Plant mediated interactions between above- and below-ground insect herbivores

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The importance of indirect interactions in determining community structure has been the subject of recent discussion (Strauss 1991). Such interactions are diverse and their consequences for community ecology are largely unknown. Recent work has shown that root- and leaf-feeding insects can interact, via a common host plant (Gange and Brown 1989, Moran and Whitham 1990, Masters and Brown 1992). These interactions could have implications for community structure, since the population dynamics of either above- or below-ground insects may be confounded by the presence of the other.

Interactions between species can have five possible outcomes (Arthur and Mitchell 1989); competition (where the two competing species have a detrimental effect on each other, a minus-minus situation), amensalism (where there is only one detrimental effect, a minus-zero situation), contramenalism (one positive and one detrimental effect, a plus-minus situation), commensalism (only one positive effect, a plus-zero situation) and mutualism (where both species have positive effects on each other, a plus-plus situation). Competition and mutualism are classically considered by ecologists to be the most widespread, but there is growing evidence that plus-minus interactions can be important. However, such interactions are not intuitive; why should one species have a competitive influence and the other have a mutualistic effect?

The model

A conceptual model illustrating a mechanism for the host-plant mediated interactions between above- and below-ground insect herbivores is shown in Fig. 1. Root herbivores remove the fine roots, either directly by chewing or indirectly by sucking (by intercepting assimilate transport to the root tips) (Brown and Gange 1990). These roots are important in taking up water and nutrients essential for plant growth. Consequently, the activities of root herbivores may induce a stress response within the host plant, which is known to lead to the accumulation of soluble amino acids and carbohydrates in the foliage (e.g. Chapin 1991). Such increased nutrient levels within foliage may in turn lead to increased performance of the insect feeding on this reservoir. Such ideas, that plant stress leads to increased insect performance, are now well documented (White 1984,

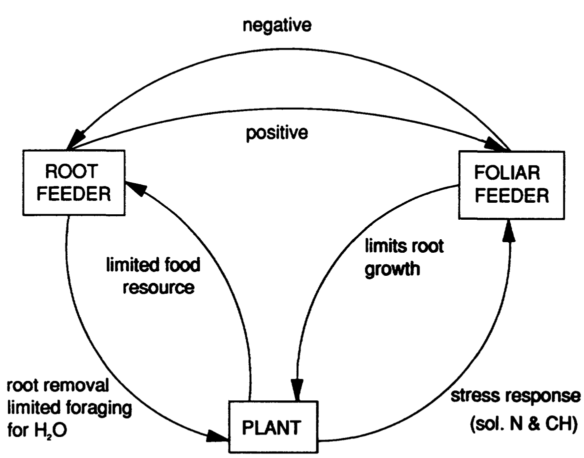

Fig. 1. A model to demonstrate the plus-minus interaction between below- and above-ground insect herbivores. Foliar feeding has a negative effect on the below-ground herbivore by reducing root growth, hence limiting food availability for the root feeder. Root feeding has a positive effect on the above-ground herbivore; removal of root biomass reduces water absorbtion, causing a stress response within the plant, thus improving food quality for the foliar feeder.

