Biogeochemistry **42:** 121–143, 1998.

Plant–Soil interactions in temperate grasslands

INGRID C. BURKE[1,2], WILLIAM K. LAUENROTH[2,3],
MARY ANN VINTON[4], PAUL B. HOOK[5], ROBIN H. KELLY[2],
HOWARD E. EPSTEIN[1,6], MARTIN R. AGUIAR[7],
MARCOS D. ROBLES[1,6], MANUEL O. AGUILERA[8],
KENNETH L. MURPHY[1,6] & RICHARD A. GILL[1,6]
[1]*Department of Forest Sciences, Colorado State University, Fort Collins, CO 80523;* [2]*Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523;* [3]*Department of Rangeland Ecosystem Science, Colorado State University, Fort Collins, CO 80523;* [4]*Department of Biology, Creighton University, Omaha, NB 68178;* [5]*Department of Animal and Range Science, Montana State University, Bozeman, MT 59717;* [6]*Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA;* [7]*Departmento de Ecologia – IFEVA, Facultdad de Agronomia, Universidad de Buenos Aires, Av. San Martin 4453 (1417) Buenos Aires, Argentina;* [8]*Instituto Nacional de Tecnologìa Agropecuaria-EEA San Luis, CC 17, RA-5730, V. Mercedes, San Luis, Argentina*

Key words: grassland soils, plant effects on soil, semiarid grassland, soil organic matter, soil resource islands, subhumid grassland, water-nutrient interactions

Abstract. We present a conceptual model in which plant–soil interactions in grasslands are characterized by the extent to which water is limiting. Plant–soil interactions in dry grasslands, those dominated by water limitation ('belowground-dominance'), are fundamentally different from plant–soil interactions in subhumid grasslands, where resource limitations vary in time and space among water, nitrogen, and light ('indeterminate dominance'). In the belowground-dominance grasslands, the strong limitation of soil water leads to complete (though uneven) occupation of the soil by roots, but insufficient resources to support continuous aboveground plant cover. Discontinuous aboveground plant cover leads to strong biological and physical forces that result in the accumulation of soil materials beneath individual plants in resource islands. The degree of accumulation in these resource islands is strongly influenced by plant functional type (lifespan, growth form, root:shoot ratio, photosynthetic pathway), with the largest resource islands accumulating under perennial bunchgrasses. Resource islands develop over decadal time scales, but may be reduced to the level of bare ground following death of an individual plant in as little as 3 years. These resource islands may have a great deal of significance as an index of recovery from disturbance, an indicator of ecosystem stability or harbinger of desertification, or may be significant because of possible feedbacks to plant establishment. In the grasslands in which the dominant resource limiting plant community dynamics is indeterminate, plant cover is relatively continuous, and thus the major force in plant–soil interactions is related to the feedbacks among plant biomass production, litter quality and nutrient availability. With increasing precipitation, the over-riding importance of water as a limiting factor diminishes, and four other factors become important in determining plant community and ecosystem dynamics: soil nitrogen, herbivory, fire, and light. Thus, several different strategies for competing for resources are present in this portion of the gradient. These strategies are represented by different plant traits, for example root:shoot allocation, height and photosynthetic pathway type (C_3 vs. C_4) and nitrogen fixation, each of which has a different influence on litter quality and thus nutrient availability. Recent work has indicated that there are strong feedbacks between plant community structure, diversity, and soil attributes including nitrogen availability and carbon storage. Across both types of grasslands, there is strong evidence that human forces that alter plant community structure, such as invasions by nonnative annual plants or changes in grazing or fire regime, alters the pattern, quantity, and quality of soil organic matter in grassland ecosystems. The reverse influence of soils on plant communities is also strong; in turn, alterations of soil nutrient supply in grasslands can have major influences on plant species composition, plant diversity, and primary productivity.

I. Introduction

Interactions of plant and soil processes in grassland ecosystems have received a great deal of attention (Wedin & Tilman 1990, 1996; Huenneke et al. 1990; Elberse & Berendse 1993; Berendse 1994; Wedin 1995; Schlesinger et al. 1990, 1996; Vinton & Burke 1995; and many others). There has been an interesting dichotomy in this research. In a first and most dominant type of work, studies have been conducted with a focus on plant species composition as it interacts with soil organic matter and nutrient availability (reviewed by Wedin 1995). Much of this work has addressed manipulations of nitrogen availability and the consequences for successional dynamics (e.g., Tilman 1987; Gleeson & Tilman 1991), or manipulations of species composition and the observed consequences for available nitrogen (e.g., Wedin & Tilman 1990; Huenneke et al. 1990).

In a second type of research, investigators have focused attention on the influence of plant presence and absence on the accumulation of organic matter and nutrient availability under individual plants, in so-called 'resource islands' (Hook et al. 1991; Vinton & Burke 1995, 1997; Schlesinger et al. 1990, 1996). For the most part, this work in grasslands to date has implicitly considered the plant–soil interaction to be one-way, i.e., plant effects on soil resources, ignoring the influence of soil resources on plant community dynamics. This work has been conducted in the arid and semiarid grasslands, where plant cover is discontinuous.

We suggest a conceptual framework for plant–soil interactions in grasslands that addresses both aspects of plant–soil interactions (Figure 1). The framework is based upon the idea that the key interactions between plants and soils change in character with the extent to which water is the important limiting resource, and is based upon a conceptual model proposed by Lauenroth and Coffin (1992) for North American grasslands. Lauenroth and Coffin (1992) distinguished between the approaches used by forest and grassland ecologists in modeling plant community dynamics. They proposed that resources limiting to plant growth may be arrayed along a precipitation axis, which differentiates among ecosystems primarily limited by belowground resources from those primarily limited by light or an 'aboveground resource'.

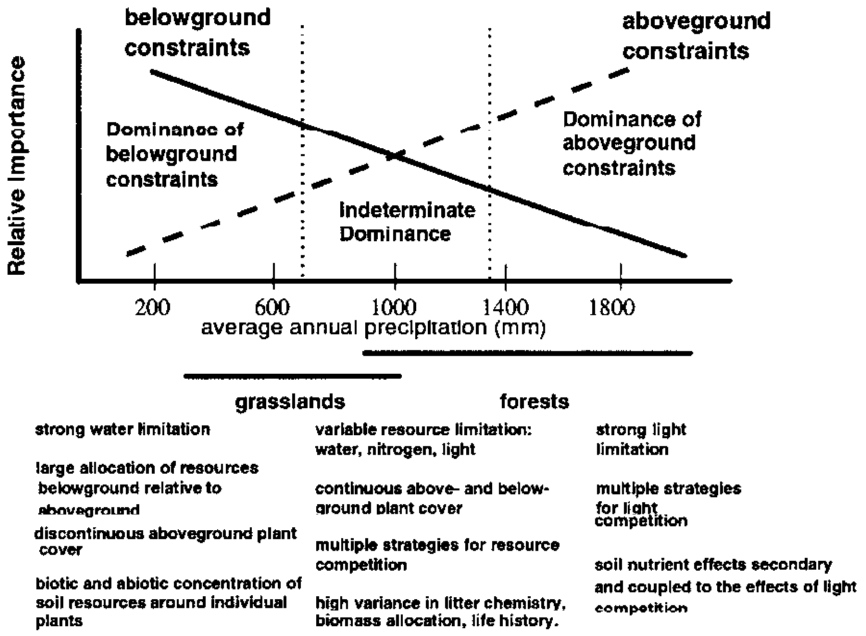

Figure 1. Conceptual model of the major resource limitations to plants across a precipitation gradient in temperate regions of the world. The importance of belowground constraints decreases with increasing precipitation. Modified from Lauenroth and Coffin (1992).

