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Modelling the effects of loss of soil biodiversity on ecosystem function

H. W. HUNT and D. H. WALL
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

Abstract

There are concerns about whether accelerating worldwide loss of biodiversity will adversely affect ecosystem functioning and services such as forage production. Theoretically, the loss of some species or functional groups might be compensated for by changes in abundance of other species or functional groups such that ecosystem processes are unaffected.

A simulation model was constructed for carbon and nitrogen transfers among plants and functional groups of microbes and soil fauna. The model was based on extensive information from shortgrass prairie, and employed stabilizing features such as prey refuges and predator switching in the trophic equations. Model parameters were derived either from the literature or were estimated to achieve a good fit between model predictions and data. The model correctly represented (i) the major effects of elevated atmospheric CO_2 and plant species on root and shoot biomass, residue pools, microbial biomass and soil inorganic nitrogen, and (ii) the effects on plant growth of manipulating the composition of the microbial and faunal community. The model was evaluated by comparing predictions to data not used in model development.

The 15 functional groups of microbes and soil fauna were deleted one at a time and the model was run to steady state. Only six of the 15 deletions led to as much as a 15% change in abundance of a remaining group, and only two deletions (bacteria and saprophytic fungi) led to extinctions of other groups. Functional groups with greater effect on abundance of other groups were those with greater biomass or greater number of consumers, regardless of trophic position. Of the six deletions affecting the abundance of other groups, only three (bacteria, saprophytic fungi, and root-feeding nematodes) caused as much as 10% changes in indices of ecosystem function (nitrogen mineralization and primary production). While the soil fauna as a whole were important for maintenance of plant production, no single faunal group had a significant effect. These results suggest that ecosystems could sustain the loss of some functional groups with little decline in ecosystem services, because of compensatory changes in the abundance of surviving groups. However, this prediction probably depends on the nature of stabilizing mechanisms in the system, and these mechanisms are not fully understood.

Keywords: ecosystem function, elevated atmospheric CO_2, functional groups, grassland, redundant groups, simulation model, soil food web

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Introduction

There is widespread concern that the worldwide loss of biodiversity may cause a degradation in the ability of ecosystems to provide goods and services such as food, fibre, clean water, and climate regulation (Myers 1996). The capacity of ecosystems to provide goods and services is closely associated with ecosystem function — whole system processes such as primary production, decom-

Correspondence: H. W. Hunt, fax +1/970 491 1965, e-mail billh@nrel.colostate.edu

position, nutrient cycling and water fluxes. Whether ecosystem functioning is influenced by biodiversity is highly controversial (Schlapfer & Schmid 1999; Wardle *et al*. 2000, Naeem 2000).

The loss or exclusion of a species from an ecosystem may have several kinds of effects: changes in (a) the abundance of other species, (b) ecosystem function, (c) both a and b, or (d) neither a nor b. A redundant species has been defined as one whose loss is compensated for by shifts in abundance of other species, such that ecosystem function is unaffected (Walker 1992). Many authors hold that some species are redundant (Lawton & Brown 1994; Andrén *et al*. 1995; Gitay *et al*. 1996; but see Tilman *et al*. 1997). Walker (1992) first raised the possibility that entire suites of species in functional groups may be redundant, and advocated the use of functional groups as a necessary means to organize information about an ecosystem and to address the relationship between biodiversity and ecosystem function. This approach has been applied to plants (Hooper & Vitousek 1997).

The potential effects of climate change on biodiversity and biogeochemistry (C and N fluxes) has focused primarily on aboveground systems. Subsurface species diversity is less often studied than in aboveground systems (Moore *et al*. 1996), but is receiving increasing attention because soils and sediments are the repository for much of the earth's biodiversity (Brussaard *et al*. 1997, Wall & Virginia 2000). Experimental evidence from agroecosystems and microcosms suggests that major components of the detrital food web in soils may be deleted with little or no decline in decomposition (Beare *et al*. 1992) or plant production (Ingham *et al*. 1985; Laakso & Setala 1999a, 1999b). However, the complexity of the soil food web makes it difficult to determine experimentally how the loss of soil functional groups in native ecosystems may influence ecosystem functioning

Tilman *et al*. (1997) used simulation models to examine the relationship between ecosystem function and the diversity of competing plant species. They stated that further theoretical work is necessary to deal with multitrophic-level interactions, keystone species, and functional groups. The present paper presents a model of a terrestrial belowground food web at the level of functional groups. There appears to be no generally accepted definition of a functional group (Wilson 1999). Functional groups are defined herein, based on the work of Gardner *et al*. (1982), as aggregates of taxa with similar diets, predators, growth rates and survival rates. Thus no *a priori* assumptions are made about the effects of functional groups on ecosystem function. The model is based on information from one particular ecosystem – native shortgrass prairie – and incorporates as much information as possible from the extensive studies carried out in this system (e.g. Albertson *et al*. 1966; Clark 1977; Woodmansee *et al*. 1978; Leetham & Milchunas 1985; Schimel *et al*. 1985; Shoop *et al*. 1989; Lauenroth & Milchunas 1991).

Paine (1980) distinguished three conceptually distinct descriptions of food webs. A 'connectedness web' merely identifies diets of each creature. An 'energy flow web' augments the connectedness web with estimates of energy or element flux rates. A 'functional web' further identifies those interactions accounting for the dynamic response of the system to perturbations such as species removals. Paine's 'functional web' is referred to herein as a 'dynamic web', to avoid confusion with the other uses of 'function' discussed above. Coleman (1985) presented a connectedness web for shortgrass prairie. Hunt *et al*. (1987a) described the 'detrital food web' (DFW), a nitrogen flow web for the same system (Fig. 1). Herein explicit carbon (energy) is added to the N fluxes of DFW and equations for the rates of processes are included. This converts the model to a dynamic web that can respond to perturbations. Previous work by the present authors includes dynamic webs for subsets of species from the complete soil food web (Hunt *et al*. 1984), and a complete dynamic web at a less detailed level of resolution (Hunt *et al*. 1991).

de Ruiter *et al*. (1995) developed a dynamic food web model based on DFW and Lotka–Volterra equations. The present model differs from theirs by including (i) both C and N cycling, (ii) a plant with variable tissue quality and shoot/root partitioning, and (iii) more mechanistic features in the consumption equations (prey saturation of predators, prey refuges and predator switching). Details of the equations governing consumption rates can have dramatic effects on model stability (May 1973; Pimm 1984; Hunt *et al*. 1987b; Lawton & Brown 1994). In the absence of biologically reasonable stabilizing mechanisms, even simple food chain models tend to be unstable over large regions of parameter space (Moore *et al*. 1993a). Based partly on these considerations, Berendse (1994) concluded that further progress in understanding food web behaviour will not come from continued study of oversimplified systems such as Lotka–Volterra equations, but will require greater attention to the biology of interacting populations.

The objectives of the present paper were to develop a model of trophic dynamics of functional groups in a soil food web of shortgrass prairie, to evaluate the performance of the model, and to use the model to examine the effects of global change, specifically elevated CO_2 and the loss of biodiversity, on the capacity of ecosystems to supply goods and services.

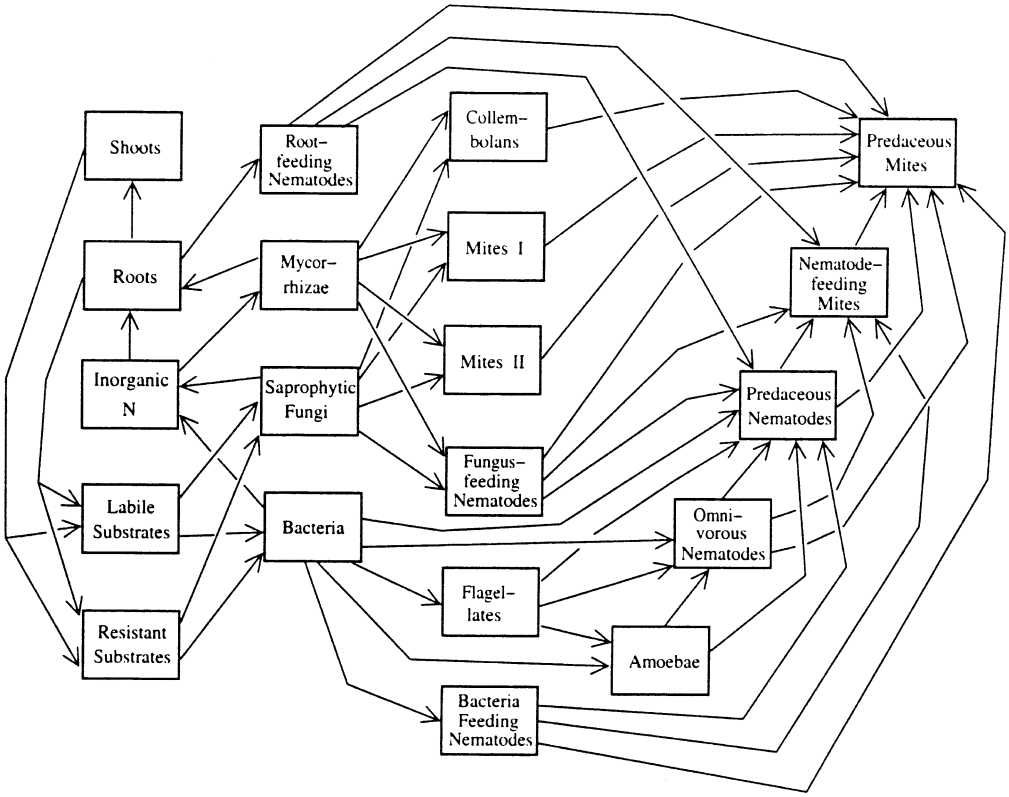

Fig. 1 Trophic relationships and major N transfers in belowground food web (Hunt *et al*. 1987a). Fungus-feeding mites are separated into two groups to distinguish the slow-growing cryptostigmatids from mesostigmatids. Flows omitted from the figure for clarity include transfers from every organism to the substrate pools (death), and from every animal to the substrate pools (defecation) and to inorganic nitrogen (mineralization). Except for soil inorganic N, every compartment has a corresponding state variable for carbon.

