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Host Choice in the Field in the Genus *Larinus* (Coleoptera: Curculionidae) Attacking *Onopordum* and *Cynara* (Asteraceae)

A.W. Sheppard,[1] D.T. Briese[1] and I. Michalakis

[1]CSIRO Biological Control Unit, Campus de Baillarguet, 34982 Montferrier-sur-Lez Cedex, France

Several members of the weevil genus *Larinus* (a genus uniquely associated with Asteraceae: Cardueae and Arctoteae) attack members of the thistle genera *Onopordum* and *Cynara* (Briese and Sheppard, *in press*). Of these, certain species are largely specific to *Onopordum* (e.g., *Larinus latus*), to *Cynara* (e.g., *L. scolymi*) or attack both genera (e.g., *L. cynarae*). This paper explores the nature of this specificity using: 1.) field observations of these species from extensive surveys; 2.) studies of genetic differentiation within *Larinus* populations in a site with more than one host plant species using electrophoresis; and 3.) field host-choice tests for these species both within and between these plant genera. The surveys revealed the existence of host-races ('biotypes') within *Larinus* species from different regions among these host-plant genera. However, no differences were found between individuals of the same *Larinus* spp. selecting different host plants at the same locality. Similarly, in the host-choice tests, these *Larinus* spp. remained faithful to the host plant genus from which they were collected. The results are discussed in relation to the consequences of race selection in the biological control of weeds and, in particular, the problems associated with artichoke for all thistle-targeted releases.

Introduction

Host-specificity among insect herbivores is highly variable (Michaud 1990), while biological control agents usually require very small host ranges. Species that are highly specialised throughout their range present little problem, but an increasing number of species have been found to have different host ranges (Thompson 1988, Katakura *et al.* 1989, Klein 1991, Zwölfer and Romstöck-Völkl 1991) or levels of specificity (Fox and Morrow 1981) in different regions within their distribution. Such variation complicates the requirement to demonstrate specificity before release in biological control.

When such differences are shown to have a genetic basis, either through host choice tests or the analysis of genetic structure within sympatric populations or along parapatric boundaries, then they are termed biotypes (Zwölfer *et al.* 1971) or host races (Diehl and Bush 1984). Such host races are common among insect herbivore families (e.g., Coleoptera: Curculionidae and Diptera: Tephritidae) attacking thistles (Asteraceae, Cardueae) (Zwölfer and Romstöck-Völkl 1991). Here we consider the situation within the thistle genera *Onopordum* and *Cynara*.

Members of these genera have been introduced from Eurasia into Australia, New Zealand, North and South America (Holm *et al.* 1979). Overall, *O. acanthium* L. and *C. cardunculus* L. are the most widespread (Fuller 1957, Gleason and Cronquist 1963, Thomsen *et al.* 1986, Le Houérou 1991), but only *O. acanthium* (Hooper *et al.* 1970, Briese *et al.* 1990) and *O. illyricum* L. (Briese *et al.* 1990) have become serious pasture weeds, restricting

[1] *Current address: CSIRO Division of Entomology, GPO Box 1700, Canberra, ACT, Australia*

within the natural distribution ranges of *L. cynarae* with *L. scolymi* Olivier (Montpellier, southern France) and *L. latus* Herbst with *L. scolymi* (Thessaloniki, northern Greece). *L. cynarae* occurs in Greece but not around Thessaloniki (Briese and Sheppard, *in press*). Mature rosettes of the host plants were arranged using 5 replicates in a Latin square on a field plot 8 months before the flowering period, following the method of Groppe *et al.* (1990). Each plant was separated by 2 m from all others. Three replicate plots were used in France and 2 in Greece. Attack levels by the different *Larinus* spp. that located the plants during the flowering period were recorded by dissecting all flower heads at the end of the flowering period and counting the number of successfully developed adults of all species/ capitulum for all the test plants.

Electrophoretic Studies

A site near Lefkonas in Macedonia, northern Greece, was used to investigate the differentiation of host races within *L. latus*. Allozyme electrophoresis was used to analyse individuals from the site where 2 species of *Onopordum* (*O. bracteatum ilex* [Janka] Franco and *O. acanthium*) and hybrids occurred together. Thirty attacked mature capitula were collected at random from each of the 3 plant taxa present. The techniques used are described in Paitier *et al.* (1987), with the exception of the staining contingency tables were used to compare the number of sites with attack on *Cynara* and *Onopordum*, for each *Larinus* spp. in each region.

