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Oogenesis requirements and weed biocontrol: an essential part in host-range evaluation of insect agents or just wasted time?

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Abstract. The ability of an insect to initiate oogenesis, i.e. become sexually mature, on a test-plant is a major factor determining its potential host range. Sixty-two papers covering host specificity of insect biocontrol agents (mostly Coleoptera), where host feeding is a prerequisite for maturation of ovarioles, were examined. These papers revealed little investigation of the oogenesis requirements of insects with a known feeding history nor of the influence of ovariole development on host acceptance. Investigations of four different herbivore-weed systems were carried out to test for differences in the experimental host-range when insect agents were kept in: (i) a no-choice situation from the day of emergence onwards; and (ii) a no-choice situation after maturation had been completed on the field host. The experiments revealed varied results depending on the herbivore-weed system studied. No case was found where a test-plant species that was accepted for continuous oviposition did not support maturation of the insects as well. When transferring sexually-mature adults onto several other critical test-plant species, only previously developed eggs were laid, but maturation itself was not supported. A general recommendation to include newly-emerged adults in maturation studies in host-specificity screening procedures does not seem to be justified.

Introduction

The use of no-choice or acceptability tests (Singer 1986) to determine the experimental host-range of insect agents has led to a number of problems in the past. For example, the rejection of agent species that developed on a broader range of plant species under laboratory conditions than they did in the field. This has led to long debates on how to interpret the results of such tests and how to improve testing procedures (Dunn 1978; Cullen 1989; Wapshere 1989). Generally, two solutions were suggested: change testing sequences and improve the choice test methodology (Dunn 1978; Wapshere 1989) or increase the use of field tests to mimic natural conditions (Briese *et al.* 1995; Clement and Christofaro 1995). However, no-choice trials are still commonly used as a basic testing method to demonstrate the physiological host range of potential biocontrol agents (e.g. Adair and Scott 1993; Gassmann 1996). Another approach in the development of host-specificity evaluation procedures might be to focus on the improvement of no-choice tests themselves.

Usually, two types of no-choice tests are conducted. Larval-transfer tests examine larval development through to adulthood, whereas adult feeding and oviposition tests investigate whether a plant species supports egg production. However, as the definition of host range presented by Hanson (1983) refers to only those plants on which an animal completes normal development in nature, no-choice tests should preferably include all developmental processes in an insect's life history. The question of whether or not development is completed is important, in that it determines the range of plant species on which the agent can exist in the absence of its field host (Cullen 1989). One aspect of insect life-history that has been largely neglected during no-choice host-range evaluations of agents where adult feeding and oviposition has been studied, is the ability of adults to reach sexual maturity (Chapman 1982), i.e. to initiate oogenesis and produce fertile eggs.

In this paper we examine the extent to which current host-specificity investigations apply to insect agents where adult feeding is a prerequisite for oogenesis. Experiments on four herbivore-weed systems are used to assess the importance of sexual maturation on the acceptability of test-plant species.

Oogenesis studies in current host-range investigations

As the experimental designs of oogenesis experiments conducted during host-range investigations differed considerably, they were divided into maturation and oogenesis experiments, and defined as follows: (i) maturation experiments are designed to investigate the ability of newly-emerged female adults to start laying fertile eggs (i.e. initiate oogenesis) when kept on test-plant species in a no-choice situation (e.g. Forno *et al.* 1992; Rizza and Pecora 1980); and (ii) oogenesis experiments are designed to investigate the extent to which females sustain egg production when kept in a no-choice situation on test-plant species, after sexual maturation on their field host or on a test-plant species (e.g. Andres and Angalet 1963; Gassmann 1996). The use of newly-emerged adults is a precondition for maturation experiments but not necessarily for oogenesis studies.

