

LINKING SPECIES & ECOSYSTEMS

edited by

Clive G. Jones

Institute of Ecosystem Studies

John H. Lawton

National Environment Research Council for Population Biology

24

SPECIES, NITROGEN, AND GRASSLAND DYNAMICS: THE CONSTRAINTS OF STUFF

David A. Wedin

Wedin, D.A. 1995. Species, nitrogen and grassland dynamics: the constraints of stuff. Pages 253-262 in C. Jones and J.H. Lawton (eds.). *Linking Species and Ecosystems*. Chapman and Hall.

SUMMARY

Herbivores, decomposers, and fire are three alternative consumers of primary production in grasslands, each with different requirements for and effects on carbon (C) and nitrogen (N). Differences between plant species in their tissue C and N chemistry can determine which of these three consumer pathways the bulk of primary production will follow in a particular system. This stoichiometric approach is applied to native humid grasslands and their dominant tall-grass species.

INTRODUCTION: THE CONSTRAINTS OF STUFF

Two dominant sets of constraints act on ecological systems: the constraints of evolution and the constraints of, for lack of a better term, stuff. To link species and ecosystems and to integrate the approaches of population/community ecologists and ecosystem ecologists both sets of constraints must be understood and acknowledged (Sternner et al., 1992; Sternner, Ch. 23; DeAngelis, 1992; Ch. 25; Holt, Ch. 26).



CHAPMAN & HALL

I(T)P An International Thomson Publishing Company

New York • Albany • Bonn • Boston • Cincinnati • Detroit • London • Madrid • Melbourne • Mexico City
Pacific Grove • San Francisco • Singapore • Tokyo • Toronto • Washington

253

The constraints of evolution are phylogeny and natural selection. Because each species has a unique phylogenetic history, only a tiny subset of the possible combinations of physiological and morphological traits currently exist. Given this phylogenetic history, the "choices" open to a species for life history or resource allocation patterns are also limited by natural selection to a reduced number of viable "strategies" (Grime, 1979; Tilman, 1988). A common criticism of ecosystem ecology is that it has generally failed to acknowledge these evolutionary constraints (McIntosh, 1981; Holt, Ch. 26). These critiques often focus on hypothesized emergent properties at the ecosystem level and successional pathways leading to greater ecosystem stability and efficiency, pathways dependent on seemingly altruistic behavior of early successional species (e.g., Odum, 1969). Because of loose evolutionary thinking, or a total lack of it, many evolutionary ecologists have ignored developments in ecosystem ecology.

But organisms are not simply sets of evolved traits. There are constraints associated with the stuff organisms are made of. Organisms are made of organic matter and require reduced C substrates for energy and cell construction. In addition, as stressed by Sterner et al. (1992), and Sterner (Ch. 23), organisms have unique requirements for elements other than C, in other words, unique elemental stoichiometries. Trophic levels, and species within trophic levels, can differ widely in both the elemental contents of their biomass, and in the residence time of various elements in living biomass. The constraints of stuff are the constraints of chemistry, the constraints involved with the transformations of energy and matter, and the constraints that biochemical pathways and biogeochemical cycles place on organisms and ultimately on entire ecosystems. Just as the constraints of evolution have been widely ignored by ecosystem ecologists, the constraints of stuff have been widely ignored by population, community, and evolutionary ecologists.

This chapter discusses the consequences of differences among grass species in their C and N chemistry for major ecosystem processes. Litter quality, forage quality (e.g., percentage crude protein), C/N stoichiometry, tissue C/N ratio, and N-use efficiency are all related ways of expressing the basic C and N chemistry of plants. Species-level differences in tissue chemistry have important consequences for plant community dynamics, plant-herbivore interactions, and the disturbance regimens of grasslands. A species' C/N stoichiometry depends not only on tissue N concentrations, however, but also on patterns of biomass allocation to various tissues (e.g., leaves, stems, and roots) and the lifespans or turnover rates of those tissues. Correlations among these traits across numerous species suggest that evolution has constrained plants to a limited number of viable strategies for dealing with the constraint of nutrient limitation (Grime, 1979; Chapin, 1980, 1987; Tilman, 1988; Tilman and Wedin, 1991).

