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Insect herbivores and plant succession

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Insect-plant interactions at the community level are discussed in terms of the life-cycle strategies of the insects at different stages in plant succession and the effects of early colonising insect herbivores on the development of the plant community. Insect life-cycle strategies are influenced by habitat permanence, habitat complexity and resource availability and diversity. These factors increase as plant succession proceeds. The life-cycle strategies of insects also change during plant succession with differences in generation time, migratory ability, overwintering stage and reproductive potential. The degree of niche specialisation and the size of the organisms also vary. The characteristic life-cycle strategies of an early colonising species are discussed and the impact of phytophagous species on early successional plant communities found to be considerable. Single species studies (e.g. *Raphanus raphanistrum*) enable this effect to be assessed more fully. Insect grazing affects the survival, growth and reproductive potential of a plant species. At a community level insect grazing has an effect comparable to that of vertebrates, namely a reduction in the rate of plant succession.

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Introduction

The changes occurring in green plants and their insect herbivores during plant succession provide an ideal means of studying insect-plant interactions at the community level. On the one hand, insect life-cycle strategies are very closely tuned to the vegetational characteristics of the habitat and on the other, the effects of insects, mainly in terms of their grazing, can influence the course and rate of plant succession (Brown 1982a). Variation in insect life-cycle strategies is commonly encountered (e.g. Dingle 1978, Brown and Hodek 1983) and has been discussed in terms of the r-K continuum (MacArthur and Wilson 1967) and bet hedging (Stearns 1976). However, studies of the insect fauna of specific habitats only rarely include consideration of the life-cycle strategies of the species involved. This is of particular relevance to herbivorous species since insect grazing is now considered, by some, to be a major selective force in the maintenance of plant diversity in time and space (e.g. Breedlove and Ehrlich 1968, 1972, Ehrlich 1970) and in the evolution of antiherbivore defence mechanisms such as secondary chemicals and morphological features of plants.

Theoretical predictions of successional processes and patterns (e.g. Clements 1916, Egler 1954, Drury and Nisbet 1973, Horn 1974, Connell and Slatyer 1977) and field studies of successional gradients (e.g. Oosting 1942, Olson 1958, Bazzaz 1975) are numerous, though mostly plant-orientated and often restricted to only a part of the gradient. Successional studies, including both plants and their insect herbivores, along an entire gradient are needed before community interactions can be clearly displayed.

At Silwood Park, Berkshire, UK a series of experimental plots of known and different successional age has been developed over the last seven years. Recently harrowed fields, created annually since 1977, and left to recolonise naturally have been used to represent early successional sites. An area of permanent pastureland with herbs represents a mid successional site while a predominantly birch (*Betula* sp.) woodland represents a late successional site. Details of the experimental sites and of sampling procedure are given in Southwood et al. (1979).

