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Nitrogen Availability and Old-Field Succession in a Shortgrass Steppe

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ABSTRACT

The relationship between soil nitrogen (N) availability and plant community structure was investigated in old-fields in the shortgrass steppe of Colorado. Nitrogen availability was manipulated by N or sucrose additions for 4 years at three old-fields (early-seral, mid-seral, and late-seral) and at an uncultivated control site. The addition of N generally resulted in increased abundance of annual forbs and grasses relative to perennials at all of the previously cultivated sites. Conversely, experimental reduction of N availability generally increased the relative abundance of perennials. Despite a lack of detectable differences in N mineralization between sites and treatments, ion-exchange resin bags confirmed that sucrose additions reduced plant-available N and that N additions increased plant-available N. This was evidenced further by similar observations for plant tissue N content. The degree to which N additions increased N availability at the various sites supported the idea that late-seral plant communities are less effective at N capture relative to earlier-seral communities. The mid-seral old-field had the lowest rates of litter decomposition and a relatively large accumulation of litter on the soil surface. This mid-seral old-field was dominated by an exotic annual grass (*Bromus tectorum*), which appears to be a major hindrance to redevelopment of the plant-soil system. By experimentally reducing N availability at this stage, we were able, in 4 years, to change the plant community into one that more closely resembled the late-seral community. We also observed that the natural recruitment of weedy annual species on the uncultivated site during an unusually wet year was suppressed by reducing N availability. Our results suggest that available N is an important factor controlling the rate and course of plant and soil community redevelopment on abandoned croplands in the shortgrass steppe, and that manipulation of N availability might be useful in restoration of rangeland vegetation.

Key words: old-field succession; nitrogen availability; plant-soil system; semiarid rangeland restoration.

INTRODUCTION

Secondary succession is the ecological process of plant community change after disturbance. In terrestrial systems, the most noticeable characteristic of this process is the change in plant species composition that takes place over time. It is often reported that plant communities change during secondary succession in response to changes in soil nutrient availability (Tilman 1982, 1987; Inouye and others 1987; Pastor and others 1987; Olff and others 1994; Brussaard and others 1996). These changes in soil nutrient availability during secondary succession are well documented (Lamb 1980; Parrish and Bazzaz 1982; Smith and Rice 1983; Tilman 1984; Inouye and others 1987; Vitousek and others 1989; Reiners and others 1994). Of particular interest is available soil nitrogen (N), which often decreases during natural secondary succession in old-fields (Foster and others 1980; Vitousek 1983; Dormaar and others 1990), or increases during secondary succession on infertile sandy soils (Tilman 1988)

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and after turf removal on European heathlands (Berendse 1990).

Nitrogen availability has been found to be inversely related to the abundance of late-seral dominants in a number of ecosystems. In European heathlands, shrub dominance decreases and perennial grasses become more abundant as available N increases (Heil and Diemont 1983; Berendse and others 1987; Heil and Bruggink 1987; Aerts and Berendse 1988). Shifts from late-seral to mid- or early-seral stages in forests have been observed to be correlated with increases in available N (Aber and others 1989; Cherfas 1991). Others have reported decreases in ericaceous shrubs and other understory vegetation with N additions in mature evergreen forests (Prescott and others 1993, 1995). Increased N availability has been shown to affect the seral process in semiarid ecosystems, slowing the replacement of annuals by herbaceous perennials (McLendon and Redente 1991, 1992; Trent and others 1992). Conversely, decreased N availability has been correlated with the replacement of early-seral species by mid-seral species in prairie and shrubland systems (Wedin and Tilman 1990; McLendon and Redente 1991, Tilman and Wedin 1991; Morgan 1994), and competitive success of shrubs over grasses is increased by lower N availability in semiarid (van Auken and Bush 1989) and arid (Ettershank and others 1978) ecosystems.

The observed patterns of species replacements during secondary succession may be attributed to changes in competitive relationships among species induced by changes in N availability (Raynal and Bazzaz 1975; Peterson and Bazzaz 1978; Tilman 1982; Miller and Werner 1987). Species with higher growth rates are favored over those with slower growth rates under conditions of high N availability (Berendse and others 1987; Heiland Bruggink 1987; Aerts and Berendse 1988; McGraw and Chapin 1989, Bobbink 1991). The high production levels in early-seral plant communities on old-fields result in high use of belowground resources (for example, N and moisture) due to their higher growth rates relative to later-seral communities (Raynal and Bazzaz 1975; Bazzaz 1979), and because relatively large amounts of the resources are often available in the upper soil after abandonment of cultivation. It is important to note that high N availability after cultivation may result not only from past N fertilization but also from the lack of an established plant community for uptake of the mineral N made available by microbial mineralization of organic N.

In the absence of frequent disturbances on old-fields, site dominance by early-seral species continues only as long as they are able to monopolize the supply of limited resources. This monopolization of resource supplies may have both temporal and spatial aspects (Juhasz-Nagy and Podani 1983). In general, early-seral species on old-fields are not effective competitors for light against mid- or late-seral species (van Hulst 1978, 1979; Bazzaz 1979). Instead, the competitive advantages of early-seral species result from their ability to deplete the supply of limiting soil resources before their competitors can use them. This can be accomplished by beginning growth earlier than their competitors (Allen and Knight 1984) or by producing more biomass more rapidly than their competitors once growth has been initiated (Grime 1973; Shipley and Peters 1990). A third competitive advantage of early-seral species might be reduced root exudation and carbon allocations for maintenance of the rhizosphere microbial community relative to late-seral species (Frederick and Klein 1994; Biondini and others 1988). All three of these processes are influenced by N availability.

OBJECTIVES

The focus of our research was the possible role of N availability as a key mechanism controlling secondary succession in these old-fields. Our primary objective was to determine if experimental manipulation of N availability on old-fields could be used to control the redevelopment of the native perennial–dominated shortgrass steppe. A supporting objective was to relate induced changes in N cycling to plant community change. The long-term goal of our research is to develop methodology for accelerating the recovery of abandoned croplands and to avoid stages in plant community development that are dominated by weedy annual species. We hypothesized that the rate and direction of plant community development on old-fields in this shortgrass steppe ecosystem could be controlled, in part, by soil N availability because plant species that are characteristic of undisturbed shortgrass steppe are better able to tolerate low available N levels than are ruderal species. From this, we also hypothesized that the redevelopment of N cycling after disturbance is an important factor in system redevelopment, and that this redevelopment can be stalled when N cycling is altered.

METHODS

Site Description

The experiment was conducted on and near the Central Plains Experimental Range (CPER) located 50 km northeast of Fort Collins, Colorado. Elevation

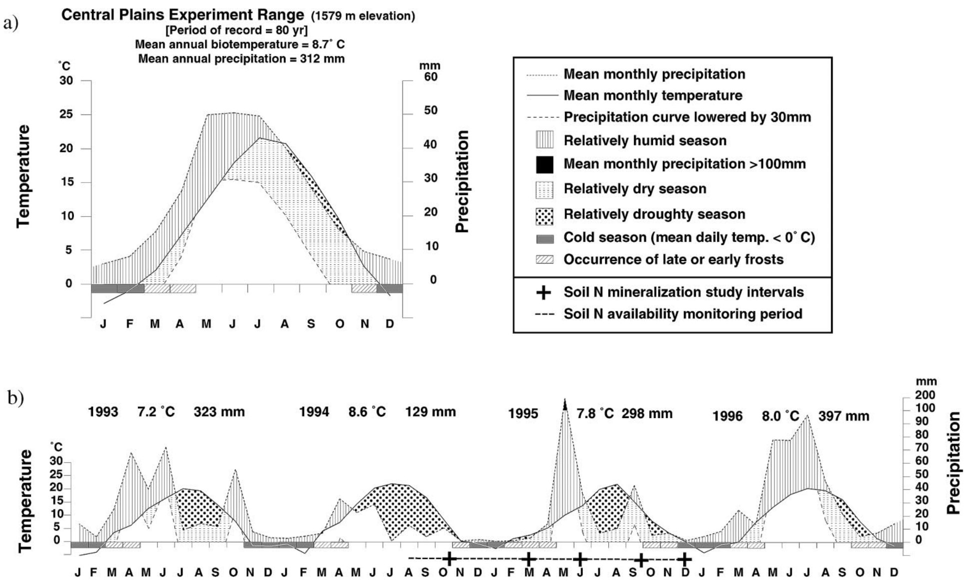

Figure 1. (a) Eighty-year average Walter climate diagram for the Central Plains Experiment Range (see Walter, 1973 for further explanation). (b) Consecutive 4-year Walter climate diagram for the period of study. Climate data was provided by the Shortgrass Steppe Long-Term Ecological Research Project, which is supported by the National Science Foundation (DEB 9632852).

