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James D. Bever, Kristi M. Westover, Janis Antonovics

Journal of Ecology, Volume 85, Issue 5 (Oct., 1997), 561-573.

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Journal of Ecology
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ESSAY REVIEW

Incorporating the soil community into plant population dynamics: the utility of the feedback approach

JAMES D. BEVER,* KRISTI M. WESTOVER and JANIS ANTONOVICS

Department of Botany, Duke University, Durham, NC 27708, USA

Summary

1 Although its importance for plant mineral nutrition and nutrient cycling has long been recognized, the soil community has rarely been integrated into dynamical frameworks of plant populations, in spite of abundant evidence for its involvement. The concept of feedback may provide theoretical and experimental tools for investigating the importance of the soil community in the population ecology and evolution of plants.

2 A mathematical model demonstrates the potential for two divergent dynamics, with positive feedback leading to the loss of diversity at a local scale and negative feedback leading to its maintenance. A linear contrast of the growth of plants in association with their own soil communities compared to the growth of plants in association with each others' soil communities can be used to differentiate between these possibilities in empirical studies.

3 Spatially explicit computer simulations demonstrate that the dynamics of a spatially structured community, as the soil community is likely to be, can differ from those predicted for a well-mixed population. Specifically, diversity can be maintained between locally homogeneous patches when positive feedback and dispersal occur at local scales.

4 Using a simple experimental protocol, we have found substantial negative feedback on plant growth through the soil community, suggesting that it may be involved in the maintenance of plant species diversity.

5 We discuss the importance of the soil community in other areas of plant ecology and evolution, including the suggestion that interactions with the soil community may be involved in the maintenance of sexual or asexual reproductive systems.

Keywords: coexistence, ecological theory, mutualism, pathogens, spatial simulations

Journal of Ecology (1997) **85**, 561–573

Introduction

The maintenance of diversity in plant communities has traditionally been assumed to result from the partitioning of abiotic resources (reviewed by Grace & Tilman 1990; Tilman & Pacala 1993). Both phenomenological and mechanistic models of competition demonstrate that competing species will coexist when intraspecific competition exceeds interspecific competition, a situation that has generally been presumed to result from abiotic niche differentiation. However, the generality of this view has been challenged and

alternative mechanisms of coexistence have been proposed (Goldberg & Werner 1983; den Boer 1986; Silvertown & Law 1987; Aarssen 1989). While several of these alternatives focus on the mediation of plant–plant interactions by organisms at higher trophic levels (herbivores and pathogens), the soil community has rarely been suggested to have an important role in the maintenance of plant diversity, in spite of the evidence that soil micro-organisms exert strong effects on plant growth and often mediate plant acquisition of abiotic soil resources. We suggest that this oversight results from difficulties of applying the standard conceptual frameworks of population and community ecology to soil organisms, where technical problems hinder the identification and enumeration

*Present address: Department of Ecology and Evolution, University of Chicago, 1101 East 57th Street, Chicago, IL 60637–1573 USA.

of such organisms. In this paper, we outline several novel conceptual and experimental approaches which have proved useful in evaluating the importance of the soil community and its components in the coexistence and dynamics of the above-ground plant community.

SOIL COMMUNITY

Micro-organisms are ubiquitous in all plant communities and exert profound effects on plant growth and reproduction. Beneficial rhizosphere bacteria influence plant performance by increasing mineral solubilization (Barr-Ness *et al.* 1991; Crowley *et al.* 1991; Derylo & Skorupska 1992), fixing nitrogen (Albrecht *et al.* 1981), producing plant growth hormones (Tein *et al.* 1979; Neitko & Frankenberg 1989), and competitively suppressing plant pathogens (Thomashow & Weller 1990; Handman *et al.* 1991). Pathogenic soil bacteria, fungi, and nematodes can greatly reduce the survival, growth, and reproduction of plants (Burdon 1987; Bruehl 1987; Augspurger 1990). Most plants absorb soil phosphorus with the assistance of mycorrhizal fungi, and some plants cannot grow without their fungal symbionts (Hetrick 1984; Brundrett 1991). However, the net effect of the soil community as a whole may not simply be the sum of the effects of its components, as synergistic (e.g. between pathogenic fungi and nematodes, Rooij-van der Goes 1995) and antagonistic (e.g. between pathogenic fungi and mycorrhizal fungi, Newsham *et al.* 1995) interactions between components have frequently been observed.

Several studies have demonstrated that the composition of the soil community can have large differential effects on plant performance. Performance of *Trifolium repens* cultivars depended upon specific associations of cultivar and symbiotic *Rhizobium* strains (Mytton 1975; Mytton & Hughes 1984; Young *et al.* 1986). The growth promotion of arbuscular mycorrhizal (hereafter AM) fungi similarly depends upon the specific matching of plant and fungal species (Nemec 1978; Ravnskov & Jakobsen 1995; Streitwolf-Engel *et al.* 1997). Furthermore, within natural communities, competitive interactions of *Trifolium repens* with particular grasses have been shown to depend upon the particular *Rhizobium* strain associated with *Trifolium* (Turkington *et al.* 1988; Chanway *et al.* 1989; Turkington & Klein 1991; Chanway & Holl 1993). The presence of AM fungi also influences the outcome of conspecific (Hall 1978) and interspecific competitive interactions (Fitter 1977; Hetrick & Wilson 1989; Allen & Allen 1990; Hartnett *et al.* 1993; Hetrick *et al.* 1994; West 1996; but see Watkinson & Freckleton 1997). The composition of the soil community was found to influence the outcome of competition between co-occurring perennial plants in an old field community (Westover 1995). Species-specific soil pathogens are also known to change the outcome of interactions between crops and weed species in

agricultural systems (Bruehl 1987) and alter seedling composition in tropical rain forests (Augspurger & Kelley 1984; Augspurger 1990).

Conversely, it has been well documented that the density and composition of the soil community can be affected by which plant species and genotypes are growing in that soil (Atkinson *et al.* 1975; Shipton 1977; Turkington *et al.* 1988; Chanway *et al.* 1991; Larkin *et al.* 1993). For example, the density (Harinikumar & Bagyaraj 1988) and composition (Johnson *et al.* 1991) of communities of AM fungi have been found to be altered by crop rotations. A similar type of host-dependence of AM fungal communities has been shown in natural situations (Sanders & Fitter 1992; Johnson *et al.* 1992; Bever *et al.* 1996). Bacterial communities have also been shown to differentiate between their hosts within a small spatial scale (Borga *et al.* 1994; Westover 1995).

CONCEPTUAL FRAMEWORK OF FEEDBACK AND THE DYNAMICS OF PLANT-SOIL INTERACTIONS

In spite of the obvious importance of the soil community for plant biology and its demonstrated importance in agricultural systems, there has been little examination of the dynamic inter-relationships between the composition of plant and soil communities. The absence of such investigations probably results from the difficulty of characterizing the soil community. While the number of microbial species present in an ounce of soil may be several thousands (Tate 1995), few of these species have been described. The quantification of the densities or frequencies of these species is even more difficult (Tate 1995). Without these essential quantities, the soil community cannot be studied within the traditional theoretical framework of population biology.

Here we suggest that the conceptual framework of feedback provides us with the theoretical and experimental tools to investigate the importance of the soil community in the ecology and evolution of plants. The feedback process involves two steps. First, a plant or populations of plants changes the composition of the soil community; secondly, this change in turn affects the rate of growth of the plant or population. The strength of this simple conceptualization is twofold: (i) it can be extended to a mathematical model that illustrates and identifies the necessary conditions for the very different dynamics of positive and negative feedback, with positive feedback leading to the loss of diversity at a local scale and negative feedback leading to the maintenance of diversity; (ii) it lends itself readily to experimentation and quantification, even though the identity of the microbial agents of feedback may not initially be known.

DYNAMIC CONSEQUENCES OF FEEDBACK

In this section, we present a heuristic model of the dynamic consequences of feedback between plants

and their soil communities. This model describes the soil community in terms of its effect on plant growth rather than in terms of the density or identity of specific components. Since this conceptualization may be unfamiliar, we indicate how parameters can be measured as they are introduced. However, we find that measurement of individual parameters is not necessary for the characterization of the net pairwise feedback dynamics.