Results

Larinus *spp. Encountered and Their Oviposition Behaviour*

Five species were recorded attacking the capitula of the genera *Onopordum* and *Cynara*. Three species in the subgenus *Larinus s. str.* oviposited on the outside of unopened flower heads and later into open flower heads (i.e., *L. latus, L. cynarae*) or only into open flower heads (i.e., *L. scolymi*). The remaining species, a new *Larinus* sp. attacking only *C. humilis* in mixed *Cynara* populations and *L. sturnus* in the subgenus *Larinodontes,* oviposited into rostrum-pierced holes in unopened flower heads in the manner typical of this subgenus (Zwölfer and Brandl 1989). *Larinus jaceae* F., and *L. turbinatus* Gyll. were observed on flowers of *Onopordum* spp. in southern France and another undetermined *Larinus* sp. was observed feeding on leaves of *Onopordum* spp. in eastern Spain.

Survey

A summary of the number of populations sampled of the different species of *Onopordum* and *Cynara* in southern Europe is given in Table 1. Ten of the 14 European species of the genus *Onopordum* and 5 of the 7 species of the genus *Cynara* were encountered. Of the sites visited, 37 contained mixtures of 2 species of *Onopordum*, 3 contained 2 species of *Cynara* and five contained species of both *Cynara* and *Onopordum*. *O. macracanthum* Schousboe, *C. algarbiensis* Cosson ex Mariz and *C. baetica* were free of *Larinus* spp. Few *C. scolymus* (artichoke) crops were sampled due to substantial existing knowledge of associated natural enemies (Paitier *et al.* 1987). Table 2 summarises the host plant-species list of the *Larinus* spp. encountered during the survey, incorporating all known literature records.

L. latus was associated only with *Onopordum* spp. in its limited eastern European distribution. *O. bracteatum* Boiss. & Heldr. and *O. illyricum carduncnlus* (Boiss.) Franco were more frequently attacked than other *Onopordum* spp. (Chi-squared = 18.2, $p = 0.0001$). Moreover, *O. argolicum* Boiss. and *O. caulescens* D'Urv. were only frequently attacked at mixed sites that also contained these species. No attack occurred on *Cynara* spp. in mixed populations.

L. scolymi was restricted to host plants of the genus *Cynara* (Fisher Exact $p<0.0001$), except at 1 French site where 2 individuals were reared from *O. illyricum* capitula. However, this species appears to have little preference within the genus *Cynara* throughout much of its geographic range. Unattacked *Cynara* spp. had relatively small capitula and were only encountered in southern Spain and Portugal near the evolutionary centre of origin of the

Table 1. A summary of the number of pure and mixed populations sampled for species of *Onopordum* and *Cynara* (* = species distributions not sympatric).

O. acanthium	**28**														
O. acaulon	5	**4**													
O. tauricum	4	*	**6**												
O. illyricum	2	*	3	**20**											
O. bracteatum	2	*	1	*	**37**										
O. nervosum	4	2	*	1	*	**9**									
O. macracanthum	*	0	*	*	*	0	**5**								
O. corymbosum	2	3	*	*	*	2	0	**6**							
O. caulescens	*	*	0	*	1	*	*	*	**1**						
O. argolicum	*	*	0	*	5	*	*	*	0	**4**					
C. cardunculus	*	*	0	1	1	0	0	0	0	1	**5**				
C. humilis	*	*	*	0	*	0	0	*	*	*	2	**7**			
C. scolymus	0	0	0	0	1	0	0	0	0	0	0	0	**3**		
C. algarbiensis	*	*	*	*	*	*	*	*	*	*	0	1	0	**3**	
C. baetica	*	0	*	0	*	0	0	*	*	*	0	0	0	*	**1**

genus (Mabberley 1989).