This general distinction between above- and belowground resource limitation influences within-plant resource allocation (root:shoot ratio, plant height, nitrogen allocation), and thus characterizes the type of competition and plant community dynamics (Tilman 1988). They used an analysis of leaf area index (LAI) to identify a theoretical zone in which plant communities are limited by soil water, termed the ‘belowground dominance’ ecosystems, and a zone dominated by light, termed the ‘aboveground dominance’ ecosystems. They suggested that the temperate zone ecosystems dominated by belowground processes occurred below 700 mm/yr annual precipitation and those dominated by aboveground processes occurred above 1200 mm/yr. Between these limits (700–1200 mm/yr) are ecosystems in which the identification of the most frequently limiting resource is unclear. They termed these ‘indeterminate dominance’ ecosystems. It is important to note that both above- and belowground resources may limit productivity anywhere along the precipitation gradient, however the emphasis of the conceptual model is the zones in which each type of resource dominates as a control over plant community dynamics. In addition, the exact location of the ‘crossover point’ (between above and belowground dominance) is likely to vary with the soil texture and mean annual temperature, as they influence water availability.

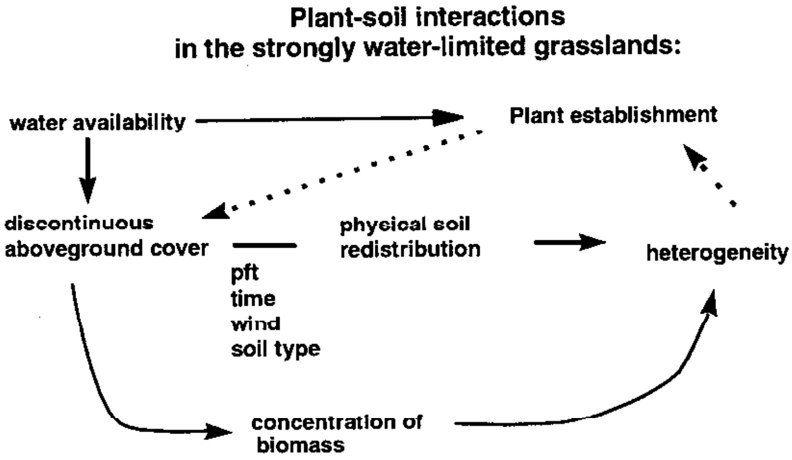

Figure 2. Plant–soil interactions in the belowground dominance grasslands. The soil water resource limits amount of biomass that can be supported, leading to discontinuous cover of plants. This discontinuous cover leads to a high degree of heterogeneity through two sets of processes, physical soil redistribution and concentration of biomass. Both of these sets of processes depend upon 4 factors: plant functional type (pft); soil type and its influence on productivity, plant functional type composition, and susceptibility to wind; wind itself; and the integrated time over which erosion and net primary productivity occur.

Temperate grasslands span a gradient from approximately 200 mm of mean annual precipitation in desert grasslands to 1500 mm per year in subhumid grasslands (Ripley 1992). Therefore they fall mainly into either the belowground dominance or indeterminate dominance categories of our conceptual model (Figure 1). We hypothesize that plant–soil interactions in dry grasslands (Figure 2), those dominated by water limitation, are fundamentally different from plant–soil interactions in subhumid grasslands of indeterminate dominance (Figure 3). In the belowground-dominance grasslands, the strong limitation of soil water leads to complete (though uneven) occupation of the soil by roots, but insufficient resources to support continuous aboveground plant cover. Discontinuous aboveground plant cover leads to strong biological and physical forces that result in the accumulation of soil materials beneath individual plants in resource islands. These resource islands have been well-described in arid and semiarid shrublands throughout the world (Charley & West 1975, 1977; Barth & Klemmedson 1978; Schlesinger et al. 1990, 1996; Burke 1989; Rostagno et al. 1991; Burke et al. 1989; Bolton et al. 1990, 1993; Coppinger et al. 1991; Jackson & Caldwell 1993; Gutierrez et al. 1993), but they have only recently been characterized in semiarid grasslands, and primarily in North American systems (Hook et al. 1991; Vinton & Burke 1995; Burke et al. 1995; Ihori et al. 1995; Kelly et al. 1996; Schlesinger et al. 1996; Kelly & Burke 1997). These resource islands may have a great deal of

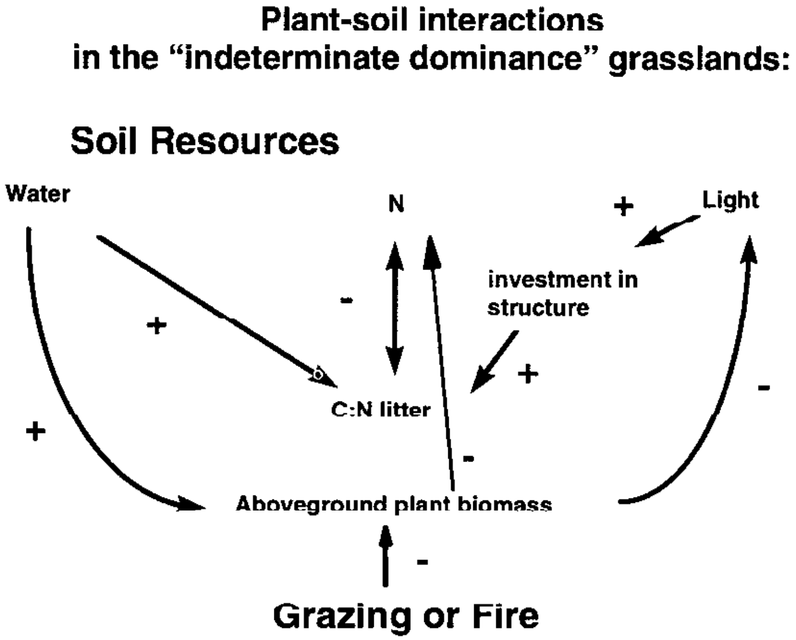

Figure 3. Plant–soil interactions in the indeterminate dominance grasslands. Negative signs denote an inverse relationship between processes, and positive signs a positive relationship. Water, nitrogen, and light vary in their importance in time and space, as major constraints over plant growth (Seastedt & Knapp 1993). As water availability increases, total aboveground biomass, lignin content (an investment in structure), and C:N ratio increase, leading to decreased relative N and light availability. These limitations, in turn, influence N availability through the plant response. Grazing and fire, important forces in the indeterminate dominance grasslands, alter plant allocation, litter quality, microbial interactions, and the relative availability of light and N (see Knapp & Seastedt 1986; Wedin 1995 for a complete discussion of the interactions of fire and grazing).

significance as an index of recovery from disturbance (Burke et al. 1995), an indicator of ecosystem stability or harbinger of desertification (Schlesinger et al. 1990), or because of possible feedbacks to plant establishment (Aguilera & Lauenroth 1995).

In the grasslands in which the dominant resource limiting plant community dynamics is indeterminate, plant cover is relatively continuous, thus the major force in plant–soil interactions is related to the feedbacks among plant biomass production, litter quality and nutrient availability (Wedin 1995; Vinton & Burke 1997) (Figure 3). Vinton and Burke (1997) demonstrated that the effects of interspecies variability in litter quality on soil nutrient dynamics is much larger in North American tallgrass prairie than in shortgrass steppe, and thus, that species composition has a larger degree of importance in these wetter grasslands. With increasing precipitation, the over-riding importance of water as a limiting factor diminishes, and four other factors become important in determining plant community and ecosystem dynamics: soil nitrogen, herbivory, fire, and light (Seastedt & Knapp 1993; Wedin 1995). Thus, several different strategies for competing for resources are present in this portion of the gradient. These strategies are represented by different plant traits, for example root:shoot allocation, height and photosynthetic pathway type (C_3 vs. C_4) and nitrogen fixation, each of which has a different influence on litter quality and thus nutrient availability (Tilman 1982; Field & Mooney 1986; Tilman & Wedin 1991a; Schimel et al. 1991; Wedin 1995).

