Restricted host range of the weevil *Aubeonymus mariaefranciscae*, a new sugar-beet pest

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Abstract

The extent of feeding, fecundity and fertility of a new sugar beet pest, *Aubeonymus mariaefranciscae* Roudier (Coleoptera: Curculionidae), on a range of plants from different families was determined. We have found that the adult weevils were only able to feed and oviposit on two closely related cultivated plants, beet and sugar beet, both subspecies of *Beta vulgaris* L., suggesting a restricted host range for this curculionid. None of 16 secondary metabolites (widely distributed among plants, and representative of different chemical groups), nor any of 19 non-host extracts from 13 different families, deterred the adults of this curculionid from feeding on sugar beet. We found a phagostimulatory effect when beet and sugar beet homogenates from various plant tissues were supplied to adult weevils on weeds that they do not feed on. Conversely, no effect was observed when sucrose was provided. These findings suggest that host selection by *A. mariaefranciscae* adults is due to the presence of an undetermined phagostimulant compound(s) in beet and sugar beet, instead of the recognition of deterrent substances among the non-host plants.

Introduction

The weevil Aubeonymus mariaefranciscae Roudier was reported to be a new sugar beet pest in 1979 (Santiago-Alvarez et al., 1982) and described as a new species in 1981 (Roudier, 1981). The adults produce characteristic notches on the leaves as well as cavities on the petioles and roots; larvae feed on and tunnel throughout the roots. Direct damage caused by the adult autumn populations of this curculionid, when population densities are high, is particularly devastating at the sugar beet seedling stage. Adults and larvae also can cause severe damage during the spring, particularly by feeding on sugar beet roots. Yield losses of 30% caused by up to 20 larvae per root have been reported in southern Spain (Giraldo & Alvarado, 1990a). It is estimated that about 3000 ha of sugar beet are affected by this curculionid, and it is spreading to other areas in this region (Giraldo & Alvarado, 1990b). All these factors make this insect one of the key pests of sugar beet crops in southern Spain.

To the best of our knowledge, damages by this curculionid have not been reported for any other cultivated plants elsewhere. Information on other food plants of *A. mariaefranciscae* is very scarce and based on casual observations of populations in the field (Giraldo & Alvarado, 1990b). Such observations are difficult to obtain because of its subterranean habits and small size, so that laboratory studies that relate potential host consumption to weevil performance are required. It would be of great interest to define its host plant range, to determine what other cultivated plants may be at risk, as well as to assess the role of weeds as potential reservoirs of infestations.

Plant chemistry plays an important role in determining the range of plants that can be exploited by an insect species (Jaenike, 1990). The host range of phytophagous insects most commonly depends on the presence or absence of a variety of secondary metabolites in plants, so that plant chemotaxonomy is probably an important factor in understanding host selection (Bernays & Chapman, 1994). Feeding activity in phytophagous insects is to a large extent governed by the presence of chemical feeding stimulants and/or the absence of feeding deterrents (Schoonhoven, 1982).

The role of both phagostimulants and deterrents in determining host selection by some phytophagous weevils has been reported. The alfalfa weevil, *Hypera brunneipennis*, is deterred from feeding by a number of plant allelochemicals (Bernays & Cornelius, 1992). Conversely, other weevils have been found to be stimulated to feed by a specific chemical or group of chemicals restricted in their distribution to a limited number of plant species (Nielsen et al., 1989; Wilson et al., 1990), or by primary plant chemicals widely distributed, such as adenine and related substances (Hsiao, 1969) and sucrose (Shanks & Doss, 1987).

In this work, the extent of feeding, as well as fecundity and fertility of *A. mariaefranciscae* adults on a range of plants from different families was determined. The effects of plant secondary compounds and non-host extracts as well as beet and sugar beet homogenates on its feeding behaviour was also studied. On the basis of these results, the host plant range of this curculionid and the chemical mechanisms that govern its host plant selection are discussed.

Materials and methods

Insects. About 800 adults of *A. mariaefranciscae* were collected in Santaella, Córdoba (Southern Spain) during the autumn of 1995 by removing them from sugar beet root wastes of the previous crop. They were maintained in a growth chamber at 22 ± 2 °C, r.h. $80 \pm 10\%$, and L16:D8 photoperiod. When needed, adults were sexed by observing the presence (males) or absence (females) of a depression between the 3rd and 4th abdominal tergites (Cabezuelo & Santiago-Alvarez, 1981)

Plants. Sugar beet plants, *Beta vulgaris vulgaris*, cv. Eva, were grown in a growth chamber, under the environmental conditions described above, to feed the stock population and to supply leaves and foliar discs as needed. Beet plants, *Beta vulgaris cicla*, free of insecticides, were obtained from a local store. The 33 species of weeds collected (Table 1) are those commonly found close to and/or in sugar beet fields in southern Spain, where *A. mariaefranciscae* is present.