L. cynarae was found attacking host plants from 3 genera, but complete development was not observed on *Silybum marianum* L. (cf. Zwölfer *et al.* 1971, Goeden 1976). In Greece, it was consistently found on *C. cardunculus* and related hybrids in all except 1 small isolated patch in the north-east, even though some sites also contained *Onopordum* spp. Where large adjacent crops of artichoke were found, they were free of attack (Fisher Exact $p<0.0001$). In Italy, where fewer sites were located, this was not so clear. Only here is this species recorded as a pest of artichoke (Martelli 1948). In southern France, only *Onopordum* spp. were attacked and, within the genus, *O. acanthium* was the least attacked (Fisher Exact $p= 0.0002$). In north-east Spain, *O. acanthium* was as equally attacked as other *Onopordum* spp., although these differed from those in France (Table 2). Comparing the 4 species of *Onopordum* in this region, *O. acaulon* (stemless) was the only species less frequently attacked (Chi-squared = 12.97 - 3/8 expected values <5 - $p= 0.005$). In southern Spain and Portugal, only *C. humilis* L. and no *Onopordum* spp. were attacked. This has lead to the identification of 3 clear host races supported by observations at sites with mixtures of host plant species (Table 3; Briese and Sheppard, *in press*).

The record for *L. sturnus*, already known to attack 4 genera of thistles (Zwölfer and Romstöck-Völkl 1991), represents a new host

Table 2. Species of *Larinus* encountered feeding in capitula of *Onopordum* and *Cynara* species during this study and their host plant range throughout their distribution from this study or from literature references.

Larinus spp.	Region	Host Plant	Proportion of Sites Attacked (or Reference)
L. cynarae F.	Greece	*O. bracteatum ilex* (Janka) Franco	0.02 (1/47)
		Onopordum spp. (5)	0.00 (0/37)
		C. cardunculus L.	0.80 (4/5)
		C. scolymus L. x *C. cardunculus*	1.00 (1/1)
		C. scolymus	0.00 (0/2)
	Italy	*O. illyricum illyricum* L.	0.33 (1/3)
		C. cardunculus	1.00 (2/2)
		Silybum marianum L.	(Zwölfer *et al.* 1971)
	S. France & Corsica	*O. acanthium* L.	0.40 (4/10)
		O. illyricum illyricum	1.00 (18/18)
		O. tauricum Willd.	1.00 (5/5)
		C. cardunculus	(Zwölfer *et al.* 1971)
		C. cardunculus (com. var. 507)	0.00 (0/3)
		C. scolymus	0.00 (0/2)
		S. marianum	0.20 (1/5)
	N.E. Spain	*O. acanthium* L.	0.53 (8/15)
		O. acaulon L.	0.11 (1/9)
		O. corymbosum	0.75 (6/8)
		O. nervosum	0.85 (11/13)
	S. Spain & Portugal	*Onopordum* spp. (3)	0.00 (0/13)
		C. cardunculus	0.00 (0/3)
		C. humilis	0.40 (4/10)
		Cynara spp. (2)	0.00 (0/5)
L. latus Herbst	Greece & Crete	*O. acanthium*	0.70 (7/10)
		O. argolicum Boiss.	0.50 (5/10)
		O. bracteatum Boiss. & Heldr. (3 subspp.)	0.96 (45/47)
		O. caulescens D'Urv.	0.50 (1/2)
		O. illyricum carduncculus	1.00 (4/4)
		O. tauricum	0.67 (4/6)
		Cynara spp. (2)	0.00 (0/6)
L. scolymi Olivier	Greece & Italy	*Onopordum* spp. (6)	0.00 (0/80)
		C. cardunculus	1.00 (7/7)
		C. scolymus	1.00 (2/2)
		C. scolymus x *C. cardunculus*	1.00 (1/1)
	France & Corsica	*O. illyricum illyricum*	0.07 (1/14)
		Onopordum spp. (2)	0.00 (0/15)
		C. cardunculus(com. var. 507)	1.00 (2/2)

Table 2. Continued.