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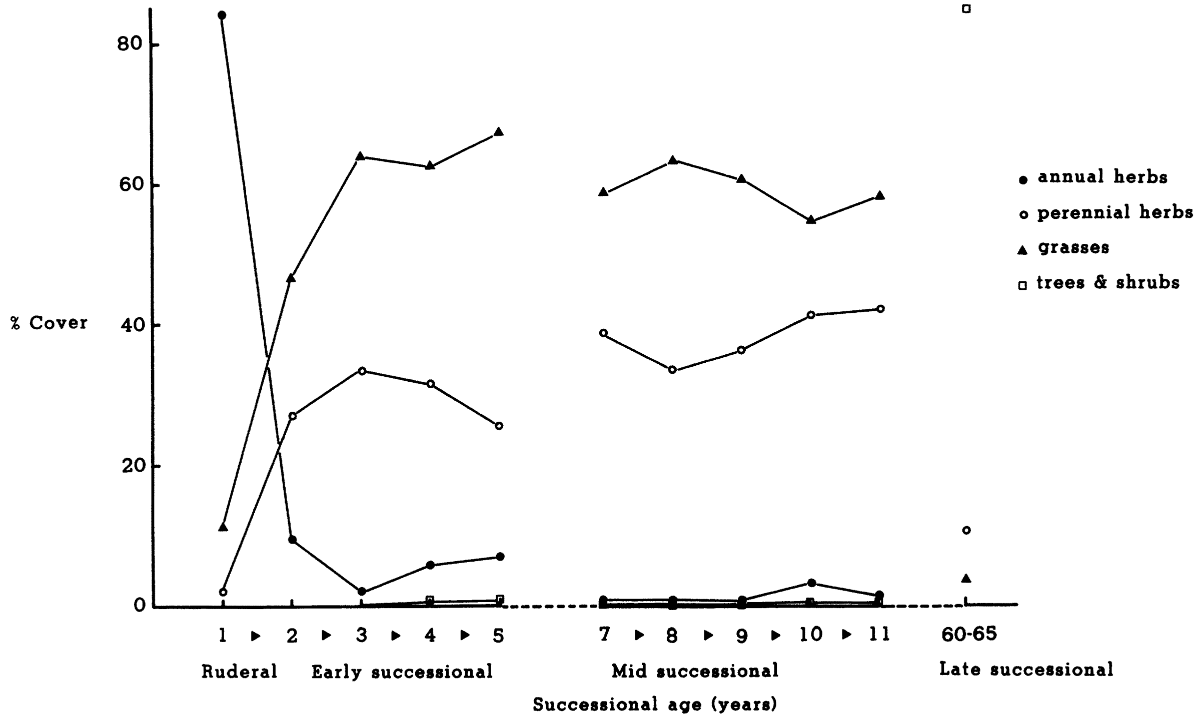

Fig. 1. Composition of the vegetation in terms of percentage cover of the major life forms from sites of different successional age. Years 1–5 and 7–11 represent changes occurring in the same sites. Years 60–65 vary very little. Annual figures are based on six monthly samples (May–October), with 225 or more sampling pins (point quadrats) per site for each sample.

Here, the insect life-cycle strategies, characteristic of these various stages in plant succession, are described; such a survey enables the specialised nature of the early colonising species to be assessed. Then, the effects of these colonising insect herbivores on early successional plant communities will be discussed.

Insect life-cycle strategies and plant succession

The life-cycle strategy of an insect is influenced by three characteristics of the habitat: habitat permanence, habitat complexity and resource diversity and availability.

In the sere under study there is a very rapid transition from an annual herb-dominated plant community to a perennial herb and grass community before tree and shrub establishment begins (Fig. 1). It is possible to recognise four major plant communities, namely ruderal, early successional, mid and late successional. Corresponding to this change in plant community organisation is an increase in habitat permanence, complexity and resource diversity and availability (Tab. 1). The former can be measured by using Sørensen's Index of Similarity (Southwood 1978), based on a comparison of the vegetation in a site for consecutive years. Habitat com-

Tab. 1. Variation in habitat characteristics, influencing insect life-cycle strategies, along the successional gradient.

Characteristic	Successional age				Source of data
	Ruderal 0–9 mo	Early 9 mo–5 yr	Mid 7–11 yr	Late 60+ yr	
Habitat permanence	0.23	0.45	0.79	0.87	Year-Year comparison (Sørensen's Index of Similarity)
Habitat complexity	1.0	1.9	1.5	4.2	Spatial diversity (data from Southwood et al. 1979)
Resource diversity/availability	4.1	3.7	4.6	9.3	Architectural diversity (for method, see Southwood et al. 1979)