We explore the dynamic consequences of feedback in its simplest form by considering two plant species, A and B, which, if present alone, would change the soil community to compositions, represented by α and β , respectively (as presented in Fig. 1). The parameters α_A and β_B represent the direction and magnitude of the direct feedback of soil communities α and β on plant A and plant B, respectively. The parameter α_A , for example, can be thought of as the difference in growth of plant A between that in a soil community that has previously been associated with plant A and one without this history. The parameters α_B and β_A represent the direction and magnitude of indirect effects of the plant species on each other through these same soil communities. The parameter α_B can therefore be considered as the difference in growth of plant B in a soil community that has previously been associated with plant A and one without this history.

The accumulated influence of plant A on the soil community, which can be thought of as the amount of α or N_α , is a function of the historical densities of plant A. Because we are assuming that α is a biotic change, we imagine that the amount of α will have the properties of populations and communities, including the capacity for exponential increase (i.e. $dN_\alpha/dt = N_\alpha N_A$, where N_A is the density of plant A). Similarly, the accumulation of the influence of plant B on the soil community is a function of the historical

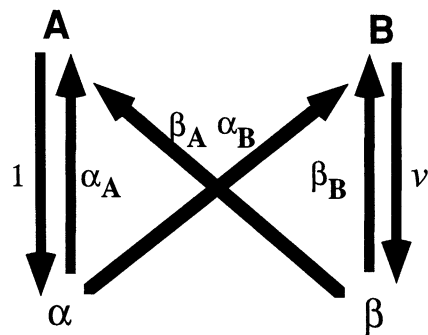


Fig. 1 Model of feedback. The letters A and B represent two plant species with the quantities α and β representing the change in the soil community resulting from the presence of A and B, respectively. The parameter v represents the strength of influence of plant B on the soil community, relative to that of plant A. The parameters α_A and β_B then represent the direction and magnitude of the direct feedback through the soil community on plant A and plant B, respectively. The parameters α_B and β_A represent the indirect effects through changes in the soil community of plant A on plant B and vice versa.

densities of plant B as well as the influence of an individual of plant species B on the soil community relative to that of an individual of plant species A, as represented by the variable v in Fig. 1. The relative influence of two plant species on the soil community could be measured by monitoring the changes in the soil community due to mixtures of the two species relative to that in pure stands. In characterizing soil community dynamics in this manner, we are ignoring many interesting interactions among the components of the soil community including competition, interference and predation. Rather, we analyse only the net consequences of the host-specific differentiation of the soil communities on plant growth.

Dynamics resulting from these relationships are most easily analysed using the assumption of continuous change over time. The rates of change of the numbers of plants of species A and B, N_A and N_B , respectively, are described as $dN_A/dt = W_A N_A$, and $dN_B/dt = W_B N_B$. This is a standard exponential growth model, where the W_A , the average fitness of plant type A, $= (\alpha_A p_\alpha + \beta_A p_\beta)$ and $W_B = (\alpha_B p_\alpha + \beta_B p_\beta)$. The variables p_α and p_β are the proportion of soil effects attributable to plant A and plant B, respectively (i.e. $p_\alpha = N_A/(N_A + N_B) = 1 - p_\beta$). In a spatial context, p_α can be thought of as the proportion of area occupied by the soil community of plant A. In this initial analysis, we are assuming that the fitness of the two plant types relative to each other does not depend upon density or on the frequency of the two plant types. The equation for instantaneous change in the frequency of plant type A, p_A , where $p_A = N_A/(N_A + N_B) = 1 - p_B$, is

$$\frac{dp_A}{dt} = \frac{d[N_A/(N_A + N_B)]}{dt} = \left(\frac{1}{(N_A + N_B)} \right) \left(\frac{dN_A}{dt} \right) - \left(\frac{N_A}{(N_A + N_B)^2} \right) \left(\frac{dN_A}{dt} + \frac{dN_B}{dt} \right). \quad (1)$$

After substituting the equations for dN_A/dt and dN_B/dt , this expression reduces to

$$\frac{dp_A}{dt} = p_A p_B [(\alpha_A - \alpha_B) p_\alpha + (\beta_A - \beta_B) p_\beta]. \quad (2)$$

Using a similar approach, we can derive the expression for the rate of change of p_α the proportion of soil effects of plant A,

$$\frac{dp_\alpha}{dt} = p_\alpha p_\beta (p_A - v p_B). \quad (3)$$

Analysis of these equations reveals several potential dynamics (Appendix, Bever 1992). If one species has much greater influence than the other on the soil (v is very large or very small) or if the feedback effects of α and β favour one species over the other (e.g. $\alpha_A > \alpha_B$ and $\beta_A > \beta_B$), then one species always has greater growth rates than the other and it will predominate in the system. These replacements cor-

respond to successional sequences, with one organism making the environment better for another which ultimately replaces it. In two other situations, which correspond to reciprocal positive and negative feedback, a single species will not necessarily replace another. Under positive feedback, the relative rate of population growth of a plant type in association with its local soil community increases over time, with the resulting prediction of a loss of diversity from the system (Fig. 2a). Alternatively, under reciprocal negative feedback the relative rate of population growth of a plant with its local environment decreases over time, resulting in the prediction that diversity would be maintained within the system (Fig. 2b). Provided that an internal equilibrium exists, the dynamics will be that of positive feedback when the sign of an interaction coefficient, I_s , is positive, where

$$I_s = (\alpha_A - \beta_A - \alpha_B + \beta_B). \tag{4}$$

Alternatively, when the interaction coefficient is negative, the resulting dynamics will be characterized by negative feedback (Appendix).

The net pairwise dynamics therefore are not constrained by the sign of the direct feedbacks. This leads to the counter-intuitive observation that pairwise negative feedback is possible even when a plant changes the soil community in a manner which results in direct positive effects on its own growth rate (i.e. α_A and $\beta_B > 0$); for example, as a result of increased densities of fungal mutualists. Such negative feedback dynamics occur provided that the changes in the soil communities (α and β) increase the growth rate of the competing species more than that of themselves, i.e.

($\alpha_B > \alpha_A$) and ($\beta_A > \beta_B$). In a similar manner, positive feedback dynamics would result in the presence of direct negative feedbacks, i.e. α_A and $\beta_B < 0$, when the change in the soil communities caused by one component decreases the growth of the other competing species more than that of itself, i.e. ($\alpha_A > \alpha_B$) and ($\beta_B > \beta_A$).

An important outcome of this analysis is that the interaction coefficient provides a convenient means to evaluate the sign, magnitude and significance of the net pairwise dynamics without specifically evaluating the component parameters. To be clear, α_A can be directly measured by comparing the growth of plant A before and after it has been grown with another individual of plant A. We can represent this symbolically as $\alpha_A = G(A)_\alpha - G(A)_0$, where $G(A)_0$ and $G(A)_\alpha$, respectively, are the growth of plant A in soil before and after it was grown with plant A. The parameters α_B , β_A and β_B can be similarly measured as $\alpha_B = G(B)_\alpha - G(B)_0$, $\beta_A = G(A)_\beta - G(A)_0$ and $\beta_B = G(B)_\beta - G(B)_0$. Substituting these equations into the eqn 4 for the interaction coefficient, we can derive an empirical test for net pairwise feedback which does not require measurement of growth in the unexposed soils, i.e. it does not include $G(A)_0$ and $G(B)_0$.

