

Soil food web components affect plant community structure during early succession

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There is a growing awareness among ecologists of the strong links that exist between above- and belowground food webs. So far, the majority of studies have considered these links from the microbial point of view, usually with single plants or very simple plant communities. Here, we report the interactions between two components of the soil food web, root-feeding insects and arbuscular mycorrhizal (AM) fungi, and their effects on the structure and development of early successional plant communities. We use long-term field experiments that employ manipulations of these organisms, both singly and in combination. Both groups have strong effects on plant community structure, with root-feeding insects increasing and AM fungi decreasing plant species richness. Root-feeding insects appear to accelerate the process of early succession, while AM fungi retard it. There are strong interactions between the insects and fungi. The effect of insects is greatest when AM fungi are present. It is suggested that this is a consequence of plant physiology, rather than any direct interaction between the groups involved. Meanwhile, AM fungi have their greatest effect on plant communities when insects are absent, suggesting that there is some disruption of the symbiosis by the invertebrates. In developing plant communities, the rate and direction of the succession is therefore determined by the relative abundance of these two members of the soil food web. The next challenge will be to understand the roles of other members of the subterranean web in terms of their interactions with insects and AM fungi and effects on plant community development.

Key words: arbuscular mycorrhiza; food web; insect; plant community; root herbivory.

INTRODUCTION

Soil food webs are remarkably complex entities (Moore & De Ruiter 1997) and it is only recently that their links with aboveground plant productivity have begun to be acknowledged (Wardle 1999; Hooper *et al.* 2000). Soil food webs differ in many ways from aboveground webs, but perhaps one of the most important differences is in their function, namely that subterranean webs are responsible for most of the decomposition and nutrient cycling in ecosystems, while aboveground webs are responsible for productivity (i.e. carbon input). This difference occurs because subterranean

webs are dominated by microbial components. It is therefore not surprising that research involving interactions between web members or between subterranean and terrestrial webs have generally involved microbial studies (Wardle 1999).

Strong and detectable interactions between microbial members of subterranean webs and the larger invertebrates that also live in soil have been found. These interactions result in changes in nutrient availability which, in turn, can affect plant growth (e.g. Alphei *et al.* 1996; Zheng *et al.* 1997; Bardgett *et al.* 1999). Furthermore, activities of detritivorous animals in soil can also have effects on foliar-feeding insects, although the nature of these is not easily predictable (Scheu *et al.* 1999). So far, however, consequences of soil food web manipulation have only been examined at the level of individual plant productivity and, as Wardle (1999) points out, there is a dearth of studies on ecosystem-level responses.

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The lack of soil food web–plant community studies is in contrast to those that have attempted to manipulate aboveground plant productivity. There are now some excellent examples of how alteration of plant productivity (usually by defoliation) affects the soil food web structure (e.g. Mikola *et al.* 2001a,b). These experiments have shown that the interactions are complex, as some components of the soil biota (e.g. enchytraeids and microbivorous nematodes) are affected by particular combinations of the defoliated plant species. Meanwhile, for others (e.g. fungal-feeding nematodes), it is not so much the plant species identity that is important, but merely the amount of foliage that is removed.

Two components of the soil food web that have known effects on plant community structure are root-feeding insects and arbuscular mycorrhizal (AM) fungi. Rhizophagous insects are the poor relation compared with terrestrial insects in the ecological literature. In reviews of root herbivory, studies on these insects represent about 1 or 2% of all insect-plant studies (Brown & Gange 1990; Hunter 2001). Nevertheless, experiments involving the careful application of soil insecticides have demonstrated that, in early succession in southern England, root-feeding insects have dramatic effects on plant community structure (Brown & Gange 1989a, 1992). Root herbivory reduces the establishment and growth of perennial forbs and thus decreases plant species richness (Brown & Gange 1989a). In this way, root-feeding insects accelerate the rate of succession during early seres, as they hasten the disappearance of perennial forbs, thereby promoting perennial grass dominance (Brown & Gange 1989b).