Materials and methods

Model structure

The trophic structure of the dynamic model is the same as in DFW (Fig. 1). Equations for the rates of processes are given in Table 1, and symbols for variables and parameters in Tables 2 and 3. Values of parameters are presented either in the text or tables. The values of some parameters were estimated using optimization procedures to achieve a good fit of the model to data (see below), and no literature citation is given. The values of other parameters were taken or derived from publications cited in the text or tables. Many processes are regulated by reduction factors (de Wit & Goudriaan 1974), which vary between zero and one, and serve to reduce the rate of a process below the maximal rate as organism N/C ratios become nonoptimal (eqn 1; Table 1). The shapes of the reduction factors (Table 4) were chosen so that organism N/C ratios in the model are regulated near the values in DFW, unless stated otherwise.

Plants. Primary production in shortgrass prairie is limited primarily by water (Lauenroth *et al*. 1978), but also may respond to N supply (Hunt *et al*. 1988). Net C assimilation was assumed to be proportional to shoot N and a feedback term representing the effect of water limitation (eqn 2; Table 1). Translocation of C from shoots to roots is proportional to shoot C and a reduction factor representing the effect of shoot N status (eqn 3; Table 1). Root respiration was taken as a fixed fraction (0.7) of C translocated to roots. Uptake of soil inorganic N occurs by a Michaelis–Menten equation with no feedback term for root N status, based on results of Hunt *et al*. (1998). Translocation of N from roots to shoots is proportional to root N and a reduction factor for the effect of root N concentration (eqn 4; Table 1).

Shoot C was assigned the value observed at the end of the growing season in growth chambers (Hunt *et al*. 1996), which approximates aboveground production because shoots were not lost through grazing or snowfall as in the field. Shoot death occurs at a rate of 110% of shoot C per year; this assumes that some shoot material is lost to the litter layer during the growing season through fragmentation of senescent leaves and shedding of reproductive tissues. Nitrogen loss from the plant associated with shoot death is only 32% of shoot N per

Table 1 Model equations. Symbols for parameters begin with letters *P*, *D* or *H* and are defined in Table 3. Symbols for state variables and auxiliary variables begin with letters other than *P*, *D* or *H*, and are defined in Table 2. Reduction factors begin with letter *E* and are defined in Table 4. Rates of processes begin with letter *R*. 'C' denotes carbon and 'N', nitrogen

$$E_N = \frac{1}{1 + P_{E1}(N/C)^{P_{E2}}}, \quad (1)^1$$

$$R_{IS} = P_{IS1}\, S_N\left(1 - \frac{S_C + T_C}{P_{IS2}}\right), \quad (2)$$

$$R_{ST} = P_{ST}\, S_C\, E_{ST}, \quad (3)$$

$$R_{TS} = P_{TS}\, T_N\, E_{TS}, \quad (4)$$

$$R_{IM} = P_{IM1}\frac{I_N}{P_{IM2} + I_N} M_C\, E_{IM}, \quad (5)$$

$$R_{ML} = P_{ML1}\, M_C^{P_{ML2}}, \quad (6)$$

$$R_{LB} = \frac{P_{LB1}\, L_C\, B_C}{P_{LB2} + L_C} E_{LB}, \quad (7)$$

$$R_{RB} = P_{RB}\, B_C\, E_{LB}\, E_{RB}, \quad (8)$$

$$R_{BI} = P_{BI}\, M_N\, E_{BI}, \quad (9)$$

$$F = \left(\frac{P_F}{B}\right)\ln\left(\frac{P_F + B}{P_F}\right), \quad (10)$$

$$A_i = P_i(B_i - G_i), \quad (11)$$

$$W_i = D_i A_i^{H_i} \quad (12)$$

[1]For a reduction factor that decreases with N/C ratio, the right-hand side of this equation is subtracted from one.

year, accounting for the observation that the majority of live shoot N is re-translocated to perennial organs in autumn (Clark 1977). These C and N loss rates, together with live shoot N/C ratios, yield the observed N/C ratios of senescent shoots (Hunt *et al*. 1996). Root death was also assumed to be proportional to root biomass, but the turnover rates for C and N were estimated via optimization, because there is little direct information about root death and root N re-translocation.

Substrate heterogeneity is represented by dividing dying plant tissue C between labile and resistant components based on N concentration (eqn 2 *in* Hunt 1977). Because the resistant component is lower in N than the labile component, the N/C ratio of the resistant component of residues was assumed to be only 70% of the N/C ratio of dying tissues.

Mycorrhizae. Release of N to roots by mycorrhizal fungi is expressed using equation (4) (Table 1), substituting mycorrhizal variables for root variables. Transfer of root C to mycorrhizal fungi is expressed by (3) (Table 1), substituting root variables for shoot variables. Fungal respiration was estimated as 70% of the C transferred from roots. The rate of uptake of soil inorganic N by mycorrhizal fungi is represented with a Michaelis–Menten equation modified by a reduction factor for the feedback effect of mycorrhizal N content (eqn 5; Table 1). Nonpredatory death of mycorrhizal fungi is density dependent according to (6) (Table 1), recommended by Bellows (1981). Dying mycorrhizal fungi are assumed to have the same N/C ratio as living fungi.

Saprophytic microbes. The assumption of DFW was retained, that bacteria are more effective decomposers of the labile (soluble) component of residues and fungi of the resistant (lignocellulose) component. The rate of decomposition of the labile fraction by bacteria (eqn 7; Table 1) follows a Michaelis–Menten equation modified by a factor (see eqn 14 *in* McGill *et al*. 1981) that accounts for substrate particle sizes and density-dependent interference among microbes. Equation (7) also is used for fungi, with substitution of fungal biomass and parameters. The equation for decomposition of the resistant fraction (eqn 8; Table 1) is that developed by McGill *et al*. (1981; eqn. 15). Respiration was estimated as 28% of residue decomposition in fungi and 30% in bacteria. Uptake of soil inorganic N is expressed by (5) (Table 1), substituting bacterial or saprophytic fungal variables for mycorrhizal variables.

Nonpredatory death of bacteria and fungi, representing losses from freezing, drying, pathogens and starvation, is assumed to be density dependent according to (6) (Table 1). Dead microbes are transferred to labile residues, except that fungi contain a fraction, estimated at 20%, of resistant compounds such as chitin and melanins (Burnett 1979; Bell & Wheeler 1986) which is sent to the resistant pool.

Fauna. The values of most physiological parameters for faunal groups, including N/C ratios, fraction of food assimilated, production to assimilation ratios, and the fractions of faeces and dead organisms transferred to the labile component of residues, are taken from DFW. Rates of N mineralization are given by (9) (Table 1).

Table 2 Definitions and units of state variables and auxiliary variables. Model equations are given in Table 1. Symbols for reduction factors begin with the letter *E*; and rates of processes with letter *R*. Symbols beginning with other letters are either state variables or auxiliary variables. 'C' denotes carbon and 'N', nitrogen

Symbol	Equation	Definition	Units
A_i	(11), (12)	available prey, item *i*	gC m^{-2}
B	(10)	prey biomass	gC m^{-2}
B_C	(7), (8)	bacterial or fungal biomass	gC m^{-2}
B_i	(11)	biomass of prey item *i*	gC m^{-2}
E_{BI}	(9)	effect of organism N/C on N mineralization	nondimensional
E_{IM}	(5)	effect of microbial N on uptake of soil inorganic N	nondimensional
E_{LB}	(7), (8)	effect of microbial density on decomposition rate	nondimensional
E_N	(1)	effect of organism N/C ratio on the rate of a process	nondimensional
E_{RB}	(8)	effect of microbial N on decomposition of resistant component of residues	nondimensional
E_{ST}	(3)	effect of shoot N on rate of C translocation	nondimensional
E_{TS}	(4)	effect of root N or mycorrhizal N on rate of N translocation	nondimensional
F	(10)	fraction of prey population in refuge	nondimensional
G_i	(11)	biomass of prey *i* in the refuge	gC m^{-2}
I_N	(5)	soil inorganic N	gN m^{-2}
L_C	(7)	labile component of residues	gC m^{-2}
M_C	(5), (6)	biomass C of a functional group	gC m^{-2}
M_N	(9)	biomass N of a functional group	gN m^{-2}
R_{BI}	(9)	rate of N mineralization	gN m^{-2} y^{-1}
R_{IM}	(5)	rate of uptake of soil inorganic N by microbes	gN m^{-2} y^{-1}
R_{IS}	(2)	rate of C assimilation by shoots	gC m^{-2} y^{-1}
R_{LB}	(7)	rate of decomposition of labile fraction of residues	gC m^{-2} y^{-1}
R_{ML}	(6)	rate of nonpredatory death	gC m^{-2} y^{-1}
R_{RB}	(8)	rate of decomposition of resistant fraction of residues	gC m^{-2} y^{-1}
R_{ST}	(3)	rate of C translocation from shoots to roots, or from roots to mycorrhizal fungi	gC m^{-2} y^{-1}
R_{TS}	(4)	rate of N translocation from roots to shoots, or from mycorrhizal fungi to roots	gN m^{-2} y^{-1}
S_C	(2)	shoot C	gC m^{-2}
S_N	(2)	shoot N	gN m^{-2}
T_C	(2)	root C	gC m^{-2}
T_N	(4)	root N, or mycorrhizal N	gN m^{-2}
W_i	(12)	weighting factor for prey *i* in diet selection	nondimensional

Nonpredatory death of all faunal groups is assumed to be density dependent according to (6) (Table 1), with power (parameter P_{ML2}) of 1.5. Values of P_{ML2} as large as 2.0 impose such strong density dependence that functional group abundances tend to be unresponsive to environmental changes, and values much smaller than 1.5 lead to extinctions of some functional groups with only moderate changes in plant characteristics. In a departure from DFW, any attempt to independently estimate nonpredatory death rates from demographic information was abandoned, because many organisms in arid systems appear to survive in an inactive condition much of the time (Hunt 1977; Whitford 1996).