Table 1. Weeds commonly found close to and/or in sugar beet fields affected by A. mariaefranciscae in southern Spain

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		Polygonum aviculare*	
Foeniculum sp.	Umbelliferae	Daucus carota*	
		Foeniculum sp.	

* Plants selected for choice feeding assays with non-host extracts.

Feeding assays

All feeding assays were performed in a growth chamber (Conviron S10H, Controlled Environments, Winnipeg, Canada) at 26 ± 1 °C, r.h. $80\pm10\%$, and L16:D8 photoperiod.

Short-term feeding on potential host plants. Ten adults were confined with leaves and roots of the weeds shown in Table 1 in a plastic box $(13 \times 9 \times 3 \text{ cm})$ containing a moistened filter paper. The containers were

held in a growth chamber for one week, and the weed pieces changed twice. Thereafter, leaves and roots were examined to determine the presence/absence of feeding activity.

Long-term feeding and determination of fecundity and *fertility.* Seven weeds of the previous experiment were selected to determine if A. mariaefranciscae adults will eventually eat some of them, if no other substrate was available, over their lifetime. Three pairs of weevils were placed in an experimental arena containing a detached leaf from one of the following plant species: sugar beet, beet, Rumex sp., Senecio sp., Sinapis arvensis L., Taraxacum sp., Atriplex patula L., Chenopodium album L. and Malva silvestris L. Each arena consisted of plastic pots (7 cm diameter \times 7 cm height), filled with moistened sand in which the leaf petioles were inserted, and covered with another plastic container (6 cm diameter \times 15.5 cm height). Four arenas for each plant species were set up in a growth chamber. Leaves were replaced weekly. The extent of feeding and the number of eggs laid per female (fecundity) were recorded each week during the lifetime of the weevils. Additionally, leaves were dissected with the aid of a microscope by peeling off the epidermis to expose the eggs. The eggs were removed by a fine camel-hair brush and transferred onto moistened filter paper inside plastic containers $(1.5 \times 3.5 \times 5.5 \text{ cm})$ and incubated at the same conditions as above to assess the percentage of egg hatching (fertility).

Choice feeding assays

General. Arenas used for these assays consisted of plastic Petri dishes $(15 \times 90 \text{ mm})$, coated on their bottom half with about 20 ml of a 2.5% agar solution (Escoubas et al., 1993). Plant leaf discs (1.77 cm^2) from the different plants examined were cut with a cork borer (No. 15), treated with the appropriate solution, and immediately after complete evaporation of the solvent each disc was fitted into a hole punched in the agar layer. Two adult weevils were placed in each arena, that contained three treated and three control discs arranged alternately, and kept in a growth chamber for 24 hours. The feeding activity was recorded as being greater on control, greater on tests, or indistinguishable. Twenty replicates were used in each bioassay, and a sign test was used to test for significance of any differences.

Deterrent activity of plant secondary compounds. Sugar beet leaf discs were treated on both surfaces with 10 μ l of the appropriate solution containing the test compound or the solvent carrier alone, as control. Chemicals representative of the major classes of secondary compounds in plants were used in this bioassay. Table 2 shows these compounds with their chemical classes and used solvents. They were applied at concentrations intended to give approximately 0.1% dry weight of discs, a typical concentration for many secondary compounds in plants (Bernays & Chapman, 1977).

Deterrent activity of non-host extracts. Non-host plants were thoroughly washed, cut into small pieces, and homogenized with distilled water (12 ml per gram of plant tissues) by a Servall Omni Mixer from Ivan Sorvall Inc. (Norwalk, Conn., USA). Sugar beet leaf discs were treated by dipping them into non-host extracts. Leaf discs dipped in distilled water were used as controls.

Phagostimulatory effect of host-plant homogenates. Leaf discs from host and non-host plants were treated by dipping them into homogenates from limb, root and petiole of beet and sugar beet plants. The homogenates were made as follows: each plant organ was thoroughly washed, cut into small pieces, and thereafter ground with distilled water (12 ml per gram of plant tissues) by a hand-held electric mixer and frozen at -20 °C until needed. Leaf discs dipped in distilled water were used as controls.