Meanwhile, in similar early successional communities, AM fungi have been shown to enhance plant species richness, through increased establishment of annual and perennial forbs (Gange *et al.* 1993). Similar results have been obtained in microcosms (Grime *et al.* 1987), although it may not be the presence of AM fungi that affects plant diversity, but rather the diversity of the fungal species (Van Der Heijden *et al.* 1998). There is thus a situation in which two members of the soil food web, when manipulated in isolation, produce contrasting effects on plant community structure and dynamics. If we are to understand how soil food web architecture affects plant community compo-

sition, then experiments in which more than one component of the web is manipulated at a time must be undertaken.

Such multitrophic experiments, although important, are difficult, because of the interactions that can occur between the web components themselves. In the case of rhizophagous insects and AM fungi, the interactions are again complex and laboratory results may not be well reflected in the field. The evidence suggests that if plants are colonized by one species of AM fungus, then growth and survival of root-feeding insects is reduced (Gange *et al.* 1994). However, if multiple combinations of fungi are present, then there is no inhibitory effect on the rhizophage (Gange 2001). It appears that in natural situations, multiple colonization of plant roots by AM species is the norm (e.g. Clapp *et al.* 1995) and so it is possible that root feeders may be unaffected by the presence of mycorrhizas in field situations.

To our knowledge, only one experiment has investigated the interaction between root-feeding insects and AM fungi in determining plant community composition. Gange and Brown (1993) found that in a ruderal plant community, AM fungi increased plant growth, but this effect was only clearly seen when insects were absent. Meanwhile, insect herbivory reduced plant growth, with the effect being most clearly seen when fungi were present. The former result suggests that insect herbivores disrupt the symbiosis in some way, while the latter suggests that AM fungi do not affect insect herbivores in the field. These experiments were relatively short term (2 years) and the intention of the current paper is to investigate trends over a longer time scale, while using a similar experimental protocol. Here, we report the effects of manipulating the root-feeding insect and AM components of the soil food web over a 5-year period, covering the development of an early successional plant community. The period also encompasses a severe drought in year 3, which enables assessment of trends under such stochastic events.

EXPERIMENTAL SYSTEM AND METHODS

An experimental site, measuring 500 m² was treated with the herbicide glyphosate in autumn,

shallow-ploughed during winter and hand-raked in spring. The soil was sandy and acidic (pH 5.4), with an available phosphate level of $3.5 \pm 0.5 \mu\text{g g}^{-1}$ (bicarbonate extractable). Four experimental treatments were established: (i) application of the granular soil insecticide Dursban 5G (containing 5% w/w chlorpyrifos; Dow Agro-Sciences, Hitchin, Hertfordshire, UK) at the rate of 18 g of product per plot; (ii) application of the granular soil fungicide Rovral (containing 10% w/w iprodione; Rhone-Poulenc, Ongar, Essex, UK) at the rate of 20 g of product per plot; (iii) application of both products; and (iv) application of neither (controls). There were four replicates of each treatment, arranged in a randomized block design. In all cases, the chemicals were applied immediately before rain was forecast, so that they were washed into the soil, to reduce activity on the surface. Applications took place at monthly intervals, beginning in April. In any experiment of this type, it is impossible to guarantee against all non-target effects of the chemicals used. However, previous work by the authors has indicated that neither pesticide has any effect on the abundance of the other target group. In current experiments, chlorpyrifos kills root-feeding insects, but not earthworms, nematodes or mites (A. F. Currie, unpubl. data, 2002), while iprodione does have small effects on total fungal biomass in the soil. However, the latter are very small in comparison with the effects seen on AM fungal colonization (e.g. Gange *et al.* 1993).

The developing vegetation was sampled at 3-weekly intervals during the first growing season (May–October) and thereafter at monthly intervals. On each occasion, a 38-cm linear steel grid, containing 10 3-mm point quadrat pins was placed randomly five times within each plot. The number of touches of all living plant material was recorded on each pin for all plant species. Data were condensed to provide information on the total cover abundance of the whole sward and that of the major life-history groups (annual and perennial forbs and perennial grasses). In each season, the abundance of each group and that of the whole sward were analyzed with a repeated measures ANOVA, employing insecticide and fungicide as main effects.

