLAINS

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11.1 Ecoregion Description

The North American Great Plains are the largest contiguous ecoregion in North America, covering 3.5 million square km^2, or 16 percent of the continental area (CEC 1997). In the United States, the Great Plains ecoregion encompasses a roughly triangular region (Figure 2.2), bordered on the west by the Rocky Mountains and the southwestern deserts in Texas and northern Mexico, on the east by the Eastern Temperate and Northern Forests ecoregions, and extending well into Canada to the north. Precipitation decreases from east to west, and the dry climate, combined with historical fire and grazing regimes, generally limits tree expansion except in localized riparian areas (Briggs and Knapp 1995, Wells 1965). Savannas and local forest cover are also possible in the wetter eastern Great Plains, though periodic fire and grazers play an important role in determining the balance of herbaceous and woody vegetation across the Great Plains (Briggs and Knapp 1995). Precipitation ranges from 320 to 1020 mm per year, and temperatures range from -5 to 30 °C; both peak during the summer growing season (Bailey 1998). Topography is generally flat, with some plateaus and slightly rolling plains. Soils are generally deep and fertile, with little leaching of minerals and strong buffering potential.

Due to the dry climate, Great Plains ecoregion vegetation is primarily composed of herbaceous species, with grasses dominant, and forbs, sedges, and shrubs subdominant. However, in the drier areas to the west and south, shrubs can codominate; in the east and north, as well as along riverbanks and depressions, trees can dominate. The Great Plains usually are subdivided into three subregions based on precipitation. From west to east (drier to wetter), these are the shortgrass prairie, mixed-grass prairie, and tallgrass prairie (CEC 1997, Samson and Knopf 1994). Shortgrass prairie is primarily dominated by the C_4 (warm season)[10] grasses blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), interspersed with succulents and dwarf shrubs. Tallgrass prairie is primarily dominated by the taller C_4 grasses: big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachyrium scoparium*), interspersed with C_3 (cool season)[11] grasses, forbs, and shrubs. Mixed-grass prairie is a mixture of the two and can shift dramatically in composition with variation in climate (Samson and Knopf 1994). The historical combination of low precipitation, frequent fires, and coevolution with native herbivores (e.g., North American bison, *Bison bison*) maintains the persistence of this generally grass-dominated ecoregion (CEC 1997, Knapp et al. 1999, Samson and Knopf 1994). More recently, reductions in fire frequency and grazing have contributed to encroachment by more woody vegetation across the Great Plains (Briggs et al. 2005).

Human activity has greatly modified the structure and function of the Great Plains. Because of its fertile soil, the Great Plains have been and continue to be heavily used for agriculture and rangelands. It is estimated that of the approximately 120 million ha of historical U. S. prairie, nearly 96 percent, 59 percent, and 50 percent, respectively, of the tallgrass, mixed-grass, and shortgrass prairie, have been lost as a result of human activity (Samson and Knopf 1994). The remaining areas exist mostly as a patchwork of prairie remnants. Many of the species on these remnants are still considered at risk due to long-term fire suppression, alteration of grazing regimes, and isolation, leading to unfavorable conditions for persistence (Briggs et al. 2005, Leach and Givnish 1996). In the Great Plains States, 61 plant species are

[10] C_4 grass: Any species of grass that uses the C_4 photosynthetic pathway, which initially produces a 4-carbon intermediary during fixation of carbon dioxide. This process is more energetically expensive but enables more efficient water usage and less degradation of photosynthetic enzymes.

[11] C_3 grass: Any species of grass that uses the C_3 photosynthetic pathway, which initially produces a 3-carbon intermediary during fixation of carbon dioxide. This process is less energetically expensive but is also less efficient at using water and leads to more degradation of photosynthetic enzymes.

listed as Federally protected (threatened, endangered, or extirpated), and 1029 are listed as state protected (NRCS 2009). The short-, mixed-, and tallgrass prairie generally correspond to the western rangelands, the wheat belt, and the corn/soybean regions (CEC 1997). Wet N deposition generally ranges from 1 to 7 kg N ha^{-1} yr^{-1}, increasing from west to east in roughly equal proportions of ammonium (NH_4^+) and nitrate (NO_3^-): 1.3:1 ratio of NH_4^+: NO_3^- (NADP 2009[12]). Dry deposition is poorly defined for the area, but site-specific studies indicate that dry deposition can account for at least half of total deposition (Gilliam 1987, Knapp et al. 1998). Consequently, we estimate total N deposition over the Great Plains at 2 to 14 kg N ha^{-1} yr^{-1}.

11.2 Ecosystem Responses to N Deposition

Grasslands characteristic of the Great Plains are commonly N-limited or co-limited by N and other resources (e.g., water, phosphorus (P)), and are dominated by plants capable of rapid response to changing conditions (Hooper and Johnson 1999, Knapp and Smith 2001, Vitousek and Howarth 1991). As such, the Great Plains are expected to be sensitive to elevated N input. Following N deposition, there is a complex cascade of potential ecosystem responses which fall into three broad categories: biogeochemical and soil microbial responses, plant population and community responses, and responses at higher trophic levels (Galloway et al. 2003).

