

A conceptual model for primary productivity, decomposition and nitrogen cycling in the Chihuahuan creosotebush desert

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Summary

The conceptual framework for a simulation model of primary productivity, decomposition and nitrogen cycling in a shrub-dominated desert ecosystem in southern New Mexico is presented. This model is based on our previous attempt to simulate carbon allocation patterns in the desert shrub *Larrea tridentata* Cov., which demonstrated that moisture patterns alone are insufficient to predict desert productivity. These results, as well as others, suggest that mineral nutrients, especially nitrogen, may also be an important determinant of productivity in arid environments. Our current research in the Chihuahuan desert is directed towards elucidating the numerous biotic and abiotic interactions that determine the rates and directions of carbon, nitrogen and water fluxes in this ecosystem. The development of this working model will serve as a tool to accomplish three major objectives: (1) to synthesize the large amount of existing data on decomposition and nitrogen cycling in deserts, (2) to quantify our present state of knowledge about the structure and function of ecosystem components important in carbon and nitrogen dynamics in deserts, and (3) to address hypotheses concerning the complex mechanisms of interactions and feedbacks among the organisms involved in carbon and nitrogen exchanges in deserts.

Introduction

Water availability has traditionally been emphasized as the major determinant of productivity and plant growth in deserts (Noy-Meir 1973, Fisher and Turner 1978, Ludwig and Whitford 1981). However, a synthesis of International Biome Project (IBP) data indicated a failure of rainfall to predict Chihuahuan desert productivity patterns (Ludwig and Flavill 1979). Recent work has shown the importance of mineral nutrients (especially nitrogen) as regulators of plant productivity in a variety of desert systems (West 1981, Penning de Vries and Djiteye 1982). In the Chihuahuan desert of southern New Mexico, the productivities of annuals and the dominant evergreen perennial shrub, creosotebush (*Larrea tridentata* Cov.), show significant interactions between quantities and availability patterns of soil moisture and nitrogen (Gutierrez and Whitford, 1986).

In terms of energy flow and nutrient cycling, *Larrea* is probably the most important plant in this ecosystem (Barbour et al. 1977, Mabry et al. 1977, Barbour 1981, Ludwig and Whitford 1981). *Larrea* affects the distribution and abundance of nutrients (West and Skujins 1978), annual plants (Muller 1953, Patten 1978, Parker et al. 1984), and available soil water (Elkins et al. 1982). Annual plant

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productivities are higher under *Larrea* shrubs than in the intershrub spaces (Guitierrez and Whitford, in press) and watering enhances these differences, with higher undershrub values corresponding to locations of greater nitrogen availability (West and Klemmedson 1978, Parker et al. 1982). However, fertilization experiments show that shallow-rooted grasses and ephemerals compete with *Larrea* for available soil nitrogen (Ettershank et al. 1978, Parker et al. 1984).

The role of nitrogen as a limiting factor to plant growth in arid systems has recently been examined in an Australian desert (Mott and McComb 1974), the Sonoran desert (Halverson and Patten 1975), the Mojave desert (Williams and Bell 1981) and a Tunisian steppe (Floret and Pontainer 1982). In the Chihuahuan desert, Ettershank et al. (1978) applied two levels of nitrogen fertilizer to a *Larrea* community and found that an application rate of 25 kg ha⁻¹ stimulated the productivity of a shallow-rooted grass (*Erioneuron pulchellum*) whereas *Larrea* growth was unaffected; and application of 100 kg ha⁻¹ stimulated growth of both species.

