

Nitrogen availability, plant–soil feedbacks and grassland stability

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Introduction

At the beginning of the 20th century, the Nebraska plant ecologist F.E. Clements presented a theory of plant community dynamics that had a large impact on grassland ecology and range science (Clements 1916). His relatively deterministic view of succession and climax community types has been widely debated in the last quarter century and rejected by many. My goal in this paper is not to pound more nails in the coffin of my Nebraskan forefather. Even if we consider Clement's theory as rejected, the basic problem with his approach persists in much of plant community ecology today. Plant ecologists, particularly those trained in North America, have consistently confused pattern with mechanism.

Consider the example of succession. For most of this century, if one had asked why we see repeatable change in plant community composition following disturbance, the answer would generally be 'it's caused by succession'. If, on the other hand, one asked for a definition of succession, it would be 'the sequence of changes on a disturbed site' (Ricklefs 1979) or a similar phrase. This is a circular argument. Succession is the pattern; it is not the mechanism or process responsible for the pattern. To be fair, my example misrepresents the treatment given succession by many ecologists, including Clements (e.g. Clements & Weaver 1938), who have studied recruitment, demography, soil fertility and other processes driving succession. However, I argue that succession is still widely thought of as a process, rather than simply a pattern.

Consider the example of the niche, which became popular conceptually in the 1960s. Why do two species coexist? Because they have different niches. How do we know these two species have separate niches? Because they coexist. Fortunately, it only took plant ecologists 20 years, rather than 50 in the case of succession, to realize that the niche was an empty explanation, a circular argument empty of mechanism and process (Peters 1991).

That brings us to today. Succession and climax models of range dynamics have been tentatively replaced by models with alternative stable states, thresholds, and transitions (Ellis & Swift 1988; Westoby *et al.* 1989; Laycock 1991; Humphreys 1997). These models present a fresh look at patterns we see over space and time in grasslands. But do we risk the same danger with these models that we had with Clements' succession model? Are we discussing pattern, but failing to grapple with underlying mechanisms? A rancher asks an ecologist why his region has seen degradation to shrubland and a loss of usable forage and why, in spite of various management approaches, he is unable to restore the native grassland community. The ecologist answers that it is because his system has passed a threshold and entered an alternative stable state. The ecologist has provided a fancier description of the pattern, but has he really told the rancher anything he didn't already know?

The goal of this session is to address the mechanisms and processes that underlie the patterns we see in rangeland plant community dynamics. In some situations these mechanisms confer stability in grasslands, while in others they cause instability. A mechanistic approach to plant community dynamics needs three components (Tilman 1987):

- plant demography (patterns of recruitment and mortality within various species' populations);
- plant resource use (a given species's performance and ability to compete under specific conditions of light, water, and nutrient availability);
- resource availability (the availability of water, nutrients, and light in a particular place and time).

In this approach, herbivory and disturbance act by affecting one or more of these three factors. Grazing, for example, simultaneously affects all three.

In this paper I will discuss plant resource use and soil resource availability. In particular, I will emphasize plant nitrogen (N) use and soil N dynamics and argue that a strong feedback links these two processes in many, if not all, grasslands.

Plant litter quality and soil nitrogen availability

In 1982, Huntley and Walker wrote that 'N has been shown in all savannas to be of great significance ... but despite many thousands of N measurements ... an understanding of the N cycle in savanna still eludes us'. I would suggest that this statement applies not just to tropical savannas (Huntley & Walker 1982), but to the various native temperate and tropical grasslands that we consider rangeland. Nitrogen limitation is so widespread that we often ignore some very basic but difficult questions (Vitousek & Howarth 1991). Why is N limitation common when grasslands are literally bathed in N₂ gas, a readily accessible source of N for both free-living and plant-associated N-fixing bacteria found in almost all grasslands? Why N limitation, when other soil nutrients, such as phosphorus, are generally immobilized by geochemical processes in ancient weathered soils and also potentially limit grassland productivity (Schlesinger 1991)? Why do semi-arid and desert grasslands commonly show a response to N fertilization when productivity in these systems is obviously moisture limited (Lauenroth *et al.* 1978; Lajtha & Schlesinger 1986)?