Our objective for this paper is to review the current information on plant–soil interactions in temperate grasslands. Our conceptual framework represents a hypothesis for worldwide grasslands that is based primarily on published studies available from North American literature, since data for semiarid grasslands on other continents are quite limited. We will focus most of our attention on those grasslands in which the plant community and ecosystem dynamics are dominated by belowground processes and resources, because plant–soil feedbacks in the subhumid, indeterminate grasslands have recently been reviewed (Wedin 1995). We will briefly summarize the indeterminate dominance grasslands.

II. Grasslands dominated by belowground processes

Heterogeneity induced by discontinuous plant cover has been shown to be a major source of spatial variability in soil organic matter quality and quantity in the semiarid, shortgrass steppe of North America, and in the semiarid steppes of Patagonia (Aguiar et al. unpubl data). Hook et al. (1991) sampled surface soils immediately under and between perennial bunchgrasses (averaging 5–15 cm across), and found that microsites under plants had up to 43% more total soil organic matter, and 150% more labile organic matter (indexed by respirable carbon) than microsites between plants. These 'resource islands' were characterized not only by higher amounts of soil organic matter and mineralizable nutrients, but also by microtopographic relief, with soil surfaces beneath bunchgrasses raised by an average of 3.0 cm relative to the interspaces (Hook et al. 1991). Such 'hummocks' have been documented for shrublands (Schlesinger et al. 1990; Rostagno & del Valle 1988) but not previously for grasslands. These data suggested that two mechanisms are likely responsible for the formation of resource islands: biological accumulation of below- and aboveground litter, and physical erosion and deposition processes that redistribute material from between to underneath individual plants. Subsequent work has evaluated both of these mechanisms. We discuss both biological and physical processes involved in resource island formation below.

Biological mechanisms in the formation of resource islands:

The accumulation of litter beneath individual plants is the source of soil heterogeneity. Is it aboveground or belowground litter that is primarily responsible for the organic matter accumulated in resource islands? An interesting paradox exists, in that our conceptual model of semiarid systems is that root biomass is more continuously distributed in the soil than is aboveground biomass. Thus one would expect that aboveground biomass may be responsible for the concentrated organic matter in resource islands. Nonetheless, another important component of our conceptual framework of grasslands is that roots are the primary source of detritus for organic matter (Dormaar 1992; Burke et al. 1997a).

Several studies suggest that the accumulation of root and crown biomass is likely the source of the small-scale heterogeneity associated with individual plants in semiarid grasslands. In the shortgrass steppe of North America, accumulations of aboveground litter are not commonly observed, due to high winds and fragmentation of leaf litter. Lee and Lauenroth (1994) and Hook et al. (1994) established that a root length and biomass gradient exists in surface soils, from the edge of an individual perennial bunchgrass, to the center of an interspace. This horizontal gradient is significant to a depth of approximately 20–30 cm (Hook et al. 1994; Lee & Lauenroth 1994; Coffin & Lauenroth 1991). Further, Kelly et al. (1996) demonstrated that a gradient in root biomass alone, in the absence of any aboveground litter inputs, is sufficient to account for an organic matter gradient similar to those observed associated with individual plants. Several studies have indicated that the influence of the resource island diminishes with depth (Burke et al. 1995), consistent with the idea that roots of adjacent plants converge at depth. Crown material, perennial tissue intermediately located between above- and belowground material, is highly concentrated under individual plants, and not subject to wind redistribution and fragmentation. Hook et al. (1991) constructed a budget of plant biomass in the surface 5 cm of soil beneath and adjacent to plants, and found that three orders of magnitude more total biomass was located under plants than between. Of the plant biomass accumulated under plants, crowns accounted for about half the material, roots about a third, and the rest leaves. We assume that at depths below 5 cm from the soil surface, crowns would not contribute to the resource island. In combination, these studies suggest that crowns and roots provide most of the material that is produced and accumulated *in situ*, forming the resource island.

An important aspect of litterfall as a biological mechanism concentrating organic matter beneath plants is the role of lateral roots in concentrating nutrients. While litterfall alone can explain carbon accumulation under plants, conservative nutrients such as nitrogen and phosphorus must be redistributed from adjacent areas. Thus, we must invoke as a mechanism the important ability of plant lateral roots to draw nutrients from the surrounding area, incorporating nutrients into biomass that is then concentrated in the soils beneath individual plants through litterfall (Gibson 1988; Hook et al. 1991).

Physical mechanisms in the formation of resource islands:

Microtopographic relief is consistently associated with resource islands in semiarid grasslands (Hook et al. 1991; Martinez-Turanzas et al. 1997; Burke et al. 1996b), with an average of 3 cm of material (Hook et al. 1991) beneath individual plants. How much of the additional resources in the resource island is present in the raised area, or 'hummock', directly beneath a plant? How long does it take for this microtopography to form? How much of the material in the hummock is moved there by physical processes, vs. biological accumulation? Is the hummock actually due to aggradation below the plant, or deflation between plants?

Recent studies suggest that the microtopography associated with individual grasses is, to a very large extent, the result of physical redistribution. Most studies of resource islands in grasslands have sampled a fixed depth down from the surface in both under-plant and interspace locations, such that soil horizons were not constant between microsites. Burke et al. (1996) sampled the hummock areas separately from other soil layers, and found that the hummocks are more than 90% mineral in composition, suggesting that physical redistribution is responsible for most of the mass of the hummock. Of course, the 10% of the material that is organic ultimately provides most of the resources in the island, and this material may have either accumulated in situ or have been physically transported. In shortgrass steppe ecosystems of North America, average windspeeds are 5–7 m s^{-1} (Lauenroth & Milchunas 1992), leading to strong forces for the physical redistribution of material. Most of the mineral material located in hummocks was in the sand-sized fraction, suggesting that these heavier materials are transported short distances, from interspaces to under plants, where canopies trap the sediments. Hummocks were largest on summit and midslope topographic positions, where wind and water erosive forces are likely to be strongest (Burke et al. 1996b). Coppinger et al. (1991) also documented the accumulation of mineral material beneath individual plants in a semiarid shrubland using ^{137}Cs, and similarly found that the highest mass under shrubs occurred at topographic positions that were most exposed to wind. Organic matter may also be transported and

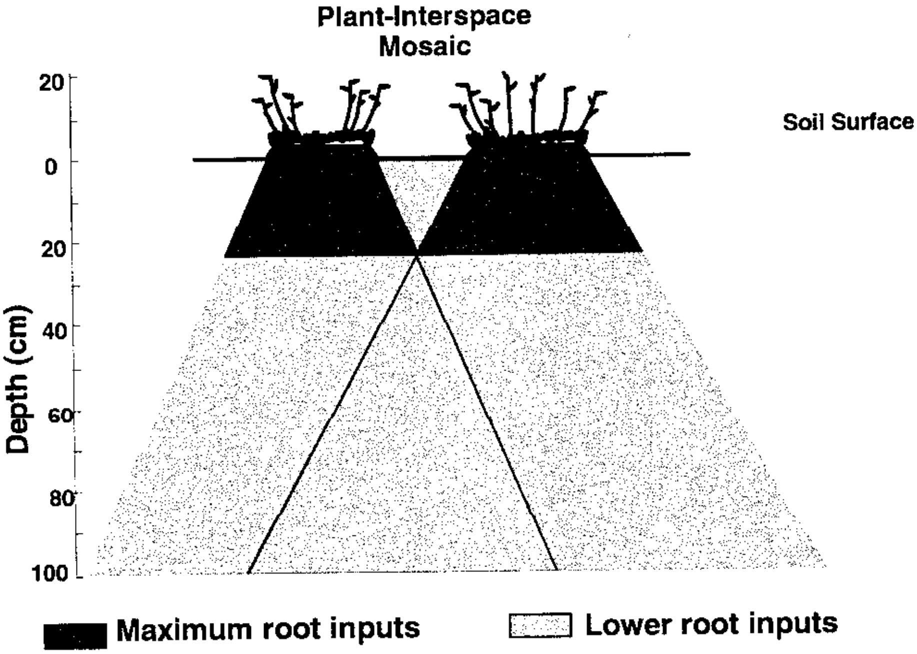

Figure 4. Schematic diagram of the exploitation of belowground space by adjacent *Bouteloua gracilis* individuals divided into two classes. Root biomass and productivity decrease exponentially with depth and with horizontal distance from the center of the plant, such that maximum root inputs are beneath plants, in the top 20–30 cm. Although roots are present throughout the solum to 100 cm, there is a clear pattern of lower root inputs in surface soils between plants, and at lower depths, which corresponds with soil organic matter and available nutrient patterns.

collected, but it will be difficult if not impossible to discern which of the organic matter in the resource island is the result of physical transport vs. biological accumulation. Finally, careful sampling with depth indicated that nearly all of the resource island was located in the 'hummock' (Burke et al. 1996).