Trophic interactions in soil are influenced strongly by soil structure and the relative sizes of prey and predator (Elliott *et al*. 1980); specifically the protection of small prey in soil pores too small to admit predators. For relatively immobile prey, this concept has been implemented through absolute prey refuges defined in terms of a fixed level of prey biomass (Hunt *et al*. 1984). A more realistic approach is to assume that the size of the population protected from predators increases continuously as prey biomass increases (eqn 10; Table 1). According to (10), both the biomass in the refuge and that outside it increase as the population increases, while the fraction in the refuge approaches one in very small populations and zero in very large populations. For mobile prey that move in and out of soil pores too small to admit their larger predators, it is assumed that there is no refuge, but that only a fraction of the prey population is apparent to the predator at any instant. For mobile prey with similar sized predators, apparency is assumed to be 100%. For immobile prey which possess a refuge, 100% of the population out of the refuge is apparent to the predator. For prey with no refuge, the fraction apparent is equal to or less than 100% depending on prey mobility and the relative size of predator and prey. Refuge levels approximate those reported by Hunt *et al*. (1984).

Table 3 Definitions and units of model parameters. Values given are for blue grama under ambient CO_2

Symbol	Equation	Definition	Value	Units	Source[1]
D_i	(12)	preference for prey *i*	see Table 6	nondimensional	estimated
H_i	(12)	switching parameter	2.0	nondimensional	Hunt *et al*. (1991)
$P_{0.1}$	(1)	N/C ratio at which reduction factor takes a value of 0.1	see Table 4	g(N)/g(C)	see Table 4
$P_{0.9}$	(1)	N/C ratio at which reduction factor takes a value of 0.9	see Table 4	g(N)/g(C)	see Table 4
P_{BI}	(9)	maximal rate of N mineralization by (a) bacteria (b) saprophytic fungi, or (c) fauna	(a) 0.6, (b) 0.6, (c) see Table 5	y^{-1}	estimated
P_{E1}, P_{E2}	(1)	parameters defining the effect of organism N/C ratio on the rate of a process	not given, see $P_{0.1}$, $P_{0.9}$	complex units (P_{E1}), nondimensional (P_{E2})	not given, see $P_{0.1}$, $P_{0.9}$
P_F	(10)	biomass at which about 69% [ln(2)] of a prey population is in the refuge	see Table 6	gC m^{-2}	see text
P_i	(11)	fraction of prey population *i* apparent to predator	see Table 6	nondimensional	see text
P_{IM1}	(5)	maximal rate of uptake of soil inorganic N by microbes	4.0	gN $(gC)^{-1}y^{-1}$	Hunt *et al.* (1986)
P_{IM2}	(5)	half-saturation constant for uptake of soil inorganic N	5.2	gN m^{-2}	Hunt *et al*. (1986)
P_{IS1}	(2)	maximal rate of C assimilation by shoots	403.	gC $(gN)^{-1}y^{-1}$	Hunt *et al.* (1998)
P_{IS2}	(2)	maximal plant biomass	404.	gC m^{-2}	estimated
P_{LB1}	(7)	maximal rate of decomposition of labile residues by (a) bacteria, or (b) saprophytic fungi	(a) 259, (b) 130	y^{-1}	Hunt *et al*. (1985), McGill *et al*. (1981)
P_{LB2}	(7)	half-saturation constant for decomposition of labile residues	115	gC m^{-2}	estimated
P_{ML1}	(6)	parameter controlling rate of nonpredatory death of (a) mycorrhizal fungi, (b) bacteria (c) saprophytic fungi, or (d) fauna	(a) 1.21, (b) 0.63, (c) 4.3, (d) see Table 5	complex units	estimated
P_{ML2}	(6)	parameter controlling rate of nonpredatory death	1.5	nondimensional	estimated
P_{RB}	(8)	maximal rate of decomposition of resistant fraction of residues by (a) bacteria or (b) saprophytic fungi	(a) 5.2, (b) 10.4	y^{-1}	estimated
P_{ST}	(3)	maximal rate of C translocation from (a) shoots to roots, or (b) roots to mycorrhizae	(a) 7.1, (b) 0.033	y^{-1}	estimated
P_{TS}	(4)	maximal rate of N translocation from (a) roots to shoots, or (b) mycorrhizae to roots	(a) 0.31, (b) 7.2	y^{-1}	estimated

[1]"estimated" parameters were estimated by optimization to achieve a good fit of model predictions to data.

Table 4 Values of N/C ratios at which reduction factors (eqn 1, Table 1; Table 2) take values of 0.1 and 0.9

Reduction factor	Process	N/C for which E_N = 0.1	N/C for which E_N = 0.9	Source
E_{BI}	N mineralization by (a) bacteria, b) saprophytic fungi, or (c) fauna	(a) 0.25 (b) 0.059 (c) see Table 5	0.33 0.070	McGill *et al*. (1981)
E_{IM}	uptake of soil inorganic N by (a) mycorrhizal fungi, (b) bacteria, or (c) saprophytic fungi	(a) 0.2 (b) 0.25 (c) 0.059	0.1 0.20 0.050	McGill *et al*. (1981)
E_{RB}	decomposition of resistant residues by (a) bacteria, or (b) saprophytic fungi	(a) 0.20 (b) 0.050	0.25 0.059	McGill *et al*. (1981)
E_{ST}	translocation of C from (a) shoots to roots, or (b) roots to mycorrhizae	(a) 0.032 (b) 0.021	0.024 0.015	Morgan *et al*. (1994)
E_{TS}	translocation of N from (a) roots to shoots, or (b) mycorrhizae to roots	(a) 0.015 (b) 0.05	0.021 0.10	(a) Hunt *et al*. (1996) (b) McGill *et al*. (1981)

Rates of prey consumption are a function of prey refuges, prey apparency, predator functional response, prey preferences and a switching mechanism. Switching, in which a predator takes the more abundant prey item

Table 5 Values of parameters controlling faunal N mineralization and death rates. The maximal rates of mineralization and the death rates were estimated by optimization. N/C ratios were derived from Hunt *et al*. (1987a)

	Parameter			
	Mineralization[1]			
		N/C Ratio[2]		
Functional group	Maximal rate (P_{BI})	$P_{0.1}$	$P_{0.9}$	Death (P_{ML1})[3]
Protozoa		0.125	0.167	
Flagellates	10.5			31.
Amoebae	11.6			5.9
Nematodes		0.091	0.111	
Root-feeding	5.0			8.0
Fungus-feeding	10.2			18.4
Bacteria-feeding	30.			4.8
Omnivorous	22.			15.2
Predatory	15.			11.3
Collembola	6.5	0.111	0.143	66.
Mites		0.111	0.143	
Fungus-feeding				
Cryptostigmatid	13.4			10.4
Mesostigmatid	7.8			11.1
Nematode-feeding	9.8			30.
Predatory	11.6			32.

[1]According to. 9, Table 1
[2]N/C ratios at which the N mineralization rate is 10% and 90% of the maximal rate.
[3]Rate constant in (6), Table 1

in a greater proportion than its abundance among all prey (May 1977), is not limited only to vertebrate predators which form search images, but can also be expressed in invertebrate predators such as microarthropods that choose among different patches of food according to food density (Bernstein 1984). Thus, switching might be an important phenomenon in soil food webs. While no direct evidence for the operation of switching in soil food webs is available, switching was incorporated in the model to help assure model stability (see below). This can be justified on the basis that soil food webs are observed to persist in nature.

The amount of prey available to a predator (eqn 11; Table 1) is a function of prey refuges and prey apparency. Total consumption is calculated as a function of total available prey biomass according to a type II functional response. Total consumption is then allocated among prey items according to preference factors and the switching mechanism by calculating a weighting factor for each prey item (eqn 12; Table 1). The switching parameter (H_i in eqn 12) is assigned a value of 2.0 for predators that switch among prey and 1.0 for those that do not (Hunt *et al*. 1991). The weighting factors are summed over prey items, and the fraction of total consumption (see above) derived from each prey is taken as the fraction of total weighting factors contributed by that prey. Figure 1 identifies trophic relationships among faunal groups, and Table 6 gives the values of parameters used in the consumption equations. Maximal feeding rates were calculated to yield maximal population growth rates observed under 'good' conditions (Hunt *et al*. 1989). In order to convert literature values of daily population growth rates to annual rates, it was assumed that a year of activity in shortgrass prairie is equivalent to 40 days with nonlimiting temperature and moisture (Cole *et al*. 1977). In the absence of information for every functional group, maximal feeding rates were assumed the same within taxonomic groups. For example, the maximal feeding rates for all groups of nematodes were based on that for fungus-feeding nematodes (Hunt *et al*. 1989). Values for the shape parameters for the functional response (the same as half saturation constants in a Michaelis–Menten equation) were estimated by optimization.

The N content of material eaten by root-feeding nematodes was assumed to be twice that of live roots. Following DFW, feeding by nematodes was assumed to cause damage resulting in the death of an additional 1.4 g of roots for every 1.0 g consumed, and the N/C ratio of killed roots was assumed to be equal to that of live roots.

Fitting the model to data

In contrast to DFW, the present model was constructed as a dynamic model, in that the equations for the rates of plant growth, decomposition, and feeding by fauna were formulated to operate over a range of possible biomass values. Thus, the model can be fitted to dynamic data. However, the model was also fitted to data representing an average or hypothetical steady state level of the state variables, which is virtually achieved in the model after 30 simulated years. The objective of fitting a dynamic model to a hypothetical steady state is that the model can then be used to examine how the steady state responds to changes in the environment, plant species, and the composition of the soil food web.