To determine the efficacy of the insecticide treatment, three 5-cm diameter soil cores were

taken from each plot at the end of each growing season and extracted using a Berlese-Tullgren funnel (Southwood & Henderson 2000). Root-feeding insects were sorted to order and counted. To provide estimates of AM colonization, three seedlings of *Plantago lanceolata* L. were planted into each plot in August of each year and removed 6 weeks later. Roots were washed and arbuscular colonization revealed with autofluorescence microscopy (Gange *et al.* 1999) and levels recorded by the cross-hair eyepiece method of McGonigle *et al.* (1990).

RESULTS

Efficacy of the treatments

Figure 1a depicts the density of root-feeding insects at the end of the fifth growing season. These data are typical of the other years of the study, with the exception of year 3 when a drought

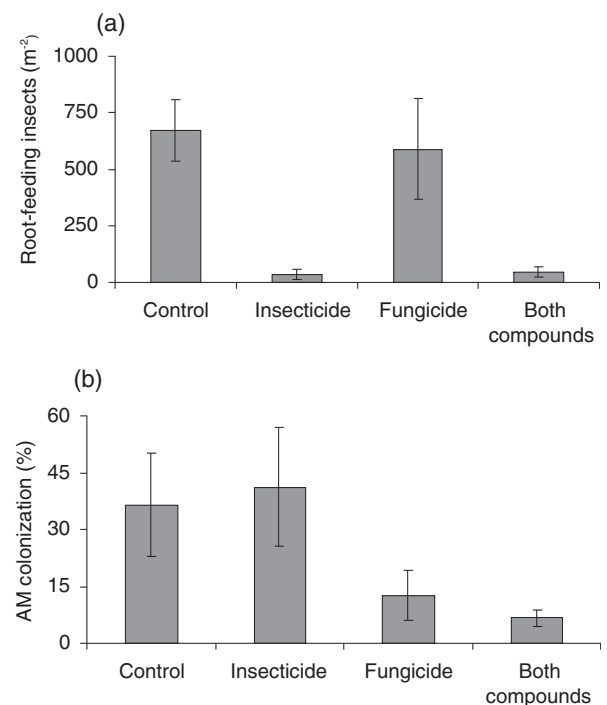


Fig. 1. Effect of insecticide and fungicide application on (a) root feeding insect density and (b) arbuscular mycorrhizal (AM) colonization of *Plantago lanceolata* in successional plots of 5 years of age. Values are mean \pm 1 SE.