Results and discussion

Host plant range of A. mariaefranciscae adults

When *A. mariaefranciscae* adults were confined for one week with most representative weeds (Table 1) of the sugar beet areas affected by this curculionid, no feeding activity was observed on any of them. The only exception was *Rumex* sp., which was slightly bitten. However, because adult weevils alternate periods of high and low feeding activity and can survive starvation for at least four months (personal observations), they were confined, during their entire lifetime, with seven of the weeds previously tested, including *A. patula* and *Ch. album*, two weeds belonging to the same family as sugar beet (Chenopodiaceae). Likewise, no feeding activity was observed, except for the sporadic feeding behaviour observed on *Rumex* sp. (0–10 notches/week/6 adults). As might be expected, adults Table 2. Chemicals and solvents used in behavioural choice feeding tests

Chemical class	Chemical	Solvent
Alkaloids	Nicotine hydrogen tartrate	50% Methanol
	Quinine chloride	50% Methanol
	Sparteine	50% Methanol
Quinones	Juglone	Methanol
Triterpenes	Diosgenin	Chloroform: methanol (1:50)
	Ursolic acid	Dimethylsulfoxid: methanol (1:50)
	Azadirachtin	Acetone
Glucosinolates	Sinigrin	50% Methanol
Amines	Hordenine hemisulphate	50% Methanol
Cyanogenic glycosides	Linamarin	50% Methanol
	Amygdalin	50% Methanol
Phenylpropanoids	Chlorogenic acid	Methanol
Flavonoids	Rutin	Ammonia sol. 30%: methanol (1:50)
Tannins	Morin	50% Methanol
Steroids	Digitonin	Methanol
Nonprotein amino acids	Mimosine	Dist. water

were able to feed on beet (*Beta vulgaris cicla*), since this cultivated plant belongs to the same species as sugar beet (*B. vulgaris vulgaris*). Moreover, they fed in a similar manner (Table 3) on both plants (> 30notches/week/6 adults).

Recent studies have suggested that host ranges in herbivorous insects may be more restricted by maternal oviposition preferences than by trade-off in larval feeding efficiency (Janz & Nylin, 1997). In insects having sedentary larvae, such as the rice weevil, Sitophilus oryzae, that feed in a single rice kernel and cannot disperse (Ryoo & Cho, 1992) and the buprestid leafmining beetle, Brachys tessellatus (Waddell & Mousseau, 1997), the mother's choice for laying eggs is particularly critical for the survival of her offspring. Similarly, we have found that in A. mariaefranciscae, whose larvae complete development at the site of oviposition, the females only laid eggs on beet and sugar beet (Table 3). No significant differences were found between weevil fecundity and fertility on both species, the percentage of egg hatching being above 90%. None of the females oviposited on any of the weeds, including Rumex sp.

Our data suggest a restricted host range for *A. mariaefranciscae* adults, as they were only able to feed and oviposit on two closely related cultivated plants, beet and sugar beet (subspecies of *B. vulgaris*). Despite beet being as good a host as sugar beet, damage from this beetle has not been reported on beet, probably due to the beet crop system (small and scattered plots) in Spain. The lack of records of this pest in other sugarbeet growing areas, where temperature regimes are lower, have been related to the finding that 4th instar larvae and pupae are unable to develop below 18 °C (Marco et al., 1997).

The non-acceptance as hosts of the weeds tested, which are the most commonly found in the area of distribution of *A. mariaefranciscae*, indicates that they are not related to weevil spreading.

Chemical basis of host selection in A. mariaefranciscae *adults*

Our finding that the host range of *A. mariaefranciscae* adults appears to be restricted to one plant species led us to determine which secondary metabolites might deter or stimulate feeding in this insect.

Table 3. Feeding activity, fecundity and fertility of *A. mariaefranciscae* adults on potential host plants

Plant ¹	Feeding activity ² (bites/week)	Fecundity ² (eggs/replicate)	Fertility ² (% hatching eggs)
Sugar beet	>30	$155\pm28~^{a}$	92.4 ± 1.7 $^{\rm a}$
Beet	>30	$181\pm56~^{\rm a}$	$90.3\pm3.6~^{a}$
Rumex sp.	0–10	no eggs	-

¹ No feeding activity or oviposition was observed on *Senecio* sp., *Sinapis* arvensis, *Taraxacum* sp., *Atriplex patula*, *Chenopodium album*, and *Malva silvestris*.

 2 Four replicates (three pairs of weevils/ replicate). Column means \pm SE followed by the same letter are not significantly different from each other (Student-Newman-Keuls test, P<0.05).