Biogeochemical and soil microbial responses:

- Increase in N availability in the soil for microbial immobilization and plant growth
- Change in microbial community structure and activity (often more bacteria)
- Increase or decrease in decomposition based on litter chemistry and other factors
- Increase in NH_3 volatilization (depending on soil pH)
- Increase in N leaching
- Increase soil acidification

Plant individual, population, and community responses:

- Increase in plant growth and allocation to aboveground structures
- Increase in tissue N content
- Decrease in light levels and alteration of germination conditions
- Shifts in competitive interactions and community composition
- Loss of species; often of rare, short, long-lived, native, and N-fixing species

Higher trophic level responses:

- Short-term increase in production at higher trophic levels due to consumption of more aboveground structures that are more nutritionally rich
- Long-term increase or decrease depending on whether plant community shifts toward or away from herbivore-preferred plant species

The above responses are general, and likely to be affected by several factors important in the Great Plains. Indeed, the structure and function of the Great Plains ecosystem is co-regulated by a complex interaction among multiple-resources, co-evolution with large populations of herbivores, and frequent punctuated disturbances, such as wildfire, that have effects on (and are affected by) responses at multiple hierarchical levels (Knapp et al.1998, Risser et al. 1981, Seastedt and Knapp 1993). As such, analysis of the effects of N deposition on the Great Plains is incomplete without incorporation of disturbance, especially from fire, herbivory, and climatic vulnerability. Unfortunately, the paucity of studies examining the effects of N addition at levels comparable to N deposition (discussed in the next section) means that little can be concluded about potential interactions with these important regulatory factors. One might expect that the removal of N via fire and/or herbivores would enhance N-limitation and therefore sensitivity to N deposition, though this likely depends on regional climatic factors, the intensity of

[12]Data from Great Plains sites were averaged over all available years to estimate N deposition and the average ratio of NH_4^+: NO_3^-.

herbivory, and the dominant mechanism regulating ecosystem structure and function (Knapp et al. 1998). Because of these uncertainties, we focus our analysis on known effects of relatively low input rates of N comparable to deposition, with some extrapolation to higher levels.

11.3 Range of Responses Observed

Few studies in the Great Plains have explicitly examined the impact of rates of N input similar to ambient N deposition rates. Indeed, of the 108 papers reviewed for this chapter that examined the effects of N enrichment on the Great Plains, only 17 included treatments ≤30 kg N ha^{-1} yr^{-1}, relevant for direct assessment of critical loads (range: 10 to 25 kg N ha^{-1} yr^{-1}). Furthermore, 9 of these 17 included other nutrient amendments in addition to N (e.g., Tilman 1987), and 12 of these 17 are from only two geographic locations (Cedar Creek Ecosystem Science Reserve, Minnesota, and the Center for Subsurface and Ecological Assessment Research, Oklahoma). These limitations warrant caution when drawing conclusions. It is unclear whether studies that also add non-N resources would underestimate the effect of N deposition (because other effects such as soil acidification and cation loss might not occur) or overestimate effects of N deposition (because co-limiting nutrients were also added). However, because (1) studies that add only N but at higher rates show qualitatively similar patterns; and (2) the site that added non-N resources is not co-limited and is largely unresponsive to addition of non-N resources (Tilman 1984, 1987), we are confident in using these studies in this review. The sections that follow in this chapter are structured by ecosystem responses, with all three prairie types grouped, owing to the small number of studies. The first few paragraphs describe the effects from low-N studies (≤30 kg N ha^{-1} yr^{-1}) and the last paragraph in each section extends the review to include notable high-N studies (>30 kg N ha^{-1} yr^{-1}).

11.3.1 Biogeochemical and Soil Microbial Responses in the Great Plains

Jorgensen et al. (2005) added N at 16.3 kg ha^{-1} yr^{-1} to a mixed-grass prairie with a background total deposition of 11 kg N ha^{-1} yr^{-1} in Oklahoma for 5 years and measured several key ecosystem responses. Soil NO_3^- increased within 1 year and remained elevated by an average of 250 percent over the next 5 years. This N was not efficiently retained in the system. Indeed, leaching of N increased nearly twelvefold, and the dominant form of N-loss shifted from dissolved organic N (DON) (75 percent of N-losses in control plots) to NO_3^- (85 percent of N-losses in fertilized plots). Although litter decomposition was not strongly affected by N addition, there was a tendency for litter N loss to be inhibited after 180 days in fertilized plots. Denitrification was not generally stimulated by added N except after large rain events or with supplemental carbon (C), thus this process appeared to be C-limited and oxygen-inhibited more than N-limited. Gross N transformation rates were not sampled within fertilized plots.

Tilman (1987) added N at a range of rates (0, 10, 20, 34, 54, 95, 170, and 270 kg N ha^{-1} yr^{-1}) to four Minnesota sites near the ecotone of mesic prairie and mixed woodland (background wet deposition 6 kg N ha^{-1} yr^{-1}). We focus our assessment on the two old fields (fields abandoned from agriculture) that most closely represent native prairie of the Great Plains, though patterns exhibited following N addition to all four fields were qualitatively similar. This experiment also included addition of non-N mineral nutrients (P, potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), and trace metals), and was resampled several times in its 28-year history to assess the impacts of eutrophication. Nitrogen addition at 10 and 20 kg N ha^{-1} yr^{-1} for 12 years did not generally increase soil NO_3^- or net N mineralization rates except in the more N-poor field, though both were elevated at higher treatment rates in both fields (Wedin and Tilman 1996). After 22 years, low rates of N addition (10 and 20 kg N ha^{-1} yr^{-1}) in the previously unresponsive old-field increased net N mineralization rates and soil extractable NO_3^- tended to increase at all treatment rates (Clark et al. 2009). The other field was not examined in this later study. Finally, although much of the added N at low rates was retained after 12 years in both fields (Wedin and Tilman 1996), this retention efficiency was diminished after 22 years, as N sinks became saturated and species composition shifted at lower treatment rates (Clark and Tilman 2008, Clark et al. 2009).