Table 1. Characteristics of the Four Sites

	Early-Seral Site	Mid-Seral Site	Late-Seral Site	Uncultivated Site
History	Last cultivated in 1989	Last cultivated in 1981	Last cultivated in 1955	Never cultivated
Soils[a]	Ascolon fine sandy loam	Ascolon fine sandy loam	Vona sandy loam	Renohill fine sandy loam
Vegetation	*Lactuca scariola, Salsola iberica, Kochia scoparia*	*Bromus tectorum, Agropyron desertorum, Sporobolus cryptandrus*	*Bouteloua gracilis, Aristida purpurea, Chrysopsis villosa*	*Opuntia polyacantha, Bouteloua gracilis, Buchloe dactyloides*

[a] *From Crabb 1982*

of the CPER is approximately 1650 m, and the annual precipitation is approximately 31 cm, with 70% occurring during the growing season (Figure 1a). Climatic conditions during the period of study are presented in Figure 1b. Vegetation in this shortgrass steppe region is dominated by bunchgrasses (64%), succulents (21%), and semishrubs (8%; Brenneman 1989). Secondary succession on oldfields in this region typically takes 50 or more years (Reichardt 1982; Coffin and others 1996) and is characterized by a transition from plant communities dominated by annual forbs and grasses to plant communities dominated by perennials (Lauenroth and Milchunas 1992). Three previously cultivated sites were used in this study, each site was selected to be as similar to the others as was possible, except for time since abandonment from cultivation (Table 1). A fourth site that has never been cultivated was used as a reference site.

Nitrogen Treatments

The experimental design was arranged as a randomized block design with blocks nested within sites. Twelve 10- x 10–m plots with 2-m buffer zones between plots were established at each of the four sites in 1993. The 12 plots at each site were arranged in four blocks of three plots each. The three available N treatments (high-N, intermediate-N, and low-N) were randomly assigned to the three plots in each block. Treatments were first applied in the summer of 1993 and continued through 1996. The low-N treatment plots received sucrose (to immobilize available N) at a rate of 3788 kg ha^{-1} y^{-1} (1600 kg C ha^{-1} y^{-1}), the high-N treatment plots received ammonium nitrate at a rate of 100 kg N ha^{-1} y^{-1}, and the intermediate-N plots, which served as controls, did not receive any amendments. The N and sucrose were hand broadcast, the N in three equal increments annually (April, June, and August) and the sucrose in eight equal increments (April through October) to provide a more temporally uniform reduction in available N through immobilization.

N Dynamics

Soil N availability. Soil N availability was monitored in each study plot by using in situ incubations of mixed-bed ion-exchange resin (IER) bags (Binkley and Matson 1983). The buried IER bags adsorb and retain mineral N from the soil solution during the incubation period. Because they are exposed to approximately the same environmental conditions as plant roots, they provide an index of relative N availability in the different study plots over time. It is important to note that IER bags compete with plant roots for available N, so changes in N availability as detected by IER bags can result from changes in N-supplying processes, as well as changes in plant N uptake. Three IER bags were buried in each of the 10- × 10–m study plots at a depth of 5–10 cm beginning in the spring of 1994. The IER bags were changed approximately monthly during periods of high rainfall and bimonthly during dry periods. One set of IER bags was left in situ over winter. At the end of the incubation period, the IER bags were air-dried overnight and extracted in 75 mL of 1 N KCl for 1.5 h on a mechanical shaker. Extracts were equilibrated overnight on a lab bench, filtered (Whatman#42 filters, Whatman International Ltd., Kent, ME, UK), and stored at −20°C until analysis. Nonincubated IER bags were extracted and used as blanks to correct for background mineral N. The extracts were analyzed for NH_4^+-N and NO_3^--N by using a Perstorp total flow solution autoanalyzer (Perstorp Analytical Inc., Silver Spring, MD, USA).

Net N mineralization. During 1995, rates of soil net N mineralization were estimated using in situ incubations of soil samples in polyethylene bags (Eno 1960). In each study plot, three 2.5- x 15–cm soil cores were removed at randomly selected points and placed into 0.04-mm-thick polyethylene bags. Because it was not possible to maintain the structural integrity of many of the dry sandy soil cores, we were unable to return the cores to their original holes. Instead, we placed the sealed bags containing the soil back into the soil profile at the point of collection by using a tile spade inserted at a 45° angle. The bags were incubated at an average depth of 10 cm for 6 mo during the winter of 1994–95, 2 mo in spring of 1995, 2.5 mo in summer, and 2 mo in autumn. At the beginning of each incubation, a soil core was removed immediately adjacent to each incubated soil sample to determine the initial levels of NH_4^+-N and NO_3^--N. Fresh and incubated soil cores were immediately cooled to 3°C and brought to the laboratory where a 5-g (moist weight) subsample was extracted with 75 mL of 1 N KCl for 1.5 h on a mechanical shaker. Samples then were equilibrated, stored, and analyzed as described for IER bag extracts. The remainder of the soil sample was weighed, dried at 105°C for 48 h, and then reweighed to correct final values for moisture content. Net N mineralization was estimated as the sum of net changes in NH_4^+-N (net ammonification) and net changes in NO_3^--N (net nitrification) for each soil sample during the incubation period.

Soil total nitrogen and pH. At the end of each growing season five 2.5 x 15–cm soil cores were collected from random points in each study plot to determine total N and soil pH. Soil total N was determined on a LECO CHN-1000 Analyzer (LECO Corp., St. Joseph, MI, USA). Soil pH was determined in a mixture of 10 g of air-dried soil in 20 mL of 0.01 M $CaCl_2$.

Decomposition

Rates of plant litter decomposition were estimated in each plot during 1994, 1995, and 1996 by using in situ incubations of local plant litter in nylon mesh bags. Litter was collected at each of the four study sites by clipping standing dead plant material in the late autumn of each year. At each site, we collected plant material from the dominant plant species in areas outside the treatment plots. Species used in litterbags were *Lactuca scariola* at the early-seral old-field, *Bromus tectorum* and *Sporobolus cryptandrus* at the mid-seral old-field (1:1 mix), *Bouteloua gracilis* and *Aristida purpurea* (1:1 mix) at the late-seral old-field, and *B. gracilis* and *Buchloe dactyloides* (1:1 mix) at the uncultivated site. Chemical characteristics of the various litter types used to construct litterbags (for the 1996 field season only) are provided in Table 2. Approximately 5 g of plant material was used in each litterbag with the mass being recorded for each bag. The moisture and ash content of the plant material was determined and used to correct the initial litterbag mass to an ash-free dry matter basis. Six replicate litterbags were placed on the soil surface in the plots at six randomly determined points. Because the bags were relatively small (10 x 10 cm), we were able to place them in contact with the soil surface between plants. To prevent disturbance by wind and grazing animals, we held the bags in place with wire mesh screens (1-cm^2 openings) that were secured in the soil with aluminum pegs. After 12 mo, the litterbags were collected, cleaned, and dried at 55°C to constant mass. After removing roots and germinating plants from the litterbags, we determined their mass. The remaining litter in each bag was ashed at 550°C for 3 h so that soil trapped in the litter material could be subtracted from the litter mass. Using the final and initial dry weights and ash contents, we calculated rates of decomposition as ash-free dry matter mass changes.