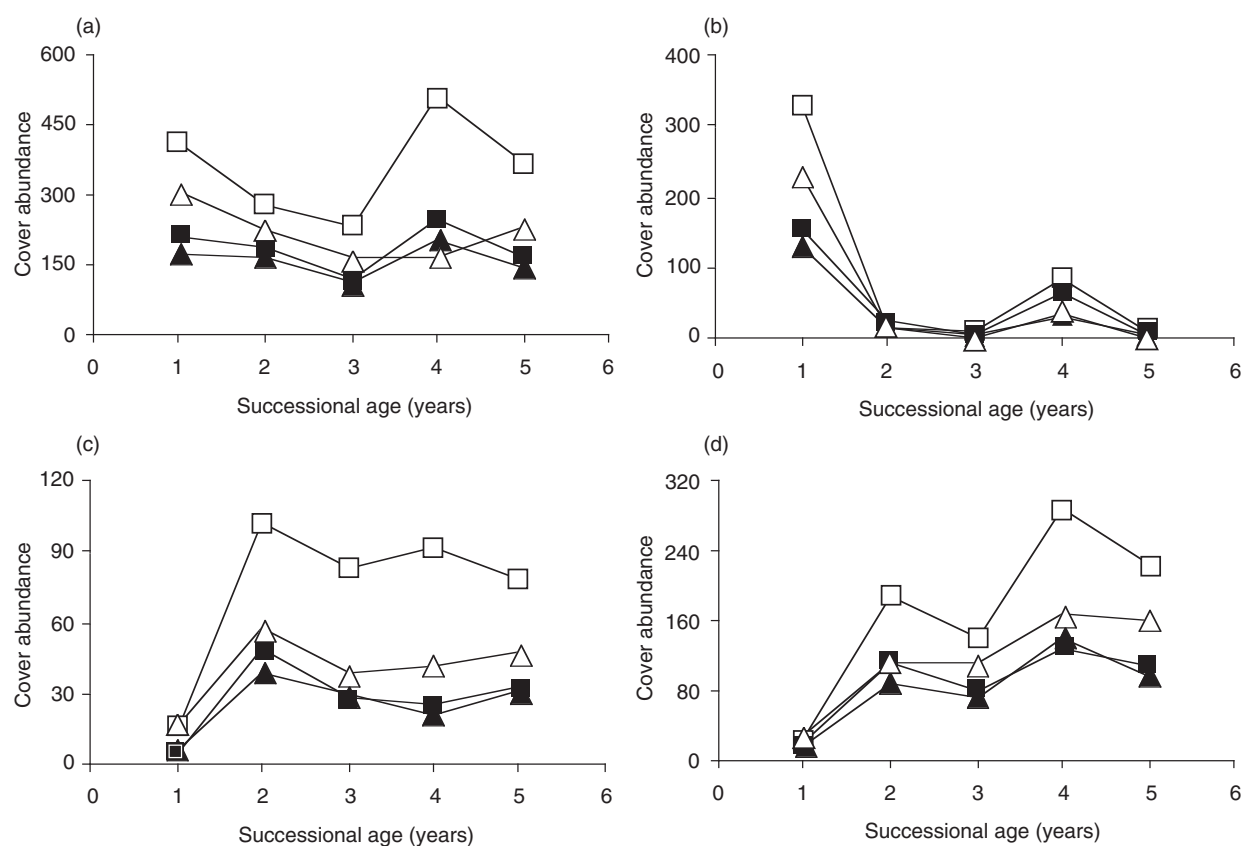


Fig. 2. Successional trends in (a) total community cover abundance, (b) cover abundance of annual forbs, (c) cover abundance of perennial forbs and (d) cover abundance of perennial grasses. Values plotted are seasonal means of treatments. (■) Control (natural levels of root-feeding insects and AM fungi); (□) soil insecticide treated; (▲) soil fungicide treated; (△) soil insecticide and fungicide treated.

affected the site for much of the summer. The density of insects was much reduced in that year and no significant treatment effects were seen. In year 5, insecticide significantly reduced the abundance of root-feeding insects ($F_{1,12} = 190.6$, $P < 0.001$), while application of fungicide had no effect. There was no interaction between the treatments. Meanwhile, fungicide application significantly reduced the AM colonization levels of *P. lanceolata* bait plants ($F_{1,12} = 83.1$, $P < 0.001$), but colonization was unaffected by insecticide application. Again, there was no interaction between the treatments. The mycorrhizal data are typical of other years of the study, with the exception of year 3, when the drought reduced levels of colonization. In year 3, the amount of rainfall between May and September (68 mm) was only 45% of the 25-year mean. Years 1, 2 and 5 were similar to the norm, but year 4 was also exceptional, with rainfall being 167% of the norm.

Plant community attributes

Seasonal means of plant community attributes over the 5-year period are shown in Fig. 2. The successional sequence was slightly unusual, because of the drought in mid summer of year 3. A statistical summary of the main effects and their interactions is presented in Table 1. Throughout the course of the study, there was a highly significant effect of reducing root herbivory on total cover abundance (Fig. 2a). Plots in which soil insects were reduced in number generally contained about twofold as much vegetation as control plots. In contrast, reduction of AM fungi significantly reduced the amount of vegetative cover in all years except year 2. In fungicide-treated plots, the amount of vegetation was generally about 80% of that in the control plots. From year 3 onwards, there were significant interactions between the two treatments (Table 1). In all cases, there was little

Table 1 Summary of ANOVA *F*-values from repeated measures ANOVA, testing for the main effects of soil insect reduction (I), AM fungal reduction (F) and the interactions between them (I*F) on plant community attributes over a 5-year successional sequence