Also in the Chihuahuan desert, Cunningham et al. (1979) and Reynolds and Cunningham (1981) conducted a two-year irrigation experiment to examine the effects of season and soil water availability on the timing and extent of reproductive and aboveground vegetative growth in *Larrea*. This led to the formulation of a *Larrea* growth model, based on various aspects of the physiological ecology of this species, to investigate carbon allocation patterns over a range of environmental conditions (Cunningham and Reynolds 1978, Reynolds and Cunningham 1979, 1981, Reynolds et al. 1979, 1980, Reynolds 1986). Growth responses, partitioning of root and shoot growth, and tissue carbon/nitrogen ratios are affected by numerous factors, including water and nitrogen availabilities. Simulation results suggested the need for including nitrogen as well as water budgets in this model since water level alone was insufficient to predict *Larrea* productivities when soil water remained high for extended periods (Reynolds and Cunningham 1981). Apparently, a nutrient deficiency (probably nitrogen) was limiting growth of plants receiving high water during the previous growing season. Comparable results were reported by Australian researchers who found plant productivity declined in the second of two wetter-than-average years (Trumble and Woodroffe 1954, Charley and Cowling 1968).

Motivated by these results, the following studies have been conducted in the Chihuahuan desert in an attempt to elucidate further the many aspects of primary productivity, decomposition and nutrient dynamics including: (1) the effects of water availability on decomposition processes (Santos and Whitford 1981, Santos et al. 1984, Schaefer et al. 1985) and belowground productivity (Fonteyn et al. 1986); (2) the effects of nitrogen fertilization on primary productivity (Ettershank et al. 1978); (3) microarthropod activity in litter (Whitford and Santos 1980, Parker et al. 1984, Steinberger et al. 1984); (4) termite removal of surface litter (Johnson and Whitford 1975, Schaefer and Whitford 1981, Whitford et al. 1982); (5) the role of nematodes in decomposition (Santos et al. 1981, Whitford et al. 1981); and (6) the significance of small mammals (Steinberger and Whitford 1983a, 1983b). Although these studies provide estimates of nitrogen pool sizes

and flow characteristics for the Chihuahuan desert ecosystem, it remains to integrate these data into a general synthesis permitting an assessment of the ecosystem dynamics. In this paper we develop a conceptual model as the initial step in this integration.

Conceptual model

A conceptual model of the major elements involved in carbon and nitrogen exchanges in the Chihuahuan desert is shown in Figures 1 and 2, respectively. This approach emphasizes the growth of *Larrea*, the dynamics of carbon and nitrogen in the soil subsystem and the interfacing of these submodels into a systems description. The internal carbon dynamics of *Larrea* are based on prior modeling work (Reynolds and Cunningham 1981).

Parker et al. (1984) proposed a possible mechanism by which nitrogen availability to *Larrea* may be influenced by ephemeral plant production. Adequate autumn and winter moisture results in abundant spring annuals, which utilize nitrogen made available by high mineralization rates during the preceding summer, wet autumn and winter (Figures 1 and 2). The spring annuals die in late spring, retaining nitrogen in decaying biomass because mineralization is low at this time. Summer rains stimulate nitrogen mineralization, but the large annual plant root component supports high densities of decomposer microorganisms (primarily fungi) which develop a dense network of hyphae around the dead ephemeral roots (Figure 2). These hyphae act as a sieve, removing essential nutrients from the downward moving water column. This nitrogen is immobilized by the microbes and is unavailable for the more deeply rooted (*Larrea*) shrubs. Data from Ludwig and Flavill (1979) and Ludwig (1986), showing maximum *Larrea* productivities in summers following dry autumns and winters (and resulting low spring ephemeral biomass), support this hypothesis.

Parker et al. (1984) present detailed information concerning nutrient pools and flows between various groups of soil biota. Root and buried litter decomposition seem to be controlled by litter quality, soil water, soil temperature and the soil biota (Figures 1 and 2). Surface litter decomposition patterns are erratic owing to fluctuating water content, low microarthropod densities and termite foraging. Therefore, surface litter decomposition processes are extrapolated from buried litter decomposition.