$$I_s = [G(A)_\alpha - G(A)_\beta - G(B)_\alpha + G(B)_\beta]. \tag{5}$$

The magnitude of feedback can thus be measured and tested using a linear contrast of the difference between growth of the two plant species in soil in which the same species has previously been cultured (to determine $G(A)_\alpha + G(B)_\beta$) and growth in soil previously cultured by the other species ($G(A)_\beta + G(B)_\alpha$); this is

$$I_s = (\alpha_A - \beta_A - \alpha_B + \beta_B)$$

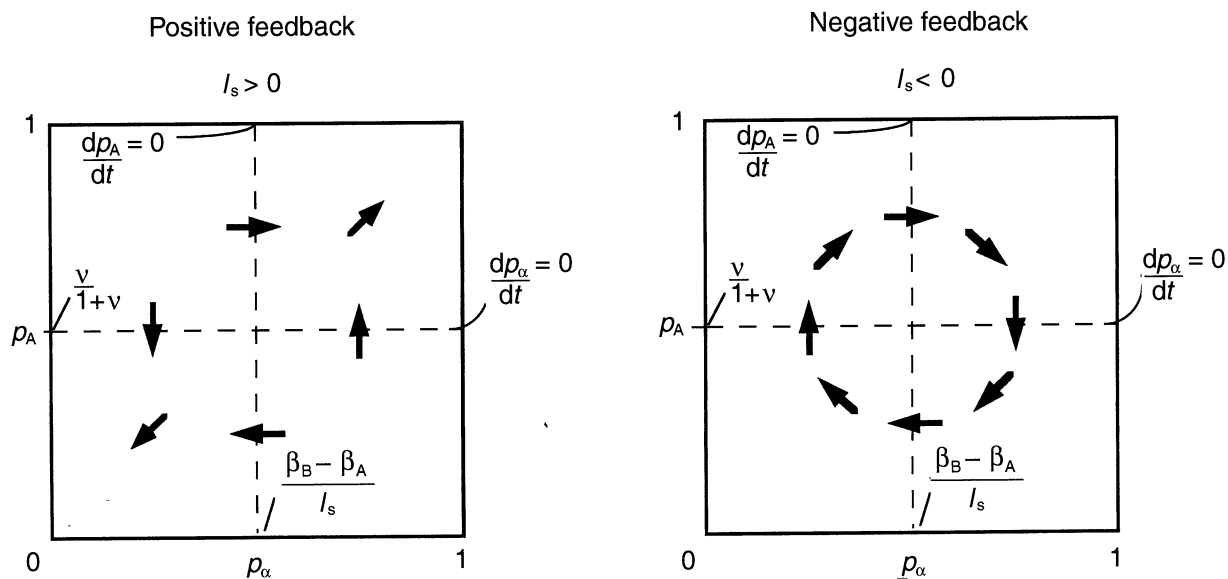


Fig. 2 Dynamics resulting from positive and negative feedback. In these phase plane diagrams, the direction of movement of the proportion of plant A, p_A , and the proportion of influence on the soil community, p_α are indicated by the arrows. The internal equilibrium is unstable under positive feedback, and diversity is lost within the system. The internal equilibrium is neutrally stable under negative feedback, resulting in cyclical dynamics which maintain diversity.

a 'home vs. away' comparison carried out with soils on which the species of interest have previously been grown (Bever 1994).

Our theoretical construction makes several simplifying assumptions about the interactions between plants and the interactions of plants with the soil community. For example, we do not explicitly include density dependence and competition, and therefore assume that the plant species share identical resources and are competitively equivalent, as has previously been argued in other contexts (e.g. Goldberg & Werner 1983). We have also assumed that changes of the soil community result in linear effects on the growth rates of plant species and that plants and soil communities change on the same time scales. Relaxation of these assumptions could alter the predicted dynamics for single populations. Nevertheless, our simple model illustrates how the soil community can play a role in the maintenance of diversity within plant communities and suggests a mechanism of evaluating this possibility.

Consequences of spatial considerations on dynamics of feedback

A further complication is that the expectations developed from single population models may not accurately represent the dynamics of systems with strong spatial structuring; such structuring is likely to be the rule in plant-soil community systems. For example, because the interaction between plants and their soil community occurs at a very local scale, it is possible that variation in plant communities could be maintained by localized positive feedback with their local soil community (Bever 1992; Molofsky 1993). We illustrate the consequences of the spatial scale of the plant-soil community interaction using a spatially explicit computer simulation. We model two annual plant species, A and B, that occupy sites on a linear habitat and which alter their soil community in ways that influence the fitness of the plants that establish at those sites the following year. Plants are initially distributed at random into the habitat (with all cells being occupied) and the nature of the soil community under any focal individual is then determined by the species at that site as well as by the species that are its immediate neighbours. We assume that the soil type in a square is an additive function of the local plant composition. Plants then establish at these sites the following season with a probability that is proportional to their frequency in the seed pool (which may come from all other plants if dispersal is 'global', or only the neighbouring plants if dispersal is 'local'). The seed output of the two species is then determined by the soil type at a particular site (Brandon & Antonovics 1996). In the case of positive feedback, the soil type favours the species that produced the soil type; in the case of negative feedback, the species that produced a given soil type is disfavoured on that site.

If both species are globally dispersed, then (as expected) negative feedback results in coexistence and a relatively uniform distribution of the two species over the habitat, whereas positive feedback results in the rapid elimination of one of the species. If there is negative feedback, but local dispersal, then plant species become aggregated (Fig. 3a). If the dispersal distances of the two species is unequal, the species which is dispersed at shorter distances is increasingly likely to go extinct by chance in spite of the stabilizing force of negative feedback; moreover, the spatial patterns are much less clumped (Fig. 3b). Alternatively, under positive feedback with local dispersal, patches of single species coalesce and the border between patches drifts, with the rate of drift and therefore the probability of extinction of one type decreasing with the decreasing scale of dispersal (Fig. 3c). While our simulation is simplified, similar results have been obtained by analogous models examining species interactions in two dimensions (Simon Levin & Richard Durrett, unpublished data). Therefore, knowledge of the temporal and spatial scale of dispersal and the scale over which the plant-soil community interactions occur is an additional and necessary ingredient for interpreting the consequences of feedback on plant community structure and dynamics.

EVIDENCE FOR FEEDBACKS THROUGH THE SOIL COMMUNITY

Work on agricultural systems provides evidence for the importance of both positive and negative feedback through soil communities. Mytton (1975) demonstrated positive feedback between cultivars of white clover and *Rhizobium* genotypes in experimental communities. Such positive feedback between legumes and their nitrogen-fixing bacteria is supported by the observation that locally coexisting bacterial genotypes are more effective at promoting plant growth than non-coexisting genotypes (Lie *et al.* 1987; Chanway *et al.* 1989). Work on agricultural systems has also demonstrated negative feedback in plant growth through the soil community. For example, Olsson & Gerhardson (1992) showed that repeated cropping with barley changed the soil community so as to decrease the growth rate of barley relative to wheat or oats. Similarly, Kollmorgen *et al.* (1985) found that pre-cropping with any plant besides wheat would reduce the density of *Gaeumannomyces graminis*, the causative agent of wheat 'take all' disease. In fact, the frequent practice of crop rotation is testimony to the importance of negative feedback in agricultural systems (Shipton 1977; Cook 1981).

In natural communities, changes in the soil community have been shown to be responsible for the successional replacement of the early pioneer species in several systems. Van der Putten and others (Van der Putten & Troelstra 1990; Van der Putten *et al.* 1993) found that the soil community associated with