We examined 62 host-specificity publications on insect agents where adult feeding is a prerequisite for egg development. Of the 62 publications, 34 are on Chrysomelidae, 19 on Curculionidae, two each on Apionidae, Cerambycidae and Tingidae and one each on Buprestidae, Agromyzidae and Lygaeidae. A list of these publications is available on request from the senior author. In 21 papers, newly emerged, unfed adults were used, whereas in 34 papers, mature or field-collected adults were tested, either for practical reasons and, or, to ensure that females were ready to oviposit (Julien *et al.* 1982; Fornasari *et al.* 1991). However, this means that the physiological host-range might be extended to plant species which support partial development of the insects but not the sexual maturation of adults (Zwölfer 1976; Forno *et al.* 1992). Seven publications did not clearly specify the attributes of the adults that were used. Only 18 papers included experiments on oogenesis requirements, 12 of which included the dissection of females for inspection of ovariole development. From these 18 host-specificity evaluations that included studies on either oogenesis and, or, maturation, two were conducted using field-collected adults, thereby excluding maturation tests. Of the remaining 16 investigations incorporating maturation tests, nine also included oogenesis studies. Only three host-range studies compared oviposition and longevity of adults in a no-choice situation on test plants prior to and after maturation on the field host (Kok *et al.* 1975; Kok *et al.* 1979; Sands *et al.* 1982).

These were the only studies providing information on the importance of maturation itself for acceptability of test-plant species. However, the three studies revealed inconsistent results: in one case, mature females laid eggs on a test-plant species, but failed to mature sexually on the same species (Sands *et al.* 1982); in the other two cases, some of the newly-emerged adults became mature and laid eggs on a critical test-plant species. However, when adults that had already matured on the field host were transferred onto the same plant species, females did not continue to lay eggs. In the latter two cases, the results were obviously influenced by other factors, such as conditioning or female behaviour. Thus, we perceived a need for additional work in this area, as reported below.

Material and methods

The effect of sexual maturation on the acceptability of critical test-plant species was studied using four herbivore-weed systems that were investigated at the IIBC European Station during 1994-1995. The systems used were: *Mogulones cruciger* Herbst (Coleoptera: Curculionidae), and *Longitarsus quadriguttatus* Pont. (Coleoptera: Chrysomelidae) mining in the roots of hound's-tongue (*Cynoglossum officinale* L.); *Microplontus edentulus* Schltz. (Coleoptera: Curculionidae) mining in the shoots of scentless chamomile (*Tripleurospermum perforatum* (Mérat) Wagenitz), and *Phytomyza vitalbae* Kltb. (Diptera: Agromyzidae), a leaf mining fly on old man's beard (*Clematis vitalba* L.).

Adults were obtained from breeding colonies. No-choice starvation tests were carried out in two treatments: (i) using newly emerged, unfed adults (NE); and (ii) using mature individuals (M) that were offered the corresponding control plant, until the females reached sexual maturity, prior to transfer onto the test plants. For each system, we used only those test-plant species on which oviposition and, or, larval development had occurred in previous tests.

Similar tests were carried out for *M. cruciger, L. quadriguttatus* and *P. vitalbae*. One pair each of *M. cruciger* and *P. vitalbae*, and five pairs each of *L. quadriguttatus* were released into plastic cylinders covered with gauze lids. Four replicates each were set up with *M. cruciger* and *L. quadriguttatus,* and five to ten with *P. vitalbae* for each test-plant species and test type. Cut leaves of either the test or the control plant were offered in moist blocks of horticultural sponge, and changed regularly. Dissections were carried out to inspect for eggs. In order to estimate the amount of adult feeding, feeding holes or feeding punctures were counted. Adult longevity was recorded for *L. quadriguttatus* and *P. vitalbae.* Since the three species are long-lived and dissections of females always revealed very low numbers of mature eggs in the ovarioles, the actual fecundity was used as a measurement for egg production.

Tests with *M. edentulus* were carried out on potted plants, using two females and one male on each plant. Before the end of the oviposition period, the weevils were removed, killed and the females were dissected to evaluate their ovariole development. Plants were examined for mines, exit holes and larvae.

Results

The results for *M. cruciger* and *L. quadriguttatus* were similar. No significant differences were found between the fecundity of females in the NE- and M-treatments. The amount of plant tissue consumed was significantly increased in the NE-treatment on *Cynoglossum amabile* and *Borago officinalis* tested with *M. cruciger* and significantly reduced on *Symphytum grandiflorum* tested with *L. quadriguttatus.* On *Lithospermum officinale* tested with *L. quadriguttatus,* longevity of the newly-emerged males and females was significantly lower compared to that of mature adults (Tables 1 and 2). In both insect species, adult feeding on *C. officinale* was not a prerequisite for initiation of egg production for the plant species tested. However, in both insect species, differences were found in the suitability of test plants to act as hosts.

