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OLFACTORY MEDIATED AGGREGATIONS OF OAK FLEA WEEVILS, *RHYNCHAENUS QUERCUS* (L.) (COLEOPTERA: CURCULIONIDAE) ON PHENOLOGICALLY EPHERMAL HOST PLANTS

ABSTRACT: Individuals of the leaf mining, oak flea weevil, *Rhynchaenus quercus* (Coleoptera: Curculionidae) aggregate on oaks bearing leaves in a proper phenological state for oviposition. As pedunculate oaks differ in the time of spring development, weevils change host trees in the course of sexual and ovipositional activity, occupying those with just appeared leaves. Olfactory stimuli (aggregation pheromone?) connected with feeding by the females on leaves are responsible for the attractance of other females (and presumably males) to such trees. Aggregative behaviour of oak flea weevils can be interpreted as a specific adaptation to phenological ephermality of pedunculate oaks.

KEY WORDS: oak flea weevil, *Rhynchaenus quercus*, olfactory attractance, host plant ephermality, aggregative behaviour, insect-plant relationships.

1. INTRODUCTION

Feeny (1976) together with Rhoades and Cates (1976) have introduced a concept of "apparency" into the debate on insect-plant interactions. This idea attracted much attention and became one of the most discussed issues in this field (Courtney 1985). According to its authors, distinction can be drawn between "apparent" and "ephermal" plants. Generally speaking, ephermal plants are, in the contrast to apparent ones, "hard to find" by herbivores in both ecological and evolutionary time. Plants of both characteristics developed different chemical strategies: apparent plants by investing much matter and energy in "quantitative" defense which employ high amounts of chemicals that form generally effective barriers, whereas ephermal plants "rely" on small quantities of specific toxins aimed at non-adapted insects.

One of the most exposed examples of an apparent plant is the pedunculate oak, *Quercus robur* (L.) – an important constituent of mid-european forests. Being "bound to find" by their enemies, oaks had developed in their evolution "solid" biochemical protection. They had made it by the production of tannins which reach 5% leaf dry weight (Feeny 1970). This barrier is effective, however, only in mature foliage. Developing leaves lack appreciable amounts of tannins and are the food of high quality for a number of insects. Consequently, oak trees suffer sometimes defoliations in the spring.

Another important feature of pedunculate oaks is their intraspecific variability in the spring initiation of leaves development (Feeny 1970, 1976; original observations). Pedunculate oaks of the same age, origin and growing conditions can form in May and the begining of June a changing mosaic of trees being in various phenological states: from closed bud stage to the stage of full grown leaves. Thus, considering this variability, oaks can be in a way ephermal in spring for many chewing insects. It has been documented, that such phenological ephermality may be fatal for certain populations of foliophagous moths due to asynchrony between eggs hatching and foliage availability (Satchell 1962, Feeny 1976).

I report here that a population of the oak flea weevil, *Rhynchaenus quercus*, a species whose larvae mine young oak leaves and are especially common on pedunculate oaks (Kozłowski 1985), form temporal, olfactory mediated aggregations on trees bearing leaves of proper developmental stage for oviposition. This behaviour can be considered as specific contradaptation to phenological ephermality of pedunculate oaks.

2. MATERIAL AND METHODS

Field observations were performed in a recreation woodland area in Sękocin near Warsaw. Young pedunculate oaks (2.2–3.5 m high) grew there as an undergrowth of pine (*Pinus silvestris* L.) forest. Four oak trees of similar appearance and growing conditions but situated at least 12 m apart from each other were chosen. It had been known from the previous years that these trees differed markedly in their phenology. Numbers of weevils on particular trees were assessed each week between May 2 and July 3 by careful shaking of all single branches above an entomological umbrella. Fallen weevils were counted, collected and examined in relation to sex. After finishing the examination, the weevils were released in the vicinity of such a tree.

To examine the role of volatiles in the finding of host-trees by oak flee weevils, attractiveness of young leaves from different trees was compared. Weevils for these tests were collected in the middle of May from trees growing in a different area of the forest. Only females were used. They were divided into groups of 20 individuals and maintained in containers with oak twiggs. Weevils were deprived of food and oviposition sites (young leaves) 24 h before a test. Tests were performed in laboratory conditions (20 ± 3°C, long day 10:14 h). Traps were 5 ml vials containing 0.5 g of cut leaves and 0.25 ml water sucked into a piece of cotton. Leaves and water were screened by a gause cloth of fine mash to protect feeding by the females. The vials were covered by disposable funnels made of filter paper. Their tips were frayed to prevent the weevils that had entered the vials from comming out. Vials were attached to the inner surface of the side wall of a plexiglass cylinder (diam. 25 cm, hight 30 cm). Their openings were directed to the middle axis of the cylinder and distributed regularly in the distance of 1 cm from the tip wall. The cylinder was illuminated from above, and the side wall was covered from the outside with opaque material.