	Year 1			Year 2			Year 3			Year 4			Year 5		
	I	F	I*F	I	F	I*F	I	F	I*F	I	F	I*F	I	F	I*F
Total cover	31.7***	5.7*	1.3	10.6**	2.4	0.93	35.5***	10.1**	4.75*	24.3***	20.6***	8.9*	101.2***	31.1***	14.9**
Annual forbs	28.4***	5.7*	2.0	0.23	1.95	0.25	0.52	2.51	1.52	0.65	5.92*	0.11	0.29	2.1	0.72
Perennial forbs	3.51	0.08	0.1	24.6***	14.8**	5.95*	9.7**	4.5*	5.1*	21.5***	8.1*	6.1*	19.2***	6.5*	5.5*
Perennial grasses	1.1	0.03	0.3	20.4***	19.3***	5.2*	7.99*	1.1	0.3	14.2**	4.9*	7.3*	51.5***	13.3**	5.4*
Species richness	15.4**	10.4**	1.9	10.8**	7.1*	0.3	1.7	0.7	0.4	17.8**	11.7**	1.3	5.2*	3.9	9.6**
Grass : forb ratio	0.38	0.06	0.18	1.67	1.08	0.31	0.04	2.06	0.18	44.6***	8.5*	1.7	14.9**	6.7*	0.13

All degrees of freedom: 1,12. ****P* < 0.001, ***P* < 0.01, **P* < 0.05.

effect of fungicide when insects were present (compare the solid symbols in Fig. 2a), but a much greater effect when insects were absent (compare the open symbols in Fig. 2a). Meanwhile, the interaction term can also be examined from the insecticide point of view. Here, it can be seen that the effect of reducing insects when AM fungi were present (compare the square symbols in Fig. 2a) was much greater than when fungi were absent (compare the triangular symbols in Fig. 2a).

The effects seen in the ruderal community of year 1 are entirely explained by the changes in the abundance of annual forbs in that year (Fig. 2b; Table 1). Thereafter, annual forbs rapidly disappeared from the aboveground vegetative community, but following the drought in year 3, there was a temporary resurgence in year 4 of the study. In this year, insecticide application had no effect on annual forb abundance, but there was a significant effect of fungicide application (Table 1). Forb abundance was significantly reduced by fungicide, irrespective of whether insects were present or absent (Fig. 2b). The main species responsible for this increase were *Vicia hirsuta* (L) S.F. Gray and *Vicia sativa* L., both of which are mycorrhizal.

Perennial forbs began to appear in the community during the latter part of year 1 and became common during year 2 (Fig. 2c). The cover of this life-history group was least affected by the drought and thus showed little increase the following year. This was probably because many of the species (e.g. *Rumex crispus* L., *Rumex obtusifolius* L., *Taraxacum* sect. *Ruderalia* Kirschner, Oellgaard & Stepanek (*Taraxacum officinale* Wigg. Group), *Sonchus arvensis* L and *Cirsium arvense* (L) Scop.) form deep tap roots. After their establishment in year 1, application of insecticide dramatically increased the abundance of this life-history group throughout the experimental period (Table 1). Application of fungicide significantly reduced the abundance of these forbs and there were significant interactions between the treatments (Table 1). These interactions were similar to those seen in the overall community analysis (above), with fungicide having the greater effect when insects were reduced and insecticide having the greater effect when AM fungi were present.

Perennial grasses also began to colonize the community in year 2, but the colonization process was temporarily arrested by the drought in year 3