NITROGEN AND THE DYNAMICS OF NATIVE HUMID GRASSLANDS

A stereotype of grasses and grasslands is that they are primarily adapted to moisture limitation and high rates of grazing. However, all grasslands are not created equal; major differences in structure and function exist across grassland types. Huntley and Walker (1982) concluded that grasslands and savannas form a continuum from high plant/low animal biomass to low plant/high animal biomass, and that this corresponds to a gradient of increasing soil nutrient availability and decreasing moisture availability. They classified African grasslands and savannas into two types: dystrophic, or nutrient-limited tall grasslands of relatively humid environments, and eutrophic, or moisture-limited short grasslands found in drier environments. This same pattern occurs in native grasslands worldwide. In most humid grasslands, N is the limiting soil nutrient.

Some of the world's most endangered ecosystems are the native humid grasslands. These include the North American tallgrass prairie, the South American pampas, the Russian tallgrass steppe, the South African high veld, and the tussock grasslands of Australia and New Zealand. All of these grasslands have, on average, very low concentrations of available soil N and show large increases in productivity in response to N additions. Dominant grasses in these systems tend to have low tissue N concentrations (i.e., high C/N ratios) in both live and senesced tissues compared to grasses of shorter arid grasslands or managed grasslands. The low tissue N concentrations reflect the species' high N-use efficiency, the ratio of net productivity to N uptake. These dominant tall grasses also maintain large root systems, with over half of annual net primary production allocated belowground, and tend to have a bunch or tussock growth form (Tilman and Wedin, 1991). Many of the native humid grasslands have been largely displaced by woody vegetation or non-native grasses, often Eurasian species, within the last century. For example, overgrazing, anthropogenic N inputs, and the exclusion of fire have all led to the displacement of native tall C₄ grasses by non-native C₃ grasses in North American tallgrass prairie, especially in its eastern distribution (east of the 95th meridian), where it is least moisture-limited.

Systems dominated by strong feedbacks often exhibit highly nonlinear responses once thresholds in the levels of driving variables are crossed (DeAngelis, 1992). I propose that the dynamics of native humid grasslands and savannas, including their widespread and rapid demise, can be understood only when we realize that strong feedbacks involving N link soils, plants, herbivores, and fire. Central to these feedbacks is the C/N ratio chemistry of the dominant grasses of native humid, tallgrass systems (Fig. 24-1). The low tissue N concentrations of these grasses leads to: (1) low forage quality and de-

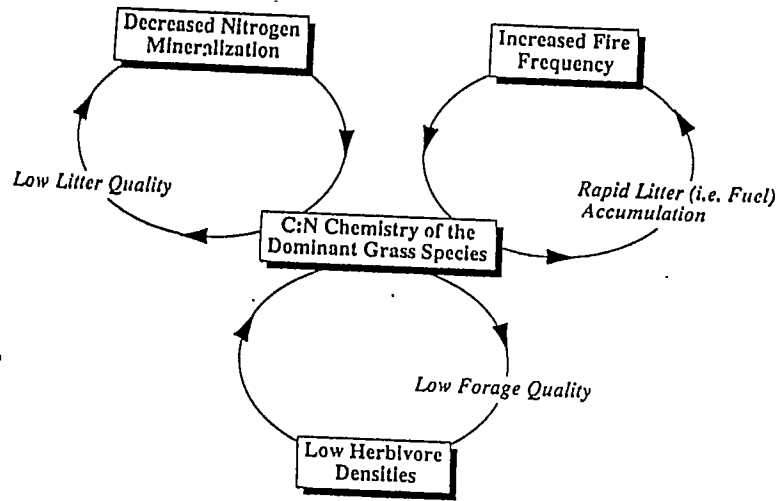


Figure 24-1. Interacting feedbacks in N-limited native tallgrass ecosystems. See text for details.

creased rates of herbivory, (2) slow litter turnover and increased fuel loads for fires, and (3) high rates of N immobilization in decomposing litter and roots and reduced soil N mineralization and availability. Not only does the N-use physiology of the dominant grasses play a major role in herbivory, fire regimens, and N cycling, these processes interact strongly. Both the complexity of the native humid grasslands and the importance of N were alluded to by Huntley and Walker (1982): "N has been shown in all savannas to be of great significance . . . but despite many thousands of N measurements, in all its forms, an understanding of the N cycle in savanna still eludes us."