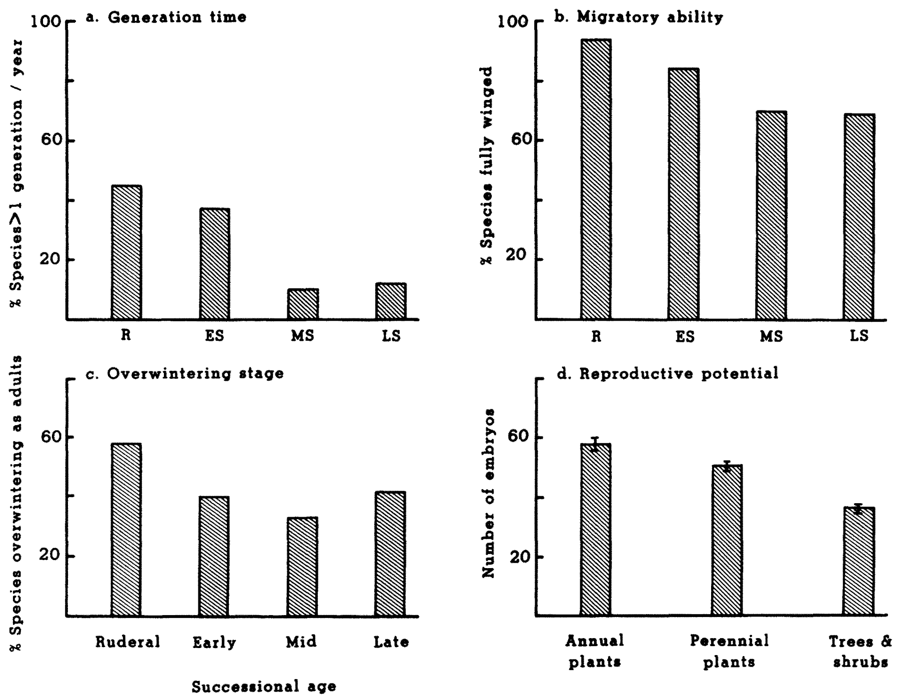

Fig. 2. Insect life-cycle strategies changing during plant succession. a–c. Heteroptera: ruderal n = 18; early successional n = 25; mid successional n = 25; late successional n = 44 species. d. Aphids (alatae and apterae): annual plants n = 137 (11); perennial plants n = 344 (36); trees and shrubs n = 191 (15) individuals, with number of species and/or host records in parenthesis. Mean ± standard error.

plexity and resource diversity and availability can be equated with spatial and architectural complexity respectively, (Southwood et al. 1979, Lawton 1983). Spatial complexity (based on the distribution of plant structures in space above ground level) and architectural complexity (based on the distribution of different types of plant structure) can be measured by the use of diversity indices as described in Southwood et al. (1979).

The insect species found to be associated with each successional plant community over a four year period have been analysed in terms of their life-cycle strategies, an approach which enables the theoretical predictions of Margalef (1968) and Odum (1969) to be tested. Essentially these predictions can be categorised in terms of the nature of the life cycle, niche specialisation and the size of the organism. However, other life-cycle features, such as those commonly associated with the r-K continuum (MacArthur and Wilson 1967), should also be considered. Thus generation time, overwintering stage, migratory ability and reproductive potential have been included.

By taking one of the dominant insect groups in the experimental sere at Silwood Park, namely the Heteroptera, it is possible to explore the patterns in life-cycle strategies seen in species associated with the four major plant communities of different successional age. The growth rate of species, expressed as the number of generations a year, is greater in early succession. Fig. 2a shows that there is a significant decrease in the proportion of species with bi- or multivoltine life cycles as succession proceeds ($\chi^2 = 11.69$, d.f. = 3, $p < 0.01$). A similar pattern was established when all exopterygote herbivores were considered (Brown and Southwood 1983). Furthermore, to complement the more rapid turnover of generations in early succession a higher proportion of species are fully winged (Fig. 2b, $\chi^2 = 2.14$, d.f. = 3, p = 0.5–0.1), and in the ruderal, early and mid successional communities a higher proportion of species overwinter as adults (Fig. 2c, $\chi^2 = 2.39$, d.f. = 2, p = 0.5–0.1). These two features combine to enable rapid invasion of the habitat and immediate reproduction. The higher architectural complexity of the habitat in later succession may explain the increase in the number of species overwintering as adults (Fig. 2c) (Brown 1982b). To my knowledge, there are no comparative accounts of the reproductive potential of insects at different stages in plant succession. An assessment of this involves the dissection of large numbers of individuals associated with a wide range of plant species. This has not yet been undertaken on the Heteroptera, but in current work on aphids (Brown and Llewellyn, unpubl.), a large number of species were collected from a range of host plants and the total number of embryos established by dissection. Fig. 2d shows the results for July, the month when most aphid species were found. Aphids (alates and apterae combined) associated with the ruderal, annual plants had significantly more embryos than those on perennial plants, characteristic of early and mid succession ($t = 3.06$, d.f. = 479, $p < 0.001$) and the latter more embryos than those on the late successional trees and shrubs ($t = 4.73$, d.f. = 596, $p < 0.001$).