Martinez-Turanzas et al. (1997) recently surveyed microtopography in a series of disturbed plots of shortgrass steppe to determine the rate at which microtopography develops, and how it is related to disturbance size (Figure 5). Plots were disturbed by the physical removal of plants. Eight years of recovery following disturbance was sufficient for microtopographic relief to develop to the same level as undisturbed plots. The largest disturbed plots (150 cm diameter) developed the largest microtopographic relief associated with individual plants, apparently due to wind and water deposition. This probably occurred because the larger disturbances had more fetch over which wind could accumulate force and materials for deposition under plants.

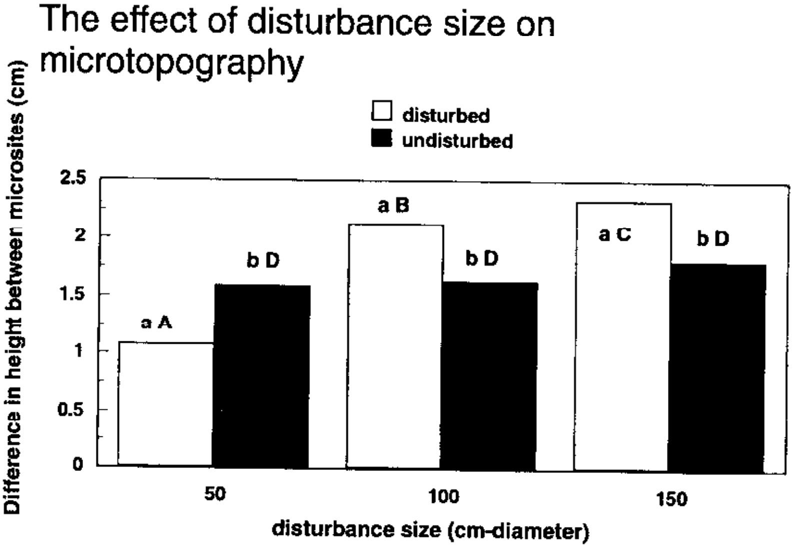

Figure 5. Microtopography or relative height of hummocks associated with individual *Bouteloua gracilis* plants in shortgrass steppe of northeastern Colorado. From Martinez-Turanzas et al. (1997). Plants in disturbed plots were removed, and height of hummocks under established plants surveyed following 8 years of recovery (see text). Small letters denote significant effects of disturbance at a particular size, relative to controls, and capital letters denote differences between disturbance sizes.

Influence of plant functional type on the resource islands:

As suggested by Vinton and Burke (1995, 1997) and our conceptual framework, one of the strongest sources of variation of soils in belowground dominance grasslands is the presence of individual plants. The type or species of individual plants causes less variability in soil characteristics than simple presence in these dry grasslands (Figure 6). However, several studies have demonstrated that plant functional type plays a significant role in the magnitude and quality of resource island that develops under individual plants (Vinton & Burke 1995; Robles & Burke 1997; Lauenroth et al. 1997). Lifespan, growth form, biomass distribution, photosynthetic pathway, and litter quality all may influence the amount and quality of organic matter that accumulates under individual plants.

With increasing lifespan, the amount of organic matter that an individual plant accumulates is likely to increase (Vinton & Burke 1995; Lauenroth et al. 1997). Although this may seem to be a subtle effect, there are at least two examples of systems in which this may be a highly significant influence on the structure of ecosystems. In the most extreme case, transition from perennial grass or shrub dominance to invasive, annual grasses has been shown to

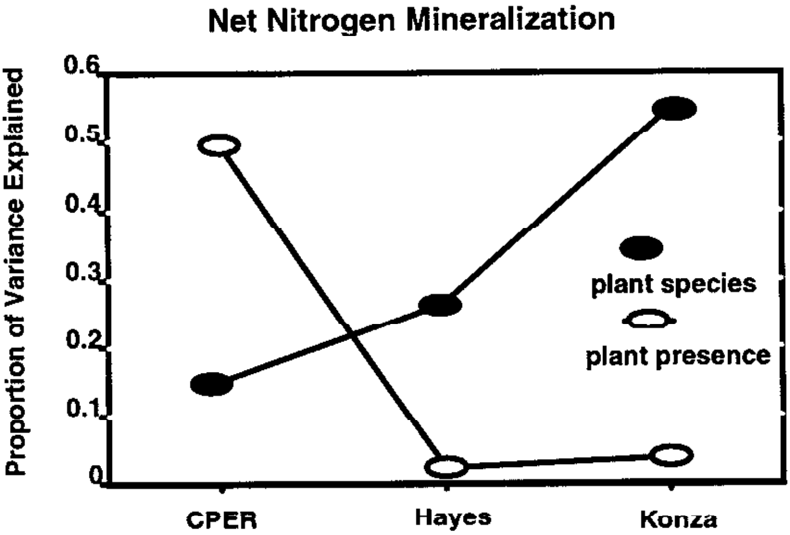

Figure 6. Variance in potential net nitrogen mineralization (derived from ANOVA R-squared, representing relative importance of different sources of variation) induced by different plant species and by individual plant presence (soils beneath or between individual plants), studied along a gradient from semiarid to subhumid grasslands in the US. CPER receives 330 mm; Hayes 550 mm; Konza Prairie Research Natural Area 900 mm. Data from Vinton and Burke (1997).

significantly reduce and even eliminate the small-scale heterogeneity associated with individual plant resource islands (Vinton & Burke 1995; Aguiar et al. 1995). Invasion of semiarid grasslands and shrublands by annual plants is a trend of considerable importance in many areas of the world (Walker et al. 1981; West 1979; Milchunas & Lauenroth 1993; Aguiar et al. 1996; Rietkerk et al. 1996). In contrast, the intensification of small-scale heterogeneity accompanying transition from grasses to shrubs has been suggested to be a key characteristic of desertification (Schlesinger et al. 1990). Recent simulation analysis (Lauenroth et al. 1997), however, suggests that low heterogeneity found by Schlesinger et al. (1990) in the grass-dominated systems of the Chihuahuan desert may be the consequence of the short life-span of the dominant grass, *Bouteloua eriopoda* (Figure 7). Arid and semiarid grasslands in other parts of the world may have soil heterogeneity that is similar to shrublands (Aguiar et al. 1995), because of the long life span of grass species such as *Bouteloua gracilis*, estimated to be 100–200 years, or possibly much longer (Coffin & Lauenroth 1989).