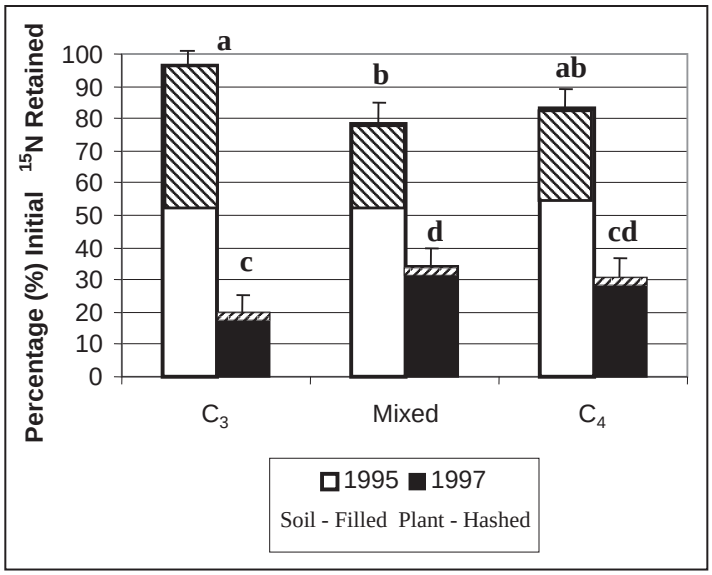

Figure 11.1—Percentage initial ^{15}N retained in soil (solid) and plant compartments (hatched) for three different plant communities (C3, mixed, C4) in 1995 (1 month after addition) and in 1997 (three growing seasons after addition). Bars are +1 SE. Difference letters represent statistically significant differences ($P<0.05$) (Epstein et al. 2001, reprinted with kind permission of Springer Science+Business Media).

The bulk of the nutrients and C in prairie ecosystems are found in the soil, suggesting the ultimate fate of deposited N is likely in complex organic matter stored in the soil. To explore this, Epstein et al. (2001) added 10 kg N ha^{-1} yr^{-1} of ^{15}N to three shortgrass steppe communities (C_3, C_4, and mixed communities) in northeastern Colorado, and sampled various pools over 3 years (background wet deposition not reported). They found that, although the C_3 community initially retained more ^{15}N after the first year (especially in plant material, Fig. 11.1), after the third year retention efficiencies were fairly low (range: 20 to 35 percent). In addition, after 3 years, more ^{15}N was retained in the C_4 and mixed C_3-C_4 communities primarily in the fine particulate organic matter fraction of the soil (Epstein et al. 2001). Another study added 25 kg N ha^{-1} yr^{-1} to five sites across the Great Plains (Table 11.1), and found after 3 years that 46 to 84 percent of the added N was retained primarily in the fine particulate organic matter of the top 20 cm of the soil, with increasing retention in soils with higher soil organic C and finer texture (Barret and Burke 2002). The lower retention efficiencies found in Epstein et al. (2001) compared with Barrett and Burke (2002; as well as others) was explained by higher losses to grazing in Epstein et al. (2001), though it is unknown whether higher herbivory led to a redistribution of ^{15}N or actual losses (i.e., increased volatilization, denitrification). Numerous tracer studies from forests corroborate the evidence that added N often resides in the soil organic or mineral layer rather than in plant tissue (Aber et al. 1998, Currie et al. 2004, Nadelhoffer et al. 2004).

Studies using higher rates of N addition than those already discussed generally confirm the above dynamics and further elucidate responses following N addition. Nitrogen addition (40 kg ha^{-1} yr^{-1}) to monocultures of prairie grassland species in Minnesota increased net N mineralization (46 percent), and respiration rates of the labile (21 percent) and recalcitrant (10 percent) soil C, and significantly decreased soil labile C (31 percent) and microbial N (20 percent) (Dijkstra et al. 2006, Reich et al. 2001). The same experiment demonstrated that although N addition also increased gross N mineralization rates (West et al. 2006) and plant tissue quantity and quality (discussed in next section), there was not an observed increase in the rate of decomposition (Knops et al. 2007). Meta-analyses have found few general relationships between N addition and decomposition, though decomposition is often inhibited in low quality tissue (high lignin:N) and when N addition rates are low compared with ambient N deposition (Knorr et al. 2005). Detailed decomposition studies using higher rates of N addition (100 kg ha^{-1} yr^{-1}) have found that fine-scale soil-substrate interactions, for example from possible shifts in microbial community composition and activity, likely determine whether N addition will generally

Table 11.1—Site characteristics and percentage of N retained 3 years after adding ^{15}N (25 kg N ha^{-1} yr^{-1}) to five prairie communities across the Great Plains. The bulk of the retention was in fine-textured soil with greater organic C content, with less N retention in plant biomass (average of 25 percent in plants across sites) (Barret and Burke 2002, reprinted with permission).