There are a number of ways of assessing niche specialisation, although some of these rely on a degree of refinement of host records not normally available in the

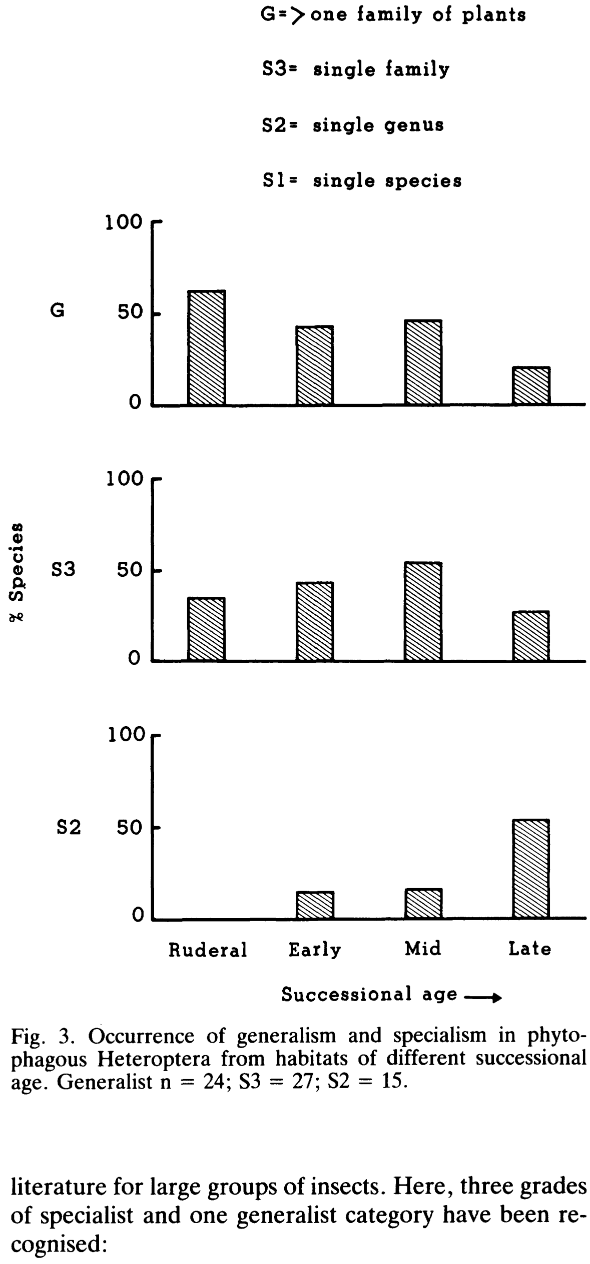

Fig. 3. Occurrence of generalism and specialism in phytophagous Heteroptera from habitats of different successional age. Generalist n = 24; S3 = 27; S2 = 15.

literature for large groups of insects. Here, three grades of specialist and one generalist category have been recognised:

Generalist (G):	associated with more than one family of plants.
Specialist Grade III (S3):	restricted to a single family (but to more than one genus).
Specialist Grade II (S2):	restricted to a single genus (but to more than one species).
Specialist Grade I (S1):	restricted to a single species.

Fig. 3 shows that in the phytophagous Heteroptera the proportion of generalist species declines along the successional gradient, whilst specialist species, particularly S2, show a marked increase in later succession ($\chi^2 = 15.67$, d.f. = 6, $p < 0.05$). A similar pattern is seen using the proportion of individuals in each category. There are very few S1 species of Heteroptera in the sere, since most specialist species feed on a single genus of plants (e.g. *Betula* feeding species probably exploit both *B. pendula* Roth. and *B. pubescens* Ehrh.). However, the inclusion of this category is important for comparison with other groups of insects, e.g. the Curculionoidea, where this degree of specialism is found (Hyman 1983).