This experimental design for litterbags was followed for the 1994 and 1995 field seasons. In 1996, a slight modification was made in that additional

Table 2. Chemical Characteristics of the Various Litter Materials Used to Construct Litterbags for the 1996 Field Season

Seral Site	Plant Species	Cellulose (%)	Lignin (%)	Cellulose + Lignin (%)	N (%)	C (%)	C:N	Lignin:N	Cellulose + Lignin:N
Early	*Lactuca scariola*	41.11	6.81	47.92	0.507	44.30	87	13	95
Mid	*Bromus tectorum* + *Sporobolus cryptandrus*	45.97	6.57	52.54	0.584	44.91	77	11	90
Late	*Bouteloua gracilis* + *Aristida purpurea*	36.93	5.38	42.31	0.673	42.03	62	8	63
Uncultivated	*Bouteloua gracilis* + *Buchloe dactyloides*	33.36	4.65	38.00	0.665	42.76	64	7	57

Plant materials were collected in October, 1995.

litterbags made from plant material from the uncultivated site was placed at all four sites. Because of these additional types of litterbags used at each site, the number of replicate bags of each type per plot was reduced from six to three. We made these modifications to better discern the relative differences in decomposition between the different sites by using a common litter type.

Litter Mass

Plant litter was collected in June and August of each year at the time of the vegetation sampling described below. After clipping vegetation, we gathered the litter by hand from each of 10 0.5-m^2 quadrats within each study plot. The litter was dried to constant mass at 55°C and weighed.

Plant Community

Annual production and N content. Aboveground plant biomass by species was collected twice annually (June and August) from 10 randomly located 0.5-m^2 quadrats within each of the 48 plots (four sites x three treatments x four replicate plots) beginning in August 1993. Each species was clipped to ground level, dried to constant mass at 55°C, weighed, ground to pass a 40-mesh sieve, and analyzed for N concentration on a LECO CHN-1000 Analyzer (LECO Corp.). Annual aboveground primary production was estimated for each plant species by taking the higher value of the two sampling dates each year. Relative biomass was calculated by dividing the annual production value for each species within a plot by the total plot production for that year. For analyses of plant community dynamics, we grouped plant species into ecologically similar groups (annual forbs, annual grasses, perennial forbs, perennial grasses, shrubs, and succulents) for the reasons discussed by Lauenroth and Dodd (1978).

Root biomass and N content. Root N pools and biomass were estimated by removing 4.5- x 15–cm soil cores from seven random points in each plot. The cores were weighed, and a 50-g subsample was removed and dried at 105°C until constant mass to determine moisture content. We estimated soil bulk density for each plot based on this and the mass and volume of the core. These bulk density values were used later to convert soil nutrient measures to mass per area values. Roots were gently separated from soil cores by hand while submerged in water. The wash water was allowed to settle so that floating fine roots could be sieved from the surface. All of the collected roots then were dried to constant mass at 55°C, weighed, and ground to pass a 40-mesh sieve. A small subsample of each root sample was analyzed for N concentration as described for vegetation. The remaining portion of the ground root sample was ashed at 550°C for 3 h to correct root weights for attached soil particles. Root biomass thus was calculated on an ash-free dry matter basis. Roots from the 50-g subsample of soil removed from the root cores for moisture determination also were sorted, dried, and weighed. These weights were added to those of the remainder of the root cores to give the total root weight per core.

Statistical Analyses

Univariate analyses were conducted on each univariate variable (grouped by site and year) by using SAS PROC GLM version 6.01 (SAS Institute, Cary, NC, USA). Differences between control and treatment plots (grouped by site and year) were tested using Tukey's tests ($\alpha = 0.05$). Because there were no significant ($\alpha = 0.05$) block effects detected for most measures, blocks were pooled to test for control and treatment plot differences within a site.

Table 3. Total Sorption of N (mg) by IER Bags from 20 April 1994 to 12 December 1995[a]

Measure	Treatment	Early-Seral	Mid-Seral	Late-Seral	Uncultivated
NH_4^+-N	High-N	10,094*	16,138*	19,450*	18,422*
	Control	492a	1333b	1402b	1070ab
	Low-N	195*	813	383*	352*
NO_3^--N	High-N	7535*	13,449*	20,807*	17,880*
	Control	736a	1388ab	1643b	1213ab
	Low-N	158*	790*	333*	236*
Total mineral N	High-N	17,629*	29,587*	40,257*	36,301*
	Control	1227a	2722b	3045b	2283ab
	Low-N	352*	1603*	716*	587*
NH_4^+-N:NO_3^--N	High-N	1.28	1.17	0.94	1.00
	Control	0.80a	1.00a	0.86a	1.10a
	Low-N	1.84*	1.30	2.17*	2.07

In the table body, treatment means within a column (site) followed by an asterisk are significantly different from the corresponding control mean for each measure at $\alpha = 0.05$ (n = 12). Site means (for control plots only) followed by different letters are significantly different from other sites at $\alpha = 0.05$ (n = 12).

[a] *Sum of eight consecutive incubations.*

RESULTS

N Dynamics

Soil N availability. Annual additions of N (100 kg ha^{-1}) significantly increased total inorganic N availability, and sucrose additions significantly decreased total inorganic N availability at all sites (Table 3) based on IER bag data. Both ammonium- and nitrate-N were detected in IER bags at a near 1:1 ratio in all control plots (Table 3). Significant changes in the ratio of sorbed NH_4^+-N to NO_3^--N, resulting from sucrose additions, at the early- and late-seral old-fields could indicate N uptake preferences of the corresponding plant and soil communities subjected to N alterations, or differential effects on the nitrification potential of the soil communities.

There was less available N (NH_4^+-N, NO_3^--N, and total mineral N) at the early-seral old-field compared with the mid- and late-seral old-fields (Table 3), indicating either lower N availability at this site or increased uptake of N by plant roots, which compete with IER bags for available N. In the N-amended plots, less N was captured in IER bags at the early-seral old-field relative to the other sites (Table 3). This general trend of increasing N availability in high-N plots with successional age is consistent with the notion that early-seral plants are more effective than mid- or late-seral plants at uptake of available soil N (Redente and others 1992). The low amounts of mineral N detected in IER bags from early-seral control plots relative to control plots at other sites (Table 3) thus are likely due to greater N uptake by vegetation.

Net N mineralization. Total in situ production of mineral N in 1995 was not significantly altered by N additions (Table 4) although net nitrification was stimulated by N addition at most sites. We, however, did observe a significant increase in the production of mineral N at the early-seral old-field in the sucrose amended plots. Because early-seral plant species release less C in root exudates than late-seral plants (Biondini and others 1988), our observations suggest that net N mineralization at the early-seral old-field may be limited by a readily available C source.

Our observation of consistent rates of net N production across the four sites in 1995 might seem to be an apparent contradiction to the IER bag data, which clearly show lower N availability at the early-seral old-field. This contradiction can be explained by the different processes that these two techniques measure. The IER bags adsorb mineral N from the soil solution and are subjected to the same conditions that plant roots and soil organisms would experience (Binkley 1984; Gibson 1986). Thus, they are an open system and must compete with other potential sinks of mineral N (leaching losses, plant roots, soil organisms, and the soil ion-exchange complex). The buried bags, however, provide a measure of the ability of the soil microbial community to produce mineral N in situ. Because the bags are a closed system, the N that is mineralized cannot be taken up by plant roots or leached out of the bags. The observed low N sorption by IER bags at the early-seral old-field despite relatively high net N mineralization is a further indication that mineral N uptake by plant roots is high in this earlier-seral plant community.

Soil total nitrogen and pH. Soil total N pools showed no clear consistent differences among sites

Table 4. Total Production of Mineral N (kg ha^{-1}) in In Situ Buried Bags during 1995[a]

Measure	Treatment	Early-Seral	Mid-Seral	Late-Seral	Uncultivated
NH_4^+-N	High-N	−20.20*	−15.08*	−49.09*	−74.97*
	Control	0.72a	2.21a	−4.05b	−0.11ab
	Low-N	5.05*	1.18	1.20	1.95
NO_3^--N	High-N	82.42*	28.82	90.69*	83.58*
	Control	41.01ab	26.49b	49.82a	27.37b
	Low-N	59.19*	25.24	37.30	29.40
Total mineral N	High-N	62.23	13.74	41.60	8.62
	Control	41.74a	28.71a	45.78a	27.26a
	Low-N	64.23*	26.42	38.51	31.35

Treatment means within a column (site) followed by an asterisk are significantly different from the corresponding control mean for each measure at $\alpha = 0.05$ (n = 12). Site means (for control plots only) followed by different letters are significantly different from other sites at $\alpha = 0.05$ (n = 12).