The Vegetation-Herbivore Feedback

A common misconception is that the high rates of primary production of native humid grasslands are correlated with high rates of herbivory. In fact, forage quantity and forage quality are strongly inversely correlated in native grasslands as one crosses regional moisture gradients (Bremen and de Wit, 1983). The dominant C₄ grasses of North American tallgrass prairie, African high veld grasslands, Australian tall tussock grasslands, and South American pampas all decrease to 4–5% crude protein (0.6–0.8% N) by mid-growing season and at senescence have dropped to 2–3% crude protein (0.3–0.4% N) (Moore, 1970; Huntley and Walker, 1982; Wedin and Tilman, 1990). Animal scientists give 6% crude protein (0.9% N) as the minimum forage protein content on which ruminant grazers can maintain their body weight (Van Soest, 1982). The high veld grasslands of Africa are called "sour" grasslands because of this unacceptably low forage quality.

The high N-use efficiencies and low tissue protein concentrations of the dominant grasses in these humid grasslands are therefore a major constraint on herbivores. Although this conclusion is best documented for large ruminant grazers, it also appears to hold for other herbivores, including aboveground and belowground invertebrates (Ritchie and Tilman, 1992; Seastedt et al., 1988). Discussing early attempts to graze native Australian tall grasslands, Gardener et al. (1990) concluded that "initially overgrazing of the grasses was not a problem as pasture quality was extremely low in the dry season and cattle tended to die at grazing pressures still safe for the majority of pasture species."

Correlated with the low tissue N concentrations of these grasses is a high concentration of structural compounds that deter grazers, including cellulose, hemicellulose, lignin, and suberin. Ultimately, forage quality is determined by the ratio of structural components such as lignin to metabolic components such as N (Van Soest, 1982). This same ratio is used as an index of litter quality in models of plant decomposition. Although patterns of plant C chemistry are beyond the discussion here, the point is that digestion by a rumen microbial community and decomposition by a soil microbial community are conceptually the same process and are regulated by the same plant chemical parameters (Pastor and Naiman, 1992).

The Vegetation-Fire Feedback

As one moves from semi-arid short grasslands to humid, taller grasslands, fire replaces grazing as the major consumer of aboveground plant biomass in native grasslands: "Fire is an herbivore that does not require protein for growth" (Bell, 1982). Fire is now accepted as critical in determining the distribution of North American tallgrass prairie and other similar systems (Axelrod, 1985; Collins and Wallace, 1990). As discussed in the next section, the high C/N and lignin/N ratios in litter of the dominant grasses in these systems causes slow decomposition, which, together with their high productivity, leads to rapid fuel accumulation. This is half of a positive feedback between these grasses and fire (Fig. 24-1). Fire also favors the dominance of these species. Their phenology, physiology, root-shoot allocation patterns, and competitive strategies are all adapted to fire and to the resulting high light—low N environment (Knapp and Seastedt, 1986; Collins and Wallace, 1990; Tilman and Wedin, 1991; Wedin and Tilman, 1993);

Although both herbivory and fire remove aboveground plant biomass, they have opposite effects on N turnover and availability in grasslands. While grazing accelerates N turnover (McNaughton et al., 1988, Holland et al., 1992), fire volatilizes most of the N in plant litter and reinforces N limitation in the system (Ojima et al., 1994). Thus, the positive feedback between certain groups

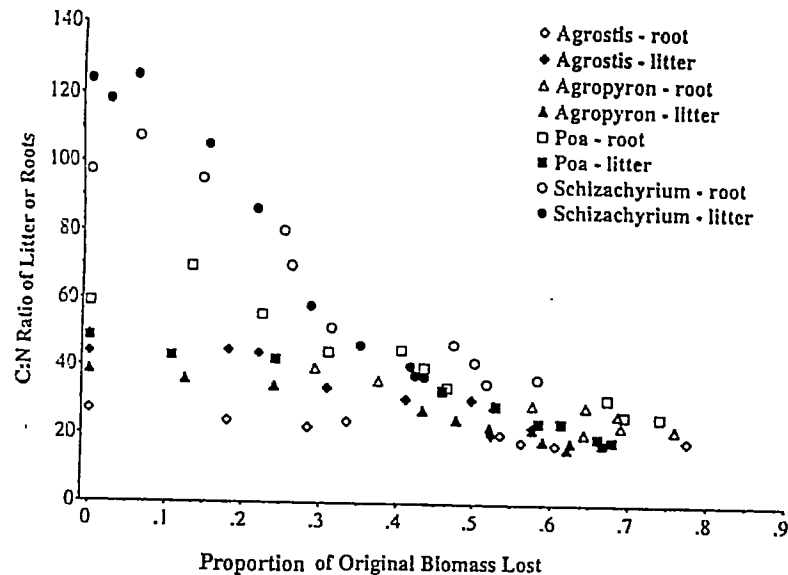
of grasses and fire as well as fire's direct effect on N cycling are central to understanding the persistence of grasslands in both tropical and temperate humid areas (D'Antonio and Vitousek, 1992).