Table 7 gives the data used. Data for average biomass C and N/C ratios of mycorrhizal fungi and all faunal groups were taken from DFW. Levels of plants, detritus, soil inorganic N, and fumigation biomass were taken from an experiment in which intact cores from native shortgrass prairie were transferred to growth chambers and subjected to various CO_2 levels, temperature

Table 6 Values of parameters controlling consumption rates in the soil food web

		Parameter[1]				
Consumer	Resource	P_{mx}	P_K	P_i	P_F	D_i
Root-feeding nematodes	Roots	132.	796.	1.0	0.0	1.0
Collembola	Saprophytic fungi	40.	7.2	1.0	2.0	1.0
	Mycorrhizal fungi			1.0	0.2	1.0
Fungus-feeding mites (cryptostigmatid)	Saprophytic fungi	30.	2.0	1.0	2.0	1.0
	Mycorrhizal fungi			1.0	0.2	1.0
Fungus-feeding mites (mesostigmatid)	Saprophytic fungi	40.	7.9	1.0	0.2	1.0
	Mycorrhizal fungi			1.0	0.2	1.0
Fungus-feeding nematodes	Saprophytic fungi	132.	53.	1.0	1.0	1.0
	Mycorrhizal fungi			1.0	0.1	1.0
Flagellates	Bacteria	80.	4.3	1.0	0.2	1.0
Amoebae	Bacteria	80.	3.5	1.0	0.5	1.0
	Flagellates			0.5	0.0	0.0003
Bacteria-feeding nematodes	Bacteria	132.	0.82	1.0	1.5	1.0
Omnivorous nematodes	Bacteria	132.	2.1	1.0	1.5	1.0
	Flagellates			0.5	0.01	1.0
	Amoebae			0.5	0.0	0.0008
Predatory nematodes	Bacteria	132.	7.6	1.0	1.5	0.99
	Flagellates			1.0	0.01	0.99
	Nematodes			1.0	0.0	1.0
Nematode-feeding mites	Nematodes	30.	0.81	0.5	0.0	1.0
Predatory mites	Nematodes	48.	2.0	0.5	0.0	1.0
	Microarthropods			1.0	0.0	1.0

[1] P_{mx} is the maximal feeding rate (y^{-1}); P_K the half-saturation constant for feeding ($g(C)\ m^{-2}$); P_i the apparency (eqn 11); P_F the prey refuge (eqn 10); and D_i is preference (eqn 12).

regimes, and water regimes (Morgan *et al*. 1994; Hunt *et al*. 1996). The cores were dominated either by *Bouteloua gracilis* (H.B.K.) Lag (blue grama) or *Pascopyrum smithii* (Rydb) A. Love (western wheatgrass). Most of the faunal data on which DFW was based were collected from upland sites dominated by blue grama. Therefore, the microbial and plant data from blue grama in the growth chamber experiment were combined with the DFW data. Application of the model to the western wheatgrass data is described below.

Rather than fitting the model to separate levels of bacteria and saprophytic fungi as in DFW, it was fitted to fumigation biomass C and N/C estimated by chloroform fumigation and extraction (Monz *et al*. 1991). A composite model variable consisting of bacteria, saprophytic fungi, one half of mycorrhizal fungi, and soil fauna excluding root-feeding nematodes, was assumed to correspond to fumigation biomass. The values of bacterial and saprophytic fungal parameters in the model were estimated to obtain the best fit of modelled fumigation biomass and biomass N/C to the data. In a similar fashion, data for detrital roots (Hunt *et al*. 1996) were assumed to correspond to the sum of the labile and resistant residue pools from the model, plus 2/3 of bacteria and saprophytic fungi. Root C and N in the model were assumed to correspond to the sum of observed large root and crown C and N.

Most model parameters were fixed at values derived from the literature. Other parameters were estimated using simplex optimization (Nelder & Mead 1965; Hunt *et al*. 1999). This procedure finds the values of parameters that minimize a measure of departure of model prediction from data. The measure of model error chosen was the sum of squared differences between the logarithm of model prediction and the logarithm of the data (Hunt *et al*. 1998). This measures the relative model error, as is appropriate for data such as those used here in which the means range over several orders of magnitude and the standard deviations tend to be proportional to the means.

Plants with the C3 photosynthetic pathway are usually considered to respond more to elevated CO_2 than those with the C4 pathway (Newton 1991). To examine the effect on the soil food web of a shift in dominance from C4 to C3 species, a situation was simulated in which plant species was changed, but other components of the

Table 7 Observed and predicted mass (gC m^{-2} or gN m^{-2}) for components of the soil food web. Data (neither bold nor italic) were available for most components of blue grama dominated soil cores under ambient CO_2, but only for the plant and substrate components in the other two treatments. The N contents of mycorrhizal fungi and groups listed below mycorrhizal fungi were treated as separate data, but were omitted from the table because C to N ratios for these groups in the model were constrained within limits (cf. Table 4). Bold italic entries are model predictions of microbial and faunal biomass. Sources of data are given in the text

	Blue grama		
Type of data	Ambient CO_2	Elevated CO_2	Western Wheatgrass
Shoot C	80.	95.	120.**
Shoot N	2.2	2.3	2.4
Root C	206.	243.*	214.
Root N	3.6	3.8*	6.2*
Detritus C	304.	304.	380.
Detritus N	13.	13.	18.6*
Soil inorganic N	1.36	0.94*	0.84**
Fumigation biomass C	19.6	19.6	35.***
Fumigation N	1.6	1.8*	3.2***
Mycorrhizal fungus C	0.70	***1.13***	***0.29***
Flagellates C	0.0161	***0.0174***	***0.0098***
Amoebae C	0.39	***0.40***	***0.21***
Nematodes			
Root-feeding C	0.29	***0.36***	***0.32***
Fungus-feeding C	0.041	***0.050***	***0.131***
Bacteria-feeding C	0.58	***0.58***	***0.38***
Omnivorous C	0.065	***0.071***	***0.031***
Predatory C	0.108	***0.121***	***0.075***
Collembola C	0.0046	***0.0051***	***0.0076***
Fungus-feeding mites			
Cryptostigmatid C	0.168	***0.176***	***0.20***
Mesostigmatid C	0.136	***0.153***	***0.23***
Nematode-feeding mites C	0.0160	***0.0176***	***0.0135***
Predatory mites C	0.0160	***0.0175***	***0.0127***
Bacteria C	***1.01***	***1.05***	***0.81***
Saprophytic fungi C	***16.6***	***18.8***	***38.***

*, **, ***Indicate treatment means differing from blue grama under ambient CO_2 at $P < 0.05$, 0.01 and 0.001, respectively

system were left largely unchanged. This was done by fitting the model to the data (Table 7) for plant, detritus, inorganic N, and fumigation biomass in western wheatgrass (C3) cores from the same growth chamber experiment providing the blue grama (C4) data. In order to achieve a fit to data, parameters controlling plant growth, residue decomposition rates and fungal death rate were estimated by optimization, while other microbial and all faunal parameters were left the same as in the blue grama simulation. Thus, the values of faunal and mycorrhizal fungal biomass were free to assume new steady-state values. The effects of elevated atmospheric CO_2 on the soil food web were simulated to achieve a fit to data for blue grama in the elevated CO_2 treatment (Table 7). All state variables were initialized as for blue grama under ambient CO_2, and the model was run for two years. All the values for parameters given above in the 'Model Structure' section apply to blue grama under ambient CO_2, and some apply as well to the other two datasets. Parameters with different values for the three datasets are listed in Table 8.

The capability of the model to represent the ecosystem level effects of functional group deletions was determined by fitting the model to dynamic data from a laboratory experiment (first experiment of Ingham *et al*. 1985) that determined the effect of the composition of the detrital web on plant growth. Blue grama was grown with the addition of different combinations of bacteria, saprophytic fungi, bacteria-feeding nematodes and fungus-feeding nematodes. The initial values of model state variables were estimated from inoculum sizes (Ingham *et al*. 1985). The model would not be expected to fit these data without parameter adjustments, because of major differences between the Ingham *et al*. experiment (growth of seedlings in sieved and sterilized soil under constant conditions, with the addition of individual species of microbes and fauna) and data on which the model was based (long established plants in intact soil cores with a full complement of microbial and faunal species, and with variable temperature, water, and photoperiod).

Model stability

The importance of prey refuges, predator switching and density-dependent death for model stability was evaluated by removing these mechanisms from the model for blue grama under ambient CO_2. Refuges were removed by calculating the fraction of prey unavailable to the predator at steady state, reducing prey apparency P_i (eqn 11) by this fraction, and then setting the fraction unavailable to zero. With these changes, the rate of consumption of each prey by each predator is unchanged at steady state. Density-dependent death was removed by changing parameter P_{ML2} (eqn 6) from a value of 1.5 to 1.0, and assigning new values to the specific death rates (P_{ML1}) so that the death rates at steady state were the same as in the density-dependent case. Switching was removed by changing all H_i (eqn 12) from 2.0 to 1.0, and estimating new values for preferences D_i so that consumption of each prey by each predator at steady state was the same as with switching. Categories of stability (May 1973) were determined subjectively, by examining plots of state variable dynamics.