Other plant functional type characteristics also influence the development of resource islands. Bunchgrasses that concentrate their aboveground and belowground productivity tend to have more distinct resource islands than do

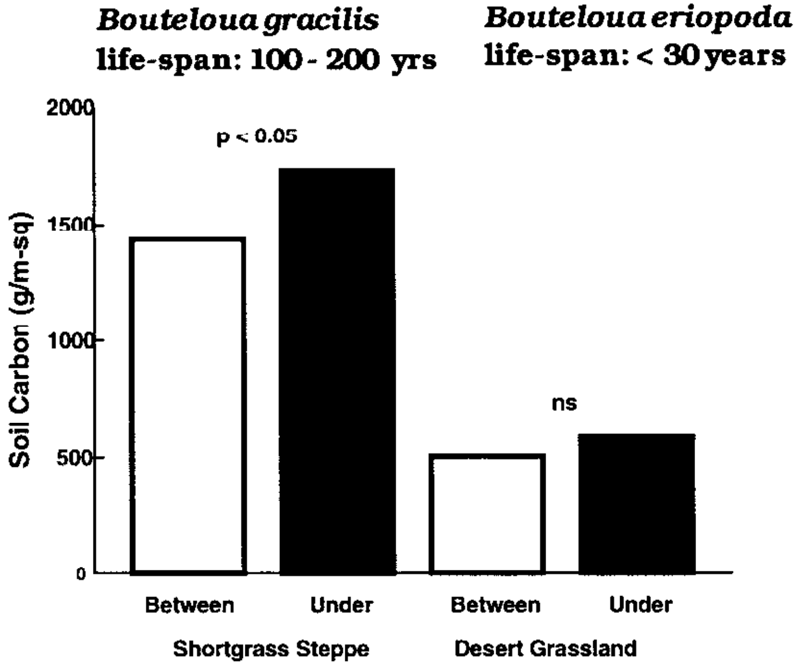

Figure 7. Soil carbon in under and between individual plants in the Chihuahuan desert (*B. eriopoda*) and shortgrass steppe (*B. gracilis*). We hypothesize that the Chihuahuan desert has insignificant resource islands because the lifespan of the dominant *B. eriopoda* is much lower than that of *B. gracilis*. From Lauenroth et al. (1997).

rhizomatous or stoloniferous species (Vinton & Burke 1995). Organic matter quality in resource islands is apparently influenced by the quality of litter, just as this is true at the field scale in the indeterminate dominance grasslands (Wedin & Tilman 1990). In the shortgrass steppe, the annual forb *Kochia scoparia* has higher N concentrations and lower lignin:N ratios in its litter than the dominant native species, leading to higher quality organic matter and higher rates of N mineralization beneath this species relative to other locations (Vinton & Burke 1995). In semiarid, perennial grasslands that are recovering from cultivation, leguminous forb species form resource islands that are enriched in N and that significantly increase organic matter quality at the field scale (Robles & Burke 1997).

How important is small-scale heterogeneity across all grasslands? Although the data are only available for North and South America, our hypothesis is that resource islands are likely to be important in semiarid grasslands worldwide, since discontinuous plant cover is a ubiquitous characteristic of semiarid regions. In addition, bunchgrass and tussock lifeforms occur in grasslands globally (Coupland 1992), albeit across precipitation gradients. Where plant cover is continuous (higher precipitation), the effect of individual bunchgrasses within a matrix of grass cover is likely to be somewhat less than in regions where plant cover is sparse (Vinton & Burke 1997).

Disturbance and the formation and dissipation of resource islands:

What is the turnover rate of resource islands, and how are they influenced by disturbance? The rate of formation of biological (organic matter) pools (as opposed to mineral soil redistribution, as discussed above) is likely limited by the growth rate and lifespan of the individual plant. In shortgrass steppe of North America, organic matter enrichment levels characteristic of native steppe (soils under plants had 200 g m^{-2} C more under than soils between plants) were present in old fields under the bunchgrass *Bouteloua gracilis* 50 years following abandonment (Burke et al. 1995). It is very likely that much less time would be required to produce a resource island that is just statistically significantly enriched, as opposed to dramatically enriched, relative to between plants. While rhizomatous grasses had not developed significant soil enrichment in total or mineralizable pools following 6 years of recovery in northeastern Wyoming, legumes did (Robles & Burke 1997). In a study evaluating how long resource islands persist following the death of individual plants, Kelly and Burke (1997) found that 36 months after the death of bunchgrasses, the enrichment of active pools of soil organic matter (mineralizable pools) in surface soils (0–5 cm) was no longer significant relative to bare ground (Figure 8). Total pools of soil organic matter were slightly enriched under dead plants 36 months following plant death. Thus, biological accumulation of organic matter occurs over relatively long time periods, but is relatively rapidly dissipated. Visual examination of these dead plants in the field suggested that wind erosion may be an important force in removing the organic material present in the 'hummock'.

Feedbacks: The influence of soil resources on plants

It is difficult to assess how important plant–soil feedbacks are, with respect to resource islands in the belowground dominance grasslands (Figure 2). There is little evidence that the presence of resource islands has relevance to plant establishment. Aguilera and Lauenroth (1995) found that seeds had a lower probability of establishing on hummocks or resource islands currently occupied by plants than they did in plant interspaces. However, on resource islands on which the plants had been killed using herbicide, there was a higher early probability of seedling emergence than for interspaces. These differences did not persist into survival of seedlings beyond one year. Given that the resource islands are relatively short-lived following plant death (Kelly

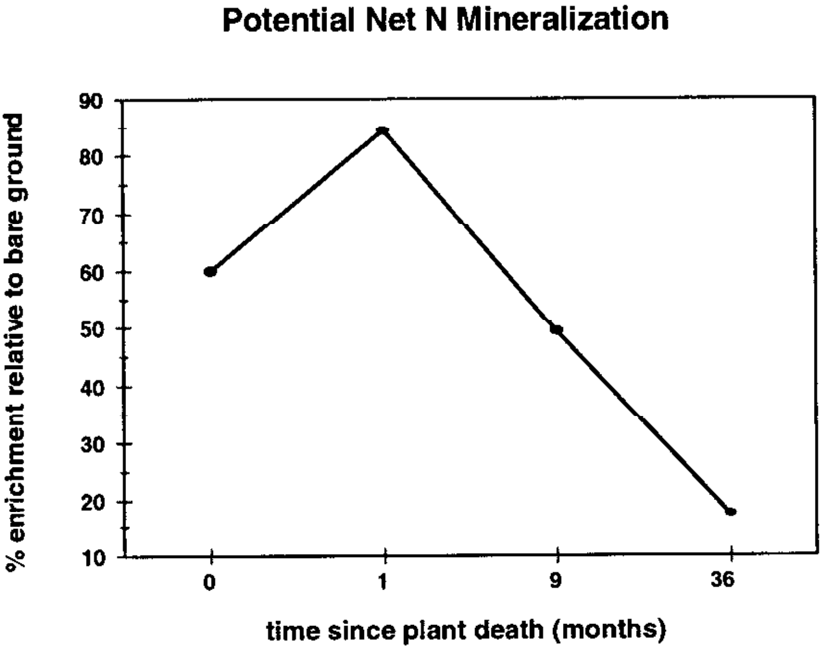

Figure 8. Intensity of the resource island effect on potential net N mineralization occurring under dead *Bouteloua gracilis* individuals in the shortgrass steppe of northeastern Colorado, 1 month, 9 months, and 36 months after death. The enrichment percentage is the difference between under-plant location and bare soil location, divided by the bare soil location. From Kelly and Burke (1997). Enrichment increases at one month because of mineralization of the fresh litterfall from the recently killed plant.

& Burke 1997), and that seedling recruitment events are rare (Lauenroth et al. 1994), it is possible that the resource islands are not important for plant community dynamics in arid or semiarid grasslands, since a recent mortality event must coincide with a seedling establishment event. In addition, two studies suggest that nitrogen availability in dry grasslands does not influence seedling survival (Hays et al. 1982; Richard 1990). Seedling survival is most closely related to the transitional point at which seedlings produce adventitious roots; nitrogen availability does not influence adventitious root growth in *Bouteloua gracilis* or *Buchloe dactyloides* (Hayes et al. 1982; Richard 1990).

The center of the resource islands associated with bunchgrasses corresponds with a zone of tiller mortality in individual bunchgrasses (Fair 1996), but the connection between this pattern and resources is unknown. This mortality pattern may be a consequence of plant morphology, rather than anything related to soil resources.