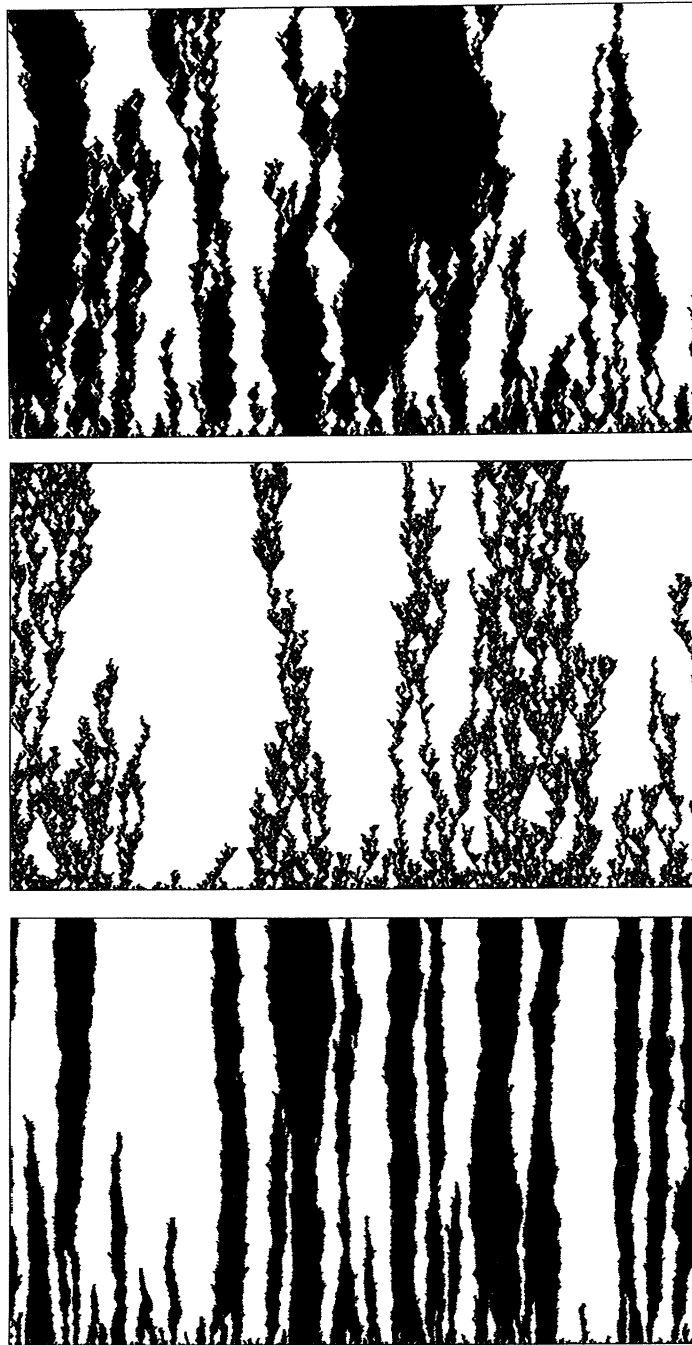


Fig. 3 Three sample runs of spatially explicit stochastic simulations of the feedback between two plant species and their local soil communities. In all figures, the plants occupy a linear array of 638 cells (with wrap around ends) represented by the horizontal axis. The vertical axis represents successive generations; the initial array is presented as the bottom row and the arrays in sequential generations are stacked immediately above them. The two plant types are represented by dark and light shades, respectively. The text describes the details of the simulation steps. (a) Negative feedback with local dispersal. (b) Negative feedback with the 'black' species locally dispersed, but the 'white' species globally dispersed. (c) Positive feedback, with both species dispersed locally.

the early coastal dune pioneer, *Ammophila arenaria*, can cause substantial reductions in its growth rate and can therefore act as an important cause of its replacement. Moreover, in her classic work on the mechanism of old field succession in North Carolina, Keever (1950) found that field-collected roots of the early successional species, horseweed (*Leptilon canadense* L.), can decrease the growth of horseweed relative to the later successional aster (*Aster pilosus*

Willd.) and broomsedge (*Andropogon virginicus* L.). We have found that plants respond similarly to roots as they do to whole soil communities (Bever 1994), suggesting that the decreased growth of horseweed, observed by Keever, was probably due to the composition of the soil and rhizosphere community associated with the roots rather than any nutrient or allelopathic effect. These studies suggest that the soil community feedbacks may be an important though

rarely studied mechanism of species replacement during succession.

Explicit tests of pairwise feedback

The role of the soil community in the coexistence of plant species is poorly understood. However, we have devised simple protocols to evaluate the importance of soil communities within the framework of feedbacks. This protocol involves two steps. First, soil communities which are initially similar (or randomly distributed in field studies) are exposed to different plant species. By growing the plants in pots with equivalent soil inocula, we can speak of the soil community as being 'cultured' by the different plant species and this 'culturing' results in the differentiation of the soil communities. Secondly, the subsequent feedback effect is measured by monitoring the growth of the plant species in pots inoculated with each type of cultured soils (or by outplanted 'phytometer' plants in field studies). The significance, direction and magnitude of feedback can then be tested by contrasting the response of plant species in their own soils against the response in each others soils (the interaction coefficient, I_s , or 'home vs. away' contrast described above).

While this second testing step could evaluate the net effect of host-induced differentiation of the biotic and abiotic components of the soil community, we have been interested in the feedbacks through the soil community in particular. We have therefore devised a method of controlling for differences in the abiotic soil community during the test experiment through inclusion of all inocula in each treatment and creating the living soil community treatments from one species by sterilizing the inocula of the other species (Bever 1994).

Using this approach, we have observed negative feedbacks on growth and survival of plant species which coexist in a North Carolina grassland community (Bever 1994). For example, *Krigia dandelion* (L.) Nutt. had a significantly higher mortality when grown with soil communities which it previously cultured than when grown with soil communities previously cultured by other plant species. There was also negative feedback on growth rates among the grass species pairs, *Anthoxanthum odoratum* L. vs. *Panicum sphaerocarpon* Ell. and *Anthoxanthum* vs. *Danthonia spicata* (L.) Beauv. (Bever 1994). We found negative feedback among seven of the eleven pairwise comparisons, indicating the importance of the process in this community (Bever 1994; Fig. 4). Moreover, we have found that the feedbacks can occur within 3 months (J. D. Bever, unpublished data) and are reproducible in both laboratory and field conditions (Westover 1995). From these quite simple experiments we have provided strong evidence for the potential importance of the soil community in maintaining diversity within plant communities.

AGENTS OF FEEDBACK ON PLANT GROWTH THROUGH THE SOIL COMMUNITY

While the simple dynamical consequences of feedback do not depend upon knowledge of the soil components that are responsible, such information is certainly desirable and could improve dynamical predictions. Feedback can result from changes in the density or composition of the communities of mutualists or pathogens (Table 1). For example, negative feedback could result when the presence of a plant causes an increase in the density of a host-specific pathogen. However, negative feedback could also result when the presence of a plant causes a change in the composition of mutualists. This possibility is not often appreciated, but can be illustrated as follows. If we imagine two plant species, A and B, and two species of soil mutualists (AM fungi for example), X and Y, such that fungal species X delivers the greatest benefit to plant A and fungal species Y delivers the greatest benefit to plant B, then positive feedback will result when the presence of plant A causes an increase in the proportion of fungus X (Fig. 5a). Alternatively, negative feedback on plant growth through changes in the composition of mutualists will result when the presence of plant A results in a decrease in the proportion of fungus X thereby decreasing the benefit received by plant A from the mycorrhizal fungi, relative to that received by Plant B (Fig. 5b; Bever 1992). In a similar manner we could get a positive feedback through changes in the composition of the community of pathogens. Thus, simple knowledge of the presence of mutualists or pathogens in the soil community does not necessarily lend itself to expectations of positive or negative feedback.

The agents of negative feedback through the soil community in agricultural systems have often been identified as species-specific pathogens (e.g. Kollmorgen *et al.* 1985), though occasionally the agent of feedback remains unclear, even in well studied systems. For example, an as yet unidentified component of the soil community has been implicated in the yield decrease due to repeated cropping of corn (Odell *et al.* 1982). Moreover, work in agricultural systems also demonstrates that it is possible to have contrary feedbacks through different components of the soil community which act over different temporal scales. For example, repeated cropping of watermelon will first result in the reduction of yield due to the accumulation of the soil pathogen, *Fusarium oxysporum*. However, the severity of this disease decreases with increasing crops of watermelon due to a change in composition of other components of the soil community (Larkin *et al.* 1993). The dynamical consequences of such contrary forces remain unexplored, but they suggest an important source of non-linearity in plant response to the cultured soil community.