The key when considering N is that plant tissue chemistry and its decomposition play a role in regulating the N cycle quite unlike their role in other nutrient cycles. The availabilities of the base cations (Ca, Mg, K, Na), phosphorus, iron, and most other elements are strongly dependent on chemical interactions with inorganic soil minerals, but N participates weakly in such geochemical interactions (Vitousek & Howarth 1991). In contrast, N availability is almost completely regulated by biotic processes. The breaking of the C–N covalent bond is relatively expensive to decomposers in terms of energy and enzymes. During decomposition, considerable N gets locked into polyphenolic ring structures as lignin and other complex molecules are slowly converted into the large recalcitrant compounds that make up soil humus. The long chain organic acids that make up humus are also readily bound to clay minerals, increasing their inaccessibility. Soil organic matter is generally an ecosystem's largest pool of N, but that nitrogen is bound in complex organic compounds and the cost of getting it is very high for microbial decomposers (Schlesinger 1991).

Thus, one cannot consider soil N availability as a 'soil' property and ignore the characteristics of present and past vegetation. Plant tissue chemistry, particularly C:N ratios and lignin

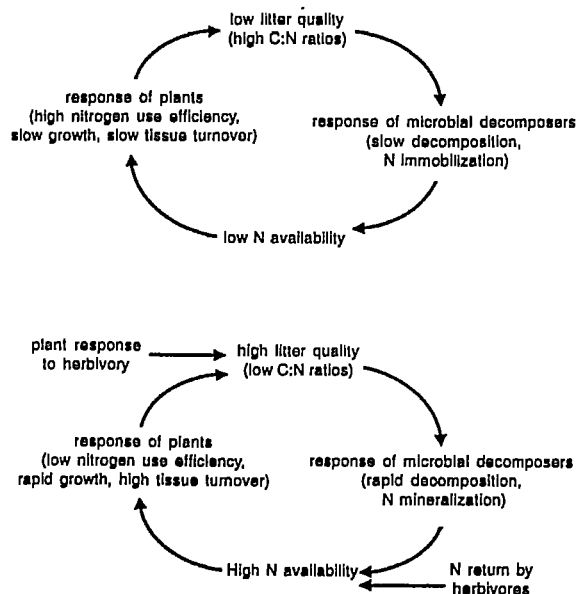


Fig. 1. (a) Positive feedback reinforces the tendency towards N limitation found in most terrestrial ecosystems; (b) herbivory can lead to an alternate positive feedback, enhancing N availability (McNaughton *et al.* 1988; Hobbie 1992; Chapin 1993).

concentrations, affect both the rate at which organic matter decomposes and the balance between the immobilization of mineral N into microbial biomass and its net release or mineralization (Aber & Melillo 1991; Hobbie 1992). If C:N ratios in plant litter are high and N is limiting to microbes relative to their energy source (labile organic C), then little, if any, net release of NH_4^+ and NO_3^- into the soil will occur. Microbial immobilization of N leads to further N limitation of plant growth and often to further decreases in plant tissue N concentrations. Nitrogen limitation and plant competition for N may also cause shifts in plant community composition. A suite of plant traits including slow growth, long-lived tissues, reduced plasticity and high nitrogen use efficiency are generally associated with species that dominate low N environments (Grime 1979; Chapin 1980; Hobbie 1992).

Is this interaction between plant nitrogen use and soil nitrogen the answer to Huntley and Walker's question about the vexing role of N in grasslands and savannas? Together, the physiological and evolutionary responses of plants to N limitation and the responses of microbial decomposers to plant tissue chemistry create a feedback that reinforces the tendency towards N limitation of most terrestrial ecosystems (Fig. 1a) (Vitousek 1982; Hobbie 1992; Chapin 1993). I suggest that one way to understand the effects of grazing, fire, moisture-limitation and soil disturbance on grassland plant communities is to analyse how these factors alter or disrupt this positive feedback between vegetation and soil N availability (Seastedt 1995; Wedin 1995).