[a] *Sum of four consecutive incubations.*

Table 5. Soil Total N and pH at the Four Seral Sites Subjected to N Manipulations

Measure	Year	Treatment	Early-Seral	Mid-Seral	Late-Seral	Uncultivated
Total N (kg ha^{-1})	1994[a]	High-N	813*	853	769	716*
		Control	674ab	761ab	805a	627b
		Low-N	798	667	822	654
	1995	High-N	1028	758	903	861
		Control	1055a	714b	881ab	829b
		Low-N	981	725	853	721
	1996	High-N	1110*	1089*	1137	1032
		Control	926a	853a	929a	957a
		Low-N	999	1043	954	1175
Soil pH	1994	High-N	6.62*	6.87*	5.57*	5.78
		Control	6.97a	7.08a	6.36b	5.63c
		Low-N	7.11*	7.11	6.53	6.01*
	1995	High-N	6.66*	7.35	6.21*	5.71
		Control	7.19ab	7.47a	6.86b	5.95c
		Low-N	7.18	7.42	6.91	5.95
	1996[a]	High-N	6.17*	7.01*	5.64*	4.78*
		Control	7.13a	7.31a	6.45b	5.82c
		Low-N	7.07	7.44	6.47	5.67

Treatment means within a column (site) followed by an asterisk are significantly different from the corresponding control mean for each measure at $\alpha = 0.05$. Site means (for control plots only) followed by different letters are significantly different from other sites at $\alpha = 0.05$.

[a] *n = 20, otherwise n = 12.*

(Table 5). There were distinct differences in soil pH between the sites, with a general trend towards decreasing pH with successional age (Table 5). We observed significant reductions in soil pH with N additions.

Decomposition and Litter Mass

Rates of decomposition of local plant litter were generally lowest for the mid-seral old-field for 3 years of study (Figure 2). In 1996, the placement of uncultivated site litter at all sites showed the same pattern of decomposition across all sites as the local litter, indicating that observed patterns of decomposition were likely due to site factors and not differences in litter types. Across the different aged sites, decomposition rates were initially high followed by the low rates at the mid-seral old-field and then an increase in decomposition rate at the late-seral and uncultivated sites. The mid-seral old-field also had the largest (although not always statistically significant) standing pool of litter mass in all years (Figure 3), suggesting that the lower decomposition rate at this site may result in larger litter pools, or conversely, that litter from this plant community (primarily *B. tectorum*) may inhibit microbial decomposition. Working in this same shortgrass steppe system, Milchunas and Lauenroth (1995) found that the cyclic abundance of exotic weeds in previously N

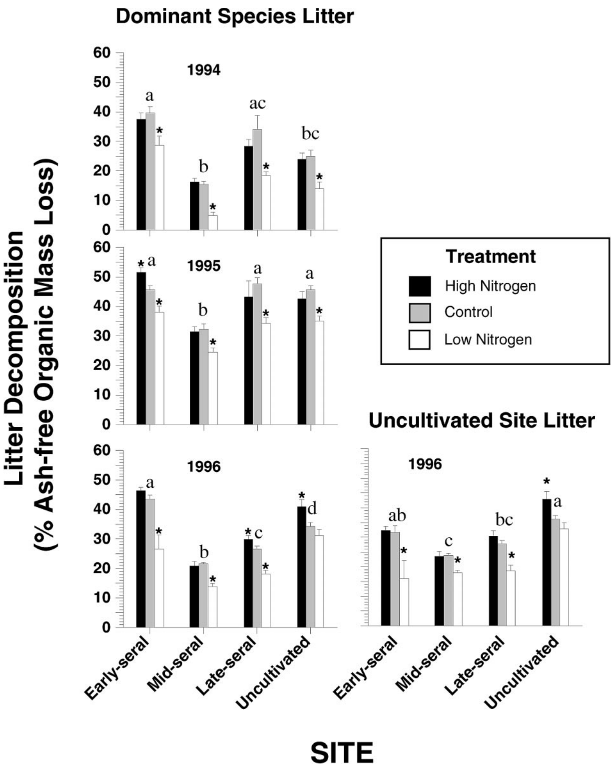

Figure 2. Decomposition of litter from the dominant plant species at the four sites subjected to N manipulation from 1994 through 1996, and for litter from the uncultivated site placed in all of the old-fields in 1996. Bars represent the standard error of the mean (n = 24 for 1994 and 1995' n = 12 for 1996). Asterisks indicate a treatment mean that is significantly different from the corresponding control mean at α = 0.05 by using a Tukey's Studentized Range test. Different letters above bars for control plots indicate significant differences between sites (control plots only) by using a Tukey's Studentized Range test (α = 0.05).

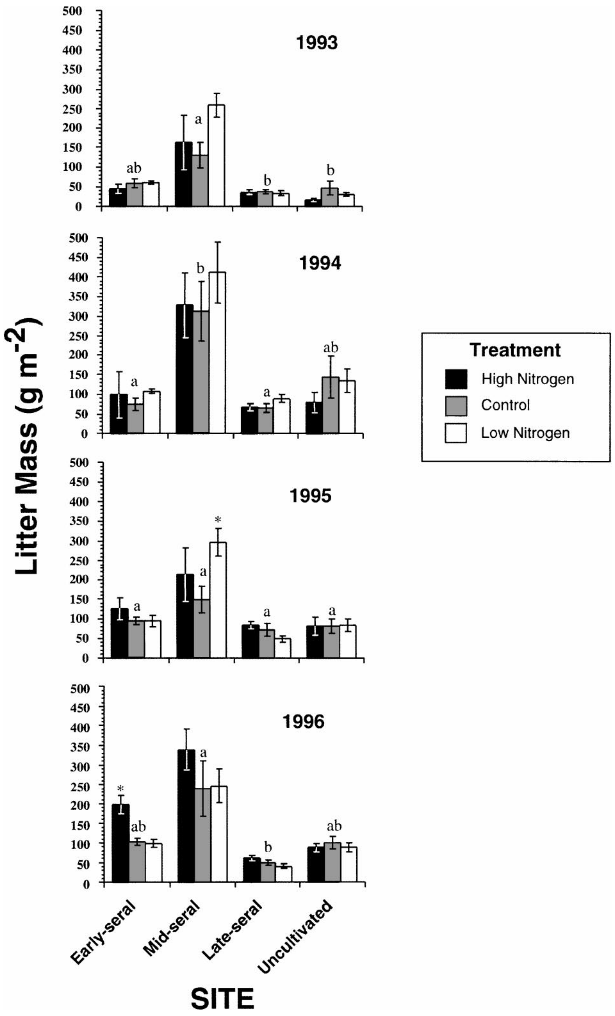

Figure 3. Standing pool of plant litter (maximum mass value from spring and summer samplings) from 1993 to 1996 at the four sites subjected to N manipulations. Bars represent the standard error of the mean (n = 4). Asterisks indicate a treatment mean that is significantly different from the corresponding control mean at α = 0.05 by using a Tukey's Studentized Range test. Different letters above bars for control plots indicate significant differences between sites (control plots only) by using a Tukey's Studentized Range test (α = 0.05).

enriched communities was related to large accumulation of plant litter.

Decreasing soil N availability significantly reduced litter decomposition rates at all sites in most years (Figure 2). Conversely, increasing soil N availability seemed to increase decomposition rates, although these increases were not always statistically significant. Our results of N availability effects on decomposition agree with those of Hunt and others (1988), because similar effects for sucrose and N additions on decomposition of various litter types in several ecosystems were observed, including a shortgrass steppe site near our sites. Turner (1977) suggested that altered decomposition rates in a Douglas-fir stand subjected to N manipulations may have been due to a pH effect. Our results, which show significant reductions in decomposition in low N plots (Figures 2 and 3) where soil pH was not significantly altered (Table 5), suggest that lower decomposition rates are not due to altered soil pH. Increases in the decomposition of surface litter in the high-N plots may have been due to the translocation of soil N to the litterbags via fungal hyphae (as suggested by Hart and others 1993), thus reducing the C:N ratio in the decomposing litter.