Table 8 Values of model parameters (Table 3) that differed among the three treatments in the experiment of Hunt *et al*. (1996)

				Treatment			
				Blue Grama			
Process	Parameter[1]	Units	Location	Ambient CO_2	Elevated CO_2	Western wheatgrass	Source[2]
Photosynthesis	P_{IS1}	gC $(gN)^{-1}y^{-1}$	(2)	403.	415.	270.	Hunt *et al*. 1998
	P_{IS2}	gC m^{-2}	(2)	404.	542.	629.	estimated
Shoot C to roots	P_{ST}	y^{-1}	(3)	7.1	4.0	5.1	estimated
	$P_{0.1}$–$P_{0.9}$	N/C	(3) (E_{ST})	0.024–0.032	0.024–0.032	0.010–0.030	Morgan *et al*. (1994)
Root uptake of inorganic N	P_V	gN $(gC)^{-1}y^{-1}$	text	0.20	0.20	0.17	Hunt *et al*. (1998)
	P_{KH}	gN m^{-2}	text	46.	34.	10.1	estimated
Root N to shoots	P_{TS}	y^{-1}	(4)	0.31	0.48	0.169	estimated
	$P_{0.1}$–$P_{0.9}$	N/C	(4) (E_{TS})	0.015–0.021	0.015–0.021	0.022–0.030	Hunt *et al*. (1996)
Shoot death (N)	P_V	y^{-1}	text	0.32	0.33	0.43	see text
Root death (C)	P_V	y^{-1}	text	0.151	0.151	0.150	estimated
Root death (N)	P_V	y^{-1}	text	0.083	0.083	0.150	estimated
	fraction N to resistant	fraction	text	0.70	0.70	0.38	estimated
Root C to mycorrhizae	$P_{0.1}$–$P_{0.9}$	N/C	(3) (E_{ST})	0.015–0.021	0.015–0.021	0.022–0.030	see text
Decomposition of labile residues	P_{LB2}	gC m^{-2}	(7)	116.	116.	191.	estimated
Resistant residues to bacteria	P_{RB}	y^{-1}	(8)	5.2	5.7	3.0	estimated
Resistant residues to fungi	P_{RB}	y^{-1}	(8)	10.4	11.4	7.0	estimated
Fungal death	P_{ML1}	complex	(6)	4.2	4.2	1.59	estimated

[1]P_V and P_{KH} are the maximal rate and half-saturation constant for a process described in the text.
[2]'estimated' denotes parameters estimated by optimization to yield a close fit of model to data (see text).

Results

Blue grama under ambient CO_2

The values of parameters giving the best model fit to the data for blue grama under ambient CO_2 are given in the text and in Tables 3–6. The measure of model error minimized during optimization (sum of squares of {log[model] – log[data]}) was transformed into a more intuitive measure by dividing by the number of data points, taking the square root, exponentiating, and subtracting 1. The result, a standard relative error (SRE), was 0.028, indicating that the model steady state was within 2.8% of most of the 35 kinds of data (Table 7). Individual errors (data not shown) ranged up to +7% for detrital N/C ratio.

Table 9 gives C and N flow rates at steady state. Net primary production (NPP) was 145 gC m^{-2} y^{-1}, of which 62% was aboveground. Microbial secondary production (uptake of residue C minus respiration) exceeded NPP because of recycling of organic residues (i.e. decomposition of dead microbes and fauna). Net mineralization by fungi was almost exactly offset by net immobilization by bacteria. Thus, fauna accounted for all of the 1.7 gN m^{-2} y^{-1} of net mineralization and 68% of gross mineralization. Bacteria-feeding nematodes accounted for 61% of the N mineralized by fauna, and the four functional groups feeding strictly on bacteria or bacteria-feeders (see Fig. 1) accounted for 83%. Most of the net mineralization was taken up by roots, and most of that taken up by mycorrhizal fungi was transferred to plants.

Western wheatgrass under ambient CO_2

The SRE for the fit of the model to the western wheatgrass data was 6.3%. Table 8 gives values of parameters that differed from blue grama under ambient CO_2. Table 7 gives predicted microbial and faunal biomass, and Table 9 gives C and N transfer rates. Wheatgrass NPP was 22% greater than that of blue grama, with all of the difference in shoots (Table 9). Total microbial biomass was greater under wheatgrass than under blue grama, the increase being entirely attributable to saprophytic fungi. The increased dominance of fungi over bacteria under wheatgrass (Tables 7 and 9) resulted from lower nonpredatory death (Table 8). Mycorrhizal fungi were much less abundant under wheatgrass. Fungus-feeding fauna had greater biomass, while bacteria-feeders and predators had lower biomass. In contrast to the situation with blue grama, microbes in western wheatgrass cores were net N mineralizers (Table 9). Thus, fauna accounted for only 40% of gross and 47% of net mineralization. Bacteria-feeding fauna

again accounted for most (57%) of N mineralization by fauna.

Blue grama under elevated CO_2

Only plant parameters and decomposition rates were estimated to achieve a fit to the data (Table 8). The SRE for the fit of the model to data was 6.3%. Net primary production increased by 36% (Table 9), but this translated into only an 18% increase in plant biomass (Table 7). Increased production under elevated CO_2 was accomplished by a 3% increase in maximal photosynthesis rate, 22% greater N uptake, and 34% greater plant carrying capacity, the latter attributable to increased water-use efficiency. Nitrogen supply to the plant increased as a result of increased uptake by both roots and mycorrhizae. Additional N was supplied by lower bacterial immobilization and slightly greater fungal and faunal mineralization, but the largest single source was depletion of soil inorganic N (Tables 7 and 9). Fauna accounted for 66% of gross and 92% of net mineralization, less than under ambient CO_2. There were small increases (3% to 24%) in biomass of all faunal groups except bacteria-feeding nematodes.

Table 9 Selected transfer rates predicted by the soil foodweb model for the three treatments in the experiment of Hunt *et al*. (1996)

	Blue grama		
Transfer	Ambient CO_2	Elevated CO_2	Western wheatgrass
Carbon (gC m^{-2} y^{-1})			
net shoot C assimilation	271.	398.	302.
shoot production	90.	110.	122
root production	54.	86.	54.
root respiration	126.	202.	126.
fungal secondary production	298.	351.	398.
bacterial secondary production	23.	25.	10.9
Nitrogen (gN m^{-2} y^{-1})			
Uptake of soil inorganic N by			
roots	1.19	1.51	2.8
mycorrhizal fungi	0.53	0.61	0.149
bacteria	0.83	0.74	0.45
fungi	~0.0	~0.0	~0.0
Net N mineralization by			
bacteria	– 0.83	– 0.74	– 0.45
saprophytic fungi	0.82	0.90	2.0
fauna	1.73	1.75	1.38
Mycorrhizal fungi to roots	0.46	0.50	0.132

Effects of food web structure on plant growth

Plant parameters estimated to achieve a fit to the data of Ingham *et al*. (1985) include lower maximal photosynthesis (lower light levels), higher carrying capacity (no water limitation), greater N uptake capacity (fewer old roots), faster C and N translocation (younger root tissues), and lower shoot and root death rates (no water or temperature stresses). Other plant parameters, including all reduction factors, were the same as presented above for blue grama under ambient CO_2. The initial values of substrates were estimated to achieve a fit to the data, but were within 20% of the values in Table 7 for blue grama under ambient CO_2. Nematode parameters were unaltered except that nonpredatory death rates were reduced by 90% (no temperature or water stresses). Microbial parameters were unaltered except that death rates were reduced by 90%, and the single bacterial species employed was assumed to be unable to attack the resistant fraction of substrates. The latter assumption was necessary to prevent the model from predicting N immobilization by bacteria, which was not observed in the experiment. Finally, it was assumed that the root system did not fully explore the soil, because there was a large pool of soil inorganic N left at the end of the experiment in the treatment with plants alone (Table 10), even though plant growth increased in treatments in

Table 10 Comparison of observed (Ingham *et al*. 1985) and simulated response of blue grama biomass (gC m^{-2}) and residual soil inorganic N (gN m^{-2}) to the inclusion of various combinations of functional groups of the soil food web. Data were converted to g m^{-2} based on the amount of soil in laboratory microcosms

	Plant biomass		Soil inorganic N	
Functional groups included	Simulated	Observed	Simulated	Observed
Plant (P) alone	1.4	1.3	4.3	4.3
P + bacteria (B)	1.5	1.4	4.4	4.2
P + B + bacteria-feeding nematodes (Nb)	3.3	3.5	5.7	5.9
P + fungi (F)	4.6	5.5	6.7	6.3
P + *F* + fungus-feeding nematodes (Nf)	5.4	4.4	8.5	6.4
P + B + Nb + *F* + Nf	5.3	5.8	8.0	6.0

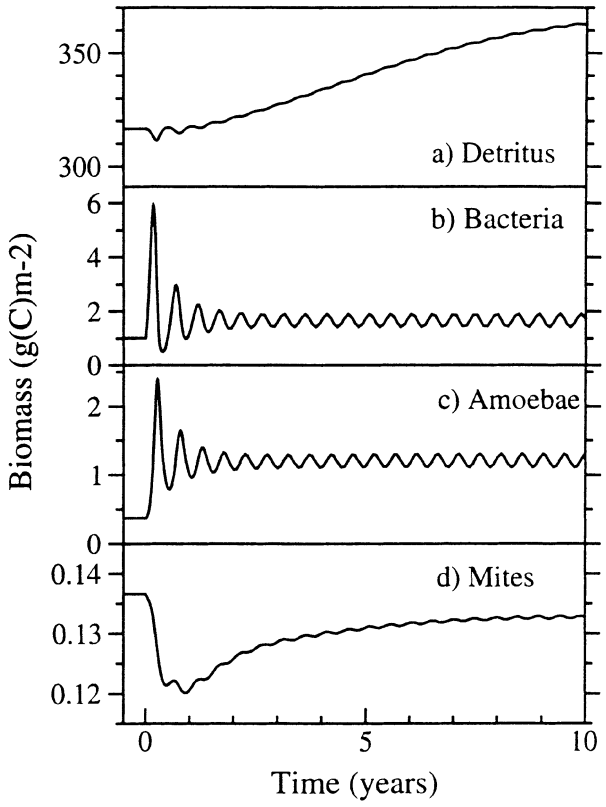

Fig. 2 Dynamics of (a) detritus, (b) bacteria, (c) amoebae and (d) mesostigmatid fungus-feeding mites after deleting bacteria-feeding nematodes at time zero. Values before time zero indicate the steady state with bacteria-feeding nematodes present.

which N supply was increased through mineralization by decomposers. Thus, only a fraction of the inorganic N initially present in the soil was available to the plants. Table 10 compares the simulation with experimental results. The correlations between model and data are positive and significant at $P < 0.05$ for plant biomass and $P < 0.10$ for residual N.

Model evaluation

The ability of the model to fit the data is not convincing evidence of its utility, because model parameters were estimated to achieve the fit. This section compares model predictions to data not used in model development.