A special factor affecting nitrogen availability to *Larrea* is termite activity. Surface foraging and subsequent predation are greatest in the autumn and early winter, providing an input of readily usable nitrogen to the soil surface in the form of gallery carton and predator excretions (Johnson and Whitford 1975, Whitford et al. 1982). Alate flights in the summer also provide a pulse of readily usable nitrogen to the soil surface by means of termite predators (Schaefer and Whitford 1981, Parker et al. 1982). These inputs precede or are concurrent with summer annual plant productivity and, as discussed above, are unlikely to be available to *Larrea* during the summer. Subterranean termites probably return as much nitro-

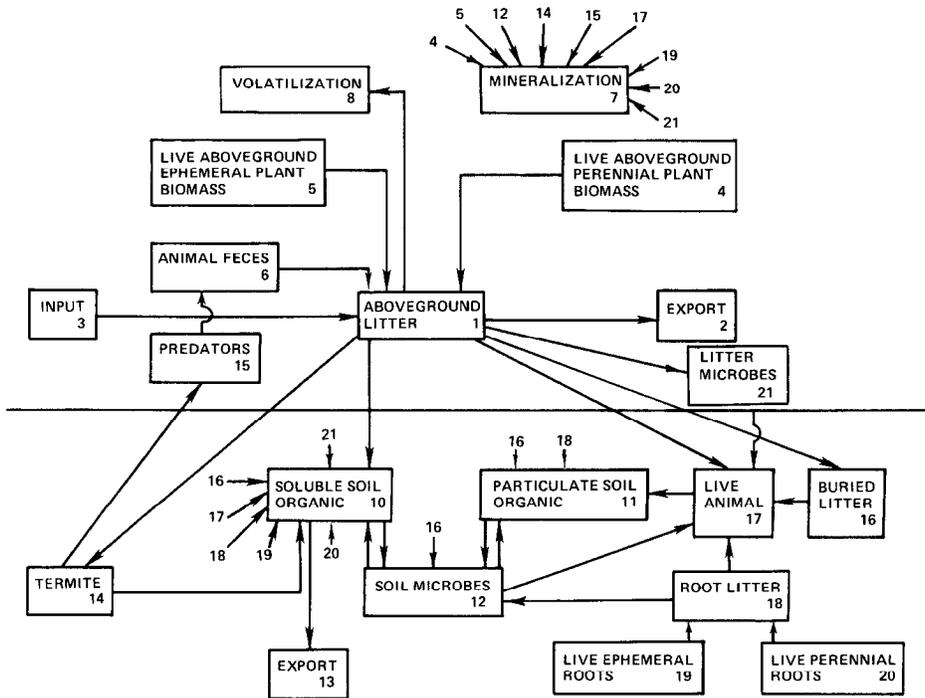


Figure 1. A conceptualization of carbon flows in a Chihuahuan desert ecosystem and their regulation by soil biota. Key to variables: 1 = Aboveground litter (containing dead plant material from ephemerals and perennials and animal feces); 2 = Exported aboveground litter (portion of 1 lost from the system by wind and water); 3 = Input of aboveground litter (portion of 1 brought into the system by wind and water); 4 = Live aboveground perennial plant biomass (dominated by *Larrea tridentata*); 5 = Live ephemeral plant biomass (predominately under shrub canopy which responds rapidly to water inputs and is short lived; essentially all material is potentially available for input into 1); 6 = Animal feces (predominately rabbit and reptile); 7 = CO₂ sink for system (derived from respiration of animals, plants, decomposers and grazers); 8 = Volatile organic compounds present on leaf surfaces and products of photodecomposition; 10 = Soluble organics either initially present in litter material, throughfall, or decomposition products (readily leached); 11 = Animal corpses and feces and dead microbial tissue (dead organisms and waste products resulting from the movement of animals from litter to soil); 12 = Soil microorganisms (primarily fungi and bacteria); 13 = Exported soluble organic (portion of 10 lost through leaching); 14 = Termites; 15 = Termite predators (ants and lizards); 16 = Aboveground litter buried by wind, water and animals; 17 = Live animal biomass (primarily microarthropods, nematodes, insects and insect larvae); 18 = Belowground root litter (dead root material from ephemerals and perennials, root sluffing); 19 = Live ephemeral roots (primarily under canopy); 20 = Live perennials roots (predominately small (<5 mm) *Larrea tridentata* roots); 21 = Surface litter microbes. KEY TO CARBON FLOWS: (1–2) = Litter export out of system (function of wind and rain); (1–8) = Volatilization of surface litter organics (abiotic weight loss by high surface temperatures and photodecomposition); (1–10) = Leaching of soluble organics, such as simple carbohydrates and microbial waste products, into soil; (1–14) = Removal of surface litter by termites; (1–16) = Burial of surface litter by wind, rain and animal activity; (1–17) = Migration of microarthropods, across litter-soil interface; (1–21) = Assimilation of surface litter by microbes; (3–1) = Litter input from outside of system (function of wind and rain); (4–1) = Perennial litter fall (mediated by wind in the spring, rain events in summer, climate in the fall and rabbits in winter); (4–7) = Live aboveground perennial plant respiration; (5–1) = Ephemeral litter fall; (5–7) = Live aboveground ephemeral plant respiration; (6–1) = Input of feces into surface litter; (10–12) = Uptake of soluble soil organics by soil microbes; (10–13) = Leaching of soluble soil organics out of system; (11–12) = Assimilation of particulate soil organics by soil microbes; (12–7) = Respiration