Plant Community

At all of the sites, a reduction of N availability from the addition of sucrose resulted in decreases in the relative biomass of annual plant species (grasses and

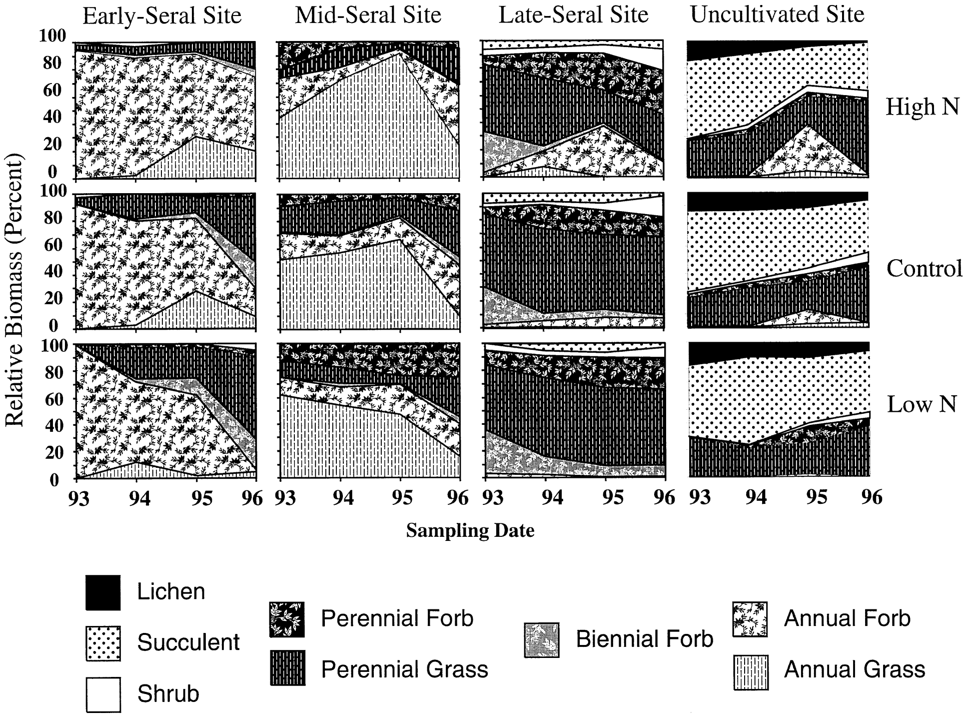

Figure 4. Relative plant community biomass composition of the four sites subjected to N manipulations plus control from 1993 through 1996. Relative biomass is based on the maximum biomass from June and August samplings each year. Each panel is the mean of four plots.

Table 6. Annual Plant Production at the Early-Seral Old-Field

	1993			1994			1995			1996		
	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N
Annual forbs	69.98	85.98	91.37	161.67	81.47	37.05[a]	235.40[a]	103.70	80.29	116.55[a]	22.67	1.19
Annual grasses	0.09	0.00	0.00	5.67	5.20	5.16	138.06	54.90	2.39	43.21[a]	8.96	2.94
Biennial forbs	0.29	0.04	0.12	3.52	1.35	1.18	5.01	8.56	16.37	11.58	21.47	23.02
Perennial forbs	0.02	0.00	0.16	0.00	0.08	1.11	0.95	0.83	2.37	0.31	1.87	2.84
Perennial grasses	2.68	3.49	0.29	9.37	10.96	10.58	23.64	21.67	30.61	39.77	44.82	69.58
Shrubs	0.00	0.00	0.00	0.00	0.00	0.02	0.06	0.00	0.00	0.00	0.00	5.71
Unknown	1.17	2.70	0.27	0.41	0.00	0.13	0.05	0.07	0.07	0.08	0.00	0.00
Total plant	74.21	92.20	92.19	180.64[a]	99.05	55.23[a]	403.16[a]	189.73	132.10[a]	214.39[a]	109.22	105.28
Native species	2.61	2.50	0.45	9.83	11.59	11.93	11.86	22.00	31.28	28.46	56.48	66.55
Introduced species	70.43	87.01	91.48	170.40	87.46	43.17[a]	391.25[a]	167.65	100.74[a]	185.85[a]	52.74	38.74
Legumes	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.15	0.03	0.00	0.00
Average number of species	6.50	5.25	5.00	11.25	11.25	10.75	18.25	15.00	15.25	18.50	21.50	17.25[a]
Litter mass	43.89	58.05	61.52	732.87	290.15	216.36	125.36	96.42	94.89	197.33[a]	101.85	98.54

*Values are plot means (*n *= 4) of oven-dried maximum biomass (g m^{-2}) for June and August samplings (except August only in 1993).*
[a] *Treatment means significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.*

forbs) and increases in perennial species (grasses, forbs, shrubs, and succulents; Figure 4). An increase of N availability from N additions resulted in increases in the relative biomass of annual plant species and decreases in perennial species (Figure 4). Similar trends can be seen in annual biomass production for annual versus perennial species as presented in Tables 6 to 9. Thus, changes due to N additions can be viewed as a successional retrogression. Conversely, reducing N availability via sucrose additions increased the rate of plant community redevelopment as measured by the relative abundance of annual versus perennial species.

Generally, additions of N to study plots increased plant N (Figure 5). Reducing N availability via sucrose additions had a less pronounced effect on plant N; however, significant reductions were observed at several sampling periods (Figure 5). Most

Table 7. Annual Plant Production at the Mid-Seral Old-Field

	1993			1994			1995			1996		
	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N
Annual forbs	27.16	16.93	10.38	14.05	28.63	20.55	16.13	57.69	56.84	140.80	82.58	29.52
Annual grasses	39.66	46.43	55.92	98.65	89.16	58.81	468.44[a]	248.61	127.06	60.08	19.18	15.04
Biennial forbs	0.00	0.90	0.00	0.32	1.15	4.12	3.48	6.63	1.12	1.61	9.93	4.63
Perennial forbs	17.16	8.94	12.02	6.20	8.52	24.07	4.74	7.23	27.93	14.96	23.11	27.73
Perennial grasses	5.54	37.90	13.99	20.45	67.94	16.48	13.19	52.16	18.80	76.81	61.12	48.99
Unknown	0.00	0.00	0.00	0.04	0.01	0.14	0.00	0.00	2.82	0.00	0.00	0.00
Total plant	89.51	111.09	92.31	139.70	195.40	124.15	507.21	372.31	234.57	294.25	195.92	125.91
Native species	24.27	34.21	27.23	28.10	35.84	38.64	18.75	69.15	41.54	103.95	89.86	69.73
Introduced species	65.24	76.88	65.09	111.57	159.56	85.38	488.46	303.16	190.22	190.30	106.06	56.18
Legumes	0.00	0.00	0.00	0.00	0.00	7.93	0.00	0.02	0.51	0.02	0.00	7.03
Average number of species	6.50	7.75	7.00	10.25	7.25	10.50	9.00	13.00	13.50	10.00	15.00	11.25
Litter mass	163.16	131.12	258.99	328.49	312.86	411.56	214.27	149.66	295.91[a]	339.30	239.87	245.59

Values are plot means (n = 4) of oven-dried maximum biomass (g m^{-2}) for June and August samplings (except August only in 1993).