As in agroecosystems, the agents of the feedbacks through the soil community in natural communities

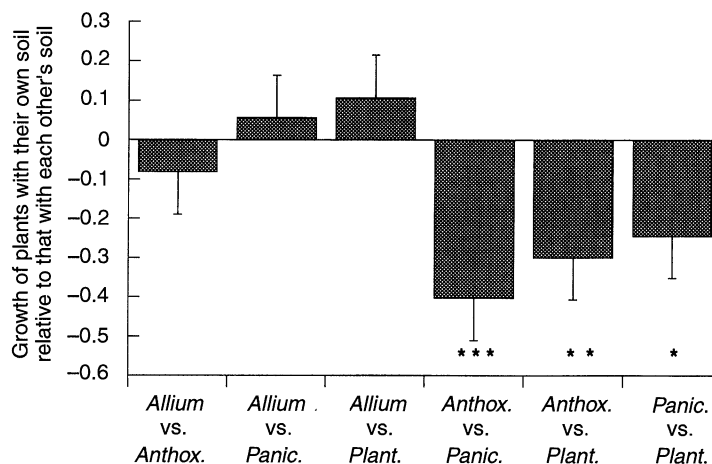


Fig. 4 Test of feedback through the soil community on growth rates of four plant species. Four perennial plant species were grown with soil communities which had been previously cultured by these same plant species (Bever *et al.* 1996). The sign and significance of feedback is tested as the difference between growth of plants with their own soil community and growth with each others soil communities for all pairs of species (the interaction coefficient, I_s). For example, in the *Anthoxanthum*–*Panicum* comparison, the magnitude and sign of feedback is determined by summing the growth of *Anthoxanthum* and *Panicum* in their own soils and subtracting the growth of *Anthoxanthum* and *Panicum* in each others soils. These differences are significantly less than zero, indicating negative feedback, for three of the six pairs of species (*, **, and *** represent $P < 0.05$, 0.01, and 0.001, respectively).

Table 1 Potential agents of feedback on plant growth through the soil community. Feedback can result from changes in the density or composition of the communities of mutualists or pathogens. For example, negative feedback could result when the presence of a plant causes an increase in the density of a host-specific pathogen. However, negative feedback could also result when the presence of a plant causes a changes in the composition of mutualists

	Positive feedback	Negative feedback
Community of mutualists	Increase in density Change in frequency	Change in frequency
Community of pathogens	Change in frequency	Increase in density Change in frequency

may be difficult to identify. For example, the degeneration of conditions for the early successional coastal dune grass, *Ammophila arenaria*, results both from accumulation of parasitic nematodes and from accumulation of fungal pathogens (Van der Putten *et al.* 1990; Rooij-van der Goes 1995). The exact identity

of the nematodes, the fungi, and the nature of their interactive effects remain unclear. The accumulation of species-specific pathogens may similarly be important in the negative feedback we have observed among coexisting grassland species in North Carolina. We have isolated five species of *Pythium* from these

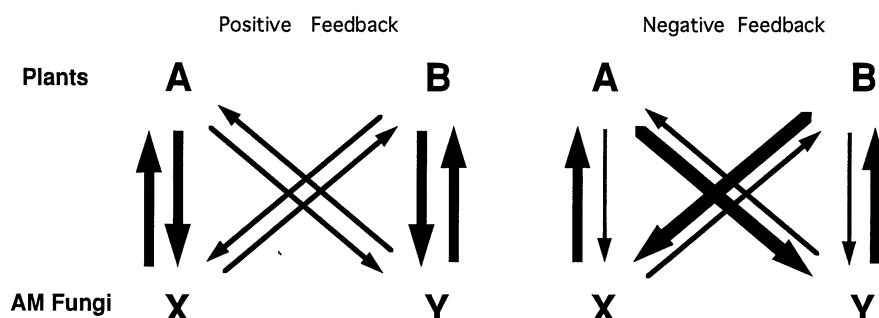


Fig 5 Feedback due to changes in composition of the community of soil mutualists. The direction of benefit delivered between two plant species, A and B, and their fungal mutualists, X and Y, are indicated by the arrows, with the thickness of the arrow indicating the magnitude of benefit. In Fig. 5a, the presence of plant A will result in an increase in the frequency of fungus X relative to fungus Y, which will then increase the rate of growth of plant A relative to plant B (resulting in positive feedback). Alternatively, in the relations represented in Fig. 5b, the presence of plant A will result in a decrease in the frequency of fungus X relative to fungus Y, which will then decrease the rate of growth of plant A relative to plant B (resulting in negative feedback).

grasses and these soil pathogens were found to exert species-specific effects on plant growth (K. Mills & J. D. Bever, unpublished data). However, we have also found the relative rates of growth of bacterial and mycorrhizal fungal species to be highly host-dependent, leading to host-specific shifts in these components of the soil community (Westover 1995; Bever *et al.* 1996). Preliminary analyses suggest that changes in the mycorrhizal community are involved in the negative feedback between *Plantago lanceolata* and *Panicum sphaerocarpon* (J. D. Bever, unpublished data). These examples illustrate that phenomenological observations of feedback can be fruitfully followed up with investigations of the detail of the microbial mechanism.

ECOLOGICAL IMPLICATIONS OF FEEDBACK

Because sessile organisms such as plants cannot escape the local and species-specific effects of their environment, positive or negative feedback through their environment may have important consequences for their population dynamics and community structure. Previous work on environmental feedback has largely focused on processes involved in the succession of plant communities. Succession in severe environments has long been considered to result from early plant communities altering the abiotic environment in a manner which increases the growth rate of other species relative to their own, i.e. negative feedback (Clements *et al.* 1928; Connell & Slayter 1977). In New England salt marshes, for example, pioneer species alleviate salt stress, which facilitates their replacement by other plant species (Bertness & Shumway 1993; Bertness & Hacker 1994). Similarly, as described previously, pioneer species in a dune community have been shown to change the soil community in a manner which facilitates their replacement by other plant species (Van der Putten *et al.* 1993). Alternatively, positive feedback through the environment is known to operate in other successional processes. For example, the invasive introduced grass, *Bromus tectorum*, replaces native sage brush communities in the arid western United States by causing an increase in the frequency of fire, a disturbance under which the grass performs exceptionally well (Stewart & Hull 1949; Melgoza *et al.* 1990; Billings 1993). While in these situations environmental feedback resulted in community replacements, we have argued that such processes might be equally important in determining coexistence within communities.

Feedback through the soil community on plant population growth rates could play an important role in the maintenance of plant species diversity through two alternate routes. Direct negative feedback between plants and their soil communities may be an important unexplored mechanism for the coexistence of plant species within an ecological neighbourhood (*sensu* Antonovics & Levin 1980). Results of our work

suggest that this mechanism may be important in the maintenance of diversity within old field communities. Furthermore, work on the incidence of damping-off disease incidence also suggests that negative feedback through an increased density of soil pathogens may be important in maintaining the high diversity of trees in tropical forests (Augsburger & Kelly 1984; Augspurger 1990). Alternatively, while positive feedback would facilitate the loss of diversity within an ecological neighbourhood, it may play an important role in maintaining species diversity between ecological neighbourhoods.

The relative importance of indirect effects through changes in the soil community and the more direct effects of competition for resources is unknown. Several studies have shown that indirect effects between plant species can be of substantial magnitude, sometimes being equivalent or even larger than direct effects (Silander & Antonovics 1982; Miller 1994). The substantial pairwise feedbacks through changes in the soil community that we have observed in our study system may result from direct effects of the soil community on the growth of an individual plant (α_A and β_B in Fig. 1). Alternatively, the change in the soil community may alter the growth rate or competitive ability of a neighbouring plant and thus may then feed back on the growth rate of the original plant (α_B and β_A in Fig. 1). In this latter scenario, negative feedback may result from indirect beneficial effects through the soil communities on the growth rate of the other species. If this occurs reciprocally, it would lead to the appearance of mutualistic interactions between plant species *sensu* Levine (1976) and Vandermeer (1980). Similarly, positive feedback through the soil community may result from indirect negative effects on a competing plant species generating the appearance of greater competition (Holt 1977, 1984).

EVOLUTIONARY IMPLICATIONS OF FEEDBACK

The consequences of natural selection are simple to understand when the environment is constant. In fact, the adaptation of plants to relatively unchanging aspects of their mineral soil environment has served as a paradigm example of the process of evolution by natural selection (Shaw 1990). It is much more difficult to predict the consequences of natural selection when the environment itself changes in response to the presence of the organism. Feedbacks through the soil community may create selective forces which run counter to those from differences in the mineral soil (Bever 1992). This problem is by no means peculiar to the plant-soil community interaction, but is true of other coevolving systems (Levin & Udovic 1977). The plant-soil community interaction, however, is ideally suited for the investigation of the evolutionary process because of the ease with which plant genotypes and the soil community can be replicated.

