Eur. J. Entomol. **91**: 53–56, 1994
ISSN 1210-5759

Resource deprival as an anti-herbivore strategy in plants, with particular reference to aphids

NEIL A.C. KIDD

School of Pure and Applied Biology, University of Wales, Cardiff CF1 3TL, UK

Aphids, chemical defence, herbivore, pine aphid, taxifolin, resource deprival

Abstract. It is generally considered that many specialist insects, such as aphids, have overcome chemical barriers to successful feeding and turned them to their own advantage as host recognition cues and phagostimulants. It is suggested that plants may counter-respond to the presence of specialised insect herbivores by manipulating recognition cues and phagostimulants to the detriment of the insect. One might expect this to involve the plant depriving the insect of access to these chemicals at critical periods in the insect's life cycle. Evidence in support of the 'resource deprival' hypothesis is presented from work carried out on the large pine aphid, *Cinara pinea*. Here, taxifolin, a possible phagostimulant, is withdrawn from the phloem to the outer shoot tissues in midsummer, with a subsequent decline in aphid growth and survival.

INTRODUCTION

The role of plant chemical defences against insect herbivores has been well established in recent years. Plants may respond to insect attack by evolving permanent (constituted) chemical defences (Levin, 1976; Rhoades & Cates, 1976; Rhoades, 1979) or, alternatively, by producing relatively short-lived 'induced' defences, which are only activated in response to immediate insect attack (Karban & Myers, 1989). With both of these strategies, plants increase the concentrations of toxic, repellent or digestibility-reducing substances in their foliage and bark.

Direct evidence in support of chemical defence theory has mostly come from studies of 'induced' defences, but most of the work has been done on generalist chewing insects (Haukioja, 1980; Schultz & Baldwin, 1982; Karban & Myers, 1989). What about attack by specialist insects? It is generally considered that many specialist insects have overcome chemical barriers to successful feeding and turned them to their own advantage as host recognition cues and phagostimulants (e.g. van Emden, 1972, 1978). In doing so, the insect herbivore becomes increasingly tied to one taxonomic group of plants, often forming an intimate and subtle physiological relationship with the host. Nevertheless, the insect is still likely to have a negative effect on plant fitness, so how might the plant respond to the insect's presence?

One possibility is that plants may respond to the presence of specialised insect herbivores by manipulating recognition cues and phagostimulants to the detriment of the insect. One might expect this to involve the plant depriving the insect of access to these chemicals at critical periods in the insect's life cycle. However, there may be circumstances where the plant has to balance the relative advantages and disadvantages of the 'resource deprival' tactic, if it simultaneously denies itself access to metabolically important substances.

Aphids, with their high degree of host-specificity and intimate chemical relationships with plants make ideal candidates for testing the resource deprival hypothesis. In this paper I present supporting evidence from studies carried out on the large pine aphid, *Cinara pinea* (Mordvilko).

EVIDENCE FOR RESOURCE DEPRIVAL

The large pine aphid is a common aphid of Scots pine, *Pinus sylvestris*, on which it feeds by extracting phloem from the current year's shoots. Populations show a single midsummer peak in abundance each year, with some trees consistently more heavily infested than others. The use of detailed simulation models has revealed plant quality to be an important factor limiting population growth in the summer, by affecting aphid development, mortality and growth rates (Kidd, 1990a,b). These changes largely account for variations in peak density from year to year and tree to tree.

Investigations into the nature of host plant quality to the aphid revealed that nymphal growth rates were positively influenced by variations in total phloem phenolics and certain amino acids (Kidd et al., 1990), the former possibly having a phagostimulatory role. Further, more detailed, analysis of the phenolic constituents have since been carried out using HPLC. Five shoot samples were taken at random from each of 8 trees during June, July and August (120 samples in all). Analysis of variance has revealed significant seasonal and between-tree differences (but not between samples), in certain individual flavonoid glycosides. These were detectable at retention times of 1.8 min, 12.5 min, 15 min (characterised as coniferyl alcohol) and 19 min (taxifolin). The peak at 1.8 min was subsequently found to be a probable artifact produced by chemical breakdown of other phenolic components. The 12.5 min peak was not completely characterised, being partly made up of coniferin plus another component, possibly catechin or dihydroconiferin or both (referred to here as coniferin+). Average concentrations of taxifolin, for example, in both current