Site	State	System	MAP (cm)[a]	MAT (°C)[b]	Total N retention (%)
Comanche National Grassland	Colorado	shortgrass	41	11.9	84
Thunder Basin National Grasslands	Wyoming	mixed-grass	32	7.9	76
Pawnee National Grasslands	Colorado	shortgrass	37	9.1	64
Fort Keogh Livestock and Range Research Laboratory	Montana	mixed-grass	35	7.1	61
Muleshoe National Wildlife Refuge	Texas	shortgrass	45	14.3	46

[a]MAP – mean annual precipitation
[b]MAT – mean annual temperature

increase or decrease decomposition (Hobbie 2005, 2008; Keeler et al. 2009). In tallgrass prairie where N addition (100 kg ha^{-1} yr^{-1}) was studied in combination with fire and simulated grazing (mowing), N availability was unaffected by burning, was elevated with burning plus N addition, and was not decreased with additional mowing (Collins et al. 1998).

Mycorrhizal responses to N deposition in the Great Plains ecoregion have been documented in gradient studies and fertilization experiments. Using grassland soil data from an N gradient in the Chicago area, Egerton-Warburton[13] reported a decline in both mycorrhizal colonization and spore density as total extractable N increased. There was a steep decline in arbuscular mycorrhizal fungal activity between 5-10 μg g^{-1} extractable soil inorganic N. While N deposition values were not available for all of these sites, National Atmospheric Deposition Program (NADP) values of 9.7 kg ha^{-1} yr^{-1} were reported from the site with highest arbuscular mycorrhizal fungal activity, and 12.4 kg ha^{-1} yr^{-1} from a site with reduced activity. Other studies using higher rates of N inputs (≥40 kg N ha^{-1} yr^{-1}) generally confirm the effects of N on microbial populations, reporting shifts in microbial communities from fungal to bacterial dominance (Bradley et al. 2006, Chung et al. 2007), increased activity for several key soil enzymes (phosphatase, β-glucosidase, and peroxidase) (Chung et al. 2007), and decreased symbiotic microbial populations (Johnson 1993, Johnson et al. 2003). These effects appear to be especially pronounced when soils are more P-rich (Egerton-Warburton et al. 2007, Johnson et al. 2003).

11.3.2 Plant Community Responses in the Great Plains

Nitrogen addition for 4 years at 16.3 kg ha^{-1} yr^{-1} to a mixed-grass prairie in Oklahoma (background total deposition of 11 kg N ha^{-1} yr^{-1}) increased total plant biomass and led to a fivefold increase in tall fescue (*Festuca arundinacea*) cover, although total cover was relatively unaffected (Clark et al. 2003, Jorgensen et al. 2005). Tall fescue cover was weakly, and often not significantly, correlated with cover of other plant functional groups (negatively with native C_4 grasses and positively with non-leguminous forbs). Species richness decreased with increased tall fescue cover in the second and third years of the study (this effect was not seen in year 1, and was not examined in later years), and was unrelated to litter biomass.

[13]Egerton-Warbuton, L.M. Unpublished data. Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL, 60022

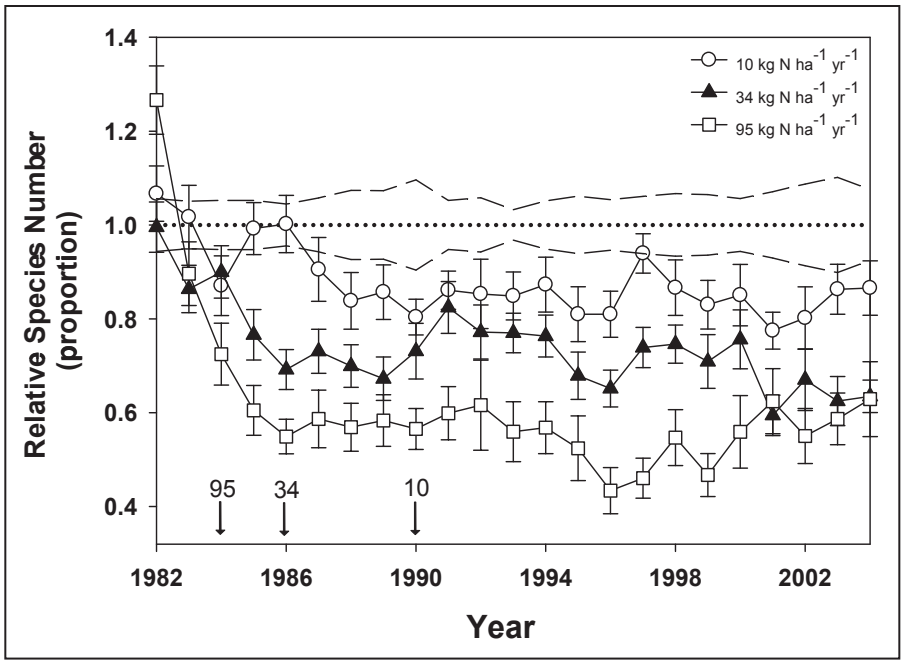

Figure 11.2—Shown are the species numbers (relative to controls) for plots receiving N at three difference rates averaged over three Minnesota fields from 1982-2004. Dashed lines correspond to annual standard errors in control plots and arrows indicate the year of first significant ($P < 0.01$) detection of species loss for that treatment rate (Clark and Tilman 2008).