Plant-soil feedbacks in Minnesota grasslands

My conclusions about the strength and significance of a plant-soil feedback involving N in grasslands is based on 12 years of research with native grasslands and abandoned agricultural fields on a sand plain in east-central Minnesota (USA). My work there with Dave Tilman initially began as a study of plant competition. Tilman had shown that by manipulating soil N availability, one could alter both the species composition and the species diversity in grasslands (Tilman 1988). To understand processes responsible for these competitive shifts, we constructed an experimental garden with replicated blocks of soil ranging from sand to a relatively rich black sandy loam. The experiment included monocultures of five perennial grasses:

two of the native dominant C_4 grasses from the tallgrass prairie (*Schizachyrium scoparium* and *Andropogon gerardii*), two non-native rhizomatous C_3 grasses (*Agropyron repens* and *Poa pratensis*), and one native, short-lived C_3 grass (*Agrostis scabra*) (nomenclature follows Ownbey & Morley 1991). In order to quantify the N availability gradient corresponding to the various soil types, we measured *in situ* net N mineralization rates in the monocultures. By year three, we were surprised to find that N mineralization rates on initially homogeneous soils had diverged sharply, ranging from less than 20 kg N/ha/year to over 100 kg N/ha/year (Wedin & Tilman 1990).

Among various plant traits, the one best correlated with this divergence in N turnover rates was root C:N ratio. The native C_4 bunch grasses, which had slowed N mineralization rates dramatically, had root C:N ratios of over 100 while the early successional native C_3 grass, which had sharply increased N mineralization, had a root C:N ratio of only 24 (Wedin & Tilman 1990). Litter decomposition studies confirmed that the low N tissues of the C_4 grasses both decomposed slowly and immobilized nitrogen for several years before beginning to mineralize (Wedin 1995). In other words, a bag of senesced leaves or roots from our dominant prairie grasses, placed out in the grassland, contained more N after two years, both as concentration and total amount, than on the day it was placed out. Our conclusion was that the competitive advantage of the native C_4 prairie grasses on these sandy soils was caused both by the effects of their litter quality on N mineralization and by their ability to deplete soil nitrate pools through efficient plant uptake (Wedin & Tilman 1993).

The most surprising aspect of these results was the rapid time frame over which the plant-soil feedbacks occurred. How, given the large quantities of organic matter in grassland soils, can major shifts in N cycling occur so quickly? Soil C and N researchers have used various approaches over the last decade to fractionate soil organic matter into active and passive fractions. These methods include size fractionations, chemical or density fractionations, laboratory incubations, and various modelling approaches (Stanford & Smith 1972; Schimel 1986; Parton *et al.* 1988; Cambardella & Elliot 1993). All of these methods point to a small active fraction of soil organic matter that dominates both C respiration and N mineralization. Wedin & Pastor (1993) performed long-term laboratory incubations with soils from the experimental monocultures described above, and concluded that changes in the pool size and turnover rate of a small labile pool of soil N (less than 3% of total soil N) accounted for the dramatic divergence in N mineralization rates observed in the field. Other grassland studies have confirmed that N mineralization or immobilization can rapidly track vegetation shifts resulting from fire (Seastedt 1995; Blair 1997) or grazing (Holland *et al.* 1992).

Another important aspect of the feedback of litter quality on N availability is that microbial resource requirements create an inherent threshold between N immobilization and net mineralization in grassland soils. This was clearly seen when we measured the C and N budgets of 164 Minnesota grassland plots that had received various levels of N fertilizer for 12 years (Wedin & Tilman 1996). Plant species composition varied with both the length of time the particular field had been abandoned from agriculture and with the amount of N added. Older fields and plots receiving less than 20–30 kg N/ha/year were dominated by native C_4 prairie grasses, while other fields were dominated by non-native C_3 grasses. Among the many parameters measured were monthly extractable soil NO_3^- and the C:N ratios both of roots and of aboveground dead plant biomass (Wedin & Tilman 1996). On these sandy soils, soil NO_3^- pools regulated both plant N availability and ecosystem N losses.