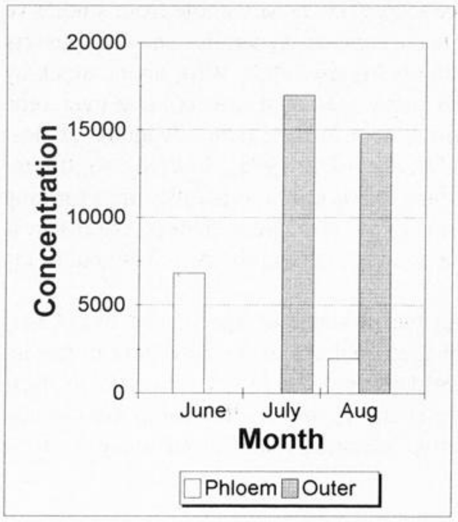

Fig. 1. Average changes in concentration of taxifolin in the current year shoots of 8 Scots pine trees (5 samples per tree). Phloem tissue was analysed separately from outer shoot tissue. Concentrations are given as arbitrary units of area (HPLC trace) and differ significantly with time (ANOVA; $P < 0.001$).

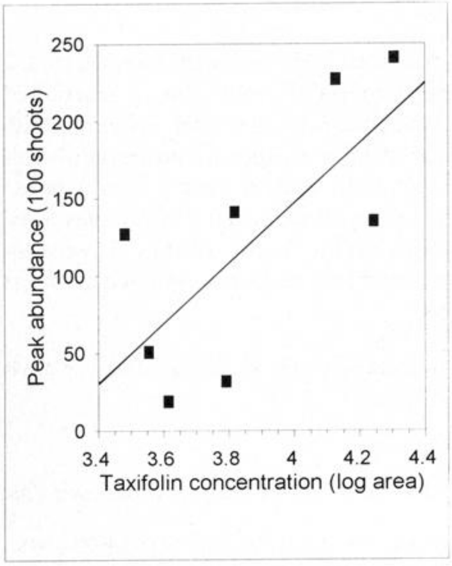

Fig. 2. Relationship between taxifolin concentration in pine shoots in June and peak abundance shown by the aphids on each of 8 trees ($Y = 190X - 612$, $r = 0.53$, $P < 0.05$).

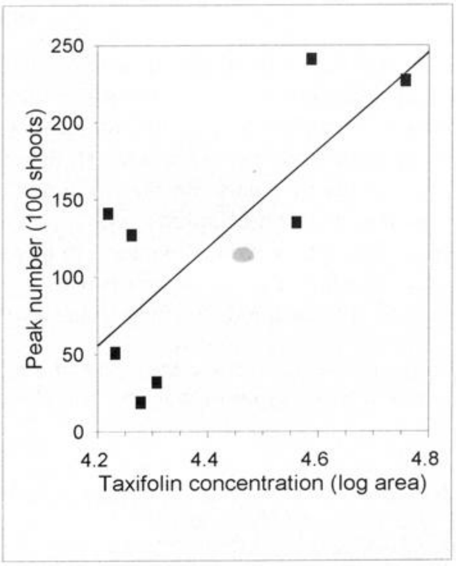

Fig. 3. Relationship between taxifolin concentration in pine shoots in July and peak abundance shown by the aphids on each of 8 trees ($Y = 310X - 1244$, $r = 0.57$, $P < 0.05$).

year outer-shoot samples (cortex + bark) and phloem extracts are shown in Figure 1. It can be seen that the concentration of taxifolin in phloem declines markedly between June and July, precisely at the time when tree quality to the aphid is also dropping. At the same time concentrations of this substance in the outer shoots increase.