Wedin and Tilman (1996) examined the impacts of 12 years of N addition at a range of rates (0 to 270 kg N ha^{-1} yr^{-1}, background wet deposition of 6 kg N ha^{-1} yr^{-1}) to two Minnesota old fields dominated by a diverse mixture of prairie grasses and forbs near the ecotone of prairie and mixed woodland. Even low rates of N addition (10 and 20 kg ha^{-1} yr^{-1}) decreased the percent abundance of C_4 grasses (dominated by the native bunchgrass little bluestem) by nearly 20 percent, and increased the abundance of C_3 grasses (primarily the invasive rhizomatous grasses Kentucky bluegrass [*Poa pratensis*] and quackgrass [*Agropyron repens*]) (Wedin and Tilman 1996). Knops and Reinhard (2000) found that the specific leaf area for all three of these grasses tended to increase with N across the N addition gradient. However, quackgrass specific leaf area increased the most at the lowest N addition rate (10 kg N ha^{-1} yr^{-1} plus 6 kg N ha^{-1} yr^{-1} background wet deposition) and demonstrated the largest proportional increase on average (86 percent for quackgrass as opposed to 40 percent and 28 percent for little bluestem and Kentucky bluegrass respectively) (Knops and Reinhart 2000). This pattern suggests plasticity as a key factor influencing compositional changes. Compositional shifts toward more productive N-rich species decreased root and litter C:N ratios, increased litter mass, decreased light penetration, and decreased species richness (Tilman 1993, Wedin and Tilman 1996). Though these changes were not readily apparent after the first few years (Clark and Tilman 2008, Tilman 1987), the losses of species and shifts in community structure increased through time, especially at lower N input levels, with a 17 percent reduction in species number at the 10 kg N ha^{-1} yr^{-1} rate after 22 years (Fig. 11.2, Clark and Tilman 2008). Tilman (1993) suggested that the loss of species was driven primarily by increased litter mass, reducing light and germination rates—a hypothesis supported by the weaker response found in the annually burned field at the same research site (Tilman 1993) and from other related studies (Foster and Gross 1998). Other research suggests light limitation from competing neighbors drives the reduction in species (Hautier et al. 2009).

Studies using high rates of N addition generally confirm the dynamics discussed above. Nitrogen addition (> 50 kg ha^{-1} yr^{-1}) to a newly restored tallgrass prairie (Baer et al. 2003) increased productivity and decreased species richness, purportedly through the same mechanism of reduced light and increased aboveground biomass and litter. Nitrogen addition at 40 kg ha^{-1} yr^{-1} to assembled prairie communities in Minnesota led to similar responses as in natural communities (increased biomass, increased plant N concentration, increased aboveground:belowground biomass ratios), and also led to decreased lignin:N ratios, increased root cellulose concentration, and short-term increases in

photosynthesis (Dijkstra et al. 2006, Knops et al. 2007, Lee et al. 2001, Reich et al. 2001). Lee et al. (2001) reported that the small increases in rates of net photosynthesis for 13 prairie species in the first year of treatment did not generally continue, even though leaf N content remained elevated. Nitrogen addition for 8 years at 50 kg ha^{-1} yr^{-1} to a restored tallgrass prairie community increased annual net primary productivity, root N, and root tissue quality, but root C:N ratios remained high enough to prevent net mineralization of N (Baer and Blair 2008). Similar to the long-term studies in Minnesota (Clark et al. 2009), there was little evidence that N enrichment increased root biomass, soil C or N accrual rates, or storage of C in total, microbial, or mineralizable pools within this time frame (Baer and Blair 2008).

Higher rates of N addition (100 kg ha-1 yr-1) have been studied extensively in many sites, with qualitatively similar results. One notable study is from the tallgrass prairie, that added high rates of N addition in combination with burning and mowing. They found that N addition greatly reduces species richness in combination with burning (especially of the diverse C_3 forb group), a decline that is mitigated with additional mowing (Collins et al. 1998).

11.3.3 Other trophic responses in the Great Plains

Nitrogen addition for 2 years (16.3 kg ha^{-1} yr^{-1}, background total deposition of 11 kg N ha^{-1} yr^{-1}) to a mixed-grass prairie in Oklahoma had variable effects on mammalian herbivores (Clark et al. 2003, Clark et al. 2005, Jorgensen et al. 2005). Nitrogen addition increased the abundance of one species of harvest mouse (*Reithrodontomys montanus*) primarily during the winter, had no effect on a second species of harvest mouse (*Reithrodontomys fulvescens*), and increased the abundance of cotton rats (*Sigmodon hispidus*) only in combination with reduced predation (i.e., fencing) (Clark et al. 2003, Jorgensen et al. 2005).

Haddad et al. (2000) examined the impacts on insect communities from fertilizer addition at a range of rates to a Minnesota old-field (0 to 270 kg N ha^{-1} yr^{-1}; background wet deposition 6 kg N ha^{-1} yr^{-1}). Nitrogen addition at low rates (≤20 kg ha^{-1} yr^{-1}) for 14 years decreased insect species diversity and increased insect numbers and biovolume. This resulted from a decrease in the diversity of food sources and oviposition sites as plant species richness declined and two species (quackgrass and Kentucky bluegrass) came to dominate. Changes in the number of insect individuals at low N addition rates (≤20 kg ha^{-1} yr^{-1}) also varied by functional type, with decreases in parasitoids and increases in herbivores (esp. dominant herbivores) (Haddad et al. 2000). Another study used a detailed biogeochemical process model to examine the effect of N deposition (1 to 5 kg N ha^{-1} yr^{-1}) and insect herbivory on ecosystem level C and N dynamics (Throop et al. 2004). Researchers found that although total C storage was less sensitive to herbivory than to N deposition, herbivory reduced production and soil organic C more as N deposition increased, influencing whether ecosystem C sequestration saturated at lower or higher N deposition rates (Fig. 11.3) (Throop et al. 2004). Short-term and long-term trophic responses to N deposition are likely to differ, and they remain understudied (Throop and Lerdau 2004). Over the short term, N addition increases plant quantity and quality without large changes in composition, which should increase insect populations. But over longer periods, compositional changes can increase or decrease herbivore activity, depending on whether there is a shift toward or away from a community dominated by herbivore-preferred species (Throop and Lerdau 2004).