Even though the experimental N additions created a continuous gradient of N inputs ranging from 10 to 270 kg N/ha/year, a threshold in the response of the plots to N loading was

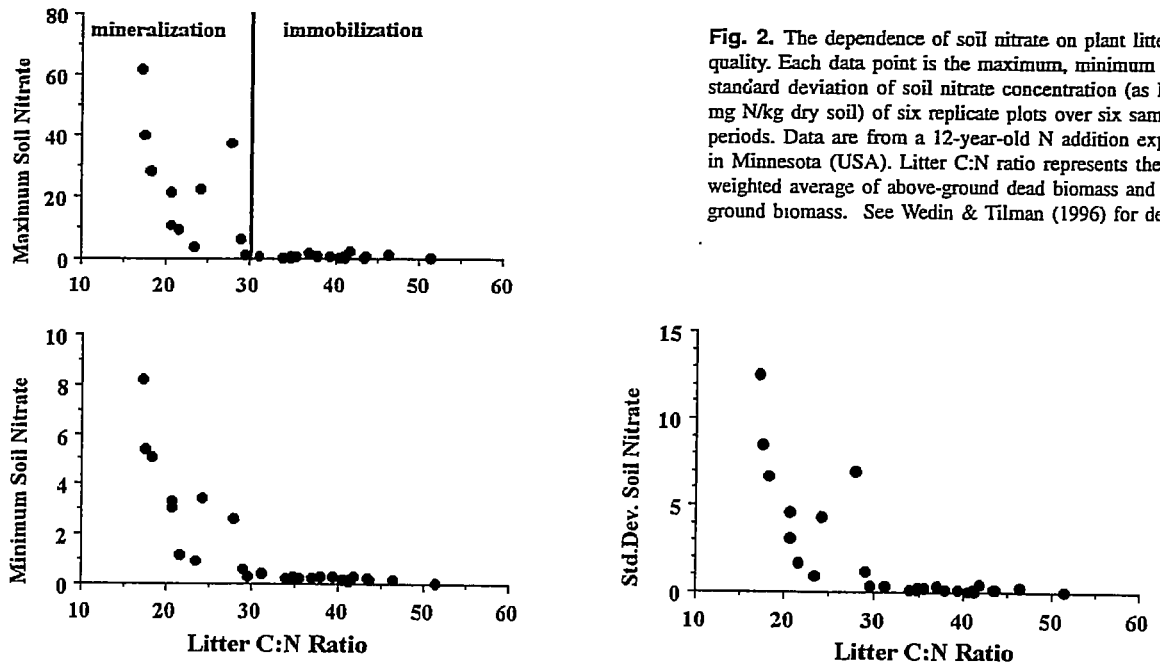


Fig. 2. The dependence of soil nitrate on plant litter quality. Each data point is the maximum, minimum or standard deviation of soil nitrate concentration (as N, mg N/kg dry soil) of six replicate plots over six sampling periods. Data are from a 12-year-old N addition experiment in Minnesota (USA). Litter C:N ratio represents the weighted average of above-ground dead biomass and below-ground biomass. See Wedin & Tilman (1996) for details.

evident. In plots where dead plant biomass had C:N ratios higher than 30 (values include roots, which have minimal N retranslocation upon senescence), soil NO_3^- concentrations were consistently low (Fig. 2). In plots with litter C:N ratios less than 30, soil NO_3^- concentrations were an order of magnitude higher and highly variable. A C:N ratio of roughly 30 for plant litter represents the breakpoint above which microbial decomposers are N-limited and immobilize mineral N and below which they are not N-limited (Aber & Melillo 1991). In our study, plots crossed this threshold when the dominance of the native C_4 grasses was lost and the system shifted to high N mineralization rates, high soil N concentrations, high N losses, and domination by rhizomatous C_3 grasses. Thus, the data show a strong linkage between patterns of N cycling and plant community dynamics in these experimental grasslands.

Implications for range ecosystems

Figure 2 is useful for generalization and speculation about the role of litter quality feedbacks and nitrogen cycling in the dynamics of grassland ecosystems globally. Let us assume that most grasslands contain a number of annuals, herbs, and shrubs that have relatively high N demands and are kept in check by competition for N with the dominant grasses. The further an ecosystem lies to the right in Fig. 2, the more microbial immobilization buffers the system against pulses of high nitrogen availability. These pulses could be caused by fertilizer application, urine hits, loss of active leaf area, localized soil disturbance, fire, drought, etc. All of these factors either directly add mineral N to the system, or they disrupt N uptake by the vegetation. If the system is not buffered (i.e. lies to the left of the threshold) or the disturbance exceeds the soil's immobilization capacity, soil mineral N pools increase dramatically and the competitive advantage of the dominant grasses is lost. This creates an opportunity for plant species with high resource requirements to gain or expand their foothold in the plant community. Small spatial and temporal excursions across the immobilization threshold are probably common in even strongly N-limited grasslands and may play a role in maintaining grassland diversity. The key question is which state, immobilization or mineralization, is dominant?