The key influence of soils on plants in shortgrass steppe may be the availability of water and nitrogen at a field scale, which can determine whether or not resource island-forming species persist in the community. Lauenroth et al. (1978) documented large shifts in plant species composition associated with increasing soil resources in shortgrass steppe, for both water and nitrogen (although primarily water). With increases in water and N availability, species composition shifted to weedy, annual species, and total biomass and cover increased, leading to a reduction in the formation of resource islands. Vinton and Burke (1995) suggested that there is possibly a significant feedback in these grasslands with weedy annual species such as *Kochia scoparia* increasing N availability, which increases its own competitiveness. The annuals also reduce heterogeneity, by growing in different locations from year to year (Vinton & Burke 1995; Aguiar et al. 1996). In any case, the key influence of soils on plant communities and composition in semiarid grasslands is through water availability, and the important influence of the plants is on soil nutrient concentration in resource islands.

III. Indeterminate dominance grasslands: An overview

Plant–soil interactions in the subhumid or indeterminate dominance grasslands have been studied a great deal, particularly from the perspective of species or plant functional type influences on soil organic matter, and the feedbacks to successional dynamics (e.g., Tilman 1984, 1986, 1987; Knapp & Seastedt 1986; Seastedt 1988; Gleeson & Tilman 1990; 1994; Seastedt et al. 1991; Schimel et al. 1991; Tilman & Wedin 1991a,b; Huenneke et al. 1990; Wedin & Tilman 1990, 1993, 1996; Ojima et al. 1994; Aerts & Caluwe 1994, 1994; Berendse 1994; Inouye & Tilman 1995; Turner et al. 1995; Schlapfer & Ryser 1996; Turner & Knapp 1996; Vinton & Burke 1997; and many others). Since a major review of plant–soil interactions in subhumid, indeterminate dominance grasslands has recently been written (Wedin 1995), here we provide only a brief overview.

The indeterminate dominance grasslands are characterized by a clear response to nitrogen additions, and clear differentiation among plant species and plant functional types with respect to their efficiencies of resource (nitrogen, light, water) acquisition (Field 1983; Field & Mooney 1986; Schimel et al. 1991; Seastedt & Knapp 1993; Wedin 1995). With respect to the spatial gradient from semiarid to subhumid grasslands, as water availability increases across the precipitation gradient, there is strong evidence of increasing light and nitrogen limitation with increasing plant height (Weaver 1954; Bremen & DeWitt 1983; Lauenroth & Coffin 1992; Lane 1995; Epstein et al. 1996; Vinton & Burke 1997; Burke et al. 1997b; Murphy et al. 1996). Increases in aboveground production and plant height are accomplished both by changes in plant species composition and by individual species increasing in height (Lane 1995). In our model of plant–soil interactions for subhumid to humid grasslands (Figure 1), as water availability increases, aboveground plant biomass increases, and light becomes more limiting. Concomitant with increasing aboveground biomass and increasing plant height, C:N ratio and lignin:N ratio of aboveground biomass increase (Vinton & Burke 1997; Murphy et al. 1996), likely contributing to decreased N mineralization relative to plant growth needs, or increased nitrogen use efficiency (Vinton & Burke 1997; Burke et al. 1997b). Thus, the feedback between plants and soils is complete: water as a soil resource alters plant features that in turn alter soil nutrient availability, as well as light availability.

These simple patterns across spatial climatic gradients are not usefully discussed in the absence of the effects of herbivory and fire, reviewed by Wedin (1995) and Burke et al. (1997a). Both grazing and fire have likely been very important controls over plant–soil interactions in subhumid and humid grasslands over evolutionary time scales (Milchunas et al. 1988; Axelrod 1985; Collins & Wallace 1990; Wedin 1995). Both grazing (Holland & Detling 1990; Holland et al. 1992) and fire (Hobbs et al. 1991; Ojima et al. 1994) increase N availability through the interactions of plants and the microbial community. Knapp and Seastedt (1986) suggest that both forces reduce detritus accumulation, which in turn reduces microbial immobilization, increasing net N mineralization and plant productivity. As a result, litter quality, as indexed by N concentrations, increases under grazing (Jaramillo & Detling 1988; Coppock et al. 1983; Polley & Detling 1989; Coughenour 1991; Milchunas et al. 1995) and moderate frequency fire (Schimel et al. 1991; Ojima et al. 1994) across a broad array of ecosystems. These responses to grazing and fire may further lead to increases in N availability through reductions in microbial immobilization, and subsequent increases in net primary productivity (Towne & Owensby 1984; Hobbs et al. 1991; Knapp & Seastedt 1986; Wedin 1995). Clearly, temporal dynamics of plant–soil interactions in the indeterminate dominance grasslands are very strongly controlled by management practices.

In addition, species or plant functional type characteristics significantly influence soil resource availability. Most studies to date have focused on N availability as the key nutrient resource in subhumid grasslands. Variation among plant species in biomass and nutrient allocation may cause significant variation in N availability (Wedin & Tilman 1990; Tilman & Wedin 1991a). Tilman and Wedin (Tilman 1982; Tilman & Wedin 1991a,b) suggest that a key mechanism in grasslands is the reduction of resources by species that are good nitrogen competitors. Generally, species with the greatest root allocation and the lowest litter quality (highest C:N) reduce soil N availability most effectively, and are hence the best competitors. Some of these differences among species may be explained by photosynthetic pathway. Subhumid grasslands may be dominated by either or both C_3 and C_4 grasses, depending upon latitude and moisture regime (Epstein et al. 1997). Litter quality strongly correlates with photosynthetic pathway (Field & Mooney 1986), with C_4 species having significantly higher C:N ratios. Wedin and Tilman (1990) found that this simple grouping of species into photosynthetic pathway was very successful in explaining the influence of plant species on nitrogen availability in tallgrass prairie, with C_4 species leading to significantly lower N mineralization. More recently, Epstein et al. (1998) have demonstrated that dominance by C_3 or C_4 species also influences methane consumption and the fluxes of nitrogen trace gases from shortgrass steppe soils, a trend that is likely to be intensified in the tallgrass systems where litter quality has even more variance (Vinton & Burke 1997).

Feedbacks: Influence of soil resources on plants

Soil nutrient and water availability clearly have strong influences on plant function and species composition in the indeterminate dominance grasslands. Species composition and net primary productivity vary strongly along topographic, management, and regional gradients that correspond with water and nutrient availability (Knapp 1985; Schimel et al. 1991; Lane 1995). Further, nitrogen availability has been shown to alter the course of secondary succession in North American tallgrass prairie (Tilman 1984, 1987), a result that has also been found in shortgrass steppe (Lauenroth et al. 1978) and annual grasslands (Huenneke et al. 1990). In the latter two cases, additions of N resulted in significant invasions of nonnative forbs. More recently, long-term nitrogen addition experiments have indicated that N availability exerts a strong ultimate control over resistance to drought in grasslands (Tilman et al. 1994; Tilman & Downing 1994). Plots with lowest N availability had different species composition and sustained largest diversity of plant communities over the long term and highest primary productivity in drought years. While the species composition may have been the direct reason for changed drought resistance, it is not possible to discern from these experiments the importance of N as a direct vs. indirect control variable. Nonetheless, N was the single variable manipulated to initiate these important interactions between plant dynamics and soil resources. Wedin and Tilman (1996) recently showed that the long-term N additions altered ecosystem properties such as N mineralization, N retention, and soil nitrate concentrations, likely through the influence of changes in plant productivity, species composition, and litter quality.