Plant responses. Net primary production of blue grama was 95% of that estimated for shortgrass prairie by fitting a more mechanistic plant model to observed shoot and root dynamics in the field (Hunt *et al*. 1991). The lower half-saturation constant for N uptake in western wheatgrass than blue grama agrees with independent estimates of Hunt *et al*. (1998). The root N turnover rate for blue grama under ambient CO_2 (23% per year including losses to nematodes) is near the 20% per year estimated from ^{15}N dynamics (Woodmansee *et al*. 1978).

Microbial responses. Assuming that the percentage mycorrrhizal infection of roots is proportional to fungal biomass, the model prediction of greater mycorrhizal biomass in blue grama than in western wheatgrass agrees with some observations (e.g. Allen *et al*. 1984), but not others (Monz *et al*. 1994). The discrepancy between studies may result from seasonal variation in percentage infection (Allen *et al*. 1984), and from differences between field and laboratory samples (Allen *et al*. 1984; Monz *et al*. 1994). The increase in mycorrhizal fungus in blue grama under elevated CO_2 agrees with the results of Monz *et al*. (1994).

Net N mineralization in blue grama cores under ambient CO_2 (1.7 gN m^{-2} y^{-1}) was considerably less than the DFW estimate of 7.6. For a system at steady state, N mineralization, plant N turnover, and N uptake must be compatible. Thus, the lower estimate of N mineralization was dictated by using lower values for plant N content. In contrast to DFW, N content of dying shoots was here based on fully senescent shoots (Hunt *et al*. 1996), and estimates of root N were reduced to account for adhering soil N (Hunt *et al*. 1999). Soil CO_2 evolution approximates net shoot C assimilation at steady state (271 gC m^{-2} y^{-1}; Table 9). This is within 15% of annual soil CO_2 evolution in shortgrass prairie estimated from a model fitted to observed seasonal dynamics of root biomass (Sauer 1978) and soil CO_2 evolution (Hunt 1977).

The dominance of bacteria in DFW was based on direct microscopic counts. Bacterial dominance is incompatible with present results, because the observed C/N ratio of fumigation biomass (12, Table 7) is closer to the C/N ratio of saprophytic fungi (17) than to that of bacteria (4). Fungal dominance is more consistent with survey results (Anderson & Domsch 1980). Greater fungus biomass in cores dominated by a C3 (western wheatgrass) than a C4 (blue grama) grass agrees with results of Hunt *et al*. (1991). Nonpredatory death causes a high turnover (17 y^{-1}) of saprophytic fungi, which may be reasonable, given the continuous production of empty hyphae during fungal growth (Paustian & Schnürer 1987). Consumers take a much greater fraction of bacterial secondary production (97%) than of fungal production (3%). Both percentages are within the ranges estimated (86–99% for bacteria and 2–33% for fungi) based on soil food web dynamics (Hunt *et al*. 1989). Bacteria-feeders have a relatively greater influence than fungus-feeders because of the 2.8-fold greater biomass of bacteria-feeders, 16-fold lower biomass of bacteria than fungi, and because the dominant bacteria-feeders (nematodes

and amebae) have greater maximal feeding rates than the dominant fungus-feeders (mites).

Faunal responses

Among fauna, only nematodes were followed in the experiment providing the data presented in Table 7 on plant and residue pools (Freckman *et al*. 1991). Observed numbers of bacteria-feeding, fungus-feeding, and root-feeding nematodes all were significantly greater in wheatgrass than blue grama cores. Ten percent more total nematodes were observed under elevated CO_2 after one growing season, but this difference was not quite significant ($P < 0.15$). In order to compare model predictions to data, nematode biomass (Table 7) was estimated from observed numbers, multiplying by literature values for body sizes, and assuming the same sizes in all treatments. The model prediction of 9% greater total nematode biomass under elevated CO_2 is compatible with the experimental result. However, the model predicted a lower biomass of bacteria-feeding nematodes under western wheatgrass than under blue grama. This discrepancy might be related to the difference in soil texture between the blue grama cores (sandy loam) and wheatgrass cores (sandy clay loam). Ingham *et al*. (1982) postulated that nematode species in heavier soils tend to have smaller individual size because of constraints on movement; if so, a smaller individual size should have been used herein in converting nematode numbers to biomass for wheatgrass cores.

Deleting functional groups

The effects of deleting individual functional groups from the full detrital web were simulated using a 30-y run of the model for blue grama under ambient CO_2. Figure 2 shows the dynamics of selected variables after the deletion of bacteria-feeding nematodes. There was an immediate increase in bacteria, a compensatory increase in amoebae (the other main group of bacteria-feeders), and other effects propagating throughout the system. Dynamics of bacteria and amoebae stabilized after about two years, while mites and detritus required about five and 10 years, respectively, to stabilize. There were small changes in some state variables between 10 and 30 years (data not shown). After 30 years, deleting bacteria-feeding nematodes led to (i) a 40% increase in bacteria, (ii) two- or threefold increases in the other bacteria feeders, (iii) a 10% decline of saprophytic fungi due to increased competition from bacteria, (iv) a 14% increase in detritus, and (v) 50% declines in nematode-feeding and predatory mites. The effects of deleting other groups varied widely.

- Deleting bacteria resulted in (i) the extinction of the four groups depending strictly on bacteria or other bacteria-feeders (Fig. 1), (ii) 62–88% declines in predators, and (iii) increases of up to 11% in fungus-feeding groups.
- Deleting predatory nematodes led to (i) 10–40% increases in the other groups of nematodes, except for omnivorous nematodes, which declined by 55%, and (ii) 40–50% declines in protozoa.
- Deleting saprophytic fungi led to (i) a five-fold increase in residues, (ii) a 12% loss of mycorrhizal fungi, (iii) 90% or greater losses of fungal feeders, and (iv) 27–75% declines in bacteria, bacteria-feeders, and predators.
- Deleting root-feeding nematodes caused (i) 20–40% declines in predators and bacteria feeders except for bacteria-feeding nematodes (ii) slight increases in saprophytic fungi and fungal feeders, and (iii) a 12% increase in plant biomass.
- Deleting amebae caused a 60% decline in omnivorous nematodes, a 30% increase in bacteria-feeding nematodes, and 20% increases in predatory microarthropods.
- Deleting either group of fungus-feeding mites caused a 13% decline in predatory mites but no more than a 3% change in any other group.
- Deleting mycorrhizal fungi caused a 9% decline in fungus-feeding nematodes and a 36% increase in soil inorganic N.
- Deleting the other functional groups (predatory mites, nematode-feeding mites, omnivorous nematodes, flagellates, Collembola, and fungus-feeding nematodes) caused no more than an 8% change in any other group.

The standard relative error SRE (omitting the deleted group from the calculation) was taken as an overall measure of the departure of state variables from their previous values after a deletion. The frequency distribution of SRE among the 15 deleted groups (not shown) had two large values (bacteria and saprophytic fungi) in the upper tail, but it was not possible to rule out a unimodal distribution. In order to determine which characteristics of functional groups were responsible for the effects of group removal, stepwise regression was used with SRE as dependent variable, and with trophic level, number of resources, number of consumers (cf. Figure 1), and biomass (Table 7) of the deleted group as independent variables. The independent variables accounted for only 39% of the variation in the effect of deletions. The deletion effect was positively correlated with biomass ($r = 0.58$, $P < 0.05$) and with number of consumers ($r = 0.63$, $P < 0.05$). There was a nonsignificant negative correlation with trophic level. The stepwise regression procedure first selected the variable for number of consumers, after which neither biomass nor

any other variable entered the equation. However, the selection of number of consumers merely indicates that the simple correlation with number of consumers was slightly higher than that with biomass, and does not indicate that the number of consumers is significantly better than biomass as an explanatory variable.

Despite some major effects of deletions on the biomass of remaining functional groups, only two of the 15 deletions resulted in as much as a 4% change in NPP. Deleting saprophytic fungi caused decreases of 60% in N mineralization and 85% in NPP. This occurred because bacteria by themselves were incapable of decomposing the resistant component of residues fast enough to prevent an accumulation of detritus and an increase in N immobilized in residues. Deleting bacteria led to reductions of 12% in N mineralization and 13% in NPP. In this case detritus declined because fungi, which are capable of faster decomposition of the resistant fraction of detritus, were relieved from competition with bacteria for the N-rich labile fraction. Nitrogen mineralization declined because the bacterial branch of the web is responsible for 83% of mineralization in the complete detrital web. Deleting mycorrhizal fungi reduced plant N uptake by 2% and NPP by 3%. Regression analysis, using the same independent variables as used above to examine effects of deletions on abundance of other groups, showed that a single variable, biomass of the deleted group, accounted for 98.8% ($P << 0.01$) of the variation in NPP.

Although deleting individual faunal groups did not affect NPP, deleting all faunal groups at once led to a shift from saprophytic fungal to bacterial dominance, and reduced N mineralization by 61% and NPP by 39%. Deleting fauna in three groups according to diet: (i) bacteria-feeding fauna (protozoans, bacteria-feeding nematodes and omnivorous nematodes), (ii) fungus-feeding fauna, and (iii) predators (predatory mites and nematodes) reduced NPP by 7%, 0%, and 2%, respectively.

Model stability

With none or with only one of the three stabilizing mechanisms in operation, the model was unstable, with five or more functional groups becoming extinct (arbitrary lower limit of 10^{-10} gC m^{-2}, about one individual per 10 m^2 for nematodes), or heading for extinction (exponential decline at a constant specific rate). Including prey refuges and switching, but not density-dependent death, led to five extinctions. Switching plus density-dependent death (excluding refuges) led to a stable limit cycle with huge amplitudes – four orders of magnitude for bacteria. Refuges plus density dependence (excluding switching) allowed model stability, but with damped oscillations. Thus, all three mechanisms together were necessary for critically damped stability of the full model. However, loss of functional groups can change these relationships. For example, when bacteria-feeding nematodes were deleted from the model with all three stabilizing mechanisms in place, model dynamics (Fig. 2) changed from a critically damped steady state to a stable limit cycle with a period of about 0.5 y and an amplitude that was relatively small except for bacteria.