I would suggest that most native humid grasslands, whether temperate or tropical, function primarily on the immobilization side of the threshold in Fig. 2. These include the North American tallgrass prairie, the Russian tallgrass steppe, the

South African high veld, and the tussock grasslands of Australia and New Zealand (Wedin 1995). 'Grassland improvement', primarily the addition of N fertilizer or legumes, has displaced many of these native grasslands, pushing them to the left hand side of Fig. 2. Although this approach has been common in humid pastureland, it has not been widely used in rangeland because of economic and, perhaps, biological constraints.

How does grazing affect the balance between mineralization and immobilization? Grazing pushes a system to the left, towards increased N availability. Not only does grazing directly add mineral or highly labile organic N to the soil, it leads to higher average plant tissue N concentrations, decreased root allocation, and, in some cases, less efficient N uptake. McNaughton and colleagues have suggested that N cycling plays a key role in the 'grazing lawn' phenomenon observed in Serengeti grasslands (McNaughton *et al.* 1988; McNaughton *et al.* 1997). Patches of fast growing, high protein, high N-demanding short grasses become established within a matrix of low nitrogen tall grasses. Grazers favour the patches with better forage quality and high N availability and avoid the low N availability regions, perpetuating a split into alternative stable states (Fig. 1b). Thus, the N mineralization-immobilization threshold created by plant litter quality can account for state and transition or threshold patterns in some rangelands (Westoby *et al.* 1989). Some studies have suggested, however, that high N availability states perpetuated by herbivores are unstable in the long run (e.g. Jefferies *et al.* 1994). In this view, the high herbivory-high N availability-high plant productivity state (Fig. 1b) is transitional to either a degraded, unproductive system or one dominated by unpalatable species (Pastor & Cohen 1997).

How does moisture limitation affect the position of grassland systems on Fig. 2? Studies from several continents clearly show that as moisture limitation increases, grassland nitrogen use efficiency and plant tissue C:N ratios decrease (e.g. Bremen & deWit 1983). Do all native grasslands, even semi-arid and arid ones, tend to generally function on the right hand side of the immobilization threshold? Or does one cross a point along precipitation gradients at which grass nitrogen use efficiency and C:N ratios are low enough that litter quality and N immobilization by microbes are irrelevant and contribute little to our understanding of plant community or ecosystem behaviour, even in historically ungrazed grasslands? These questions will remain unanswered until more research is conducted.

If we reconsider Fig. 2 and the N immobilization–mineralization threshold, this model suggests that adding grazers, adding nitrogen or taking away moisture will all push a grassland system to the left, towards a high N availability state. Many semi-arid grasslands, even in the absence of grazers, may function near that threshold and be essentially co-limited by water and nitrogen. For example, the displacement of native perennial grasslands by annual grasslands in California following the introduction of domestic livestock could have corresponded to a shift from nitrogen limitation or co-limitation to a system dominated solely by moisture limitation (Baker 1978; Huenneke *et al.* 1990). The perennial grasses could out-compete the fast-growing annual grasses for nitrogen, but not for soil moisture in a Mediterranean climate. Once annuals were established, their very high litter quality (i.e. low C:N ratios) would rapidly have pushed these grasslands far to the left on Fig. 2 (i.e. from Fig. 1a to Fig. 1b).