gen by means of predators as they remove by detritus consumption (Schaefer and Whitford 1981, Whitford et al. 1982). Because the decomposition of surface litter generally provides a more continuous mineralization of nitrogen during the late spring and summer (during the period of greatest *Larrea* productivity), termite activity could have an inhibitory effect on *Larrea* growth by pulsing the system with nitrogen just prior to summer annual germination and growth.

In summary, there are numerous studies that point to the importance of nitrogen and water interactions in controlling productivity patterns in arid ecosystems, e.g., the northern Sahara (Floret and Pontainer 1982), the sub-Sahara Sahel (Penning de Vries and Djiteye 1982) and the Chihuahuan desert. We have developed a preliminary model for quantifying carbon and nitrogen cycling in the belowground decomposer community of an arid ecosystem, based on the approaches of Parnas (1975), Smith (1979), Bosatta (1981), McGill et al. (1981), Tanji (1982) and Knapp et al. (1983). This model will utilize the broad data base provided from numerous studies of the Chihuahuan desert ecosystem. Separate verification and validation data sets currently exist for: (1) plant productivities and litter production; (2) termite activities; and (3) decomposition processes. Current and proposed work includes examination of: (1) additional plant productivities and litter production; (2) aboveground insect herbivory; (3) root parasite populations; (4) root exudates; (5) soil nitrogen mineralization; and (6) the effects of continued nitrogen fertilization on desert productivity, all of which will be needed for further model refinement. Many of these data are provided as a part of the Long Term Ecological Research (LTER) project being conducted on the Chihuahuan desert. The establishment of a quantitative framework in which carbon, nitrogen, and water availabilities could be examined with respect to ecosystem dynamics would greatly enhance the overall understanding of ecosystem processes in arid regions.

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tion of soil microbes (mineralization); (12-10) = Excretion by soil microbes; (12-11) = Death of soil microbes; (12-17) = Predation of soil microbes; (14-7) = Termite respiration; (14-10) = Production of gallery carton material; (14-15) = Predation of termite workers and alates; (15-6) = Termite predator feces; (15-7) = Termite predator respiration; (16-10) = Leaching of soluble organic compounds from buried litter; (16-11) = Fragmentation of buried litter (primarily by the actions of soil microarthropods); (16-12) = Assimilation of buried litter by microbes; (16-17) = Assimilation of buried litter by microarthropods, insect larvae, nematodes; (17-7) = Respiration of soil animals; (17-10) = Soil animal excretion; (17-11) = Death of soil animals; (18-10) = Leaching of soluble organics from dead roots; (18-11) = Fragmentation of dead roots; (18-12) = Assimilation of root litter by microbes; (18-17) = Assimilation of dead root organics by soil animals; (19-7) = Live ephemeral root respiration; (19-10) = Ephemeral root exudation; (19-18) = Death of ephemeral roots; (20-7) = Live perennial root respiration; (20-10) = Perennial root exudation; (20-18) = Perennial root death; (21-7) = Respiration of surface litter microbes; (21-10) = Excretion of surface litter microbes (leaching from surface); and (21-17) = Assimilation of surface litter microbes by soil animals.