Litter Chemistry and the Vegetation-Soil N Feedback

The previous sections emphasize the importance of N limitation in native humid grasslands. Our recent studies of long-term grass monocultures suggests that the C/N chemistry of the dominant grasses is both a cause and a consequence of this N-limitation (Wedin and Tilman, 1990; Wedin and Pastor, 1993).

For example, we have followed the C and N dynamics of litterbags containing either aboveground litter or roots of four grass species (D.A. Wedin and J. Pastor, unpublished). *Schizachyrium scoparium* is a dominant C_4 grass of North American tallgrass prairie, whereas *Agropyron repens*, *Poa pratensis*, and *Agrostis scabra* are C_3 species that displace *Schizachyrium* following major soil disturbance (e.g., cultivation) or N fertilization. During the course of decomposition, the broad initial differences among species and tissue types in C/N ratios disappeared (Fig. 24-2). By the time litterbags had reached approximately

Figure 24-2. Convergence of C/N ratios in decomposing litter and roots for four grass species during a 3-year litterbag study in east-central Minnesota, U.S.A. (Unpublished data of D.A. Wedin and J. Pastor.) Aboveground litter was placed in 1-mm mesh bags on the soil surface, and roots were buried in polyester bags. See Wedin and Tilman (1990) for details of the species and experimental monocultures from which plant materials were taken. Complete species names: *Schizachyrium scoparium*, *Agropyron repens*, *Poa pratensis*, and *Agrostis scabra*.



60% mass loss, all tissue types had converged on a similar chemistry with C/N ratios of about 20. Thus, considering the endpoint of grass litter decomposition alone, species differences in litter chemistry appear to be insignificant. Instead, the endpoint of decomposition is presumably regulated by the nutritional requirements and energetics of the microbial decomposer community.

However, the rates of decomposition and N dynamics during decomposition differed sharply among species. Low-quality litter from the prairie grass *Schizachyrium* decomposed slowly (60% still remaining after 2 years) and immobilized large amounts of N. There was no net release of N from *Schizachyrium* within 3 years (see also Pastor et al., 1987). In contrast, higher quality litter from the C_3 grass *Agropyron repens* decomposed faster (40% remaining after 2 years) and showed no net immobilization of N.

The high potential for N immobilization in the litter and root detritus of dominant tallgrass prairie species such as *Schizachyrium* translates into decreased N turnover and reduced N availability in tallgrass prairie. Wedin and Tilman (1990) found that *in situ* N mineralization diverged significantly within 3 years among monocultures of five grass species growing on initially homogeneous soils. Net N mineralization rates decreased sharply in soils under *Schizachyrium* and *Andropogon gerardi*, another tallgrass prairie dominant. In contrast, *Agrostis scabra*, a native early successional C_3 species, had much higher litter quality (C/N ratio = 24 for roots) and significantly increased N mineralization rates. Based on laboratory incubations with soils from these same monocultures, Wedin and Pastor (1993) concluded that the grass species need affect only a small labile pool of soil organic matter (in this case <3% of total soil organic matter) to cause the 10-fold divergence in N mineralization rates observed in the field (Wedin and Tilman, 1990). This suggests that soil N dynamics can rapidly track shifts in the species composition of grassland vegetation, and that feedbacks between plant species and soils may be quite strong (see also Hobbie, 1992).

C/N Stoichiometry and Grassland Consumer-Resource Interactions

The assertion that detrital pathways, trophic dynamics and disturbance regimens interact to determine grassland dynamics suggests that ecologists must dive into a system of overwhelming complexity, especially if one is interested in processes at the species level for one or more trophic levels (McNaughton et al., 1988). Alternatively, a stoichiometric approach to consumer-resource interactions (sensu Sterner, Ch. 23) in grasslands may generate a useful simplification of the system. Herbivores, decomposers, and fire are, in essence, three alternative consumers of primary production in grasslands, each with a unique C/N stoichiometry. The proportion of plant biomass consumed by each varies widely across grassland types and differences among

plant species in C/N chemistry may be a major determinant of the relative strengths of these three sinks for primary production.