Studies using higher rates of N addition than those discussed above generally confirm the aforementioned dynamics, with some notable exceptions. In particular, Lau et al. (2008) found no effect of N addition (40 kg ha^{-1} yr^{-1}) on herbivory of a common N-fixing prairie legume (roundhead lespedeza [*Lespedeza capitata*]). This suggests that higher trophic responses to N deposition are likely to depend on specific plant-herbivore interactions. Nonetheless, a review of studies on the effect of high rates of N addition on insect herbivory found a generally stimulatory effect through increased foliar N and decreased secondary compounds (Throop and Lerdau 2004). Macroinvertebrates in the tallgrass prairie of Kansas yielded complex treatment responses between N addition (100 kg ha^{-1} yr^{-1}) and other treatments (burning, mowing, and P addition).

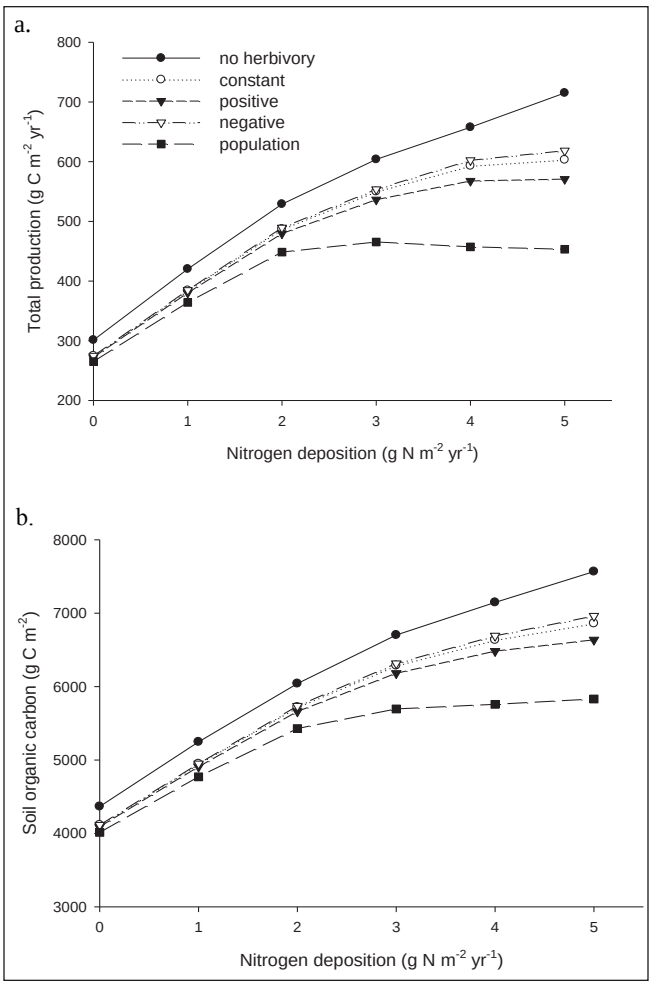

Figure 11.3—Influences of N deposition and the four herbivore functions on C dynamics. The four functions describe whether the intensity of herbivory is independent of the rate of N deposition (constant), increases linearly with N deposition (positive), decreases linearly with N deposition (negative), increases multiplicatively with N deposition (population), or whether herbivory is absent (no herbivory). Values are from the final year of a simulation run that included a 2500-year climate stabilization, 30 years of N deposition, and 30 years of herbivory and N deposition. (a) Total annual biomass production (sum of above-and belowground production) in terms of C accumulation in g m^{-2} yr^{-1}; (b) Total pools of soil organic C (Throop et al. 2004, reprinted with permission of John Wiley and Sons).

Generally, exotic earthworms and herbivorous beetle larvae tended to increase with fertilization, while cicadas were relatively unresponsive (Callaham et al. 2002, 2003). Nitrogen addition (80 kg ha^{-1} yr^{-1}) to a tallgrass prairie in Texas led to a decrease in arthropod richness as a result of an increase in nonpreferred woody species (Hartley et al. 2007). One of the few long-term studies to date of small mammal responses found a long-term decrease in the population of voles after 9 years of high-N treatment (336 kg ha^{-1} yr^{-1}) to an Ohio old-field (Hall et al. 1991). The decrease in the vole population was attributed to a shift in the plant population from edible species (70 percent edible species such as Canada goldenrod [*Solidago canadensis*] and clover [*Trifolium* spp.] in control plots) to inedible species (63 to 99 percent inedible species such as annual ragweed [*Ambrosia artemisiifolia*] and great ragweed [*Ambrosia trifida*] in fertilized plots).