We have evidence that feedback through the soil

community might be involved in the maintenance of dominant modes of reproduction in two plant species. Sexual reproduction may be advantageous when genotypes within a population experience strong negative environmental feedback on fitness (which would generate negative frequency dependence). In *Anthoxanthum odoratum*, which predominantly reproduces sexually, we have found both negative frequency-dependent selection in the field (Antonovics & Ellstrand 1984; Kelley *et al.* 1988) and negative feedback through soil community between genotypes in the laboratory (Fig. 6). Alternatively, asexual reproduction may be advantageous when genotypes within a population experience a strong positive environmental feedback on fitness (which would generate positive frequency dependence). Ronsheim (1996) has found positive frequency-dependent selection in the field within *Allium vineale*, which predominantly reproduces through asexual bulbils. Using components from this same site, we have found positive feedback through the soil community between genotypes of *Allium* (Fig. 6).

While the nature of the environmental feedback will influence the evolution of plant growth form and life histories, it is also true that the growth form and life history of a species will influence the evolution of the interaction of the plant and soil. In one example, Van der Putten *et al.* (1988) notes that the dune grass, *Ammophila*, grows vertically through accreting sand and, in the process, escapes the negative effects of its soil community. In this case, it seems likely that *Ammophila* evolved the vertical rhizomes as an adaptation to its dune environment. Alternatively, given its habit of growing away from its previous rhizo-

sphere, it is possible that it reduced investment in chemical or other defences for its root system, making it vulnerable to pathogenic fungi and nematodes.

In summary, we have introduced the theoretical and experimental framework of feedback as a tool to assess the importance of the soil community in critical issues concerning the ecology and evolution of plants. For example, our observations of strong negative feedback between plant species suggest that feedback through changes in the soil community may play an important role in the maintenance of diversity in plant communities. Thus, while previous empirical and theoretical work on the maintenance of plant species diversity has focused almost exclusively on competition for abiotic resources, we present evidence for the potential importance of the soil community. Moreover, using this framework, we have obtained evidence suggesting that the soil community could be involved in such evolutionary phenomena as the maintenance of dominant modes of reproduction in plant populations. Finally, our conceptualization links major questions in population and community ecology to the wealth of data on negative feedback and the common practice of crop rotation in agricultural settings. Further work on the environmental feedback in natural systems, particularly on its spatial and temporal scale, agents and consequences, may in turn provide important insights into the workings and management of sustainable agricultural systems.

Acknowledgements

Previous versions of this manuscript were improved by the suggestions and conversations with H. Alex-

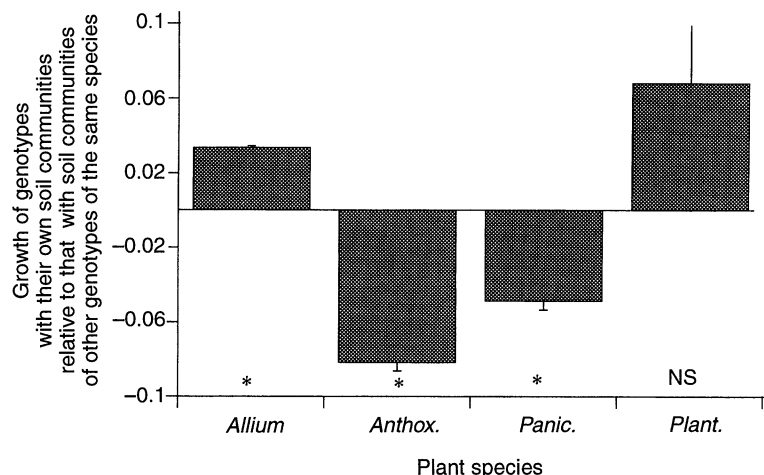


Fig 6 Test of feedback through the soil community between individual genotypes of four plant species. For each of four perennial plant species, replicates of six genotypes were grown with soil communities which had been previously cultured by these same genotypes (Bever *et al.* 1996). The sign and significance of feedback is tested within each species separately as the difference between growth of plants with soil communities previously cultured by their own genotype and growth with the soil communities previously cultured by other genotypes of the same species. For example, the magnitude and sign of feedback between genotypes of *Allium* is determined by summing the growth of the six *Allium* genotypes in their own soils and subtracting the growth of these genotypes in each others soils. This difference is significantly greater than zero, indicating positive feedback among genotypes of *Allium*, a species which predominantly reproduces through asexual reproduction. For *Anthoxanthum* and *Panicum*, the difference is significantly less than zero indicating negative feedback between genotypes within these predominantly sexually reproducing species (* represents $P < 0.05$).

ander, P. Thrall, M. Rausher, A. Pringle, E. Macklin, P. Schultz, A. Fitter, L. Haddon and two anonymous referees. We are grateful for the support of USDA grants 92-37101-7461 and 94-37101-0354 and NSF grant DEB-9615941.

