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

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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 Here, taxifolin, a possible phagostimulant, is withdrawn from the phloem to the outer shoot tissues in midsummer, with a subsequent decline in aphid growth and survival.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 import-ant 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 mid-summer 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 im-portant 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 sea-sonal and between-tree differences (but not between samples), in certain individual flavo-noid 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 subse-quently 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
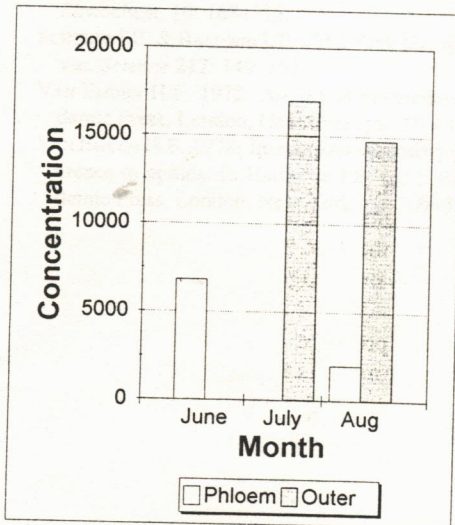

Fig. 1. Average changes in concentration of taxifolin in the current year shoots of 8 Scots pine trees (5 samples per tree). Phloem tissue was analysed separately from outer shoot tissue. Concentrations are given as arbitrary units of area (HPLC trace) and differ significantly with time (ANOVA; $P < 0.001$).
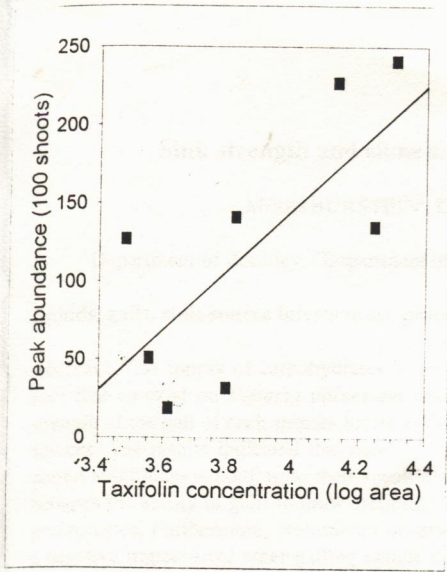
54

Fig. 2. Relationship between taxifolin concentration in pine shoots in June and peak abundance shown by the aphids on each of 8 trees ($Y = 190X - 612$, $r = 0.53$, $P < 0.05$).
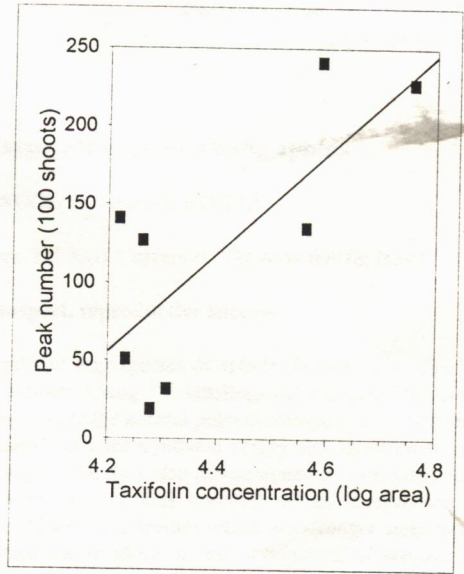
Fig. 3. Relationship between taxifolin concentration in pine shoots in July and peak abundance shown by the aphids on each of 8 trees ($Y = 310X - 1244$, $r = 0.57$, $P < 0.05$).

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.

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Sink strength and clone size of sympatric, gall-forming aphids

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Aphids, galls, sink-source interactions, phloem transport, reproductive success

Abstract. The supply of carbohydrates to growing galls of four species of aphids (Pemphigidae: Fordinae) that co-exist on *Pistacia palaestina* trees was studied. Using ^{14}C labelling we compared the sink strength of the gall of each species for its ability to manipulate the normal phloem transport from different sources. The results indicated that none of the galls had net photosynthetic ability and all of them imported assimilates according to their specific sink strength. The data also demonstrated a correspondence between the ability of galls to draw assimilates from wider sources (sink strength) and aphid reproductive performance. Furthermore, preliminary observations indicated that species which are stronger sinks have a negative impact over other galling aphids on the same leaf or shoot through withdrawal of assimilates and nutrients.

INTRODUCTION

Aphid galls act as sinks which sustain aphid nutrition by manipulation of phloem transport from different sources into the galls (Larson & Whitham, 1991). Mature leaves which export assimilates may serve as the sources. Although the mechanisms which regulate sink-source interactions are not fully known, it is generally accepted that phloem sap flows according to sucrose gradients and depends on the distance between the sink and the source, the vascular connections between them, and sink strength. Differences in source utilization and sink strength of four species of gall-forming aphids of the subfamily Fordinae, (Pemphigidae) which coexist on the same shoots of their primary host: *Pistacia palaestina* (Anacardiaceae) are described in this preliminary paper. The galls of *Baizongia pistaciae* (Bp) are formed near the terminal bud. *Geoica utricularia* (Gu) galls are located on the leaflet midrib. *Forda formicaria* (Ff) and *Paracletus cimiciformis* (Pc) galls are located on the leaflet margins. The three latter species may coexist on the same leaves or even the same leaflets, and share a similar life history (Koach & Wool, 1977).

MATERIALS AND METHODS

Sink strength of each gall was defined by its ability to draw assimilates from different sources. It was measured by [14]CO$_2$ labelling technique during June–September 1992. Source organs (single leaves or leaflets) were enclosed in nylon bags tightly sealed with putty and thread. [14]CO$_2$ gas was released by the reaction of sodium carbonate (Na$_2$[14]CO$_3$) solution with lactic acid injected into the bag. CO$_2$ fixation was allowed to take place under natural conditions for about four hours (10 am–2 pm). All shoots were removed two days after labelling and were deep frozen. Distribution of ^{14}C in every shoot was first qualitatively estimated by autoradiography, then extracted for 24 h by DMF (N,N-Dimethylformamid). Radioactivity was determined by liquid scintillation counting. All ^{14}C measurements are expressed as ratios of activity in the gall tissue (dpm/mg. dry weight) to activity (dpm/mg. dry weight) of the source tissue, after 48 h of transport. For brevity we refer to the measure as AR (assimilation ratio).