Herbivores, fire, and microbial decomposers have different minimum N requirements below which consumption of plant biomass will not occur. As alluded to above, fire has no minimum N requirement for its resource (litter). The detrital pathway can also generally consume plant biomass, such as wood, with very low tissue N, often as low as 0.1%. Herbivores, however, have minimum N requirements for their forage, with actual levels depending on body size, physiological status, ruminant vs. nonruminant classification, and other factors. As the mean N concentration of primary production decreases, consumption is therefore shifted to greater detrital and fire consumption.

Secondly, these three consumers differ in the rates at which consumption occurs, organic C-N bonds are broken, and reaction endproducts are released. Fire has the highest rate of consumption and the rate is independent of plant tissue N concentration. Herbivores have the next highest rate of consumption, although the rate at which consumption and digestion occurs may be quite dependent on plant tissue chemistry. The rate at which litter decomposes and mineralizes C and N appears to be highly dependent on tissue chemistry, and is generally quite slow in N-limited systems.

Finally, these three consumers differ dramatically in the final form in which consumed N is released. All three mineralize N in the sense that they break organic C-N bonds and release part or all of the N they consume in nonorganic forms. For both decomposers and herbivores, consumed N in excess of that required for growth is released in forms readily taken up by vegetation (i.e., urea, ammonium, or nitrate). In contrast, fire volatilizes organic N to a poorly defined combination of ammonium, NO_x gases, and particulates. These forms are essentially unavailable, at least in the short term, to terrestrial vegetation.

Thus each of the three consumer-resource interactions discussed here (herbivore-grass, decomposer-grass, and fire-grass) has a unique stoichiometry. Each has different requirements for and effects on C and N. Differences among grass species in C/N ratio can determine both which pathway their above or belowground biomass will take and the rate of consumption and mineralization of N by the consumer. Although this stoichiometric approach ignores vast differences in the ecology of herbivores, fire and decomposers, it may be a powerful simplification based on the underlying chemical and mass balance constraints all three processes face.

CONCLUSIONS

By considering an ecosystem's underlying chemical constraints while resisting the temptation to fragment the study into traditional ecological subdisciplines (e.g., disturbance regimes, trophic dynamics, nutrient cycling, and plant com-

munity dynamics), ecologists may find key parameters or processes that can explain much of that system's dynamics. Identifying those key processes also brings clarity to the question "Do species differences matter to overall ecosystem dynamics and stability?" In this case, we can focus on how and why grasses differ in their C and N chemistry.

Because all plants have some plasticity in nutrient and biomass allocation patterns, part of our answer is below the species level. Recent studies have shown that physiological shifts in N-use efficiency and allocation pattern among populations within grass species have led to rapid shifts in soil N availability in response to fire (Ojima et al., 1994) and grazing (Holland et al., 1992). These shifts in N availability in turn affect plant community and trophic dynamics. As stressed by Chapin (1980), plasticity in nutrient use is itself a trait selected for or against under different conditions. More research is needed on inter- vs. intraspecific variation in plant resource use and tissue chemistry. However, it appears that much of the variance is at interspecific or higher levels for natural vegetation. For example, differences in litter chemistry among species are usually larger than differences among individuals or populations within species (e.g., Pastor et al., 1984).

Wedin and Tilman (1990) found that differences in photosynthetic pathway (C_3 vs. C_4) explained much of the divergence in N cycling under the grass species they studied. In most native humid grasslands, the dominant species are C_4 grasses. Because C_4 species have reduced requirements for N-containing photosynthetic enzymes, they generally have lower leaf N concentrations than C_3 species (Field and Mooney, 1986). Thus, the high N-use efficiency of these C_4 grasses is partly explained by their high photosynthetic N-use efficiency (rate of CO_2 uptake per unit leaf N).

The overall C/N stoichiometry or N-use efficiency of a species depends not just on its photosynthetic N-use efficiency, however, but also on its biomass allocation pattern, tissue longevity, and rates of N retranslocation (Acerts, 1989). These traits have evolved under strong selection in plants (Chapin, 1980; Tilman, 1988). For example, among 21 grass species from successional grasslands in Minnesota, all of the early successional species had relatively low litter C/N ratios (i.e., low N-use efficiencies) regardless of photosynthetic pathway (D.A. Wedin, unpublished). Physiological and biochemical constraints alone cannot account for this pattern. There is no constraint of stuff that says old field colonists cannot have high tissue C/N ratios. Rather, evolutionary constraints may dictate an unavoidable tradeoff between the high allocation to reproduction and high growth rates required by successful old field colonists and a high N-use efficiency (Tilman, 1988; Tilman and Wedin, 1991).