IV. Summary

Grassland ecosystems encompass a broad spectrum of plant–soil interactions, because the key constraints to plant growth (water, nutrients, and light) vary in their importance both spatially and temporally. In the semiarid to arid grasslands, which are dominated by belowground constraints, there is strong coupling between the structure of plant communities and the spatial distribution of soil resources that results in the formation of 'resource islands' associated with individual plants. Data from both shrublands and grasslands suggests that plant functional type has a large influence on the formation of resource islands, with long-lived shrubs and perennial bunchgrasses having the highest capability for accumulating resources. In many areas of the world, perennial bunchgrass and shrub communities are susceptible to invasion by annual plants in the wake of mortality induced by fire or grazing (Walker et al. 1981; West 1979; Milchunas & Lauenroth 1993; Aguiar et al. 1996; Rietkerk et al. 1996). These annuals do not generate the resource islands characteristic of the original ecosystem (Vinton & Burke 1995; Aguiar et al. 1996). In other parts of the globe, human influences are shifting grasslands to shrublands, which is apparently altering the scale of resource islands (Schlesinger et al. 1990, 1996). What is the significance of changing the scale of soil heterogeneity induced by individual plants? Schlesinger et al. (1990) suggest that the magnification of individual resource islands associated with desertification of the Chihuahuan desert is an indicator of reduced ecosystem stability. If resource islands were to serve as important locations for seedling establishment, however, increasing their occurrence could be interpreted as a positive attribute. Further, resource islands could be considered to be conserving resources within an ecosystem that would otherwise be transported away via wind or water erosion. While research has now been conducted on the formation and persistence of resource islands, little information exists on their ecosystem significance. It is clear, however, that explicit sampling of resource islands in grasslands is crucial to assessments of ecosystem organic matter and nutrient capital (Vinton & Burke 1995; Robles & Burke 1997).

In subhumid grasslands, characterized by indeterminate constraints that vary in both time and space (Seastedt & Knapp 1993), plant species characteristics have a strong influence on soil nutrient availability and ecosystem carbon storage (Wedin & Tilman 1990, 1996). Soil nutrient availability, in turn, has a strong feedback to plant growth and plant community dynamics (Tilman & Wedin 1991a,b). Thus, changes in either plant species composition through invasions or other human-mediated effects, or manipulations of soil resources through cultivation, may have large consequences for the interactions between plants and soils. Large-scale manipulations of N availability, through either N deposition or temperature-induced increases in decomposition, may thus have significant consequences for plant community dynamics and carbon storage in subhumid grasslands (Wedin & Tilman 1996).

References

Aerts R & De Caluwe H (1997) Nutritional and plant-mediated controls on leaf litter decomposition of Carex species. Ecol. 78: 244–260

Aguiar MR, Burke IC, Lauenroth WK & Anderson JE (1995) Changes in plant functional types and the fate of the soil organic matter in the sagebrush steppe. Ecol. Bull. 76: 2

Aguiar MR, Paruelo JM, Sala OE & Lauenroth WK (1996) Ecosystem responses in plant functional type composition: An example from the Patagonian steppe. J. Veg. Sci. 7: 381–390

Aguilera MO & Lauenroth WK (1995) Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. J. Ecol. 83: 87–97

Axelrod DI (1985) Rise of the grassland biome. Bot. Rev. 51: 163–201

Barth RC & Klemmedson JO (1978) Shrub-induced spatial patterns of dry matter, nitrogen and organic carbon. Soil Sci. Soc. Am. J. 42: 804–809

Berendse F (1994) Litter decomposability – a neglected component of plant fitness. J. Ecol. 82: 187–190

Bolton H Jr, Smith JL & Wildung RE (1990) Nitrogen mineralization potentials of shrub-steppe soils with different disturbance histories. Soil Sci. Soc. Am. J. 54: 887–891

Bolton H, Smith JL & Link SO (1993) Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biol. Biochem. 25: 545–552

Bremen H & DeWit CT (1983) Rangeland productivity and exploitation in the Sahel. Sci. 221(4618): 1341–1347

Burke IC (1989) Control of nitrogen mineralization in a sagebrush steppe landscape. Ecol. 70(4): 1115–1126

Burke IC, Reiners WA & Schimel DS (1989) Organic matter turnover in a sagebrush steppe landscape. Biogeochem. 7: 11–31

Burke IC, Lauenroth WK & Coffin DP (1995) Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. Ecol. Appl. 5(3): 793–801

Burke IC, Lauenroth WK, Brannen P, Madigan B & Riggle B (1996b) Interactions among plant species, topography, and grazing in soil redistribution and organic matter accumulation in shortgrass steppe. Ecol. Bull. 77: 61

Burke IC, Lauenroth WK & Milchunas DG (1997a) Biogeochemistry of managed grasslands in the Central Grasslands of the U.S. In: Paul E, Paustian K, Elliott ET & Cole CV (Eds) Organic Matter in U.S. Agroecosystems (pp 85–101). CRC Press, Boca Raton, FL

Burke IC, Lauenroth WK & Parton WJ (1997b) Regional and temporal variability in aboveground net primary productivity and net N mineralization in grasslands. Ecol. 78: 1330–1340

Charley JL & West NE (1977) Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. Soil Biol. Biochem. 9(5): 357–365

Charley JL & West NE (1975) Plant induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. J. Ecol. 63: 945–964

Coffin DP & Lauenroth DS (1989) The effects of disturbance size and frequency on a shortgrass plant community. Ecol. 69: 1609–1617

Coffin DP & Lauenroth WK (1991) Effects of competition on spatial distribution of roots of blue grama. J. Range Manage. 44: 68–71

Collins SL & Wallace LL (1990) Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, Oklahoma

Coppinger KD, Reiners WA, Burke IC & Olson RK (1991) Net erosion on a sagebrush steppe landscape as determined by cesium-137 distribution. Soil Sci. Soc. Am. J. 55: 254–258

Coppock DL, Detling JK, Ellis JE & Dyer MI (1983) Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of prairie dogs on intraseasonal aboveground plant biomass, nutrient dynamics and plant species diversity. Oecol. 56: 1–9

Coughenour MB (1991) Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. J. Appl. Ecol. 28: 71–82

Coupland RT (1992) Natural Grasslands. Volumes 8A and 8B in Ecosystems of the World. Elsevier. Amsterdam, The Netherlands

Dormaar JF (1992) Decomposition as a process in natural grasslands. In: Coupland RT (Ed) Natural Grasslands: Introduction and Western Hemisphere. Volume 8A, Ecosystems of the World (pp 121–136). Elsevier, Amsterdam, The Netherlands

Elberse, WT & Berendse F (1993) A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. Funct. Ecol. 7: 223–229

Epstein HE, Lauenroth WK, Burke IC & Coffin DP (1996) Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. J. Veg. Sci. 7: 777–788

Epstein HE, Lauenroth WK, Burke IC & Coffin DP (1997) Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains. Ecol. 78: 722–731

Epstein HE, Burke IC, Mosier AR & Hutchinson GL (1998) Plant functional type effects on trace gas fluxes in the shortgrass steppe. Biogeochemistry, this issue, 145–168

Fair J (1996) Demography of *Bouteloua gracilis* in shortgrass steppe and mixedgrass prairie. Unpublished Master's Thesis, Fort Collins

Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecol. 56: 341–347

Field C & Mooney HS (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givinish TJ (Ed) On the Economy of Form and Function (pp 25–55). Cambridge University Press, Cambridge, England

Gibson (1988) The maintenance of plant and soil heterogeneity in dune grassland. J. Ecol. 76: 497–508

Gleeson SK & Tilman D (1991) Plant allocation and the multiple limitation hypothesis. Amer. Nat. 139: 1323–1343

Gleeson SK & Tilman D (1990.) Allocation and the transient dynamics of succession on poor soils. Ecol. 71: 1144–1155

Gleeson SK and Tilman D (1994) Plant allocation, growth rate and successional status. Funct. Ecol. 8: 543–550

Gutierrez JR, Meserve PL, Contreras LC, Vasquez H & Jaksic FM (1993) Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. Oecol. 95: 347–352

Hays R, Ried CPP, St. John TV & Coleman DC (1982) Effects of nitrogen and phosphorus on blue grama growth and mycorrhizal infection. Oecol. 54: 260–265

Hobbs NT, Schimel DS, Owensby CE & Ojima CE (1991) Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecol. 72: 1374–1382

Holland EA & Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecol. 71: 1040–1049

Holland EA, Parton WJ, Detling JK & Coppock DL (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am. Nat. 140: 685–706

Hook PB, Burke IC & Lauenroth WK (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. Plant Soil 138: 247–256

