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Gorse pod susceptibility and oviposition preference to the gorse seed weevil, *Apion ulicis* (Forster) (Coleoptera: Apionidae)

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Abstract Gorse (*Ulex europaeus* L.) is an economically important weed in New Zealand. To contain its spread, the gorse seed weevil, *Apion ulicis* (Forster) was released in 1931. Some aspects of the bionomics of this insect have been studied previously, but the oviposition behaviour of *A. ulicis* was not investigated. Results indicated that *A. ulicis* can oviposit in gorse pods in the age range 10–35 days. Pods 21 days old and pods that have not been previously attacked by other females were preferred. The implications of these results are discussed in relation to the biological control of gorse in New Zealand.

INTRODUCTION

In many holometabolous insects the selection of a feeding site for the larval stage is determined by the ovipositing female and not the larva. This is true of the gorse seed weevil, *Apion ulicis*, whose larvae cannot move between gorse pods and must complete their development in the pod chosen by the female. Larval survival is therefore dependent on adult oviposition behaviour.

Gorse (*Ulex europaeus* L.) produces a pubescent seed pod or legume (Jones 1945) approximately 15–20 mm long (Schauer 1982) and 6–8 mm wide (Wagner et al. 1990) when mature. In New Zealand, eggs of the gorse seed weevil are found in pods from mid August to early December (Cowley 1983). When ovipositing, the female bores a small hole with her rostrum into the seed chamber or locule of the pod. When the hole is complete the ovipositor is orientated into it. Eggs are deposited on the inside walls of the seed chamber or directly on the seeds. The hole gradually closes as the pod matures. It takes up to 5 h to bore a hole and ovipositing females may utilise those already present from the activity of other females (Davies 1928).

Eggs are laid in young green pods only, with the hole occasionally being bored through the calyx that surrounds the developing pod (Davies 1928; Miller 1947, 1970; Forster 1977). Cowley (1983) has estimated, from field observations, that pods up to 1 month old may be used before they become too tough to penetrate. Stevenson (1973) has shown that *Apion* does not discriminate between pods at different positions on a gorse branch.

Gorse produces a bright yellow inflorescence that arises in the axils of spines from the previous years growth. The flower is typical of the Leguminosae being characterised by lateral wings or alae and an anterior keel or carina (Jones 1945). The flower is amphisporangiate with the 10 stamens being fused forming a staminal tube around the gynoecium.

The gynoecium consists of a single carpel with a short, densely-haired ovary bearing 14 ovules (Chater 1931). Pollination of the flower occurs primarily by bees searching for pollen. The carina is depressed when the insect lands on the alae causing the style to emerge. Pollen is collected ventrally off the pollinator on the stigma, with the stamens depositing pollen on the insect (Jones 1945). Gorse has two flowering periods in New Zealand from which fruit is set. The spring fruit set occurs from July–December and the autumn set February–May (Cowley 1983; Hoddle 1991).

The purpose of this investigation was to determine the age range of pods that female weevils could

utilise for oviposition, and whether *A. ulicis* would discriminate preferentially between susceptible pods of varying ages and susceptible pods that had been attacked previously by other females.

METHODS AND MATERIALS

Gorse flowers can be pollinated artificially. The keel of a "virgin" flower was depressed between the thumb and forefinger, resulting in the emergence of the stigma and the explosive release of pollen. The pollen was collected with a fine paint brush and painted on to the stigmas of other "virgin" flowers. Consequently, the exact date of pollination was known.

Flowers were pollinated in this manner on potted gorse plants outdoors. These plants had been beaten and inspected carefully to ensure that they were weevil-free for this experiment. The calyx of each pollinated flower was painted with a coloured nail polish. This tagging programme allowed rapid identification of pods pollinated on set dates. Artificial pollination had a success rate ranging from 48–67%. The development of pollinated flowers was observed daily and recorded. Pods were opened at regular intervals and the seed maturation times were recorded.