20 females were released into the cylinder in each of the 6 replicates of the test. After 24 h weevils inside the vials were counted. Two experiments were performed. In the first one, the effectiveness of vials containing juvenile leaves from 6 different trees (*Q. robur, Fagus silvatica* L., *Populus pyramidalis* Rozier, *Malus* sp., *Alnus glutinosa* (L.), *Larix decidua* Miller) and a control vial containing destilated water only was assesed.

In the second experiment, attractiveness of vials enclosing screened oak leaves together with single, hungry females separated from the leaves versus traps with leaves of the same origin and equally hungry females that could feed on them was compared. Vials of both types were located alternately on the cylinder wall in the manner analogical to that from the first test. Differences in the numbers of females traped into vials with feeding and starving females were analized. The tests were repeated 6 times.

3. RESULTS

First weevils had appeared on pedunculate oaks some one week before the earliest trees opened their buds. At this time weevils set motionless near the tops of the oak branches mimicking precisely oak buds. As soon as the first trees started to open their buds, weevils started to appear on such trees in greater numbers. They fed, mated and after some 2–3 days first ovipositions were to observe.

As Figure 1 shows, numbers of individuals changed markedly on particular trees in the course of the leafing season. Weevils were more abundant on trees bearing young, just shot leaves. Both sexes were represented on such trees in approximately equal proportions ($\chi^2 = 1.18$; $n = 122$). Frequently, copulating or tandeming pairs were seen throughout this period. Flying weevils that approached and landed on such trees were sometimes observed, especially in warm days. This made the impression that weevils were able to localize proper plants from a distance.

Olfactory component engaged in the aggregation behaviour of oak flea weevils can be evidenced by the results of the laboratory tests together with the electro-antennogram study which have proved high capacity of the olfactory system in this weevil to perceive leaf derived volatiles (Kozłowski and Visser 1981). The comparison of vials that contained leaves from different trees (Table 1) can suggest that the odour from oak leaves evoked certain degree of positive reaction from the tested females. However, this response was not specific as vials with leaves from other

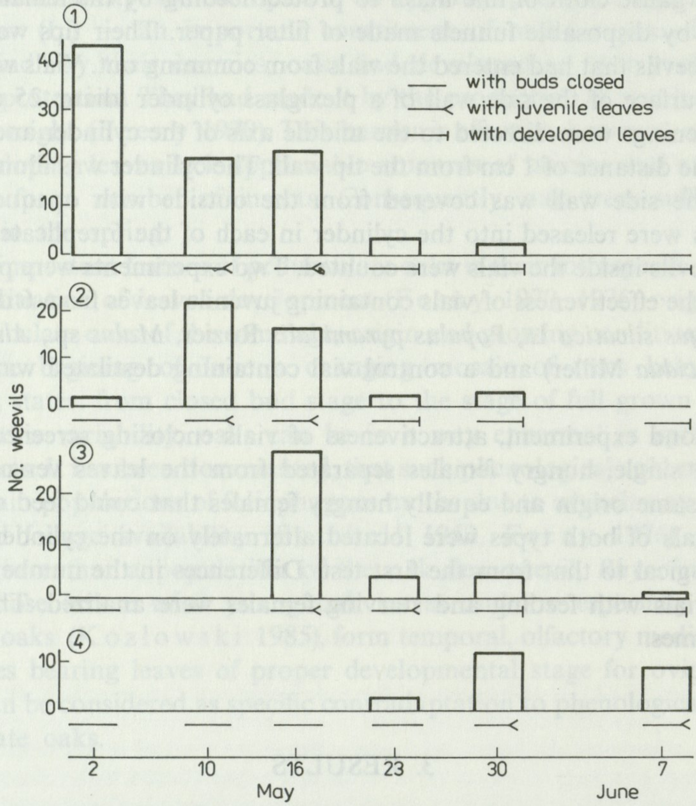

Fig. 1. Numbers of adult oak flea weevils, *Rhynchaenus quercus* collected from four pedunculate oaks which differed in spring bud burst

Table 1. Mean numbers ($n=6$) of female oak flea weevils, *Rhynchaenus quercus* that have been found in traps containing young leaves from various trees. Different letters following the values indicate significant ($p<0.05$) differences, according to the Duncan's test of data transformed to $\sqrt{x+1}$

Tree species	Mean
Quercus robur	1.75[a]
Fagus silvatica	1.46[a]
Populus pyramidalis	1.32[a]
Malus domestica	0.87[ab]
Alnus glutinosa	0.99[a]
Larix decidua	0.00[c]
Aqua destilata (control)	0.05[bc]

trees lured females in similar proportions (except for *Larix* leaves that probably were deterrent).

Oak flea weevils are finical in host plant choice and never accept other plants than oaks for food and oviposition in the field (Kozłowski 1985). As the tests have not revealed any specific action of volatiles from oak leaves, one can suppose that their role in host plant localization is limited when they occur alone. Results of the second test showed, however, that the attractiveness of oaks can essentially enhance with the presence of feeding females. Numbers of females that were found in vials containing leaves with single feeding females were much higher then in control vials in each of the 6 replicates of the test. Mean difference $\pm$ standard deviation was 12.8 ± 4.2, i.e. highly significant ($p < 0.001$) according to both Wilcoxon and Student paired data test.