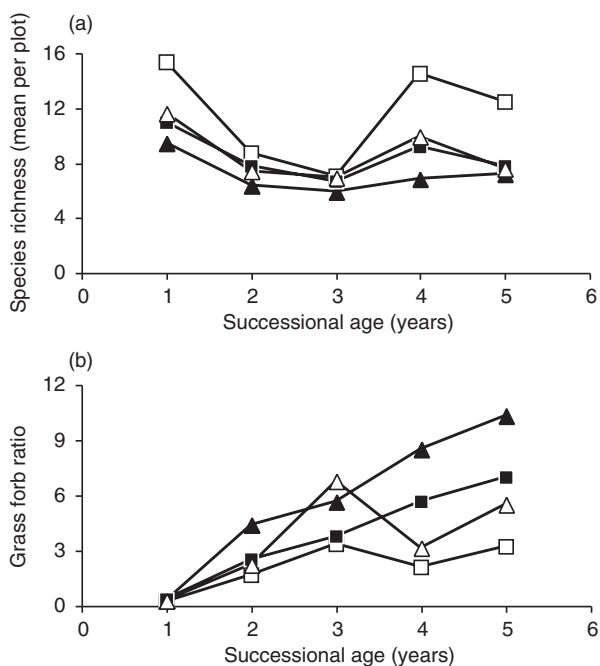


Fig. 3. Successional trends in (a) plant species richness (mean per plot) and (b) grass forb ratio. Values plotted are seasonal means of treatments. (■) Control (natural levels of root-feeding insects and AM fungi); (□) soil insecticide treated; (▲) soil fungicide treated; (△) soil insecticide and fungicide treated.

(Fig. 2d). From year 2 onwards, application of soil insecticide significantly increased the abundance of this life-history group, while (with the exception of year 3) application of fungicide reduced it. With the exception of the drought year, there were also interactions between the treatments, with fungicide only having an effect if insects were reduced, while the insecticide effect was greatest in the presence of the fungi (Fig. 2d).

Mean total species richness per plot in each treatment is shown in Fig. 3a. The effect of the drought in year 3 can be clearly seen, with a reduction in the number of extant plant species in that year. With the exception of year 3, application of soil insecticide increased plant species richness (Table 1). Fungicide application decreased species richness in years 1, 2 and 4 (Fig. 3a). The only occasion on which there was an interaction between the treatments was year 5. In that year, application of insecticide increased species richness only when AM fungi were present, because if the fungi were reduced, insecticide had no measurable effect (Fig. 3a).

The ratio between the abundance of grasses and forbs is depicted in Fig. 3b. Here, it can be seen that the treatments showed distinctly different patterns over the 5-year period, indicating that the structure of the plant community in each was quite different. In years 4 and 5 the application of insecticide significantly decreased the grass : forb ratio, while application of fungicide increased it (Table 1). No interactions were found between the treatments in any year. By the end of the experiment, the ratio in fungicide-treated plots was nearly twice that of control plots, whereas in insecticide-treated plots, the ratio was approximately half that in controls. Fungicide application therefore led to communities dominated by perennial grasses, while insecticide application led to more forb-dominated communities.

DISCUSSION

It is clear from these experimental results that manipulation of the root-feeding insect and AM fungal members of the soil food web can have a dramatic effect on the structure of aboveground plant communities. Both experimental treatments were very effective in reducing the abundance of their target groups, while neither had an effect on the other group. We appreciate that there may be other components of the soil food web that may be affected by chemical application and that results have to be interpreted with this in mind. However, we feel that such an approach is justified, given the logistical problems of assembling complete model communities involving manipulation of many members of the soil food web, with the inherent problems this method brings.

There are several encouraging aspects of these results, which lend support to those of other experiments. The first is that the patterns we have observed are repeatable in early successional communities in southern England. For example, Brown and Gange (1989a,b) have shown that root-feeding insects depress plant species richness, the mechanism appearing to be one of selective perennial forb establishment. When these insects are present, many emerging seedlings are damaged or consumed beneath the soil surface (Gange *et al.* 1991), meaning that fewer emerge aboveground. The process of seedling loss leads to reduced forb

establishment, a reduction in plant species richness and an acceleration of the successional process, as grasses are allowed to dominate the community (Brown & Gange 1992). Although root-feeding insects may be at lower densities than their foliar-feeding counterparts (Brown & Gange 1992), the effects that they have on plant species richness are more dramatic. Indeed, the relative effects of rhizophagous insects, in relation to their biomass, may approach that of vertebrate grazers (Brown & Gange 1990). Meanwhile, the enhancement of plant species richness by AM fungi in the current experiments has also been found in similar early successional communities (Gange *et al.* 1990, 1993). Such repeatable results across years suggest that the patterns observed must be real and not artefacts of particular climatic conditions prevailing at the time. The effects of climate were particularly noticeable in the current experiment, when a severe drought afflicted the site in year 3. Root-feeding insects are extremely susceptible to reduced soil moisture availability (Brown & Gange 1990), whereas their feeding activities generally impose water stress reactions in plants (Masters & Brown 1997). If the former mechanism is most important, one might expect to see relatively small effects of insecticide application during a drought, but if the latter occurs, one would expect to see enhanced effects. It was noticeable that the effects of insecticide treatment under drought were no greater than or less, than during other years of the study. Therefore, it appears that the effect of root-feeding insects in a plant community is more a function of their number, rather than the physiological effects that these insects have on plants.