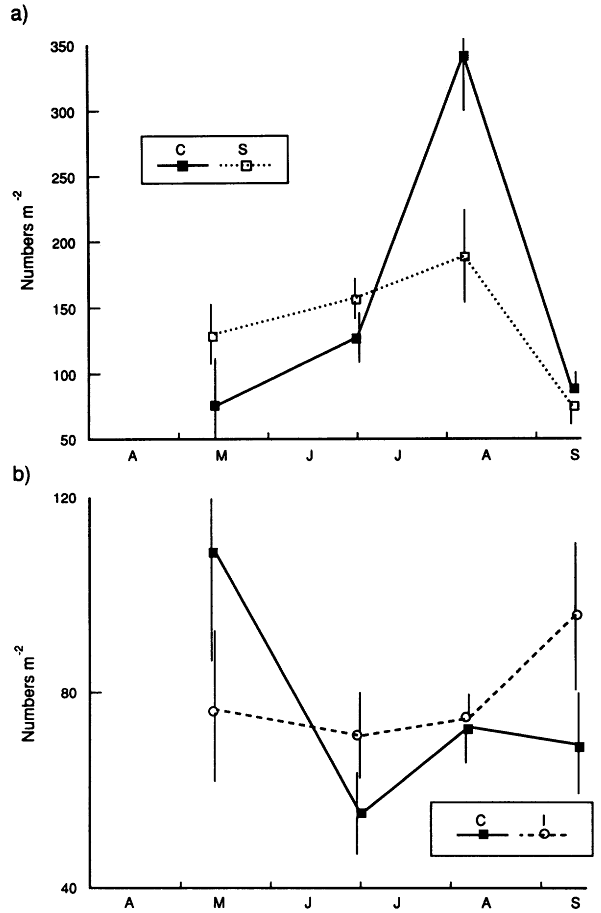

Fig. 2. The effect of above- and below-ground herbivory on the population dynamics of the insect fauna associated with a ruderal plant community over one season, (a) the response of the above-ground insects and (b) the response of the below-ground insects. Values are means of 5 replicate plots, bars indicate one standard error. C: control plots with both above- and below-ground insects, S: soil insecticide application, I: foliar insecticide application.

Mattson and Haack 1987), but have been the subject of debate (Larsson 1989, McQuate and Connor 1990). Indeed, Larsson (1989) has suggested that chewing insects would be less responsive to plant stress than sucking insects. This could be of importance in determining the response of a foliar feeder to root herbivory. However, foliar herbivory may cause a decrease in root biomass and, as the roots are a poor quality food resource (Andersen 1987), then any reduction in root quantity will have a negative effect on the root feeder (Brown and Gange 1990). Thus, we suggest that below- and above-ground insect herbivores interact in a plus-minus fashion; where root herbivory has a positive effect on foliar feeders, by increasing their performance, and foliar herbivory has a detrimental effect on root feeders, by decreasing their growth (Fig. 1).

Direct evidence

Only a few studies have directly tested the interaction between above- and below-ground insects. Masters and Brown (1992) used a controlled environment experiment to illustrate that root and leaf feeders can interact, via the host plant, in a plus-minus fashion. Root feeding (by chafer larvae) was found to cause an increase in the fecundity of the folivorous insect (a leafminer), whereas leaf feeding caused a decrease in the growth rate of the below-ground insect herbivore. Such above- and below-ground interactions are only of consequence if they occur in natural situations. We have conducted a manipulative, factorially designed, field experiment involving the judicious application of foliar and soil insecticide to an early successional plant community at Silwood Park, Berkshire, U.K. The experiment employed the same design and replication as that of Brown and Gange (1989). In this paper, details of the insecticides, their application and screening for direct effects on vegetation and foliar feeding insects are also described. Reduction of root-feeding insects led to a mid season density of above-ground insects which was significantly less ($t = 2.62$, $p < 0.05$, df. $= 8$) than in the control situation, where root herbivores were present (Fig. 2a). The difference was largely due to an increased abundance of multivoltine, generalist homopteran species (e.g. Aphididae). Reduction of foliar feeders had no significant overall effect on the numbers of subterranean insects, although there was a suggestion that foliar herbivory depressed root herbivore abundance at the end of the season (Fig. 2b). Due to the nature of the life cycles exhibited by many root herbivores (Brown and Gange 1990), colonization early in the season would not be expected. A more detailed study was conducted during 1991, with the initial results supporting those already found, both studies will be published in due course. These results therefore conform with the plus-minus model and provide evidence that contramensalistic interactions can occur in the field.

Indirect evidence

Considerably more studies provide evidence for one or other part of the plus-minus model. The evidence for root herbivory causing a stress response within the plant is growing. Gange and Brown (1989) studied the effects of root herbivory (by chafer larvae) on an annual forb (*Capsella bursa-pastoris* L.) and an associated foliar feeder, the black bean aphid (*Aphis fabae* Scop.). They found that root herbivory led to a drought response within the plant, which increased foliar nutrient levels sufficiently to increase aphid growth and fecundity. Evidence from the agricultural literature has yielded similar results (e.g. Ridsdill Smith 1977, Goldson et al. 1987) and there is also evidence for excess water mitigating the effects of root herbivory (Ladd and Buriff 1979, Brown and Gange 1990). These results support the plus half of the model.