Hook PB, Lauenroth WK & Burke IC (1994) Spatial patterns of plant cover and roots in a semiarid grassland: abundance of canopy openings, root gaps, and resources gaps. J. Ecol. 82: 485–494

Huenneke LF, Hamburg SP, Koide R, Mooney HA & Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecol. 71: 478–491

Ihori T, Burke IC & Hook PB (1995) Nitrogen mineralization in native, cultivated, and abandoned fields in shortgrass steppe. Plant Soil 171: 203–208

Inouye RS & Tilman D (1995) Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. Ecol. 76: 1872–1887

Jackson RB & Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecol. 74: 612–614

Jaramillo VJ & Detling JK (1988) Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. Ecol. 69: 1599–1608

Kelly RH & Burke IC (1997) Heterogeneity of soil organic matter following death of individual plants in shortgrass steppe. Ecol. in press

Kelly RH, Burke IC & Lauenroth WK (1996) Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. Ecol. 77: 2516–2527

Knapp AK & Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. BioSci. 36: 662–668

Lane DR (1995) Aboveground net primary production across a precipitation gradient in the Central Grassland Region. Thesis, CSU, Fort Collins, CO

Lauenroth WK & Coffin DP (1992) Belowground processes and the recovery of semiarid grasslands from disturbance. Eco. Rehab. 2: 131–150

Lauenroth WK, Coffin DP, Burke IC & Virginia RA (1997) Interactions between demographic and ecosystem processes: a challenge for functional types. In: Smith TM & Shugart HH (Eds) Plant Functional Types (pp 234–254). Cambridge University Press, Cambridge, UK

Lauenroth WK, Dodd JL & Simms PL (1978) The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecol. 36: 211–222

Lauenroth WK & Milchunas DG (1992) Short-Grass steppe. In: Coupland RT (Ed) Natural Grasslands: Introduction and Western Hemisphere. Ecosystems of the World, Volume 8A (pp 183–226). Elsevier, Amsterdam – London – NY – Tokyo

Lauenroth WK, Sala OE, Coffin DP & Kirchner TB (1994) The importance of soil water in the recruitment of Bouteloua Gracilis in the shortgrass steppe. Ecol. Appl. 4: 741–749

Lee CA & Lauenroth WK (1994) Spatial distributions of grass and shrub root systems in the shortgrass steppe. Am. Midl. Nat 132: 117–123

Martinez-Turanzas GA, Coffin DP & Burke IC (1997) Development of microtopography in a semiarid grassland: effects of disturbance size and soil texture. Plant Soil 191: 163–171

Milchunas DG & Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63: 327–366

Milchunas DG, Sala OE & Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am. Nat. 132: 87–106

Milchunas DG, Varnamkhasti AS, Lauenroth WK & Goetz H (1995) Forage quality in relation to long-term grazing history, current-year defoliation, and water resource. Oecol. 101: 366–374

Murphy KL, Burke IC, Vinton MA, Lauenroth WK & Aguiar M (1996) Regional analysis of plant tissue chemistry in the central grasslands of the U.S. Bull. Ecol. Soc. Am. 77: 317

Ojima DS, Schimel DS, Parton WJ & Owensby CE (1994) Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochem. 24: 67–84

Polley, HW & Detling JK (1989) Defoliation, nitrogen, and competition: effects on plant growth and nitrogen nutrition. Ecol. 70: 721–727

Richard CE (1990) Nitrogen and phosphorus effects on blue grama and buffalo grass interactions. M.S. Thesis. Colorado State University. Fort Collins, CO

Rietkerk M, Ketner P, Stroosnijder L & Prins HHT (1996) Sahelian rangeland development: a catastrophe? J. Range Manage 49: 512–519

Ripley EA (1992) Grassland Climate. In: Coupland RT (Ed) Natural Grasslands: Introduction and Western Hemisphere. Ecosystems of the World 8A (pp 7–24). Elsevier, Amsterdam, The Netherlands

Robles MD & Burke IC (1997) Legume, grass, and Conservation Reserve Program effects on recovery of soil organic matter pools and nutrient availability. Ecol. Appl. 7: 345–357

Rostagno CM & del Valle HF (1988) Mounds associated with shrubs in aridic soils of northeastern Patagonia: characteristics and probable genesis. Catena 15: 347–359

Rostagno CM, del Valle HF & Videla L (1991) The influence of shrubs on some chemical and physical properties of an aridic soil in northeastern Patagonia, Argentina. J. Arid Env. 20: 179–188

Schimel DS, Kittel TGF, Knapp AK, Seastedt TR, Parton WJ & Brown VB (1991) Physiological interactions along resource gradients in a tallgrass prairie. Ecol. 72: 672–684

Schlapfer B & Ryser P (1996) Leaf and root turnover of three ecologically contrasting species in relation to their performance along a productivity gradient. Oikos 75: 398–406

Schlesinger WH, Raikes JA, Hartley AE & Cross AF (1996) On the spatial pattern of soil nutrients in desert ecosystems. Ecol. 77: 364–374

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA & Whitford WG (1990) Biological feedbacks in global desertification. Sci. 247: 1043–1048

Seastedt TR (1988) Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecol. 69: 59–65

Seastedt TR, Briggs JM & Gibson DJ (1991) Controls of nitrogen limitation in tallgrass prairie. Oecol. 87: 72–79

Seastedt TR & Knapp AK (1993) Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. Am. Nat. 141: 621–633

Tilman D (1986) Nitrogen-limited growth in plants from different successional stages. Ecol. 67: 55–563

Tilman D (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Monographs in Population Biology 26, Princeton University Press. Princeton, NJ

Tilman D (1982) Resource Competition and Community Structure. Princeton University Press, Princeton, NJ

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

Tilman D & Wedin D (1991a) Dynamics of nitrogen competition between successional grasses. Ecol. 72: 1038–1049

Tilman D, Wedin D & Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nat. 379: 718–720

Tilman D. Downing A & Wedin DA (1994) Does diversity beget stability? Nature 371: 113–114

Tilman D & Downing JA (1994) Biodiversity and stability in grasslands. Nature 367: 363–365

Tilman GD (1984) Plant dominance along an experimental nutrient gradient. Ecol. 65: 1445–1453

Towne G & Owensby CE (1984) Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. J. Range Manage. 37: 392–397

Turner CL & Knapp AK (1996) Responses of a C_4 grass and three C_3 forbs to variation in nitrogen and light in tallgrass prairie. Ecol. 77: 1738–1749

Turner CL, Kneisler JR & Knapp AK (1995) Comparative gas exchange and nitrogen responses of the dominant C_4 grass, *Andropogon gerardii*, and five C_3 forbs to fire and topographic position in tallgrass prairie during a wet year. Int. J. Plant Sci. 156: 216–226

Vinton MA & Burke IC (1995) Interactions between individual plant species and soil nutrient status in shortgrass steppe. Ecol. 76: 1116–1133

Vinton MA & Burke IC (1997) Plant effects on soil nutrient dynamics along a precipitation gradient in Great Plains grasslands. Oecol. (in press)

Walker BH, Ludwig IC, Holling CS & Peterman RM (1981) Stability of semi-arid savanna grazing systems. J. Ecol. 69: 473–498

Weaver JE (1954) North American Prairie. Johnsen Publishing Company, Lincoln, NB

Wedin D & Tilman D (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Eco. Mono. 63: 199–229

Wedin DA (1995) Species, nitrogen, and grassland dynamics: the constraints of stuff. In: Jones CG & Lawton JH (Eds) Linking Species and Ecosystems (pp 253 262). Chapman and Hall, New York, NY

Wedin DA & Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecol. 84: 433–441

Wedin DA & Tilman D (1996) Influence of nitrogen loading and species composition on the carbon balance of grasslands. Sci. 274: 1720–1723

West NE (1979) Basic synecological relationships of sagebrush-dominated lands in the Great Basin and the Colorado Plateau. In: The Sagebrush Ecosystem. A Symposium. Utah State University, Logan, Utah, pp 33–41