Arbuscular mycorrhizal fungi are similarly detrimentally affected by lack of soil moisture, but are also known to alleviate the effects of drought stress in plants (Smith & Read 1997). Reduction of the fungi in year 3 only had a measurable effect on plant abundance when insects were also reduced. The physiological benefits of AM fungi on plants may therefore only be important in natural communities when climatic conditions are suitable and when other soil organisms are present at particular levels of abundance.

The overriding role of climate is clearly demonstrated by considering the results obtained in year 4 of this experiment. That summer was much wetter than the norm (and thus year 5, when less

dramatic results were obtained) and the community that developed was unusual in an early successional sequence. The vegetative dominance that was beginning to be established by perennial forbs and grasses was broken during year 3, allowing a reversal of succession and a resurgence of annual forbs in year 4. When conditions were appropriate (i.e. plentiful soil moisture), root feeding insects were abundant and their effects on the community dramatic. This was probably due to the fact that high soil moisture allowed successful egg hatch and larval development (Brown & Gange 1990). It is interesting that the presence of AM fungi significantly increased the abundance of annual forbs in this year, but that the effect was not dependent on the presence of root-feeding insects. The dominant annual forbs that established at this time were *Vicia hirsuta*, *V. sativa* and *Tripleurospermum perforatum* Mérat. All three are mycorrhizal (Harley & Harley 1987; Gange *et al.* 1990) and appeared to benefit greatly from the fungal presence. *Tripleurospermum perforatum* has also been shown to respond positively to a reduction in root herbivory (Müller-Schärer & Brown 1995) and this effect was repeated in the present study. Clearly, in natural plant communities, such effects will depend on the spatial distribution of AM fungi, and root-feeding insects, both of which are often aggregated (Brown & Gange 1990; Brundrett 1991). Therefore, the clumped distributions of insects and fungi may lead to heterogeneity of vegetation, creating natural mosaics, although these effects may only be manifest after times of stress to the community (the 'ecologic crunch' of Allen 1991).

On a smaller scale, another ecological crunch for AM fungi could be the presence of subterranean insects. One feature of the present experiment was the number of interactions seen between the experimental treatments. In general, it was found that root-feeding insects had their greatest effect when AM fungi were also present and that AM fungi had the greatest effect when the insects were absent. There are relatively few laboratory experiments that have investigated the interactions between these two trophic groups. The limited evidence suggests that AM fungi may reduce the growth and survival of rhizophagous insects, but that this depends on the identity of the fungal species involved in the symbiosis. It appears that colonization of the root system by one mycorrhizal

species may have a detrimental effect on insects, whereas multiple colonization may have no effect (Gange *et al.* 1994; Gange 2001). In natural situations, multiple mycorrhizal species colonization of roots is likely to be the norm (Clapp *et al.* 1995) and the results presented here lend support for the idea that mycorrhizal fungi have little effect on insects. We found that insects had the greatest effect on plants when AM fungi were present, something one would not expect to find if the mycorrhiza was antagonistic to insects. Instead, we suggest that the explanation for the interactions is that plant growth is determined by the size and functional capability of the root system. In the insecticide treatment, reduced herbivory means that root systems would be larger. The larger root systems would be able to take full advantage of the mycorrhizal condition in the relatively poor nutrient soil. However, if root-feeding insects were present, then the benefit of being mycorrhizal is not seen, due to the smaller nature of the root system. Therefore, in this case, the interaction between treatments is not a result of direct interactions between the insects and fungi, but one that is mitigated through host plant physiology.