[a] *Treatment means significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.*

Table 8. Annual Plant Production at the Late-Seral Old-Field

	1993			1994			1995			1996		
	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N
Annual forbs	2.63	2.41	3.27	15.50[a]	5.94	1.95	70.47	7.98	0.34[a]	15.83	8.50	1.03
Annual grasses	0.00	0.00	0.00	14.40	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Biennial forbs	25.84	26.22	32.71	4.81	6.23	10.53	3.14	6.55	4.87	2.19	2.32	7.05
Perennial forbs	5.65	4.20	11.20	23.27	19.15	12.78	42.99[a]	19.45	12.85	47.71[a]	12.86	18.39
Perennial grasses	42.25	51.40	47.69	68.05	75.22	47.10	38.31[a]	59.47	33.87[a]	49.19	58.72	45.19
Shrubs	3.45	2.90	5.19	5.34	3.15	3.12	9.62	5.83	2.77	23.70	15.66	6.09
Succulents	5.29	7.26	0.05	7.22	6.77	4.10	5.55	7.84	5.02	9.90	2.50	2.64
Unknown	0.03	0.10	0.00	0.07	0.61	0.12	0.00	0.06	0.00	0.00	0.00	0.00
Total plant	85.12	94.48	100.09	138.64	117.72	79.68[a]	170.08	107.18	59.71[a]	148.52[a]	100.56	80.38
Native species	57.37	66.76	64.31	119.30	109.35	67.59	134.83	99.54	53.69	143.97	96.68	72.64
Introduced species	27.73	27.62	35.78	19.28	7.65	11.97	35.26	7.58	6.03	4.55	5.88	7.74
Legumes	26.43	26.43	33.68	6.16	6.81	12.94	4.45	6.96	5.33	4.74	2.42	10.40
Average number of species	13.00	14.25	12.75	17.25[a]	21.75	20.00	22.25	21.25	17.25	22.00	21.50	18.75
Litter mass	36.22	38.14	33.59	471.15	396.48	294.62	84.20	73.39	48.62	61.47	48.29	40.77

Values are plot means (n = 4) of oven-dried maximum biomass (g m^{-2}) for June and August samplings (except August only in 1993).

[a] *Treatment means significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.*

plant N across all sites was detected in belowground structures, and this root pool of N showed dramatic increases during the wet spring of 1995 (Figure 1) at all of the sites but was more pronounced at the younger old-fields (Figure 5).

In addition to changes in the species composition of these plant communities with N manipulations, we observed functional and structural changes as suggested by altered above- and belowground plant community biomass (Figure 6). There was a general positive response of aboveground plant growth to N additions, especially at the early-seral old-field (Figure 6). There were also differences in biomass allocation between the different sites with early- and mid-seral communities having most biomass aboveground, whereas the late-seral and uncultivated communities allocated most biomass belowground. Annual variation in total plant biomass was also apparent. The wet spring of 1995 resulted in increased biomass (relative to 1994) at

Table 9. Annual Plant Production at the Uncultivated Site

	1993			1994			1995			1996		
	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N	High N	Control	Low N
Annual forbs	0.31	0.64	0.39	1.48	0.84	0.30	69.25[a]	19.01	2.39[a]	0.60[a]	0.13	0.04
Annual grasses	0.00	0.00	0.00	0.15	0.11	0.01[a]	11.17	4.02	0.15[a]	1.44	5.20	0.28[a]
Biennial forbs	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.06	0.00	0.00	0.02	0.00
Perennial forbs	0.92	2.78	0.66	3.57	4.52	3.13	7.33	7.46	14.73	1.44[a]	3.82	5.48
Perennial grasses	27.68[a]	33.87	31.14	46.34	40.93	43.96	43.93	37.18	29.38	51.60	58.23	38.73[a]
Shrubs	0.81[a]	3.07	0.40[a]	4.98	2.68	1.43	13.38	7.10	2.19	5.20	10.62	4.33
Succulents	64.92	95.40	57.06[a]	74.10	77.15	138.01	66.15	86.62	62.85	37.03	56.83	47.03
Unknown	0.07	0.00	0.00	0.02	0.02	0.00	0.46	0.00	0.10	0.00	0.00	0.00
Total plant	94.70	135.74	89.64[a]	130.64	126.23	186.83	211.69	161.44	111.78	97.31	134.84	95.88
Native species	94.63	135.74	89.64	130.59	126.18	186.83	210.81	161.33	111.65	97.23	134.83	95.87
Introduced species	0.00	0.00	0.00	0.03	0.04	0.00	0.43	0.12	0.04	0.08	0.01	0.01
Legumes	0.85	2.46	0.56	2.26	3.01	1.81	2.97	4.26	11.95	0.26[a]	1.67	3.21
Average number of species	12.75	13.75	12.00	20.00	20.50	17.50	28.25	26.25	22.25	19.25	22.00	19.50
Lichens	17.63	22.23	19.81	14.16	17.84	23.53	10.44	21.97	15.68	1.53	9.35	7.92
Litter mass	16.13	45.84	31.24	78.83	144.89	134.18	81.55	81.87	155.28	87.42	100.65	88.71

Values are plot means ($n = 4$) of oven-dried maximum biomass ($g\ m^{-2}$) for June and August samplings (except August only in 1993).

[a] *Treatment means significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.*

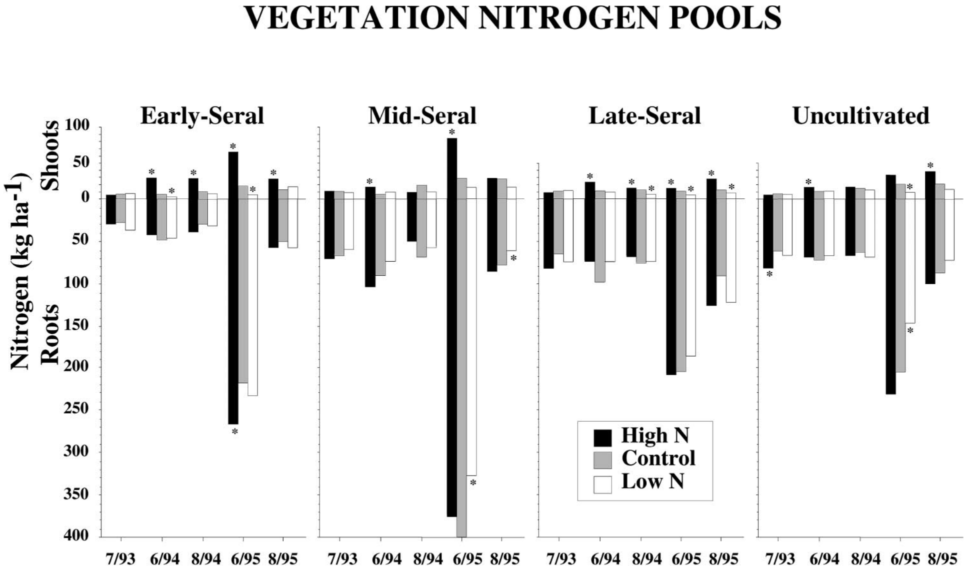

Figure 5. Nitrogen content of roots and shoots for different treatments at three old-fields and an uncultivated shortgrass steppe site for five sampling dates between 1993 and 1995. Asterisks indicate a treatment mean that is significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.

all sites. This growth response was only apparent below ground at the late-seral and uncultivated sites.

DISCUSSION

N as a Regulator of Old-Field Succession

The pattern of old-field succession that we observed in this study was similar to that reported by Costello (1944) for this region. Our early-seral old-field was initially dominated by annual forbs. By the fourth year, it contained a mix of annual forbs, annual grasses, and perennial grasses. The mid-seral old-field in comparison was dominated by an annual grass (*B. tectorum*) until the wet spring of 1995 (Figure 1) when it declined and was replaced by annual forbs and perennial forbs and grasses (Figure 4). The late-seral old-field was dominated by perennial grasses and did not appear to undergo any major compositional changes during the study period. The uncultivated reference site was dominated by perennial grasses and succulents (Figure 4).

As measured by the relative abundance of annual versus perennial species, the experimental reduc-

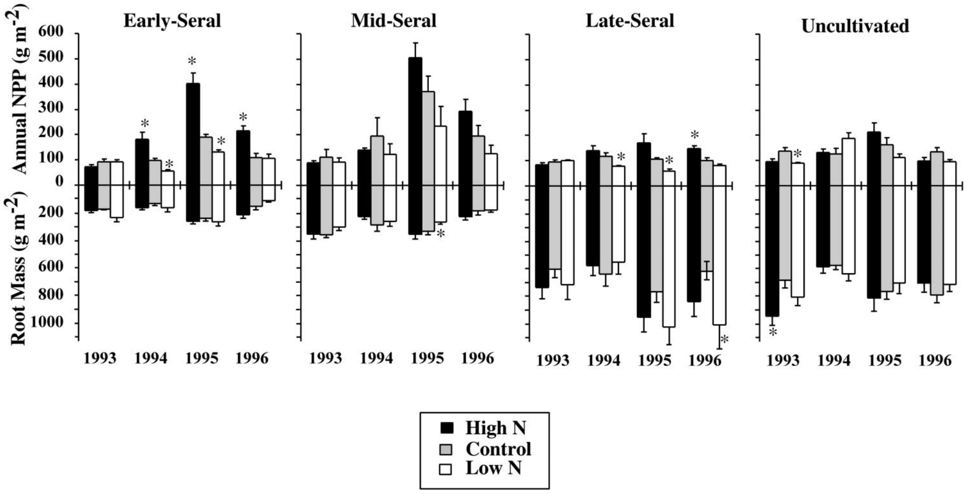

Figure 6. Plant community biomass allocation (above and below ground) at the four sites subjected to N manipulations plus control from 1993 through 1996. Thin bars represent the standard error of the mean. Asterisks indicate a treatment mean that is significantly different from the corresponding control mean at $\alpha = 0.05$ by using a Tukey's Studentized Range test.

tion of available soil N resulted in increased rates of succession at the early-, mid-, and late-seral old-fields and minimized compositional instability at the uncultivated site (Figure 4). Experimental increases in N availability resulted in species composition in all four communities shifting in the direction of earlier seral conditions. These results are very similar to those of a comparable study conducted in a semiarid shrubland in Western Colorado by McLendon and Redente (1992).