11.4 Critical Loads Estimates

We estimate the critical loads for shifts in ecosystem structure and function at 10 to 25 kg N ha^{-1} yr^{-1} for mixed- and shortgrass prairie and 5 to 15 kg N ha^{-1} yr^{-1} for tallgrass prairie. These overall estimates are based on observed shifts in several key biogeochemical, plant, and trophic indicators following N inputs just above these levels (Table 11.2, 11.3). Total N input at 27.3 kg ha^{-1} yr^{-1} (16.3 kg N ha^{-1} yr^{-1} treated and 11.0 kg N ha^{-1} yr^{-1} of ambient N deposition) to a mixed-grass prairie site increased plant community biomass, increased NO_3^- leaching, and had variable effects on higher trophic levels, suggesting that the N critical load must be below this level. Thus, we set the critical load at 10 to 25 kg N ha^{-1} yr^{-1}. It is difficult to assign a lower value to this range, as we do not have a treatment level for which there was no negative effect, nor do we know whether ambient N deposition has caused alterations in the ecosystem from a prior unimpacted condition. We regard this estimate as fairly reliable rather than reliable because of this uncertainty and because it is based on the only known empirical study examining the response of mixed-grass prairie to such low levels of N. We use the same estimate for the shortgrass prairie (10 to 25 kg N ha^{-1} yr^{-1}) because we expect these ecosystems to respond similarly and we have no other empirical studies to consult. This reduces the reliability for the shortgrass prairie critical loads to expert judgment. The critical load for shortgrass prairie may be slightly higher or co-dependent on water availability, as this system is less sensitive to high rates of N addition (100 kg ha^{-1} yr^{-1}) than the tallgrass prairie (Clark et al. 2007), and likely has a greater tendency for water limitation or co-limitation of water and N (Hooper and Johnson 1999, Lauenroth et al. 1978). However, we urge caution due to the lack of studies and suggest using the 10 to 25 kg

Table 11.2—Responses to low rates of N addition (N-add; ≤25 kg N ha^{-1} yr^{-1}) for the Great Plains ecoregion. Rates of N deposition (N-dep) are shown for comparison.

Ecosystem component	Site	N input *kg N ha^{-1} yr^{-1}* N-add/N-dep	Indicator	Measured Response	Study
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Biogeochemical and microbial	Elevated net N mineralization rates after 22 years, not after 12 years	Clark et al. 2009, Wedin and Tilman 1996
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Plant community	Increased biomass, C_3 (cool season grass) abundance, litter mass, decreased C_4 (warm season grass) biomass, light penetration, tissue C:N, and species richness	Clark and Tilman 2008, Wedin and Tilman 1996, Tilman 1993, Tilman 1987
Ecotone (tallgrass prairie and oak woodland)	Cedar Creek Ecosystem Science Reserve LTER, MN	10-20/6[a]	Higher trophic levels	Decreased insect diversity, and number of parasitoids, increase in total numbers of insects and number of herbivorous insects	Haddad et al. 2000
Shortgrass prairie (3)	Short-grass steppe LTER, CO	10/3[a]	Biogeochemical	Retention of ^{15}N in organic soil layers more than in plants after 3 years	Epstein et al. 2001
Arbuscular mycorrhizal fungi	Chicago, IL area N gradient	12[a]	microbial	Decline in both mycorrhizal colonization and spore density	Egerton-Warburton[c]
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Biogeochemical and microbial	Increased soil NO_3^- and leaching, inconclusive effects on decomposition, no effect on denitrification	Jorgensen et. al. 2005
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Plant community	Increased plant biomass and tall fescue cover, decreased richness, weaker effects on cover of other species	Jorgensen et. al. 2005
Mixed-grass prairie	Center for Ecological Assessment Research, OK	16.3/11[b]	Higher trophic levels	Increases of harvest mouse (*Reithrodontomys montanus*) in winter, no effects on other mammals	Jorgensen et. al. 2005
Mixed-grass (2) and shortgrass (3) prairies	Various (Table 11.1)	25/1-4[a]	Biogeochemical	Retention of ^{15}N in organic soil layers more than in plants	Barret and Burke 2002

[a]Locally measured wet deposition
[b]Total (wet+dry) N deposition
[c]See footnote 13 on page 121

Table 11.3—Critical loads for nutrient N for the Great Plains ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Tallgrass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts	Need more low-N studies without other nutrients	Clark et al. 2009, Clark and Tilman 2008, Tilman 1993, Tilman 1987, Wedin and Tilman 1996
Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts	More studies needed	Clark et al. 2003, 2005; Jorgenson et al. 2005
Shortgrass prairie	10-25	(#)		Inferred from mixed grass	Barret and Burke 2002, Epstein et al. 2001
Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton[a]

[a]See footnote 13 on page 121

N ha^{-1} yr^{-1} level as the critical load. Total N input at 16 kg N ha^{-1} yr^{-1} (10 kg N ha^{-1} yr^{-1} treated and 6 kg N ha^{-1} yr^{-1} ambient N deposition) to a northeastern tallgrass prairie site led to reductions in plant richness, shifts in biogeochemical cycling, and changes in the insect community, suggesting that the N critical load must be below this level. Researchers at this site estimated the critical threshold to these old fields at 5.3 kg N ha^{-1} yr^{-1}. However, due to the extremely low N status of this site, resulting from its geomorphology and past use for agriculture, we think this estimate is likely low for the tallgrass prairie as a whole. Thus, we estimate the critical load for tallgrass prairie at 5 to 15 kg N ha^{-1} yr^{-1}. We regard this estimate as fairly reliable rather than reliable because the only available study also added non-N resources, and because the site is nutrient poor compared to other tallgrass prairie sites (Grigal et al. 1974).

Based on research by Egerton-Warburton[13] and NADP wet deposition, we suggest a provisional N critical load of 12 kg ha^{-1} yr^{-1} for mycorrhizal effects in this ecoregion. However, the lack of sites with lower N deposition in the gradient studied may give us an unrealistically high value for the critical load, as communities in the low deposition sites may have already been altered. Clearly, additional factors such as soil type, fire history, and agricultural and other land-use history will have a large influence on the N status of the Great Plains grassland ecosystem types, and thus on the responsiveness of mycorrhizal fungi to N deposition.