An understanding of why grass species differ in C and N chemistry in some cases and not in others requires consideration of both the constraints of evo-

lution and the constraints of biochemistry/biogeochemistry (i.e., stuff). Understanding the consequences of these species differences for grassland dynamics requires a clearer and more integrated picture of the stoichiometry of grass–consumer (herbivore, fire, and decomposer) relations.

ACKNOWLEDGMENTS

This chapter grew out of numerous discussions with collaborators D. Tilman and J. Pastor. Our research was supported by the University of Minnesota and the National Science Foundation (BSR-8811884).

LITERATURE CITED

- Aerts, R. 1989. Nitrogen use efficiency in relation to nitrogen availability and plant community composition. Pages 285-297 in H. Lambers, editor. Causes and consequences of variation in growth rate and productivity in higher plants. SPB Academic Publishing, The Hague, The Netherlands.
- Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:164-196.
- Bell, R.H.V. 1982. The effect of soil nutrient availability on community structure in African savannas. Pages 193-216 in Huntley, B.J. and B.H. Walker, editors. Ecology of tropical savannas (Ecological Studies 42). Springer-Verlag, Berlin.
- Bremen, H. and C.T. de Wit. 1983. Rangeland productivity and exploitation in the Sahel. *Science* 221:1341-1347.
- Chapin, F.S. III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233-260.
- Chapin, F.S. III. 1987. Plant responses to multiple environmental factors. *Bioscience* 37:49-57.
- Collins, S.L. and L.L. Wallace (editors). 1990. Fire in North American tallgrass prairie. U. of Oklahoma Press, Norman, Oklahoma.
- DeAngelis, D.L. 1992. Dynamics of nutrient cycling and food webs. Chapman and Hall, London.
- D'Antonio, C.M. and P.M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-88.
- Field, C. and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25-55 in T.J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge.
- Gardener, G.J., J.G. McIvor, and J. Williams. 1990. Dry tropical rangelands: solving one problem and creating another. Pages 279-286 in D.A. Saunders, A.J.M. Hopkins and R.A. How, editors. Australian ecosystems: 200 years of utilization, degradation and reconstruction. Surrey Beatty and Sons (Ecological Society of Australia), Chipping Norton, Australia.
- Grime, J.P. 1979. Plant strategies and vegetation processes. J. Wiley and Sons, Chichester, England.
- Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7:336-339.
- Holland, E.A., W.J. Parton, J.K. Detling, and D.L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *American Naturalist* 140:685-706.
- Huntley, B.J. and B.H. Walker. 1982. Ecology of tropical savannas (Ecological Studies 42). Springer-Verlag, Berlin.
- Knapp, A.K. and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36:662-668.
- McIntosh, R.P. 1981. Succession and ecological theory. Pages 10-23 in West, D.C., H.H. Shugart and D.B. Botkin. Forest succession: concepts and application. Springer-Verlag, Berlin.

- McNaughton, S.J., R.W. Reuss, and S.W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* 38:794-800.
- Moore, R.M.: 1970. Australian grasslands. Australian National University Press, Canberra.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1993. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, in press.
- Pastor, J., J.D. Aber, C.A. McLaugherty, and J.M. Melillo. 1984. Aboveground production and N and P dynamics along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65:256-268.
- Pastor, J., M.A. Stillwell, and D. Tilman. 1987. Little bluestem litter dynamics in Minnesota old fields. *Oecologia* 72:327-330.
- Pastor, J. and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forest. *American Naturalist* 139:690-705.
- Ritchie, M.E. and D. Tilman. 1992. Interspecific competition among grasshoppers and their effect on plant abundance in experimental field communities. *Oecologia* 1992:524-532.
- Seastedt, T.R., S.W. James and T.C. Todd. 1988. Interactions among soil invertebrates, microbes and plant growth in the tallgrass prairie. *Agriculture, Ecosystems and Environment* 24:219-228.
- Sterner, R.W., J.J. Elser and D.O. Hessen. 1992. Stoichiometric relationships among producers and consumers in food webs. *Biogeochemistry* 17:49-67.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.
- Tilman, D. and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72:685-700.
- Van Soest, P.J. 1982. Nutritional ecology of the ruminant. Cornell University Press, Ithaca, New York.
- Wedin, D. and J. Pastor. 1993. Nitrogen mineralization dynamics in grass monocultures. *Oecologia*, in press
- Wedin, D. and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84:433-441.
- Wedin, D. and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* 63:199-229.