The changes in plant community composition in treated plots correspond to a gradient of available soil N that was detected by IER bags (Table 3). Given the high levels of available N detected in the N treated plots (relative to controls) and the low levels of available N in the sucrose-treated plots, we presume that N limitations occurred in the low-N plots. In most cases, supplemental N resulted in increased plant tissue N content (Figure 5) and increased plant biomass (Figure 6), whereas sucrose addition (low-N plots) tended to reduce plant biomass (Figure 6) and N storage (Figure 5).

The observed increase in abundance of rapidly growing annual plants with increasing N availability, and their corresponding decrease with N reduction does not appear to simply be a result of competitive displacement by slower-growing perennials. Instead, the annuals appeared to loose dominance when their strategy of high production of aboveground biomass (Grime 1973; Shipley and Peters 1990), as occurred in the wet spring of 1995 (Figures 4 and 6), resulted in increased incorporation of N into plant biomass (Figure 5). This rapid growth and N uptake likely resulted in a depletion of soil mineral N by the annuals. Supporting this suggestion was the minimum mineral N detected in IER bags during the wet spring of 1995 (seasonal data not shown). The N-uptake efficiency of early-seral plants relative to later-seral species also is evidenced further by the trend of increased N availability in N amended plots with site age (Table 3; this observation emphasizes the importance of recognizing IER bags as an open system where plant roots are competing with IER bags for mineral N so that low recovery of N in IER bags can be interpreted either as low N supply or high N uptake by vegetation). Because early-seral annual plants have low root to shoot ratios relative to later-seral perennials (Figure 6), the rapid depletion of N from their root zone causes N to become insufficient to support the high biomass production that they require to dominate aboveground competition for light. The result of experimentally reduced N availability was a shift in plant community composition toward an increase in slower-growing perennial species (Figure 4) with more extensive root systems (Figure 6) that are better adapted to reduced N availability.

This shift in biomass allocation from aboveground to belowground during community changes in these old-fields (Figure 6) was coupled with shifts in soil microbial community composition and responses to N treatments (see Klein and others 1995, 1996, 1998). The microbial communities at the early- and mid-seral old-fields, with primarily aboveground plant biomass allocation (Figure 6), responded differently to N treatments than did the late-seral old-field and the uncultivated sites (Klein and others 1996) where plant biomass allocation was primarily belowground (Figure 6).

Our observations of plant community composition during the unusual spring of 1995 give further insight into the importance of N availability in controlling plant community dynamics. At the uncultivated site, this wet period coincided with the appearance of a significant annual component that was not present in other years (Figure 4). This annual component of the community was even more predominant in the N amended plots. However, the application of sucrose suppressed these annuals (Figure 4). These observations suggest that the appearance of weedy annual plants in the native shortgrass steppe during wet periods may not be entirely attributable to moisture availability as might be assumed. Instead, there may be a moisture–N availability relationship, with the control being water limitation of microbes that perform N mineralization or biological N_2 fixation.

The changes in plant species composition shown in Figure 4 for the younger old-fields can be attributed primarily to just a few plant species, the annual forbs *Lactuca scariola* and *Sisymbrium altissimum* at the early-seral old-field, and the annual grass *B. tectorum* at the mid-seral old-field (Tables 6 and 7). *B. tectorum* is an exotic annual grass that is an aggressive invader and a major concern in the Western US (Billings 1994; Monsen 1994; Pyke and Novak 1994; Young 1994). At the time that we began this study, *B. tectorum* appeared to have just arrived at the early-seral old-field and was the dominant species at the mid-seral old-field. The mid-seral old-field also was characterized by low rates of litter decomposition (Figure 2), high litter mass (Figure 3), and very low active fungal biomass in soils relative to the younger (early-seral) old-field (Klein and others 1995, 1996, 1998). These observations suggest that *B. tectorum* might increase its competitive advantage and thus slow recovery by negatively impacting the soil microbial community and N-cycling processes. Such effects of *B. tectorum* on the microbial community might be due to factors such as soil shading by the dense litter layer resulting in lower soil temperature and decreased decomposition, greater competition for moisture, or plant-produced allomones. As a likely result of the wet spring of 1995, annual litter decomposition rates increased (Figure 2), the layer of accumulated litter on the soil surface decreased (Figure 3), and *B. tectorum* abundance sharply declined at the mid-seral old-field (Figure 4 and Table 7) indicating that the dense litter layer created *by B. tectorum* may be important to its dominance of a site.

N Manipulation as a Management Tool

Reducing soil N availability caused the plant and soil communities to take on later-seral characteristics, whereas, increasing soil N availability caused plant and soil communities to take on earlier-seral characteristics. This suggests that N manipulation has potential to be a useful tool for altering the rate and course of old-field succession on similar abandoned croplands. Morgan (1994) made a similar suggestion based on N manipulation of tallgrass prairie in Manitoba, Canada. Hastening the recovery of abandoned croplands to native shortgrass steppe has many economic, environmental, and social benefits, because later-seral shortgrass steppe is more productive rangeland, is less susceptible to soil erosion, and provides better wildlife habitat than earlier-seral communities.

The application of sucrose, as was done in this study, to large areas of abandoned croplands is not an economically feasible option for hastening recovery. However, the application of other materials that have the potential to stimulate microbial growth and immobilize mineral N might be feasible in certain circumstances. We currently are evaluating the feasibility of such materials in ongoing studies.

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REFERENCES

Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM. 1989. Nitrogen saturation in northern forest ecosystems. Bioscience 39: 378–86.

Aerts R, Berendse F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio 76:63–9.

Allen EB, Knight DH. 1984. The effects of introduced annuals on secondary succession in sagebrush-grassland, Wyoming. Southwestern Nat 29:407–21.

Bazzaz FA. 1979. The physiological ecology of plant succession. Ann Rev Ecol Syst 10:351–71.

Berendse F. 1990. Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J Ecol 78:413–27.

Berendse F, Oudhof H, Bol J. 1987. A comparative study on nutrient cycling in wet heathland ecosystems. I. Litter production and nutrient loss from the plant. Oecologia 74:174–84.

Billings WD. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the Western Great Basin. In: Monson SB, Kitchen SG, eds. Proceedings—ecology and management of annual rangelands. US Forest Service, Intermountain Res Stat Gen Tech Rep INT-GTR-313. Ogden, Utah. p 22–30.

Binkley D. 1984. Ion exchange resin bags: factors affecting estimates of nitrogen availability. Soil Sci Soc Am J 48:1181–4.

Binkley D, Matson P. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. Soil Sci Soc Am J 47:1050–2.

Biondini M, Klein DA, Redente EF. 1988. Carbon and nitrogen losses through root exudation by *Agropyron cristatum, A. smithii* and *Bouteloua gracilis*. Soil Biol Biochem 20:477–82.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. J Appl Ecol 28:28–41.

Brenneman J. 1989. Long-term ecological research in the United States: a network of research sites. 5th ed. Seattle, WA: University Washington, College of Forestry Resources AR-10.

Brussaard L, Bakker JP, Olff H. 1996. Biodiversity of soil biota and plants in abandoned arable fields and grasslands under restoration management. Biodiversity Conserv 5: 211–21.