Recently, a means of calculating niche breadth, based on a numerical scale according to the range of host plants used, was described by Brown and Southwood (1983). The application of this scale to the entire exopterygote fauna (including the Heteroptera) revealed a decline in niche breadth as succession proceeds.

The size, and also shape, of heteropteran species from habitats of different successional age has already been described (Brown 1982b). It was found that, contrary to theoretical predictions in which small species were assumed characteristic of early successional habitats and large species of late successional habitats, the range in size and shape increased along the successional gradient. Species characteristic of early successional habitats were somewhat intermediate in size and tended to be fairly consistent in size and shape.

An assessment of these life-cycle strategies displayed by the Heteroptera provides a means of defining an early colonising species (Fig. 4). Such a definition is likely to be similar for other insect groups, but data are lacking.

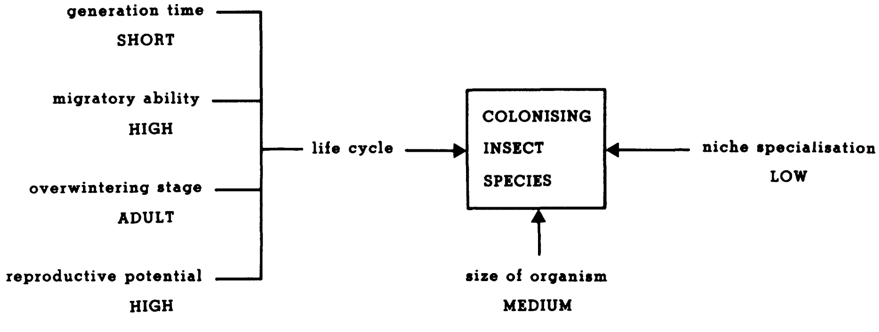

Fig. 4. Summary of life-cycle strategies displayed by colonising Heteroptera.

Effects of colonising species on early successional plant communities

In contrast to a range of studies on vertebrates (e.g. Patton and Frame 1981, Watt 1981a, b) there have been relatively few describing the effects of insect herbivores on the structure and development of natural plant communities. One such study during early succession has been undertaken by Stinson (1983) using the experimental system at Silwood Park.

Insect herbivores can be broadly categorised as defoliators, miners and gall formers and sap-feeders. Whereas the impact of the first two types can readily be seen and quantified in terms of leaf area or biomass removed, the effect of sap-feeding species is more subtle and can only be assessed by the manipulation of insect populations. Furthermore, the sap-feeding groups (Heteroptera, Homoptera and Thysanoptera) are numerically the most important in the early stages of this sere (Brown 1982a). The chemical exclusion of all insects from an experimental site, already protected from birds and rabbits and with very small populations of Molluscs, resulted in dramatic differences in the plant communitiy when compared with an insect-grazed site (Stinson 1983). For example, plant species were accumulated more quickly in the insect-free site and the percentage cover of vegetation was greater. These differences were thought to be due to the greater survival of seedlings in the insect-free site. Another major difference was seen in the grass/herb index, expressed as the proportion of touches (point quadrats) of grasses to herbs. Grasses were seen to invade the insect-free site more rapidly than the insect-grazed site. There were also differences in the number and timing of the reproductive structures of plants, with the insect-free site being characterised by the earlier production of larger numbers of flowers and fruits than the insect-grazed site (Brown 1982a). The use of smaller plots in 1983 (8 plots, 1 m^2) has enabled single plant species studies in natural, early successional communities to be undertaken and the development of individual plants to be monitored. The exclusion of insects, by the regular use of non-persistent insecticides in adjacent plots, has permitted direct comparisons between insect-grazed and insect-free plots. Grazing by other herbivores was prevented. There are several common ruderal species occurring in the experimental sere at Silwood Park (Southwood et al. 1979). One example of these, the wild radish, *Raphanus raphanistrum* L., can be used as an example of the pattern seen in a number of species. Insect grazing affects the plant species in terms of survival, growth and reproductive potential. The number of individual plants is significantly lower for most of the season in the insect-grazed plots (Fig. 5, $F = 47.9$, $p < 0.001$). The difference is almost solely due to extensive herbivore pressure on young plants in the insect-grazed plots, within a week in early May, and at a time when further germination is occurring in the insect-free plots. A difference also occurs in the rate of growth of the plant which can be seen by an examination of the height profiles of the species under the two conditions (Fig. 6). Growth is advanced in the insect-free plots, with a flowering 'canopy' developing by June, a feature only seen in the insect-grazed plots by