Leaves that were screen together with females had, as a role traces of intensive feeding and defecation. This "feeding factor", responsible for the attraction can be related in the field to vulgar, alimentary or ovipositional feeding connected with egg hole formation in the main vain of a leaf. It is not yet clear what was the source of the attractant. It was not possible to test frass alone because of the shortage of the experimental insects due to their seasonality and sharp decline of their population density in the field that have been sustaining already for several years. It is highly possible that the frass contained the attractant since volatiles which function as aggregation pheromones have been found in the frass of related insects: certain Curculionidae (Tumlison et al. 1969, Chang and Curtis 1972) or Scolytidae (c.f. Birch 1984).

4. DISCUSSION

Oak flea weevils are rather exceptions among the miners of oak leaves. Most of the species that adopted mining habits in oaks derive from Mictolepidoptera. They develop in mature or even senescent leaves, depending probably on food of worse quality than insect consuming juvenile foliage. But at the same time, the miners of older leaves seem to avoid in an appreciable extent to be "accidentally devoured" by numbers of young foliage feeders. Oak flea weevils take this risk but can instead profit from food of a better sort.

Young oak flea weevil larvae were never observed in mature leaves. Development in such leaves is perhaps for them even impossible due to high degree of veins sclerotisation, as it has been described for the larvae of a related species: beach flea weevil, *Rh. fagi* (Kleine 1925). Careful analysis of the oviposition and feeding traces left by beech flea weevils on beech trees that differed in bud burst data showed that these insects could actively select suitable trees for oviposition (Bale 1984). Also oak flea weevils, being dependent on juvenile leaves, should heave been expected to include in their developmental habits elements connected with spring ephermality of their prevailing hosts – pedunculate oaks.

Feeny (1976) suggested that the reduction of wings in certain species of

Geometridae (e.g. *Operophtera brumata*) that larvae grow on juvenile oak leaves can be regarded as adaptative since arised in the course of relationships with phenologically ephermal hosts. Such females being "attached" to a particular tree may increase chance to produce progeny that hutch in a coincidence with the appearance of leaves. Females of the oak flea weevil have developed quite different strategy. They search actively for trees being in proper phenologicas states. They use olfactory cues to approach and locate trees that had been already accepted by the other individuals of the same population.

Aggregative behaviour and its biological meaning may posses several aspects when to consider individual selection (Alcock 1982). It is obviously profitable for host searching females. Joining other females on a particular tree, newcommers increase chance of finding suitable leaves for oviposition (given that density of the resident females is not too high since in one leaf only one larva can develop and ovipositing females are capable to discriminate occupied leaves: Kozłowski – unpublished data). Assemblance of moderate number of females do not seem to impend over both residents and newcommers regarding relatively low numbers of eggs laid per day in relation to the abundance of leaves on an average tree.

Another aspect which can be profitable for the both types of females is the attraction of males and of females to males. The presence of male assemblance can theoretically promote epigamic selection and this way increase fitness of the females (Thornhill and Alcock 1983). These suppositions should be however experimentally verified.

5. SUMMARY

Trees of the pedunculate oak, *Quercus robur* can differ markedly in their time of spring foliage development. This phenological ephermality of particular trees had been interpreted as an adaptation related with the avoidance of spring defoliation by certain chewing insects. Females of the oak flea weevil, *Rhynchaenus quercus* (a species which larvae mine young oak leaves) deposit their eggs exclusively into developing, just shot leaves. Weevils of the both sexes form temporal aggregations on pedunculate oaks bearing leaves in a proper stage of development (Fig. 1). It has been proved that moderate and unspecific olfactory attractivity of oak leaves to the weevils (Table 1) can be appreciably enhanced when leaves are submited as food for the females. These olfactory cues promote aggregation on oaks that had been already accepted by other weevils. Such behaviour can be regarded as specific contradaptation to phenological ephermality of pedunculate oaks.

6. POLISH SUMMARY

Poszczególne drzewa dębu szypułkowego *Quercus robur* mogą się znacznie różnić czasem wiosennego rozwoju liści. Ta fenologiczna efemeryczność jest tłumaczona jako adaptacja pozwalająca unikać intensywnego żerowania owadów zjadających młode liście dębu. Samice skoczonosa dębowca, *Rhynchaenus quercus* – gatunku, którego larwy minują młode liście dębów – składają jaja wyłącznie do rozwijających się liści, zaraz po pęknięciu pąków. Chrząszcze obu płci tworzą czasowe skupiska na dębach znajdujących się w odpowiednich dla owipozycji fazach rozwoju (rys. 1). Wykazano, że zapachowa atrakcyjność liści dębu szypułkowego dla samic skoczonosa dębowca, która była umiarkowana

i niespecyficzna (tab. 1), wzrastała znacznie, gdy na liściach tych żerowały inne samice skoczonosa dębowca. Zdolność do skupiania się chrząszczy na drzewach znajdujących się w odpowiednim stadium rozwoju liści może być uważana jako swoista dla skoczonosa dębowca kontradaptacja na fenologiczną efemeryczność dębów szypułkowych.

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