11.5 Comparison to Critical Loads for Other Regions

The European ecosystems most comparable to the U.S. Great Plains are the EUNIS (European Nature Information System) coded habitats E1.2 (perennial calcareous grassland and basic steppes) and E1.7 (non-Mediterranean dry acid and neutral grassland) (European Environmental Agency 2010). Bobbink et al. (2003) estimated a moderately reliable critical load for perennial calcareous grassland and basic steppes at 15 to 25 kg N ha^{-1} yr^{-1}, and a reliable critical load for non-Mediterranean dry acid and neutral grassland at 10 to 20 kg N ha^{-1} yr^{-1} (Bobbink et al. 2003). Other ecosystems comparable to the U.S. Great Plains (especially short- and mixed-grass prairie) include the Eurasian steppe that stretches from Asia into Eastern Europe. Nitrogen addition at 17.5 kg N ha^{-1} yr^{-1} to a representative site in rural China led to increases in plant biomass and reductions in species richness (critical load less than 20 kg N ha^{-1} yr^{-1}) (Bai et al. 2010). Our estimates for the Great Plains are similar to those from China and slightly lower than those from Europe, as we have long-term field experiments in these lower ranges, and it is likely that responses in Europe may be somewhat attenuated due to higher historical levels of N deposition (Galloway et al. 2004). Indeed, several observational studies across

current N deposition gradients (Stevens et al. 2004) and at different time periods (Bennie et al. 2006, Smart et al. 2005) suggest that current and historical N deposition may lower species richness across European systems, though more research is sorely needed.

11.6 Future Research Directions and Gaps in Data

Currently, native communities of the Great Plains are highly fragmented as a result of extensive agricultural activity across this large region and are threatened by several global-change factors in addition to N deposition, including continued land-use change, alterations of historic fire and grazing regimes, and regional climate change. Although fire and grazing are expected to alter ecosystem sensitivity to N deposition, no studies to date have examined these critical interactions at rates comparable to deposition levels. The few high N addition studies suggest that ecosystems may be maximally sensitive if fire regimes alone are restored, suggesting effective conservation likely requires the re-establishment of multiple regulating factors (Collins et al. 1998, Suding et al. 2004). Elevated carbon dioxide (CO_2) under future global change has been hypothesized to both favor and disfavor the currently subordinate C_3 grasses in this ecoregion, depending on the dominant ecological response. On one hand, C_3 grasses may be favored if the fertilization effect of CO_2 predominates and water does not become limiting, resulting in dramatic reductions of ecosystem C-sequestration (Knapp et al. 1998). However, several other lines of research suggest that elevated CO_2 may actually favor the continued dominance of the C_4 grasses of this system through their elevated water use efficiency during dry years (Ham et al. 1995; Knapp et al.1993, 1996), an effect that is likely dependent on future climate patterns (Knapp et al. 1998). Each of these dynamics requires further investigation, but is beyond the scope of this report. Nevertheless, there are several future research directions that will improve our ability to predict the impacts of N deposition. Most importantly, we stress the need for more empirical studies in more geographic locations examining the long term (≥10 years) impacts from low rates of N input (≤20 kg N ha^{-1} yr^{-1}) comparable to N deposition over this region. This should be pursued both in isolation and in combination with the multiple factors that regulate ecosystem structure and function across the Great Plains. This experimental work, however, is not enough, and should be coordinated with dynamic ecosystem-vegetation models to direct limited resources towards areas of greater sensitivity. The wide range of ecosystem responses to high rates of N addition observed (Clark et al. 2007) demonstrate that not all ecosystems are equally N sensitive. Prior research suggests that fine-scale as well as regional-scale factors likely moderate ecosystem responses (Gough et al. 2000). Nonetheless, there are several specific areas that would benefit from additional study as they relate to N deposition:

- Shifts in phenology: A few studies in other systems have examined changes in the timing of ecological interactions with added N which can greatly influence ecosystem functioning (Cleland et al. 2006).
- Decomposition: The impact of N addition on decomposition is still unresolved and largely unstudied at low input rates (Hobbie 2008, Keeler 2010, Knorr et al. 2005).
- Shifts in belowground communities and processes: Although fungal:bacterial population ratios often decrease with N addition (e.g., Bradley et al. 2006), no studies to date have addressed these dynamics at low rates.
- Modulating responses to N deposition: Historical and altered regimes of fire and herbivory are likely to modulate ecosystem sensitivity to N deposition. In addition, grasslands are known to often be co-limited by other resources in addition to N (primarily water), though it is unknown whether critical thresholds for N deposition will decrease or increase under changing climatic regimes (Bobbink et al. 1998).
- Higher-order responses to N deposition: Most of the research to date has focused on plant and soil responses to N deposition. However, higher order responses, such as N-induced shifts in herbivory, pathogens, and drought stress, as well as modulating influences from fire,

herbivory, and climatic variability, are likely to greatly modify the total ecosystem response to N deposition (Bobbink et al. 1998, Knapp et al. 1998, Throop and Lerdau 2004).

- Predictive modeling: As briefly mentioned above, more effort directed to predictive modeling of ecosystem sensitivity to N addition needs to be pursued across ecosystem types and indicators (Heil and Bobbink 1993).

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