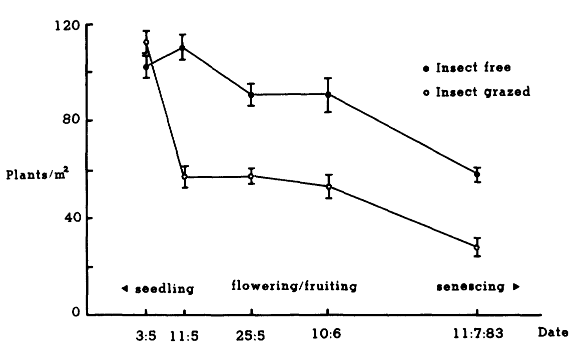

Fig. 5. Comparison of number of plants of *Raphanus raphanistrum* in insect-free and insect-grazed plots. Mean ± standard error.

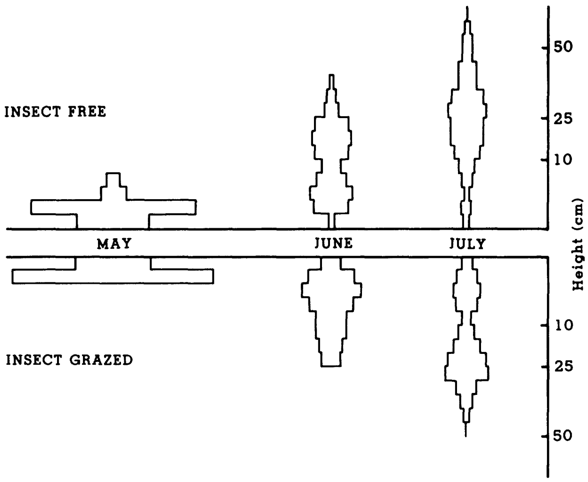

Fig. 6. Growth of *Raphanus raphanistrum*, shown by height profiles, in insect-free and insect-grazed plots.

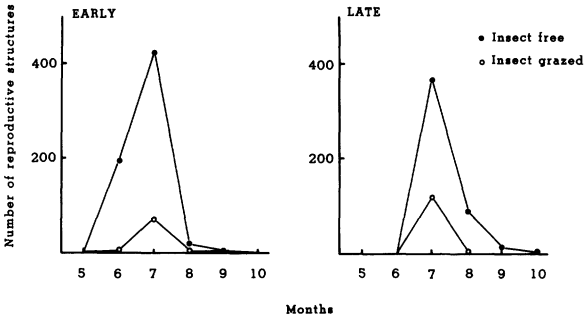

Fig. 7. The effect of insect herbivores on the timing and production of reproductive structures of *Raphanus raphanistrum*. (a. from Brown 1982a).

July. Senescence is well under way in all plots by August. The number of reproductive structures, both early (flowering stem, pre-anthesis and anthesis) and late (post-anthesis, fruiting) is significantly higher in the insect-free plots (Fig. 7, early: $F = 210.1$, $p < 0.001$; late: $F = 43.7$, $p < 0.001$). The advance in timing of flowering in the insect-free plots can also be seen.

Conclusions

The interactions between plants and insects along a successional gradient are complex and are yet to be fully explored. In one example discussed here, the vegetation provides a templet which moulds the life-cycle strategy of the insect, while at the same time the insect may have a dramatic effect on shaping that templet.

The impact of insect herbivores on early plant succession appears to be considerable. Recent single species studies have displayed a reduction in the number of individual plants, a decrease in growth rate and a lowering of reproductive potential by insect herbivores. These features together with the community characteristics displayed in earlier work on the whole plant community have indicated the effects of insect herbivores to be similar to those of vertebrates, namely a reduction in the rate of secondary plant succession. If we couple this with some of the insect life-cycle strategies described earlier, especially those enabling the rapid build up of populations, we may predict that insect herbivory may display its greatest impact on early succession – but this remains to be tested.

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