Mogulones cruciger laid significantly more eggs on the control plant than on *Amsincksia tessalata* or on *B. officinalis* (Mann-Whitney, $P << 0.05$, $n = 4$). The differences were not significant for the other plant species tested. Comparable results were found for adult feeding and for leaf-tissue consumed per egg laid (Table 1). No significant differences were found between the control and test-plant species during the time required to initiate oviposition, i.e. 14.5±2.9SE days on *C. amabile* to 34.5±9.1SE days on *Amsincksia tessalata.*

In *L. quadriguttatus,* the actual fecundity was significantly reduced on all three test-plant species compared to the control, irrespective of treatment. Comparable results were found for adult feeding and longevity (Table 2).

Table 1. Fecundity and adult feeding of *M. cruciger* on different test-plant species prior to and after ovariole development. NE - newly emerged adults. M - mature adults. One feeding hole is approximately 2 mm^2. * significant differences between the test-plant species and the control (Mann-Whitney, $P<0.05$), a - significant difference between the NE- and M-tests (Mann-Whitney, $P<0.05$). $N = 4$ in all cases except for *C. offininale* (M) where $N = 3$.

Plant species	Type of test	Mean ±SE number of eggs laid per female	Mean ±SE number of feeding holes per pair	Mean ±SE number of feeding holes per egg laid
Cynoglossum officinale	NE	69.7±31.5	739.3±155.2	26.8±7.7
	M	39.0±11.8	797.5±39.2	18.3±8.4
Cynoglossum amabile	NE	13.5±1.8	1821.5±82.7* a	71.3±19.2*
	M	21.8±5.7	1230.3±169.8 a	144.3±23.3*
Anchusa azurea	NE	19.5±5.3	689.3±52.8	35.0±13.3
	M	19.5±5.5	471.8±56.0*	48.0±17.4
Amzincksia tesselata	NE	1.0±0.6*	570.5±102.8	195.0±107.1*
	M	7.0±2.7*	647.8±47.1	468.8±157.1*
Borago officinalis	NE	4.3±3.1*	795.5±35.0	124.0±42.5
	M	3.8±0.5*	633.0±34.6*	455.5±186.6*
Lappula deflexa	NE	23.3±5.7	978.8±99.9	60.3±16.4
	M	15.3±4.5	759.5±124.2	47.3±7.7

Of the five plant species tested, *P. vitalbae* laid eggs exclusively in the tests carried out with sexually matured females (Table 3). Significant differences in the number of eggs laid in the different treatments were found in *Clematis maximowicziana* and *C. orientalis*. Highly significant differences in fecundity, adult feeding and longevity, were found in *C. orientalis* only. Examination of the original data set disclosed that seven of the ten NE-females fed on *C. orientalis* failed to produce any eggs on this plant species, whereas mean fecundity, adult feeding, and longevity of the remaining three females were no different to those for the nine matured females. Hence, the differences between treatments arose from differences amongst individuals of the newly-emerged females in their ability to feed and oviposit on *C. orientalis*.

Mature females of *M. edentulus* accepted all plant species they were offered for oviposition (Table 4). Except for *Matricaria maritima*, the number of mature eggs per female still present upon dissection was always lower in the NE- than in the M-treatment. The difference was only significant for *Anthemis cotula* (Mann-Whitney, P = 0.042). In the NE-treatment with *A. cotula* and *Leucanthemum vulgare*, dissected females did not contain any mature eggs or ovarioles, whereas the mines found in *M. maritima* and *Chamomilla recutita* indicated that these plant species supported maturation of newly-emerged females. However, fewer mines were found in the NE-treatment compared to the M-treatment.

Discussion

The experiments gave varying results on the importance of sexual maturation for the acceptance of test-plant species.

The results were similar for the two beetle species developing in the roots of hound's-tongue. All test-plant species used supported the maturation of *L. quadriguttatus* and *M. cruciger*, with the probable exception of *A. tessalata*, where a mean of only one egg was laid. No differences were found in the time period required until first oviposition, indicating that the test-plant tissues were capable of supporting the process of sexual maturation (Chapman 1982). However, significant differences were found in the actual fecundity (total number of eggs laid) for insects on the control and the test-plant species, and thus in the suitability of the test-plant species to act as alternative hosts. Although the physiological mechanisms underlying nutritional requirements for oogenesis and their interaction with host selection are still not well understood, the results suggest a likely difference in host-plant preferences of the ovipositing females.