Larinus spp.	Region	Host Plant	Proportion of Sites Attacked (or Reference)
		C. scolymus	1.00 (2/2)
	N.E. Spain	*Onopordum* spp. (4)	0.00 (0/45)
	S. Spain & Portugal	*Onopordum* spp. (3)	0.00 (0/13)
		C. cardunculus	1.00 (4/4)
		C. humilis	0.60 (6/10)
		Cynara spp. (2)	0.00 (0/5)
Larinus sp. nov.	S. Spain & Portugal	*Onopordum* spp. (3)	0.00 (0/13)
		C. humilis	0.90 (9/10)
		Cynara spp. (3)	0.00 (0/7)
L. sturnus Schaller	N. Spain	*O. acaulon*	0.11 (1/9)
	Austria	*Arctium* sp.	(Zwölfer *et al.* 1991)
	European Alps	*Cirsium spinosissimum*	(Zwölfer *et al.* 1991)
		Centaurea spp.	(Zwölfer *et al.* 1991)
	Greece, S.W. Germany & S. and C. France	*Carduus* spp.	(Sheppard, unpublished data)
		Cirsium eriophorum	(Zwölfer & Brandl 1989)

genus for this weevil. Whether this represents a new "*O. acaulon*" race requires confirmation through a detailed survey of the surrounding thistle genera.

In only 15 of the 146 sites observed were >1 species of *Larinus* found attacking the same host. Thirteen involved partitioning of the host plant by 2 *Larinus* spp. (Table 4). In the genus *Onopordum,* the trend was toward exclusive use of the host plant by a single *Larinus* species, because in all but 1 case of resource sharing the host involved belonged to the genus *Cynara* (Table 4).

Host-Choice Experiment

Under conditions of equal access to all potential host plants, the weevils chose the host genus on which they themselves had developed (Table 5). The *L. latus* and *L. cynarae* that were present came from subspecies of *O. illyricum.* Next generation adults emerged only from plants of this genus. Oviposition was also limited to these species (unpublished data). Similarly, adults of *L. scolymi* emerged only from *Cynara* spp. For all *Larinus* spp., no difference was found in the number of adults emerging per head between species in the genus attacked.

Electrophoresis of L. latus *from a Mixed* Onopordum *Site*

Weevils reared to adulthood provided 22 adults from *O. bracteatum*, 33 from *O. acanthium* and 18 from the hybrids. Nine polymorphic loci were detected using standard horizontal starch gel protein electrophoresis (GOT, IDH, MDH-1, MDH-2, PGI, ME, ADH, GPD and LAP). None of the 3 *L. latus* groups collected showed a significant deviation from expected genotype frequencies under random mating between groups (Fisher Exact test not significant for all loci).

Wright's F_{st} statistic (Wright 1951), a measure of population subdivision, was calculated. This estimation was done using the Weir and Cockerham (1984) procedure, which includes corrections for small sample size. The overall F_{st} for all loci was very low ($F_{st} = 0.019$, SD obtained by jackknifing over loci = 0.0081). Since the distribution of F_{st} was not known, 95% confidence intervals were estimated by bootstrapping over loci (Weir 1990). One thousand samples were generated providing an interval between -0.0086 and 0.0446. The absence of significant subdivision indicated a lack of host race formation. However, 1 locus (IDH) showed significant heterogeneity of allele frequencies between populations (Chi-squared = 7.1, p=0.029), but, given that 9 loci were screened, this locus may have shown differentiation by chance.

Table 3. Three host races of *L. cynarae* adapted from (Briese and Sheppard 1991).

Principal Host Plant of Race	Unattacked Sympatric Species	Region
I. *Cynara cardunculus* L.	*Onopordum* spp.	Greece, Italy
II. *Cynara humilis* L.	*C. cardunculus*	S. Spain, Portugal
III. *Onopordum* spp.	Cultivated *Cynara* spp.	S. France, Corsica, N.E. Spain[1]

[1] Authors discuss the possibility of a division of this race into 2 parts based on allopatry across the Pyrenees.

Table 4. Partitioning host plant utilisation amongst 5 species of *Larinus* attacking thistles of the genera *Onopordum* and *Cynara* in Mediterranean Europe; I-III are host races from Table 3.

Larinus spp.	Number of Observations On	
	Onopordum spp.	*Cynara* spp.
1 species host[1]		
L. latus Herbst	66	
L. cynarae Fabricius III	54	
L. scolymi Olivier		7
Larinus sp. nov.		3
L. sturnus Schaller	1	
2 species host[1]		
L. cynarae III + *L. scolymi*	1	
L. cynarae I + *L. scolymi*		6
Larinus sp. nov. + *L. scolymi*		6
3 species host[1]		
L. cynarae II + *L. scolymi* + *Larinus* sp. nov.		2

Table 5. The number of adult *Larinus* that emerged per capitula from the replicated Latin square field host-specificity test. (*O. tauricum* was not tested in France.)