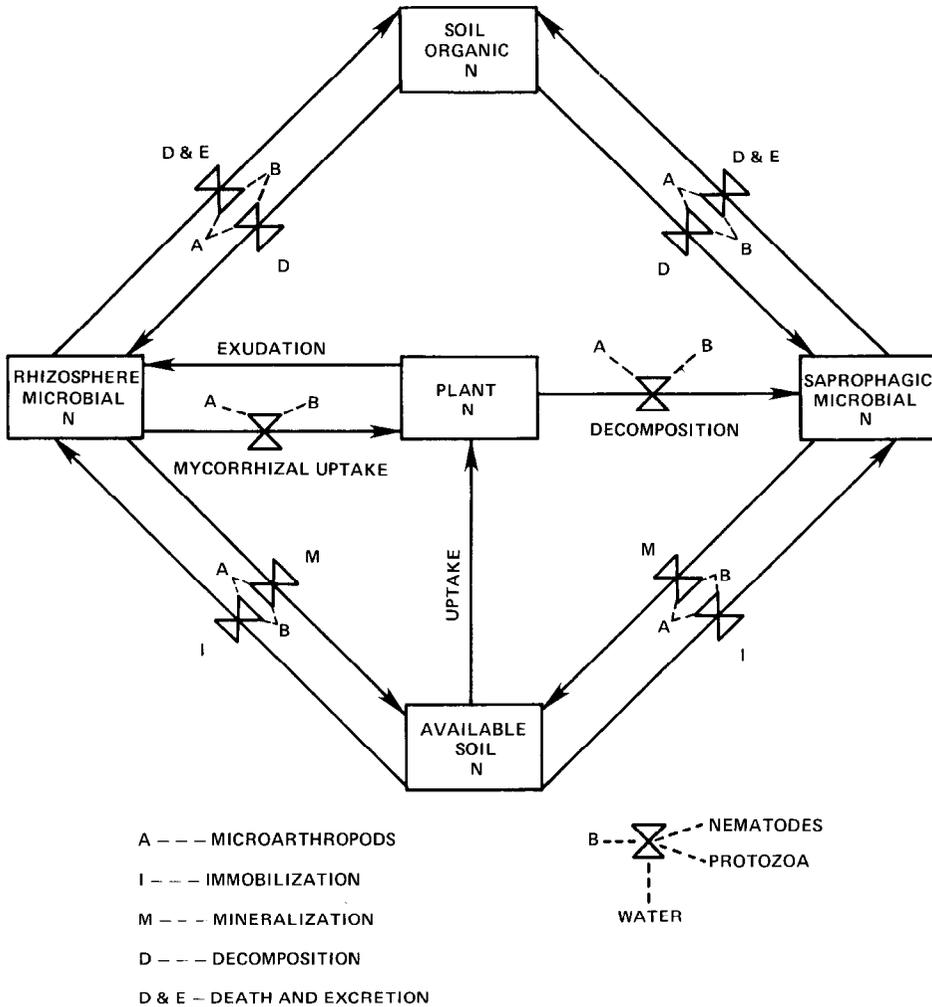


Figure 2. A conceptualization of flows of nitrogen in a Chihuahuan desert ecosystem and their regulation by soil biota.

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