The results for *M. cruciger* and *L. quadriguttatus* are similar to the findings of Kok *et al.* (1979) and Forno *et al.* (1992) where the quality of critical test-plant species to act as alternative hosts was low compared to the controls, but sexual maturation was supported. Studies by Blossey *et al.* (1994a, b), comparing the suitability of a critical test-plant species

Table 2. Fecundity, adult feeding and longevity of *L. quadriguttatus* on different test-plant species prior to and after ovariole development. NE - newly emerged adults. M - mature adults. One feeding hole is approximately 1 mm^2. * significant differences between the test-plant species and the control (Mann-Whitney, P<0.05), a - significant difference between the NE- and M-tests (Mann-Whitney, P<0.05). N = 4 in all cases except for *E. vulgare* (M) where N = 3.

Plant species	Type of test	Mean ±SE number of eggs laid per five females	Mean ±SE of feeding holes per five pairs	Mean ±SE longevity of females (days)	Mean ±SE longevity of males (days)
Cynoglossum officinale	NE	632.8±184.0	6738.8±392.1	64.6±0.9	52.5±10.1
	M	633.8±35.0	6510.8±972.1	67.0±8.1	42.7±5.8
Echium vulgare	NE	115.8±16.8*	2477.0±144.3*	30.8±4.6*	22.3±3.9
	M	47.3±22.5*	2646.0±496.3*	32.1±0.6*	27.9±0.4*
Lithospermum officinale	NE	51.8±32.1*	1683.3±140.9*	20.2±3.4* a	19.8±4.3* a
	M	16.8±5.9*	2429.3±274.6*	42.2±8.3* a	40.7±4.2 a
Symphytum grandiflorum	NE	102.0±35.3*	2477.0±144.3* a	28.1±3.1*	28.6±3.8
	M	174.5±25.4*	4206.5±371.4 a	42.2±4.7*	35.6±5.5

Table 3. Fecundity, adult feeding and longevity of *P. vitalbae* on different test-plant species prior to and after ovariole development. NE - newly emerged adults. M - mature adults. *, ** - significant differences between the test-plant species and the control (Mann-Whitney, * = $P<0.05$; ** $P<0.01$). a, aa - significant differences between the NE- and M-treatments (Mann-Whitney, a = $P<0.05$; aa = $P<0.01$). N = 5 except where indicated in parentheses after the notations NE and M.

Plant species	Type of test	Mean ±SE number of eggs laid per female	Mean ±SE number of feeding punctures per female	Mean ±SE longevity of females (days)
Clementis vitalba	NE/M	978.0±257.6	7470.2±1501.6	35.2±7.0
C. marata	NE	0.0±0.0**	7.2±7.0**	6.8±2.6*
	M	1.0±1.0**	17.8±17.8**	4.4±1.0*
C. maximowicziana	NE (4)	0.0±0.0* a	8.0±8.0**	4.0±2.0*
	M (3)	4.0±2.0* a	50.0±34.3**	4.0±0.0*
C. montana	NE	0.0±0.0**	0.0±0.0** a	2.0±0.4**
	M	12.8±10.7**	14.0±6.9** a	3.4±0.4**
C. orientalis	NE (10)	177.6±99.7**aa	1495±819.6** aa	8.2±3.6** aa
	M (9)	787.3±108.5 aa	5987.2±833.2 aa	24.0±3.2 aa
C. recta	NE	0.0±0.0**	3.0±3.0**	8.0±4.5*
	M	6.0±4.8**	73.8±49.2**	7.0±3.1*
C. viticella	NE	0.0±0.0**	0.0±0.0**	3.4±0.2**
	M	6.2±6.0**	4.4±3.0**	3.2±0.4**

with that of the control, led to the same conclusion. Based on these data, the recommendation to use newly-emerged adults for feeding and oviposition tests would not be justified.