References

- Aarssen, L.W. (1989) Competitive ability and species coexistence: a 'plant's-eye view.' *Oikos*, **56**, 386-401.
- Albrecht, S.L., Okon, Y., Lonnquist, J. & Burton, R.H. (1981) Nitrogen fixation by corn-*Azospirillum* associations in a temperate climate. *Crop Science*, **21**, 301-306.
- Allen, E.B. & Allen, M.F. (1990) The mediation of competition by mycorrhizae in successional and patchy environments. *Perspectives on Plant Competition* (eds J. B. Grace & D. Tilman), pp. 367-390. Academic Press, San Diego, California, USA.
- Antonovics, J. & Levin, D.A. (1980) The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics*, **11**, 411-452.
- Antonovics, J. & Ellstrand, N.C. (1984) Experimental studies of the evolutionary significance of sexual reproduction. I. A test of the frequency-dependent selection hypothesis. *Evolution*, **38**, 103-115.
- Atkinson, T.G., Neal, J.L. & Larson, R.L. (1975) Genetic control of the rhizosphere microflora of wheat. *Biology and Control of Soil-Borne Plant Pathogens* (ed. G. W. Bruehl), pp. 116-122. American Phytopathology Society, St. Paul, Minnesota.
- Augsburger, C.K. (1990) Spatial patterns of damping-off disease during seedling recruitment in tropical forests. *Pests, Pathogens and Plant Communities* (eds J. J. Burdon & S. R. Leather), pp. 131-144. Blackwell Scientific Publications, Oxford.
- Augsburger, C.K. & Kelley, C.K. (1984) Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, **61**, 211-217.
- Barr-Ness, E., Chen, Y., Hadar, Y., Marschner, H. & Roemheld, V. (1991) Siderophores of *Pseudomonas putida* as an iron source for dicot and monocot plants. *Plant and Soil*, **130**, 231-241.
- Bertness, M.D. & Shumway, S.W. (1993) Competition and facilitation in marsh plants. *American Naturalist*, **142**, 718-724.
- Bertness, M.D. & Hacker, S.D. (1994) Physical stress and positive associations among marsh plants. *American Naturalist*, **144**, 363-372.
- Bever, J.D. (1992) *Ecological and evolutionary dynamics of plants and their soil communities*. PhD thesis. Duke University, Durham.
- Bever, J.D. (1994) Feedback between plants and their soil communities in an old field community. *Ecology*, **75**, 1965-1977.
- Bever, J.D., Morton, J., Antonovics, J. & Schultz, P. (1996) Host-specificity and diversity of glomalean fungi: an experimental approach in an old field community. *Journal of Ecology*, **84**, 71-82.
- Billings, W.D. (1993) Ecological impacts of *Bromus tectorum* and resultant fire on ecosystems in the Western Great Basin. *Ecology, Management, and Restoration of Inter-Mountain Annual Rangelands* (ed. S. Monsen). US Forest Service, Ogden, Utah.
- Borga, P., Nilsson, M. & A. Tunlid. (1994) Bacterial communities in peat in relation to botanical composition as revealed by phospholipid fatty acid analysis. *Soil Biology and Biochemistry*, **26**, 841-848.
- Brandon, R. & Antonovics, J. (1996) The coevolution of organism and environment. *Concepts and Methods in Evolutionary Biology* (ed. R. Brandon), pp. 161-178. Cambridge University Press, Cambridge.
- Bruehl, G.W. (1987) *Soilborne Plant Pathogens*. Macmillan Publishing Co., New York, New York.
- Brundrett, M. (1991) Mycorrhizas in natural ecosystems. *Advances in Ecological Research*, **21**, 171-313.
- Burdon, J.J. (1987) *Diseases and Plant Population Biology*. Cambridge University Press, Cambridge, Massachusetts.
- Chanway, C.P. & Holl, F.B. (1993) First year performance of spruce seedlings inoculated with plant growth promoting rhizobacteria. *Canadian Journal of Microbiology*, **39**, 1084-1088.
- Chanway, C.P., Holl, F.B. & Turkington, R. (1989) Effect of *Rhizobium leguminosarum* biovar *trifoli* genotype on specificity between *Trifolium repens* and *Lolium perenne*. *Journal of Ecology*, **77**, 1150-1160.
- Chanway, C.P., Turkington, R. & Holl, F.B. (1991) Ecological implications of specificity between plants and rhizosphere micro-organisms. *Advances in Ecological Research*, **21**, 121-169.
- Clements, F.E., Weaver, J. & Hansson, H. (1928) *Plant competition: an analysis of the development of vegetation*. Carnegie Institute, Washington, DC, USA.
- Connell, J.H. & Slayter, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119-1144.
- Cook, R.J. (1981) The influence of rotation crops on take-all decline phenomenon. *Phytopathology*, **71**, 189-192.
- Crowley, D.E., Want, Y.C., Reid, C.P.P. & Szanislo, P.J. (1991) Mechanisms for iron acquisition from siderophores by micro-organisms and plants. *Plant and Soil*, **130**, 179-198.
- den Boer, P.J. (1986) The present status of the competitive exclusion principle. *Trends in Ecology and Evolution*, **1**, 25-28.
- Derylo, M. & Skorupska, A. (1992) Rhizobial siderophore as an iron source for clover. *Physiology of Plants*, **85**, 549-553.
- Edelstein-Keshet, L. (1988) *Mathematical Models in Biology*. Random House, New York.
- Fitter, A.H. (1977) Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. *New Phytologist*, **79**, 119-125.
- Goldberg, D. & Werner, P.A. (1983) Equivalence of competitors in plant communities: a null hypothesis and an experimental field approach. *American Journal of Botany*, **70**, 1098-1104.
- Grace, J.B. & Tilman, D. (1990) *Perspectives on Plant Competition*. Academic Press, San Diego, California, USA.
- Hall, J.R. (1978) Effects of endomycorrhizas on the competitive ability of white clover. *New Zealand Journal of Agricultural Research*, **21**, 509-515.
- Handman, H., Weller, D.M. & Thomashow, L.S. (1991) Relative importance of fluorescent siderophores and other factors in biological control of *Gaeumannomyces graminis* var. *tritici* by *Pseudomonas fluorescens* 2-79 and M4-80R. *Applied Environmental Microbiology*, **57**, 3270-3277.
- Harinikumar, K.M. & Bagyaraj, D.J. (1988) Effect of crop rotation on native vesicular arbuscular mycorrhizal propagules in soil. *Plant and Soil*, **110**, 77-80.
- Hartnett, D.C., Hetrick, B.A.D., Wilson, G.W.T. & Gibson, D.J. (1993) Mycorrhizal influence on intra- and inter-specific neighbour interactions among co-occurring prairie grasses. *Journal of Ecology*, **81**, 787-795.

- Hetrick, B.A.D. (1984) Ecology of VA mycorrhizal fungi. *VA Mycorrhizae* (eds C. L. Powell & D. J. Bagyaraj), pp. 35–56. CRC Press, Boca Raton, Louisiana, USA.
- Hetrick, B.A.D., Hartnett, D.C., Wilson, G.W.T. & Gibson, D.J. (1994) Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. *Canadian Journal of Botany*, **72**, 168–176.
- Hetrick, B. & Wilson, G. (1989) Relationship between mycorrhizal dependence and competitive ability of two tall prairie grasses. *Canadian Journal of Botany*, **67**, 2608–2615.
- Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Holt, R.D. (1984) Spatial heterogeneity, indirect interactions and the coexistence of prey species. *American Naturalist*, **124**, 377–406.
- Johnson, N.C., Pflieger, F.L., Crookston, R.K., Simmons, S.R. & Copeland, P.J. (1991) Vesicular-arbuscular mycorrhizas respond to corn and soybean cropping history. *New Phytologist*, **117**, 657–663.
- Johnson, N.C., Tilman, D. & Wedin, D. (1992) Plant and soil controls on mycorrhizal fungal communities. *Ecology*, **73**, 2034–2042.
- Keever, C. (1950) Causes of succession on old fields of the piedmont, North Carolina. *Ecological Monographs*, **20**, 229–250.
- Kelley, S.E., Antonovics, J. & Schmitt, J. (1988) A test of the short-term advantage of sexual reproduction. *Nature*, **331**, 714–716.
- Kollmorgen, J.F., Griffiths, J.B. & Walsgott, D.N. (1985) Effects of cropping sequence on saprophytic survival and carry over of *Gaeumannomyces graminis* var. *tritici*. *Ecology and Management of Soilborne Plant Pathogens* (eds C. A. Parker, A. D. Rovira, K. J. Moore, P. T. Wong & J. F. Kollmorgen), pp. 240–242. American Phytopathology Society, St. Paul, Minnesota.
- Larkin, R.P., Hopkins, D.L. & Martin, F.N. (1993) Effect of successive watermelon plantings on *Fusarium oxysporum* and other micro-organisms in soils suppressive and conducive to *Fusarium* wilt of watermelon. *Phytopathology*, **83**, 1097–1105.
- Levine, S.H. (1976) Competitive interactions in ecosystems. *American Naturalist*, **110**, 903–910.
- Levin, S.A. & Udovic, J.D. (1977) A mathematical model of coevolving populations. *American Naturalist*, **111**, 657–675.
- Lie, T.A., Götkan, D., Emgin, M., Pijnenborg, J. & Anlarsal, E. (1987) Co-evolution of the legume–*Rhizobium* association. *Plant and Soil*, **100**, 171–181.
- Melgoza, G., Nowak, R.S. & Tausch, R.J. (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia*, **83**, 7–13.
- Miller, T.E. (1994) Direct and indirect species interactions in an early old-field plant community. *American Naturalist*, **143**, 1007–1025.
- Molofsky, J. (1993) *Population dynamics and pattern formation in populations: theoretical models and empirical tests using Cardamine pennsylvanica*. PhD thesis. Duke University, Durham.
- Mytton, L.R. (1975) Plant genotype \times *Rhizobium* strain interactions in white clover. *Annals of Applied Biology*, **80**, 103–107.
- Mytton, L.R. & Hughes, D.M. (1984) Inoculation of white clover with different strains of *Rhizobium trifoli* on a mineral hill soil. *The Journal of Agricultural Science*, **102**, 455–459.
- Neitko, K.F. & Frankenberg, W.T. Jr (1989) Biosynthesis of cytokinins in soil. *Journal of the Soil Science Society of America*, **53**, 735–740.
- Nemec, S. (1978) Response of six citrus rootstocks to three species of *Glomus*, a mycorrhizal fungus. *Proceedings of the Florida State Horticulture Society*, **91**, 10–14.
- Newsham, K.K., Fitter, A.H. & Watkinson, A.R. (1995) Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. *Journal of Ecology*, **83**, 991–1000.
- Odell, R.T., Walter, W.M., Boone, L.V. & Oldham, M.G. (1982) The morrow plots: a century of learning. *Bulletin of the University of Illinois Agriculture Experiment Station*, **775**, 22.
- Olsson, S. & Gerhardson, B. (1992) Effects of long-term barley monoculture on plant-affecting soil microbiota. *Plant and Soil*, **143**, 99–108.
- Ravnskov, S. & Jakobsen, I. (1995) Functional compatibility in arbuscular mycorrhizas measured as hyphal P transport to the plant. *New Phytologist*, **129**, 611–618.
- Ronsheim, M.L. (1996) Evidence against a frequency dependent advantage for sexual reproduction in *Allium vineale*. *American Naturalist*, **147**, 718–733.
- Rooij-van der Goes, P.C.E.M. (1995) The role of plant-parasitic nematodes and soil-borne fungi in the decline of *Ammophila arenaria* (L.) Link. *New Phytologist*, **129**, 661–669.
- Roughgarden, J. (1979) *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan, New York.
- Sanders, I.R. & Fitter, A.H. (1992) Evidence for differential responses between host-fungus combinations of vesicular-arbuscular mycorrhizas from a grassland. *Mycological Research*, **96**, 415–419.
- Silander, J.A. & Antonovics, J. (1982) Analysis of interspecific interactions in a coastal plant community – a perturbation approach. *Nature*, **298**, 557–560.
- Shaw, A.J. (1990) *Heavy Metal Tolerance in Plants: Evolutionary Aspects*. CRC Press, Boca Raton, Florida.
- Shipton, P.J. (1977) Monoculture and soilborne plant pathogens. *Annual Review of Phytopathology*, **15**, 387–407.
- Silvertown, J. & Law, R. (1987) Do plants need niches? Some recent developments in plant community ecology. *Trends in Ecology and Evolution*, **2**, 24–26.
- Stewart, G. & Hull, A.C. (1949) Cheatgrass (*Bromus tectorum* L.) – An ecological intruder in southern Idaho. *Ecology*, **30**, 58–74.
- Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. (1997) Clonal growth traits of two *Prunella* species are determined by co-occurring arbuscular mycorrhizal fungi from a calcareous grassland. *Journal of Ecology*, in press.
- Tate, R.L. (1995) *Soil Microbiology*. Wiley and Sons, Inc. New York, New York.
- Tein, T.M., Gaskins, M.H. & Hubbell, D.H. (1979) Plant growth substances produced by *Azospirillum brasilense* and their effect on the growth of pearl millet (*Pennisetum americanum*). *Applied Environmental Microbiology*, **37**, 1016–1024.
- Thomashow, L.S. & Weller, D.M. (1990) Role of antibiotics and siderophores in biocontrol of take-all disease in wheat. *Plant and Soil*, **129**, 93–99.
- Tilman, D. & Pacala, S. (1993) The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R. E. Ricklefs & D. Schluter), pp. 13–25. University of Chicago Press, Chicago, Illinois, USA.
- Turkington, R., Holl, F.B., Chanway, C.P. & Thompson, J.D. (1988) The influence of microorganisms, particularly *Rhizobium*, on plant competition in grass-legume communities. *Plant Population Ecology* (eds A. J.