There is substantial evidence for foliar herbivory reducing root biomass. Moran and Whitham (1990) conducted a garden experiment to study the effect of leaf-galling aphids on root-feeding aphids, mediated through the annual forb, *Chenopodium album* (L.). They found that foliar herbivory reduced root biomass and with it populations of subterranean aphids, even to the point of extinction. In another field experiment, Seastedt and Reddy (1991) found that the density of soil-dwelling aphids and scale insects was significantly increased in plots treated with a foliar insecticide. These results are similar to those recorded at Silwood Park and are consistent with the negative half of the model.

Exceptions

Evans (1991) conducted a factorial field experiment in the native tallgrass prairie of Kansas. He found that, while the numbers of leafhoppers and planthoppers were significantly increased in plots treated with soil insecticides, the number of aphids did not increase when root herbivory was reduced. These results are contrary to those reported here (Fig. 2), but are likely to be due to the stated ineffectiveness of the soil insecticides used (Evans 1991). In addition, insects are known to have variable responses to plants which are stressed, such that if root herbivory does cause plant stress, the foliar feeder may not necessarily increase in abundance (McQuate and Connor 1990). Unfortunately, Evans did not monitor the response of the below-ground insect herbivores.

Other discrepancies lie with the response of the root herbivore population to foliar herbivory, or defoliation, with workers recording an increase in below-ground insect abundance in response to above-ground herbivory, in tallgrass prairie (e.g. Seastedt et al. 1988). In cases such as these, a more complex interaction involving other organisms, such as fungi, may be occurring. It has recently been demonstrated that foliar herbivory can result in a reduced infection of roots by mycorrhizal fungi (Gehring and Whitham 1991). These fungi have been shown to confer resistance in a root system to nematodes (e.g. Carling et al. 1989) and we have recent evidence that subterranean insect survival is also reduced by mycorrhizal infection (Gange and Brown unpubl.). Thus, foliar feeding by insects may result in increased performance of root feeders, mediated through reduced infection by mycorrhizal fungi. It is interesting to note that mycorrhizal fungi would be expected to be abundant in prairie ecosystems (Allen 1991), where exceptions to the plus-minus model have been recorded.

The response of plants with different life-history strategies may also be important. When a perennial plant is defoliated, an immediate response is to restore the root/shoot ratio by increasing shoot growth by translocating stored assimilates from the roots, thus reducing root biomass (McNaughton 1983). This has the effect of decreasing the root C:N ratio (Seastedt et al. 1988), hence increasing the food quality for the root herbivores. However, annual plants do not transport a high proportion of primary productivity to their root system for storage (Mooney 1972). Thus, when defoliation occurs, annuals are more likely to restore the root/shoot ratio by diverting the products of primary productivity to the shoot for foliar regrowth, thereby decreasing root biomass. In this situation, neither the nitrogen content or quality of the roots will be increased. Thus, root herbivores will have a reduced growth rate on annual plants, due to limited food quantity. It is likely that differences in life-history strategy of the plant community being studied may have a dominant role and explain some of the anomalies between recent results. For example, the community we studied is annual dominated, while that of Seastedt et al. (1988) is perennial dominated.

Conclusion

The above results indicate that the plus-minus model not only occurs in the laboratory or garden experiments, but can occur in the field. Since it is generally accepted that the majority of plants in the field are water stressed (Hsiao et al. 1976), then the presence of root herbivores may well exacerbate this response, leading to an increased density of foliar feeders. Likewise, since below-ground arthropods are governed by a series of complex interactions, which are dominated by quality and quantity of the roots, then root herbivore densities could be reduced by foliar feeding insects. The implication of these interactions in community processes could be considerable.

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