The results for the agromyzid fly differed considerably from those for the two beetles. Only one of the tested plant species, *Clematis orientalis*, supported maturation of a portion of the fly population. The significant differences in mean longevity and consequently in total fecundity between the NE- and M-treatment were not due to reduced fitness of the flies in general, but indicated genetic variation in the ability of the *P. vitalbae* population tested to adopt *C. orientalis* as an alternative host (Bernays and Chapman 1994). Similar results were found for the weevil *Ceutorhynchus trimaculatus* when kept on artichoke, a critical test plant for this species (Kok *et al.* 1979).

In the M-treatment with *P. vitalbae*, a few eggs were laid on a further five test-plant species. It is assumed that these eggs developed in the ovarioles of the females that were provided with the control prior to transfer onto test-plant species. Similar results were found when using mature adults for no-choice oviposition tests (e.g. Zwölfer 1976; Zwölfer and Harris 1984; Jayanth and Nagarkatti 1987; Gassmann 1996). Although the number of eggs laid was very low compared with the number laid on the controls, the results would not allow the exclusion of these five plant species from further testing, since they had supported partial development in previous tests. Thus, in the case of *Phytomyza vitalbae* it would be highly advisable to use newly-emerged adults, since, from the six plant species tested, five could have been excluded immediately, compared to none that could be excluded when using mature adults.

The results of the tests with *M. edentulus* allow only qualitative conclusions. Two test-plant species supported sexual maturation, i.e. *M. maritima* and *C. recutita*, whereas *L. vulgare* and, possibly, *A. cotula* did not. Reproductive organs appeared to have been resorbed due to the unsuitability of the latter test-plant species (Chapman 1982). Therefore, based on the results for this species, the use of newly-emerged adults should also be advocated, especially since one of the test-plant species, where the female ovarioles were completely resorbed in the NE-treatment (Bell and Bohm 1975), had supported larval development to adulthood in previous tests.

When assessing the results of these studies it seems important to distinguish between three possible responses: firstly, the suitability of critical test-plant

Table 4. Attack by *M. edentulus* on different test-plant species prior to and after ovariole development. NE - newly emerged adults. M - mature adults. Number of mature eggs and ovarioles derived from dissections of females. Number of ovarioles expected per female was four. 'Mines and exit holes' refer to shoot dissections. N = 3 in all cases.

Plant species	Type of test	No. of females found alive/dead	No. mature eggs per female	No ovarioles found/ expected	Mines and exit holes
Tripleurospermum	NE	4/0	1.0±0.7	10/16	20
perforatum	M	6/0	4.7±1.1	16/24	15
Matricaria	NE	4/0	2.3±1.6	12/16	10
maritima	M	6/0	2.0±0.6	20/24	22
Chamomilla	NE	6/0	1.2±0.6	12/24	3
recutita	M	6/0	2.2±0.5	24/24	12
Anthemis	NE	3/0	0	0/12	0
cotula	M	6/0	3.0±0.7	16/24	8
Leucanthemum	NE	3/1	0	0/16	0
vulgare	M	4/1	1.2±0.7	8/20	7

species for insects to reach sexual maturity and sustain egg production, which was demonstrated for the two beetle species feeding on *C. officinale*; secondly, the inability of newly-emerged adults to produce eggs on critical test-plant species, on which matured adults laid previously-ripened eggs; and thirdly, the rejection of test-plant species by newly-emerged adults, on which egg production could be maintained by matured adults. The second response was observed for five *Clematis* species tested with *Phytomyza vitalbae* and for *A. cotula* and *L. vulgare* tested with *M. edentulus*, whereas the third response was only partly demonstrated for *Clematis orientalis*. There is an indication that those test-plant species on which oviposition can be maintained do not support sexual maturation of adults. It would therefore seem unimportant whether or not newly-emerged or matured adults are used in adult feeding and oviposition tests, since the ability of adults to mature on a test plant might be sufficiently predicted by measuring their oviposition performance. However, by using newly-emerged adults, test-plant species may be excluded faster and with greater certainty from further screening tests.

The experiments revealed preliminary results only and further studies on this topic are necessary. In addition, the ability of an insect species to complete its development on a test-plant species is not an absolute criterion. The level of damage needs to be taken into consideration (Cullen 1989), as well as the fact that behavioural factors such as conditioning might override physiological suitability (Kok *et al.* 1975, 1979). Therefore, for pragmatic reasons, a general recommendation to use only newly-emerged adults when conducting feeding and oviposition tests with insect agents does not seem to be justified.

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