- Davy, M. J. Hutchings & A. R. Watkinson), pp. 343–366. Blackwell Scientific Publications, Oxford.
- Turkington, R. & Klein, E. (1991) Competitive outcome among four pasture species in sterilized and unsterilized soils. *Soil Biology and Biochemistry*, **23**, 837–843.
- Vandermeer, J.H. (1980) Indirect mutualisms: variations on a theme by Stephen Levine. *American Naturalist*, **116**, 441–448.
- Vandermeer, J.H. (1981) *Elementary Mathematical Ecology*. John Wiley and Sons, New York.
- Van der Putten, W.H., Mass, P.W. Th., Van Gulik, W.J.M. & Brinkman, H. (1990) Characterization of soil organisms involved in the degeneration of *Ammophila arenaria*. *Soil Biology and Biochemistry*, **22**, 845–852.
- Van der Putten, W.H. & Troelstra, S.R. (1990) Harmful soil organisms in coastal foredunes involved in degeneration of *Ammophila arenaria* and *Calammophila baltica*. *Canadian Journal of Botany*, **68**, 1560–1568.
- Van der Putten, W.H., Van Dijk, C. & Peters, B.A.M. (1993) Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature*, **362**, 53–56.
- Van der Putten, W.H., Van Dijk, C. & Troelstra, S.R. (1988) Biotic soil factors affecting the growth and development of *Ammophila arenaria*. *Oecologia*, **76**, 313–320.
- Watkinson, A.R. & Freckleton, R.P. (1997) Quantifying the impacts of arbuscular mycorrhizal fungi on plant competition. *Journal of Ecology*, **85**, 000–000.
- West, H.M. (1996) Influence of arbuscular mycorrhizal infection on competition between *Holcus lanatus* and *Dactylis glomerata*. *Journal of Ecology*, **84**, 429–438.
- Westover, K.M. (1995) *The role of rhizosphere soil microorganisms in plant competition and coexistence*. PhD thesis. Washington State University, Pullman.
- Young, N.R., Hughes, D.M. & Mytton, L.R. (1986) The response of white clover to different strains of *Rhizobium trifoli* in hill-land reseeded: a second trial. *Plant and Soil*, **94**, 277–284.

Received 5 November 1996
revision accepted 17 April 1997

Appendix

ANALYSES OF DYNAMICS DUE TO SOIL COMMUNITY FEEDBACK

As derived in the text, the expressions for instantaneous change of the frequency of plant type A among all plant

types (A and B), p_A , and of the frequency of soil effects of plant A, p_x are written as follows:

$$F_1 = \frac{dp_A}{dt} = p_A p_B [(\alpha_A - \alpha_B) p_x + (\beta_A - \beta_B) p_B] \quad (A1)$$

$$F_2 = \frac{dp_x}{dt} = p_x p_B (p_A - v p_B). \quad (A2)$$

The equilibrium conditions of these equations are derived by setting F_1 and F_2 equal to zero and then solving for p_A or p_x . Instantaneous change in p_A is zero where $p_A = 0$ or 1, or where $p_x = \hat{p}_x$, where

$$\hat{p}_x = \frac{\beta_B - \beta_A}{\alpha_A - \alpha_B - \beta_A + \beta_B} = \frac{\beta_B - \beta_A}{I_s}. \quad (A3)$$

Instantaneous change in p_x is zero where $p_x = 0$ or 1, or $p_A = \hat{p}_A$, where

$$\hat{p}_A = \frac{v}{1+v}. \quad (A4)$$

There will be an internal equilibrium when \hat{p}_x and \hat{p}_A are between 0 and 1. The value \hat{p}_x will be between 0 and 1 so long as one plant does not have higher fitness in both soil types (i.e. when $\alpha_A > \alpha_B$ and $\beta_B > \beta_A$ or when $\alpha_B > \alpha_A$ and $\beta_A > \beta_B$). The value \hat{p}_A will be between 0 and 1 provided $v > 0$.

The stability of the corner and internal equilibria can be assessed by evaluating the Jacobian Matrix of partial derivatives, \mathbf{J} at the equilibria (Roughgarden 1979; Vandermeer 1981; Edelman-Keshet 1988). The Jacobian Matrix,

$$\mathbf{J}_{(p_A, p_x)} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \quad (A5)$$

where

$$a_{11} = \partial F_1 / \partial p_A = [(\alpha_A - \alpha_B) p_x + (\beta_A - \beta_B) p_B](1 - 2p_A), \quad (A6)$$

$$a_{12} = \partial F_1 / \partial p_x = p_A p_B I_s \quad (A7)$$

$$a_{21} = \partial F_2 / \partial p_A = p_x p_B (1 + v), \text{ and} \quad (A8)$$

$$a_{22} = \partial F_2 / \partial p_x = [p_A - v p_B](1 - 2p_x). \quad (A9)$$

We identify the criteria for stability by evaluating the eigenvalues at the equilibria. At the internal equilibrium, a_{11} and a_{22} are equal to zero (therefore the trace of the matrix is also zero) and a_{21} is positive. Therefore, the stability of the internal equilibrium depends upon the sign of the interaction coefficient, I_s . When the interaction coefficient is positive ($I_s > 0$), the internal equilibrium is an unstable node (Fig. 2a). When the interaction coefficient is negative ($I_s < 0$), the internal equilibrium is a neutrally stable (Fig. 2b). Greater details of analysis and criteria for stability of corner equilibria are given in Bever (1992).