We also found that AM fungi appeared to have a very large beneficial effect on plant community growth when insects were reduced, but that this effect virtually disappeared when insects were present. It is encouraging that this result repeats that of, to our knowledge, the only other similar experiment (Gange & Brown 1993). The most plausible explanation is that insects may disrupt the functioning of the symbiosis in some way. Obvious candidates for such disruption are the Collembola, or springtails, which can be very abundant. In the past, it has been suggested that they are consumers of mycorrhizas and thus detrimental to the functioning of the symbiosis. A recent review (Gange 2000) concludes that there is actually no evidence to support this view and that it is more likely that Collembola, through feeding on competitor non-AM fungi, are beneficial to the mycorrhiza. If Collembola (or, indeed, larger root-feeding insects) do feed on AM fungi, then application of insecticide ought to result in an increase in AM colonization of plants. However, no such effect was seen in this study. Instead, we believe that it is more likely that larger insects

disrupt the AM symbiosis as an occupational hazard of root feeding. Arbuscular mycorrhizal fragments and spores have been found within the guts of several larger soil insects (Rabatin & Stinner 1991; Harinikumar & Bagyraj 1994) and it is likely that disruption of the mycorrhiza occurs through physical movement of invertebrates through soil, consumption of mycelium or severing of hyphal links at the root surface. For larger invertebrates, one might expect the former possibility to be most likely, but Pattinson *et al.* (1997) could find no evidence that earthworms acted in this way. Whatever the mechanism, these results show that one reason why so many field-based AM-plant growth experiments have failed in the past (McGonigle 1988) is that insects were not controlled in the experimental designs.

It is clear that root-feeding insects and AM fungi can affect the structure of plant communities in early succession and the most likely mechanisms are differential seedling establishment and the subsequent competitive interactions between perennial forbs and grasses (Brown & Gange 1992). What is also clear is that these organisms can also affect the rate of the successional development. In the present study, we used the grass : forb ratio as an indicator of successional change and clear differences emerged between the experimental treatments. Reduction of mycorrhizas caused a switch to a community dominated by perennial grasses (i.e. a more advanced sere than the forb-dominated insecticide treatment). These results are in contrast to those of Hartnett and Wilson (1999) who found that AM fungi depress plant species richness in old-field tallgrass prairie because strongly mycotrophic grasses dominated in plots where mycorrhizas were present. In the early successional sequence reported here, AM fungi increased plant species richness, because mycotrophic forbs were more able to compete with the grasses when the fungi were present. Indeed, it was noticeable that by year 5 of the study, fungicide application no longer had any effect on plant species richness. It is therefore possible that as grasses come to dominate the communities in mid or late succession, the role of AM fungi will change (Johnson *et al.* 1991; Barni & Siniscalco 2000). Certainly, we know that the nature and role of root-feeding insects change, as the communities become perennial grass dominated. In these com-

munities, root herbivory is concentrated on the grasses and insect exclusion thus results in a decrease in plant species richness as a few perennial grasses are allowed to dominate (Brown & Gange 1993). Such temporal variation in effects was seen in the grass : forb ratio in combined treatment plots. In early succession (years 1–3), when root-feeding insects are rare (Brown & Gange 1990), these plots were similar to those treated with fungicide alone. However, in later years, as insects became more abundant, the herbivory effect appeared to take over, and these plots then became more similar to those treated only with insecticide.

Our conclusions are that in early succession, the root-feeding insect and AM fungal members of the soil food web affect the structure of plant communities. There are many interactions between them, as the insect effect is greatest when fungi are present, but the fungal effect is greatest when insects are absent. Root-feeding insects accelerate the process of succession, while AM fungi retard it. The dynamics of early successional communities are therefore determined by a balance in the relative abundance of each group, in the same way as it is by root- and foliar-feeding insects (Brown & Gange 1992). Overlying the often intricate interactions is the unpredictable and varying effect of climate. The next challenge will be to perform realistic manipulative experiments to investigate how other members of the soil food web fit into the process of plant succession. The other components of the food web may modify the interactions we have described and/or have important direct effects on plant communities. Only when we start to understand the complexity of biotic interactions in the soil and the way in which they are mediated via the plant community will we be able to predict the development of successional communities and manage the process effectively.

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