A recent review of plant–soil feedbacks in temperate grasslands (Burke *et al.* 1998) suggests that the positive feedback proposed here between litter quality and N cycling plays only a minor role in plant community dynamics and stability in semi-arid grasslands. In the short-grass steppe of eastern Colorado (USA), grass tussocks represent zones of N cycling and biological activity in a matrix of bare soil. Differences in tissue chemistry and N use among plant species appear to have little importance in the short-grass steppe, where the key question is whether or not a particular spot has a living plant at all (Vinton & Burke 1995). Schlesinger & Pilmanis (1998) discussed plant–soil feedbacks and vegetation dynamics in even drier systems, contrasting desert grasslands with the shrublands that have widely displaced them in the American south-west. In intact desert grassland, soil mineral N concentrations appear to be consistently low, while in shrublands (i.e. following desertification) concentrations are higher and much more spatially variable (Schlesinger & Pilmanis 1998). It is unclear, however, whether microbial immobilization is playing a key role in maintaining low soil N availability in desert grassland and whether the disruption of litter quality feedbacks contribute to the desertification process.

Intensive grazing is widely assumed to precipitate shrub expansion and desertification in arid grasslands by reducing grass biomass and eliminating the competitive advantage of grasses over potentially invading shrub species, particularly at the shrub's seedling stage. Recent studies, however, suggest that shrub invasion cannot be accounted for by a simple model in which grazing tilts the competitive balance between grasses and shrubs (Brown & Archer 1989; Archer 1995; O'Connor 1995; Brown & Archer 1999). Perhaps it is more useful to think of grazing in these situations as disrupting a plant–soil system, an important part of which is the feedback effects of grass litter quality on N cycling.

Conclusion

The insights of F.E. Clements invigorated plant ecology at the beginning of the 20th century (Clements 1916). New insights into the spatial and temporal patterns of grassland plant communities are welcome and needed at the beginning of the 21st century. I hope, however, that grassland ecology has matured sufficiently as a discipline that these new insights into vegetation pattern will encourage new process-based research into the underlying mechanisms of grassland dynamics and not become an end in themselves.

Vegetation–soil feedbacks play a central role in current grassland ecology. A synthesis is emerging among fields as diverse as ecophysiology, soil organic matter dynamics, herbivory, plant competition, and fire ecology. Similar conclusions have been reached by agronomists in the last two decades (Ball & Ryden 1984; van der Meer *et al.* 1986). Central to this synthesis in grassland ecology is the linkage between the N use and physi-

ology of grasses on the one hand and the controls over N cycling and soil organic matter dynamics on the other (Hobbie 1992; Wedin 1995; Seastedt 1995). I argue that this linkage is potentially important in all grassland types. It remains to be seen, however, what light this approach will shed on problems in diverse rangeland ecosystems. The role of N limitation remains particularly problematic in semi-arid and arid grasslands.

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Facilitation in rangelands: direct and indirect effects

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Introduction

The structure of rangeland plant communities is highly altered by competitive interactions among plants and the modification of competitive interactions by herbivory (Scholes & Archer 1997). However, by emphasizing competitive interactions and herbivory, the positive effects that plants may have on each other have been largely overlooked until recently. Positive interactions, or facilitation, among plants have been shown to be important in many ecosystems around the world (Callaway 1995). Plants have been shown to directly enhance the fitness of other plants by providing shade, substrate, nutrients, soil oxygen, or shelter from harsh weather, and plants may indirectly enhance the fitness of other plants by protecting them from herbivores, via mycorrhizal connections, by attracting pollinators, or through interconnected webs of competitors. Neither direct nor indirect facilitation occurs independently of competitive effects (Callaway 1995, 1997).

Direct facilitation in savanna rangelands often occurs when overstorey trees provide shade, nutrients, or water via hydrau-

lic lift to herbaceous plants in their understoreys (Parker & Muller 1982; Joffre & Rambal 1988; Callaway *et al.* 1991; Vetaas 1992; Belsky 1994; Caldwell *et al.* 1998). In oak-dominated savannas in California, the effects of *Quercus douglasii* H. & A. (blue oak) have been reported as both competitive (Murphy & Crampton 1964; Kay 1987) and facilitative (Holland 1980; Holland & Morton 1980). At the landscape-scale much of this variation appears to be correlated with climate (McClaran & Bartolome 1989), but individual 'facilitating' and 'competing' blue oaks have been observed with metres of each other (Callaway *et al.* 1991). In the first part of this paper I focus on a suite of positive and negative effects that may determine whether a blue oak facilitates or competes with understorey plants (see Callaway *et al.* 1991).

Intense grazing of rangelands often results in highly competitive palatable species being replaced by less palatable species, which are often considered 'less desirable or even worthless plants'