These observations yield detailed insights into the way in which taxifolin is mobilised in Scots pine during the season. Taxifolin is present in relative abundance during June, declines markedly in July and increases slightly again in August. Outer shoot tissues show the inverse of this relationship, indicating that the chemical is being mobilised quickly through the phloem in early summer, to be concentrated in the outer shoot tissues. This general pattern is repeated in all trees examined, although there may be considerable variation in precise concentrations. The significance of taxifolin to the aphid becomes clear when we relate aphid performance to the concentrations of specific phenolic glycosides. Using peak aphid density as a performance indicator (previously established as correlating well with nymphal growth rates), the only substance to correlate consistently well with aphid performance on a seasonal and between-tree basis was taxifolin (Figs 2, 3). This is consistent with our previously held view (Kidd et al., 1990) that one or more phenolic substances may be acting as a phagostimulant. Removal of taxifolin from the phloem tissue in July may, therefore, be a tactic by the tree to deprive the aphid of a required substance, thereby limiting its population growth and potential damaging effects on the tree. Certainly, the results of extensive simulation modelling show that, without such seasonal changes in plant chemistry, populations would be capable of growing to 10 times observed levels (Kidd, 1990b).

DISCUSSION

Is it possible then, that at least in the above described herbivore-plant interaction, the plant has taken the next step in the coevolutionary process? By overcoming generalised chemical barriers to feeding and turning specific chemicals to their own advantage (e.g. recognition cues, phagostimulants), insects may lay themselves open to further anti-herbivore tactics by plants. Resource deprival is one such tactic open to plants. We might expect insects, such as aphids, which specialise in feeding on particular plant tissues to be more susceptible to manipulation in this way than unspecific feeders such as chewing insects. Testing of the resource deprival hypothesis should perhaps be concentrated on insect groups such as aphids, leafhoppers and leaf-miners.

ACKNOWLEDGEMENTS. I thank Mark Jervis for his critical comments on the manuscript. The pine aphid work was funded by the Natural Environment Research Council.

REFERENCES

HAUKIOJA E. 1980: On the role of plant defences in the fluctuation of herbivore populations. *Oikos* **35**: 202–214.

KARBAN R. & MYERS J.H. 1989: Induced plant responses to herbivory. *Annu. Rev. Ecol. Syst.* **20**: 331–348.

KIDD N.A.C. 1990a: The population dynamics of the large pine aphid, Cinara pinea (Mordv.). I. Simulation of laboratory populations. *Res. Popul. Ecol.* **32**: 189–208.

KIDD N.A.C. 1990b: The population dynamics of the large pine aphid, Cinara pinea (Mordv.). II. Simulation of field populations. *Res. Popul. Ecol.* **32**: 209–226.

KIDD N.A.C., SMITH S.D.J., LEWIS G.B. & CARTER C.I. 1990: Interactions between host-plant chemistry and the population dynamics of conifer aphids. In Watt A.D., Leather S.R., Hunter M.D. & Kidd N.A.C. (eds): *Population Dynamics of Forest Insects.* Intercept, Andover, pp. 183–193.

LEVIN D.A. 1976: The chemical defence of plants to pathogens and herbivores. *Annu. Rev. Ecol. Syst.* **7**: 121–159.

RHOADES D.F. 1979: Evaluation of plant chemical defences against herbivores. In Rosenthal G.A. & Janzen D.H. (eds): *Herbivores: their Interaction with Secondary Plant Metabolites.* Academic Press, London, New York, pp. 3–54.

RHOADES D.F. & CATES R.G. 1976: Towards a general theory of plant antiherbivore chemistry. *Recent Adv. Phytochem.* **10**: 168–213.

SCHULTZ J.C. & BALDWIN I.T. 1982: Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* **217**: 149–151.

VAN EMDEN H.F. 1972: Aphids as phytochemists. In Harborne J.B. (ed.): *Phytochemical Ecology.* Academic Press, London, New York, pp. 25–43.

VAN EMDEN H.F. 1978: Insects and secondary plant substances – an alternative viewpoint with special reference to aphids. In Harborne J.B. (ed.): *Biochemical Aspects of Plant and Animal Coevolution.* Academic Press, London, New York, pp. 309–323.