Test Plant	*L. cynarae* (*Onopordum* Host Race)	*L. latus*	*L. scolymi*
O. illyricum L.	0.233 ± 0.056	0.011± 0.011	0.0
O. acanthium L.	0.244 ± 0.062	0.005 ± 0.003	0.0
O. tauricum Willd.	not tested	0.019 ± 0.005	not tested
C. cardunculus L.	0.0	0.0	0.321 ± 0.121
C. scolymus L.	0.0	0.0	0.800 ± 0.800

Discussion

Host Partitioning

The *Larinus* spp. attacking these 2 plant genera do not all conform to the 2 "types" described by Zwölfer and Brandl (1989). Both *L. latus* and *L. cynarae* have intermediate oviposition behaviours, medium length rostra and no sexual dimorphism and may represent a third functional sub-guild within the genus (Zwölfer and Brandl 1989). However, evidence is poor as to what might explain the way *Larinus* species are distributed among the European members of these host plant genera.

Only on *Cynara* spp. with large capitula was there scope for direct competition between *Larinus* spp. Where partitioning of *Cynara* spp. by *Larinus* spp. occurred, however, contrasting oviposition strategies were always observed. For example, on *C. humilis* in Portugal, where 3 *Larinus* spp. co-occurred, all 3 recognised oviposition strategies existed, giving rise to variation in the timing of attack. *L. scolymi*, laying into the flowers, was generally 1 month later than the other species. These subtle differences may permit coexistence, but there is evidence that heavy early attack by 1 *Larinus* spp. may disadvantage subsequent attack by another. At the 2 sites where most heads were destroyed, the ratio of emerging adults of *L. cynarae, L.* sp. nov. and *L. scolymi* was 18:28:2 and 32:5:4 respectively. Although it might appear that *L scolymi* always fared worst, the presence of nearby populations of the later flowering *C. cardunculus,* which appeared only to be attacked by *L. scolymi,* could indicate that *C. humilis* is only its secondary host.

Onopordum spp. never appear to accommodate >1 species of *Larinus.* This was particularly evident in Greece, where *L. latus* is the sole member of this genus attacking *Onopordum* spp., and *L. cynarae* is represented only by its "*Cynara*" host race. Historic competitive exclusion may have been witnessed here if similarity of oviposition strategy is the key to species distribution in *Larinus,* but there are several other equally plausible explanations for the pattern observed (Briese and Sheppard, *in press*). More detailed study would be needed to quantify any competitive interactions and their possible impact on community structure and host race formation.

Host-Specificity and Taxonomic Level

The field observations suggest that, although most species and host races remain restricted to 1 host plant genus and may show a "preference" within that genus, occasional attack on a related genus can occur in mixed populations. Intuition suggests that it would be less likely for a species to shift hosts than for a host race, especially if other conspecific host races exist elsewhere on the new host genus (i.e., as with *L. cynarae*). The data presented here do not clearly support this intuition. In Italy, the existing "*Cynara*" host race of *L. cynarae* was observed to use *Onopordum,* while *L. scolymi* was restricted to *Cynara* spp. In southern France, however, *L. scolymi* attacked novel hosts while the "*Onopordum*" host race of *L. cynarae* did not. The host choice experiments also showed the "*Onopordum*" host race of *L. cynarae* was as selective for hosts as the other *Larinus* spp. without known host races.

Although it is risky, when target and crop species are so closely related, to extrapolate ecological observations about host-specificity into evolutionary predictions about the stability of this specificity, there is no reason to suggest that predictions should be any more risky at a subspecific than a specific level of the agent. The electrophoretic study supports the idea that host race formation is not a simple process of sympatric speciation, but requires other allopatric or geographic boundaries for isolating sub-units within a species. While evidence and support from another thistle head-weevil species, *Rhinocyllus conicus* (Froelich) (Coleoptera: Curculionidae), shows that not only are subspecific races clearly separable genetic and ecologically distinct groups, they can also be useful in biological control (Goeden *et al.* 1985, Klein 1991). If we can scientifically test these "intuitions" about the importance of the species division in agents, as we are starting to do in other ecological aspects of biological control, then it may well be possible to use host-races of agents to help control weeds that are closely related to agricultural crops.

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