We have tested the deterrent effect of 16 secondary metabolites (Table 2) on feeding activity of *A. mariae-franciscae* adults on sugar beet. These plant chemicals were selected because they are widely distributed among plants, and are representative of different chemical groups (Bernays & Chapman, 1977). When tested in choice-feeding assays, none of the secondary metabolites deterred this curculionid from feeding on sugar beet (P>0.025, n = 20, sign test). Any result which showed smaller differences was considered unimportant, since P-values < 0.01–0.001 are usually reported for other insect herbivores with these compounds at equal doses (Bernays & Chapman, 1977; Bernays & Cornelius, 1992).

It may be argued that plant chemicals act in Nature primarily as a biochemical profile rather than single compounds. It has been shown that, for instance, feeding and oviposition of reproductive boll weevils, *Anthonomus grandis*, on cotton was reduced by extracts of several non-host and alternate hosts plants (Bird et al., 1987; Palumbo et al., 1990; Honda & Bowers, 1996). Therefore, we have also tested the deterrent effect of extracts from 19 species of non-host plants (Table 1) on the feeding activity of *A. mariae-franciscae* adults on sugar beet. None of the extracts deterred this curculionid from feeding on sugar beet (P>0.025).

We also tested if root extracts from sugar beet would enhance feeding responses of *A. mariaefranciscae* adults on species of weeds on which we showed above that they do not feed. We recorded a strong phagostimulatory effect (P<0.001) on *S. arvensis, Taraxacum* sp. and *Rumex* sp. and a moderate phagostimulatory effect (0.001 < P < 0.025) on *Senecio* sp. and *M. silvestris* (Table 4). Interestingly, no increase in the

Table 4. Effects of sugar beet root homogenate on the feeding behaviour of *A. mariaefranciscae* adults on leaves of several non-host plant species

Phagostimulatory effect ¹	Plant species
at P<0.001	Sinapis arvensis
	Taraxacum sp.
	Rumex sp.
at P<0.005	Senecio sp.
	Malva sylvestris
No effect	sugar beet

¹ Choice feeding assay between control leaves of different plant species and the same leaves treated with sugar beet root homogenate (n = 20, sign test).

feeding activity was observed when sugar beet leaves were treated with sugar beet root extracts.

In a complementary experiment, crude extracts from roots, petioles and limbs from beet as well as sucrose were tested on *Senecio* sp. leaves (Table 5). A phagostimulatory effect was obtained with all extracts tested, except with that from beet petioles. In addition, we have shown that a 20% sucrose solution, similar to that found in sugar beet roots, lacked stimulatory feeding activity.

Our results suggest that host selection by *A. mari-aefranciscae* adults is based on the presence of a phagostimulant compound(s) in beet and sugar beet, instead of the recognition of deterrent substances among the non-host plants. We have proved that the phagostimulant is not sucrose, despite the fact that this substance is the principal component of sugar beet roots, and sugars are the nutrients most commonly used by insects as phagostimulants (Bernays & Chapman, 1994). Moreover, petioles and limbs of sugar beet and

Table 5. Effects of homogenates from different parts of beet and sugar beet plants on feeding behavior of *A. mariaefranciscae* adults on *Senecio* sp. leaves

Phagostimulatory effect ¹	Homogenate
at P<0.001	Beet limb
	Sugar beet root
	Beet root
at P<0.005	Sugar beet limb
	Sugar beet petiole
No effect	Sucrose
	Beet petiole

¹ Choice feeding assay between untreated and homogenate treated *Senecio* sp. leaves (n = 20, sign test).

roots and limbs of beet, whose sugar concentrations are low, also stimulate feeding. Thus, we may conclude that the phagostimulatory effect reported here is due to other types of compounds: nutrients and/or secondary metabolites.

There are records in other phytophagous weevils, where secondary metabolites restricted to few plant taxa act as phagostimulants, such as the monophagous weevil Ceutorhynchus constrictus that is stimulated by the glucosinolate sinigrin to feed on garlic mustard, Alliaria petiolata (Nielsen et al., 1989). Similarly, a pentacyclic triterpenoid, present in the periderm of sweet potato storage roots, induced feeding and oviposition by females of the sweet potato weevil, Cylas formicarius (Nottingham et al., 1987; Wilson et al., 1990). In other cases, the phagostimulants are widely distributed primary plant chemicals, such as adenine and related substances for the alfalfa weevil, Hypera postica (Hsiao, 1969), and sucrose for some species of curculionids (Shanks & Doss, 1987). Further research is needed to elicit which compound(s) are implicated in the phagostimulatory effect reported here.

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