Cherfas J. 1991. Disappearing mushrooms: another mass extinction? Science 254:1458.

Coffin DP Lauenroth WK, Burke IC. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. Ecol Appl 6:538–55.

Costello DF. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of Northeastern Colorado. Ecology 25:312–26.

Crabb JA. 1982. Soil survey of Weld County, Colorado, Northern Part. USDA-SCS and Forest Service, US Government Printing Office, Washington, DC.

Dormarr JF, Smoliak S, Wilms WD. 1990. Soil chemical properties during succession from abandoned cropland to native range. J Range Manage 43:260–65.

Eno CF. 1960. Nitrate production in the field by incubating soil in polyethylene bags. Soil Sci Soc Am Proc 24:277–9.

Ettershank G, Ettershank JA, Bryant M, Whitford WG. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan Desert ecosystem. J Arid Environ 1:135–9.

Foster MM, Vitousek PM, Randolph PA. 1980. The effect of ragweed (*Ambrosia artemisiifolia* L.) on nutrient cycling in a 1st-yr old-field. Am Midl Nat 103:106–13.

Frederick BA, Klein DA. 1994. Nitrogen effects on rhizosphere processes of range grasses from different successional seres. Plant Soil 161:241–50.

Gibson DJ. 1986. Spatial and temporal heterogeneity in soil nutrient supply measured using in situ ion-exchange resin bags. Plant Soil 96:445–50.

Grime JP. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–7.

Hart SC, Firestone MK, Paul EA, Smith JL. 1993. Flow and fate of soil nitrogen in an annual grassland and a young mixed-conifer forest. Soil Biol Biochem 25:431–42.

Heil GW, Bruggink M. 1987. Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. Oecologia 73:105–7.

Heil GW, Diemont WH. 1983. Raised nutrient levels change heathland into grassland. Vegetatio 53:113–20.

Hunt HW, Ingham ER, Coleman DC, Elliot ET, Reid CPP. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69:1009–16.

Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell M, Zinnel KC. 1987. Old-field succession on a Minnesota sand plain. Ecology 68:12–26.

Juhasz-Nagy P, Podani J. 1983. Information theory methods for the study of spatial processes and succession. Vegetatio 51: 129–40.

Klein DA, McLendon T, Paschke MW, Redente EF. 1995. Saprophytic fungal-bacterial biomass variations in successional communities of a semi-arid steppe ecosystem. Biol Fertil Soils 19:253–6.

Klein DA, McLendon T, Paschke MW, Redente EF. 1996. Nitrogen availability and fungal-bacterial responses in successional semi-arid steppe soils. Arid Soil Res Rehab 10:321–32.

Klein DA, Paschke MW, Redente EF. 1998. Assessment of fungal-bacterial development in a successional semi-arid grassland by direct integration of chloroform-fumigation extraction (FE) and microscopically derived data. Soil Biol Biochem 30:573–81.

Lamb D. 1980. Soil nitrogen mineralization in a secondary rain forest succession. Oecologia 47:257–63.

Lauenroth WK, Dodd, JL. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36:211–22.

Lauenroth WK, Milchunas, DG. 1992. Short-grass steppe. In: Coupland RT, editor. Ecosystems of the world 8A: natural grasslands—introduction and Western hemisphere. Amsterdam: Elsevier. p 183–226.

McGraw JB, Chapin FS III. 1989. Competitive ability and adaptation to fertile and infertile soils in two Eriophorum species. Ecology 70:736–49.

McLendon T, Redente EF. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology 72:2016–24.

McLendon T, Redente EF. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91:312–7.

Milchunas DC, Lauenroth WK. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Ecol Appl 5:452–8.

Miller TE, Werner PA. 1987. Competitive effects and responses between plant species in a first-year old-field community. Ecology 68:1201–10.

Monsen SB. 1994. The competitive influences of cheatgrass. Bromus tectorum. on site restoration. In: Monson SB, Kitchen SG, editors. Proceedings—ecology and management of annual rangelands. Ogden, UT: US For Serv, Intermountain Res Sta, Gen Tech Rep INT-GTR-313. p 43–50.

Morgan JP. 1994. Soil impoverishment: a little known technique holds potential for establishing prairie. Restoration Manage Notes 12:55–6.

Olff H, Berendse F, De Visser W. 1994. Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. J Ecol 82:611–20.

Parrish JAD, Bazzaz FA. 1982. Competitive interactions in plant communities of different successional ages. Ecology 63: 314–20.

Pastor J, Stillwell MA, Tilman D. 1987. Little bluestem litter dynamics in Minnesota old fields. Oecologia 72:327–30.

Peterson DL, Bazzaz FA. 1978. Life cycle characteristics of Aster pilosis in early successional habitats. Ecology 58:1005–13.

Prescott CE, Coward LP, Weetman GF, Gessel SP. 1993. Effect of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*), in two coastal Douglas-fir forests. For Ecol Manag 61:45–60.

Prescott CE, Kumi JW, Weetman GF. 1995. Long-term effects of repeated N fertilization and straw application in a jack pine forest. 2. Changes in the ericaceous ground vegetation. Can J For Res 25:1984–90.

Pyke DA, Novak SJ. 1994. Cheatgrass demography—establishment attributes, recruitment, ecotypes, and genetic variability. In: Monson SB, Kitchen SG. editors. Proceedings—ecology and management of annual rangelands. Ogden, UT: US Forest Service, Intermountain Res Sta, Gen Tech Rep INT-GTR-313. p 12–21.

Raynal DJ, Bazzaz FA. 1975. Interference of winter annuals with Ambrosia artemisiifolia in early successional fields. Ecology 56:35–49.

Redente EF, Friedlander JE, McLendon T. 1992. Response of early and late semiarid seral species to nitrogen and phosphorus gradients. Plant Soil 140:127–35.

Reichardt KL. 1982. Succession of abandoned fields on the shortgrass prairie, Northeastern Colorado. Southwestern Nat 27:299–304.

Reiners WA, Bouman AF, Parsons WFJ, M Keller. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecol Appl 4:363–77.

Shipley B, Peters RH. 1990. A test of the Tilman model of plant strategies: relative growth rate and biomass partitioning. Am Nat 136:139–53.

Smith JL, Rice EL. 1983. Differences in nitrate reductase activity between species of different stages of old field succession. Oecologia 57:43–8.

Tilman D. 1982. Resource competition and community structure. Monographs in population biology 17. Princeton, NJ: Princeton University Press.

Tilman D. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65:1445–53.

Tilman D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol Monog 57:189–214.

Tilman D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton, NJ: Princeton University Press.

Tilman D, Wedin DA. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72:685–700.

Trent JD, Young JA, Blank RR. 1992. Potential role of soil microorganisms in medusahead invasion. In: Monson SB, Kitchen SG, editors. Proceedings—ecology and management of annual rangelands. Ogden, UT: US For Serv, Intermountain Res Sta, Gen Tech Rep INT-GTR-313. p 140–2.

Turner J. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. For Sci 23:307–16.

van Auken OW, Bush JK. 1989. Prosopis glandulosa growth: influence of nutrients and simulated grazing of Bouteloua curtipendula. Ecology 70:512–6.

van Hulst R. 1978. On the dynamics of vegetation: patterns of environmental and vegetational change. Vegetatio 38:65–75.

van Hulst R. 1979. On the dynamics of vegetation and succession in model communities. Vegetatio 39:85–96.

Vitousek PM. 1983. Nitrogen turnover in a ragweed-dominated 1st-year old field in southern Indiana. Am Midl Nat 110:46–53.

Vitousek PM, Matson PA, Van Cleve K. 1989. Nitrogen availability and nitrification during succession: primary, secondary, and old-field seres. Plant Soil 115:229–39.

Walter H. 1973. Vegetation of the Earth in relation to climate and the eco-physiological conditions. New York: Springer-Verlag.

Wedin DA, Tilman D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84:433–41.

Young JA. 1994. History and use of semiarid plant communities—changes in vegetation. In: Monson SB, Kitchen SG, editors. Proceedings—ecology and management of annual rangelands. US For Serv, Intermountain Res Sta, Gen Tech Rep INT-GTR-313. Ogden.