Discussion

Responses to elevated CO_2

In agreement with experimental results, simulated plant biomass increased under elevated CO_2, while plant N concentration and soil inorganic N level decreased. These changes suggest greater N limitation of primary production relative to water limitation (Hunt *et al*. 1996), which has been postulated to ultimately limit plant response to elevated CO_2 in the field (Strain & Bazzaz 1983). According to the model, net primary production increased by 36%, mostly as a result of greater water-use efficiency under elevated CO_2. Other model changes included greater biomass of saprophytic fungi and most faunal groups, 11% greater net N mineralization, and greater mycorrhizal biomass and N transfer from mycorrhizae to roots. Thus, changes in the soil food web served to increase N availability to the plant and partially to offset the increase in relative plant N limitation under elevated CO_2. If this homeostatic model response is realistic, it suggests that N limitation will be less constraining to ecosystem response to elevated CO_2 than previously thought. Model response to elevated CO_2 is reminiscent of apparently adaptive homeostatic changes observed by Watson & Lovelock (1983) in a simple model of plant community adjustment to changes in radiative forcing.

Effects of functional group deletions

Although there are examples in the soil food web (Wall & Moore 1999) of species deletions that lead to changes in the abundance of other species and in ecosystem function (decomposition), there is little doubt that many species can be lost with little effect on abundance of other species (Bond 1994; Ehrlich 1994; but see Pimm 1980). The model's predictions about the effects of deleting decomposer functional groups agree with experimental results (Ingham *et al*. 1985; Beare *et al*. 1992; Laakso & Setala 1999a, 1999b) that some groups in the soil food web can be deleted without much effect on ecosystem function. The small effect of deleting mycorrhizal fungi on NPP of blue grama is consistent with the lack of strong mycorrhizal dependence in some prairie grasses (Hetrick *et al*. 1987), and with observations in this

particular species (Hays *et al*. 1982). The lack of a large positive response to mycorrhizae has been postulated to result from 'efficient soil exploration by finely branched root systems' (Hays *et al*. 1982), and may also be related to the lack of phosphorus limitation at the field site represented by the model (Clark *et al*. 1980).

Deletion of nine of the 15 groups in the soil food web model (all five microarthropod groups, flagellates, mycorrhizae, and two out of five nematode groups) caused no more than a 15% change in biomass of another group, and no significant effects on mineralization or NPP. The deletion of six groups (bacteria, saprophytic fungi, amoebae, bacteria-feeding nematodes, root-feeding nematodes, and predatory nematodes) caused at least a 15% change in another group. Only two functional groups, bacteria and saprophytic fungi, caused large enough changes in NPP (– 13% and –85%, respectively) to be detectable in an experimental study and thus to be considered nonredundant. Four of the six groups which caused at least a 15% change in abundance of another group caused less than a 3% change in NPP, and thus appear to qualify as redundant functional groups.

The model is useful in (i) showing that ordinary trophic dynamic mechanisms among functional groups are sufficient to account for observed redundancy, and (ii) providing a theoretical tool for examining redundancy. Compensatory responses to deletions can be identified in most cases. For example, deleting bacteria-feeding nematodes led to increases in the other bacteria-feeding fauna. It is surprising that root-feeding nematodes were redundant, because there is no other herbivorous group in the model. Apparently the phenomenon of redundancy can result from situations other than that in which two similar groups can substitute for each other in carrying out the same ecosystem process.

The apparent lack of bimodality in the frequency distribution of size of deletion effects supports the hypothesis of Hurlbert (1997) that there may be no qualitative distinction between groups with large and small effects. However, only 15 deletions were examined, which may not be enough to detect weak bimodality. The lack of an unambiguous relationship between biomass of the deleted group and the effect of deletion on the abundance of other groups supports the opinion (Hurlbert 1997; but see Power *et al*. 1996 for opposite opinion) that indices of system response to deletions should not be scaled *a priori* to biomass. Identification of taxa whose preservation may be critical to maintenance of biodiversity and ecosystem function is an important challenge for conservation biology (Power *et al*. 1996). Only 39% of variation in effects of deleting functional groups from the model could be accounted for statistically in terms of simple properties (biomass and the architecture of trophic relationships) of the deleted group, even though there was no measurement error because the model is deterministic. This suggests that system properties governing the size of deletion effects are not localized at the deleted group, and may be distributed diffusely throughout the food web.

It might be inferred that fauna must exert dynamic control over N mineralization, because they account for most of net mineralization. Indeed, removing all fauna dramatically reduced net mineralization and NPP. Nevertheless, no one faunal group had significant effects on system function. This result differs from that of de Ruiter *et al*. (1993) and Moore *et al*. (1993b), who found that deleting individual faunal groups from an N flow model of the detrital web caused reductions of up to 40% in N mineralization. However, their analyses were not based on a dynamic model and did not fully allow for compensatory changes in the remaining groups. O. J. Andrén (pers. comm.) has suggested that the redundancy exhibited by faunal groups in the present model helps to explain the observation (Andrén *et al*. 1999) that major ecosystem fluxes can be predicted with models such as Century (Parton *et al*. 1987), which disregard the bewildering species numbers and population dynamics of soil organisms, but only include (implicitly) their overall activity.

Model stability

May (1973) pointed out that including the 'realistic complications' of species interactions such as switching, density-dependent death and spatial heterogeneity 'can easily stabilize' models. Full stability (critical damping) of the soil food web model required three stabilizing mechanisms: density-dependent death, prey refuges, and predator switching. Of these mechanisms, the best experimental evidence exists for refuges. Density-dependent death can be considered a surrogate for mechanisms known to operate in soil food webs, such as disease, parasites, and, for some groups, predation among species within a functional group. Switching is a plausible but undocumented mechanism. O. J. Andrén (pers. comm.) has pointed out that the inclusion of stabilizing mechanisms is probably responsible for the tolerance of the model to the loss of many of the functional groups. If this is correct, greater attention to stabilizing mechanisms is warranted in studies of the relationship between biodiversity and ecosystem function. Stabilizing mechanisms not yet included in our model are seasonal variation in resource availability (Ebenhoh 1988) and explicit spatial heterogeneity (Huston & DeAngelis 1994) such as rhizosphere vs. nonrhizosphere soil, litter vs. soil layers, and soil pore size distributions.

The results presented herein must be qualified in several important ways. First, deletions of multiple functional groups, which may have more severe consequences than single deletions, have not been systematically examined. Second, the effects of deleting functional groups were tested in a single system (blue grama under ambient CO_2 and a constant environment), and the relationships between decomposer groups and ecosystem function may vary significantly among ecosystems (González & Seastedt, 2001). Finally, the stability of the simplified systems remaining after deleting groups has not been examined systematically, and such stability may be critically important to ecosystem function in a changing environment (Berendse 1994; Andrén *et al*. 1995).

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References

Albertson FW, Riegel DA, Tomanek GW (1966) *Ecological Studies of Blue Grama Grass (Bouteloua Gracilis).* Fort Hays Studies-New Series: Science Series No. 5. Fort Hays Kansas State College, KS.

Allen MF, Allen EB, Stahl PD (1984) Differential niche response of *Bouteloua gracilis* and *Pascopyrum smithii* to *VA* mycorrhizae. *Bulletin of the Torrey Botanical Club*, **111**, 361–365.

Anderson JPE, Domsch KH (1980) Quantities of plant nutrients in the microbial biomass of selected soils. *Soil Science*, **130**, 211–216.

Andrén OJ, Bengtsson J, Clarholm M (1995) Biodiversity and species redundancy among litter decomposers. In: *The Significance and Regulation of Soil Biodiversity* (eds Collins HP *et al*.), pp. 141–151. Kluwer, Dordrecht.

Andrén OJ, Brussaard L, Clarholm M (1999) Soil organism influence on ecosystem-level processes — bypassing the ecological hierarchy? *Applied Soil Ecology*, **11**, 177–188.

Beare MH, Parmelee RW, Hendrix PF, Cheng W, Coleman DC, Crossley DA Jr (1992) Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. *Ecological Monographs*, **62**, 569–591.

Bell AA, Wheeler H (1986) Biosynthesis and functions of fungal melanins. *Annual Reviews in Phytopathology*, **24**, 411–451.

Bellows TS Jr (1981) The descriptive properties of some models for density dependence. *Journal of Animal Ecology*, **50**, 139–156.

Berendse F (1994) Ecosystem stability, competition, and nutrient cycling. In: *Biodiversity and Ecosystem Function* (eds Schulze ED, Mooney HA), pp. 409–431. Springer, New York.

Bernstein C (1984) Prey and predator emigration responses in the acarine system {*Tetranychus urticae – Phytoseiulus persimilis*}. *Oecologia*, **61**, 134–142.

Bond WJ (1994) Keystone species. In: *Biodiversity and Ecosystem Function* (eds Schulze ED, Mooney HA), pp. 237–253. Springer, New York.

Burnett JH (1979) Aspects of the structure and growth of hyphal walls. In: *Fungal Walls and Hyphal Growth* (eds Burnett JH, Trinci APJ), pp. 1–25. Cambridge University Press, New York.

Clark FE (1977) Internal cycling of 15nitrogen in shortgrass prairie. *Ecology*, **58**, 1322–1333.

Clark FE, Cole CV, Bowman RA (1980) Nutrient Cycling. In: *Grasslands, Systems Analysis and Man* (eds Breymeyer AJ, Van Dyne GM), International Biological Programme, pp. 659–712. Cambridge University Press, Cambirdge.

Cole CV, Innis GS, Stewart JWB (1977) Simulation of phosphorus cycling in semiarid grasslands. *Ecology*, **58**, 1–15.

Coleman DC (1985) Through a ped darkly: an ecological assessment of root-soil-microbial–faunal interactions. In: *Ecological Interactions in Soil* (ed. Fitter AH), Special Publication No. 4 of the British Ecological Society, pp. 1–21. Blackwell Scientific Publications, Oxford.

de Ruiter PC, Moore JC, Zwart KB *et al.* (1993) Simulation of nitrogen mineralization in the belowground food webs of two winter wheat fields. *Journal of Applied Ecology*, **30**, 95–106.

de Ruiter PC, Neutel A-M, Moore JC (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, **269**, 1257–1260.

Ebenhoh W (1988) Coexistence of an unlimited number of algal species in a model ecosystem. *Theoretical Population Biology*, **34**, 130–144.

Ehrlich PR (1994) Biodiversity and ecosystem function: Need we know more? In: *Biodiversity and Ecosystem Function* (eds Schulze E-D, Mooney HA), pp. vii–xi. Springer, New York.

Elliott ET, Anderson RV, Coleman DC, Cole CV (1980) Habitable pore space and microbial trophic interactions. *Oikos*, **35**, 327–335.

Freckman DW, Moore JC, Hunt HW, Elliott ET (1991) The effects of elevated CO_2 and climate change on soil nematode community structure of prairie sod. *Supplemental Bulletin Ecological Society of America*, **72**, 119(Abstract).

Gitay H, Wilson JB, Lee WG (1996) Species redundancy: a redundant concept? *Journal of Ecology*, **84**, 121–124.

Gardner RH, Cale WG, O'Neill RV (1982) Robust analysis of aggregation error. *Ecology*, **63**, 771–779.

González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. *Ecology*, **82**, 955–964.

Hetrick BAD, Kitt DG, Wilson GT (1987) Mycorrhizal dependence and growth of warm-season and cool-season tallgrass prairie plants. *Canadian Journal of Botany*, **66**, 1376–1380.

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

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Hunt HW (1977) A simulation model for decomposition in grasslands. *Ecology*, **58**, 469–484.

Hunt HW, Coleman DC, Cole CV, Ingham RE, Elliott ET, Woods LE (1984) Simulation model of a foodweb with bacteria, amoebae and nematodes in soil. In: *Current Perspectives in Microbial Ecology* (eds Klug MJ, Reddy CA), pp. 346–352. American Society for Microbiology, Washington, DC.

Hunt HW, Cole CV, Elliott ET (1985) Models for growth of bacteria inoculated into sterilized soil. *Soil Science*, **139**, 156–165.

Hunt HW, Stewart JWB, Cole CV (1986) Concepts of sulfur,

carbon, and nitrogen transformations in soil: Evaluation by simulation modeling. *Biogeochemistry*, **2**, 163–178.

Hunt HW, Coleman DC, Ingham ER *et al.* (1987a) The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils*, **3**, 57–68.

Hunt HW, Logan JA, Walter DE, Elliott ET, Moore JC (1987b) Stability of simulation models of detrital food webs in soil. *Bulletin Ecological Society of America*, **68**, 328(Abstract).

Hunt HW, Ingham ER, Coleman DC, Elliott ET, Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology*, **69**, 1009–1016.

Hunt HW, Elliott ET, Walter DE (1989) Inferring trophic transfers from pulse-dynamics in detrital food webs. *Plant and Soil*, **115**, 247–259.

Hunt HW, Trlica MJ, Redente EF *et al.* (1991) Simulation model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling*, **53**, 205–246.

Hunt HW, Elliott ET, Detling JK, Morgan JA, Chen D-X (1996) Responses of a C3 and a C4 perennial grass to elevated CO_2 and temperature under different water regimes. *Global Change Biology*, **2**, 35–47.

Hunt HW, Morgan JA, Read JJ (1998) Simulating growth and root-shoot partitioning in prairie grasses under elevated CO_2 and water stress. *Annals Botany*, **81**, 489–501.

Hunt HW, Reuss DE, Elliott ET (1999) Correcting estimates of root chemical composition for soil contamination. *Ecology*, **80**, 702–707.

Hurlbert SH (1997) Functional importance vs. keystoneness: Reformulating some questions in theoretical biocenology. *Australian Journal of Ecology*, **22**, 369–382.

Huston MA, DeAngelis DL (1994) Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist*, **144**, 954–977.

Ingham RE, Trofymow JA, Anderson RV, Coleman DC (1982) Relationships between soil type and nematodes in a short-grass prairie. *Pedobiologia*, **24**, 139–144.

Ingham RE, Trofymow JA, Ingham ER, Coleman DC (1985) Interactions of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. *Ecological Monographs*, **55**, 119–140.

Laakso J, Setala H (1999a) Population- and ecosystem-level effects of predation on microbial-feeding nematodes. *Oecologia*, **120**, 279–286.

Laakso J, Setala H (1999b) Sensitivity of primary production to changes in the architecture of belowground food webs. *Oikos*, **87**, 57–64.

Lauenroth WK, Milchunas DG (1991) Shortgrass steppe. In: *Natural Grasslands: Introduction and Western Hemisphere* (ed. Coupland RT), pp. 183–226. Elsevier, New York.

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

Lauenroth WK, Hunt HW, Swift DM, Singh JS (1986) Estimating aboveground net primary production in grasslands: a simulation approach. *Ecological Modelling*, **33**, 297–314.

Lawton JH, Brown VK (1994) Redundancy in ecosystems. In: *Biodiversity and Ecosystem Function* (eds Schulze E-D, Mooney HA), pp. 255–270. Springer, New York.

Leetham JW, Milchunas. DG (1985) The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass and grazing by cattle. *Pedobiologia*, **28**, 311–325.

May RM (1973) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

May RM (1977) Predators that switch. *Nature*, **269**, 103–104.

McGill WB, Hunt HW, Woodmansee RG, Reuss JO (1981) PHOENIX, a model of the dynamics of carbon and nitrogen in grasslands. *Ecological Bulletin (Stockholm)*, **33**, 49–115.

Monz CA, Reuss DE, Elliott ET (1991) Soil microbial biomass carbon and nitrogen estimates using 2450 MHz microwave irradiation or chloroform fumigation followed by direct extraction. *Agriculture, Ecosystems and Environment*, **34**, 55–63.

Monz CA, Hunt HW, Reeves FB, Elliott ET (1994) The response of mycorrhizal colonization to elevated CO_2 and climate change in *Pascopyrum smithii and Bouteloua gracilis*. *Plant and Soil*, **165**, 75–80.

Moore JC, de Ruiter PC, Hunt HW (1993a) Influence of productivity on the stability of real and model ecosystems. *Science*, **261**, 906–908.

Moore JC, de Ruiter PC, Hunt HW (1993b) Soil invertebrate/micro–invertebrate interactions: disproportionate effects of species on food web structure and function. *Veterinary Parasitology*, **48**, 247–260.

Morgan JA, Hunt HW, Monz CA, LeCain DR (1994) Consequences of growth at two carbon dioxide concentrations and two temperatures for leaf gas exchange in *Pascopyrum smithii* (C3) and *Bouteloua gracilis* (C4). *Plant, Cell and Environment*, **17**, 1023–1033.

Myers N (1996) Environmental services of biodiversity. *Proceedings of the National Academy of Sciences USA*, **93**, 2764–2769.

Naeem S (2000) Reply to Wardle et al. *Bulletin of the Ecological Society of America*, **81**, 241–246.

Nelder JA, Mead R (1965) A simplex method for function minimization. *Computer Journal*, **7**, 308–313.

Newton PCD (1991) Direct effects of increasing carbon dioxide on pasture plants and communities. *New Zealand Journal of Agricultural Research*, **34**, 1–24.

Paine RT (1980) Food webs: linkage interaction strength and community infrastructure. *Journal of Animal Ecology*, **49**, 667–685.

Parton WJ, Schimel DS, Cole CV, Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains Grasslands. *Soil Science Society of America Journal*, **51**, 1173–1179.

Paustian K, Schnürer J (1987) Fungal growth response to carbon and nitrogen limitation: application of a model to laboratory and field data. *Soil Biology and Biochemistry*, **19**, 621–629.

Pimm SL (1980) Food web design and the effect of species deletion. *Oikos*, **35**, 139–149.

Pimm SL (1984) The complexity and stability of ecosystems. *Nature*, **307**, 321–326.

Power ME, Tilman D, Estes JA *et al.* (1996) Challenges in the quest for keystones. *Bioscience*, **46**, 609–620.

Sauer RH (1978) A simulation model for grassland primary producer phenology and biomass dynamics. In: *Grassland Simulation Model* (ed. Innis GS), pp. 55–87. Springer, New York.

Schimel D, Stillwell MA, Woodmansee RG (1985) Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology*, **66**, 276–282.

Schlapfer F, Schmid B (1999) Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications*, **9**, 893–912.

Shoop M, Kanode S, Calvert M (1989) Central Plains Experimental Range: 50 years of research. *Rangelands*, **11**, 112–117.

Strain BR, Bazzaz FA (1983) Terrestrial plant communities. The response of plants to rising levels of atmospheric carbon dioxide. In: *CO_2 and Plants* (ed. Lemon ER), American Association for the Advancement of Science, Selected Symposium no. 84, pp. 177–222. Westview Press, Boulder, CO.

Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity. Theoretical considerations. *Proceedings of the National Academy of Science*, **94**, 1857–1861.

Walker BH (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Wall DH, Moore JC (1999) Interactions underground. *Bioscience*, **49**, 109–117.

Wardle DA, Huston MA, Grime JP *et al.* (2000) Biodiversity and ecosystem function: An issue in ecology. *Bulletin of the Ecological Society of America*, **81**, 235–239.

Watson AJ, Lovelock JE (1983) Biological homeostasis of the global environment: the parable of Daisyworld. *Tellus*, **35B**, 284–289.

Whitford WG (1996) The importance of the biodiversity of soil biota in arid ecosystems. *Biodiversity and Conservation*, **5**, 185–195.

Wilson JB (1999) Guilds, functional types and ecological groups. *Oikos*, **86**, 507–522.

de Wit CT, Goudriaan J (1974) *Simulation of Ecological Processes*. Centre for Agricultural Publishing and Documentation, Wageningen.

Woodmansee RG, Dodd JL, Bowman RA, Clark FE (1978) Nitrogen budget of a shortgrass prairie ecosystem. *Oecologia*, **34**, 363–376.