Davies (1928) noted that females readily oviposited in pods when held in captivity. Twigs with developing pods of known age were picked and enclosed with one female in a clear plastic container (height 62 mm, radius 25 mm) with 40/40 stainless steel mesh replacing most of the screw lid. The base of each container had a 4 mm hole allowing the gorse branch bearing the pod(s) to pass into a vial of water. The aperture was sealed with cotton wool. Pods from artificially pollinated flowers were first presented to female weevils at 7 days of age, then at 3–4 day intervals up to 38 days of age.

Female weevils have a selection of pod ages to choose from when ovipositing in the field. Caged female weevils were presented simultaneously with three pods aged 14, 21, and 28 days, to determine if preference with respect to pod age exists. In the field, female weevils encounter pods that have already been attacked by other females. The ovipositing female is faced with a decision: to lay in an infected susceptible pod and risk reducing reproductive fitness through increased larval competition, or to maximise reproductive success by searching for virgin pods.

Two 3-week old pods were presented to 10 individually caged female weevils for a 24 h. The number of oviposition marks on each pod was recorded after this time. Two of these pods were then presented randomly to another female along with two unattacked 3-week old pods for a further 24 h. The number of oviposition attacks was then recorded for both sets of pods. The pods used were picked at the same time so pod condition would not be a biasing factor.

Pods were examined after 24 h for oviposition holes, oviposition scars (unsuccessful attempts at boring an oviposition hole), and eggs, using a Bausch & Lomb stereomicroscope at ×10.5 magnification.

RESULTS

Flower senescence and pod development

Twenty four hours after pollination, the calyx of each flower started to close in towards the ovary. The large posterior petal was pushed downwards and the alae were forced in towards the carina, both extended beyond the closing calyx.

Within 4–5 days of pollination the petals started to senesce. This was indicated by a deepening of the yellow colour and a characteristic wilting. After 6–7 days, unfertilised flowers aborted and petal senescence was complete. By day 8–9, the calyx was tightly closed around the developing pod with the dead floral material extending beyond the calyx.

The pod develops in the protection of the calyx until about 17 days of age, when its tip starts to extend beyond the calyx. The sides of the pod are exposed by day 21 as it widens, forcing the calyx apart. The seeds are fully developed by day 35, having enlarged to completely fill the seed chamber.

Seed maturation

There are three chronologically distinct colour classes for seeds: green, yellow, and black.

The spring set of seed. Flowers were pollinated at the begining of October. The mean number of days for the seed to yellow was 53.25 ±1.70 days (range 50–58 days, temperature 17.30°C ±0.91°C). Seeds remained yellow for 3–6 days.

The autumn set of seed. Flowers were pollinated in mid April. The mean number of days for the seed to yellow was 75.66 days ±2.8 days (range 56–88 days, temperature 14.68°C ±0.80°C). Seeds remained yellow for 9–18 days. The time for seed to yellow for the spring and autumn seed set is significantly different ($t = 6.38$, df = 14, $P < 0.05$). Yellowing is accompanied by a distinctive browning of the pod. Seeds darken, dehydrate, and remain in the blackened pod until it dehisces.

Pod susceptibility to weevil attack

Oviposition holes, eggs, and oviposition scars were recorded for pods 10–35 days old. Pods that were 7 days old were not attacked. Oviposition activity therefore first occurred on pods that were 10 days of age, the age that unfertilised ovules are aborted and fertilised ovules start to develop. Pods that were 38 days of age were attacked but only oviposition scarring occurred, suggesting that oviposition stimuli were still present, but the pod was too tough to penetrate.

Pod age discrimination by ovipositing weevils

Female weevils show a bias in oviposition attacks. They preferentially attack and lay eggs in gorse pods of a particular age, choosing those 21 days old instead of 14 or 28 days old ($\chi^2 = 16.09$, df = 2, $P < 0.05$) (Table 1). As a consequence, more eggs were laid in the 21 day old pods (Table 2).

Discrimination between previously attacked and unattacked pods

The proportion of new oviposition attacks on the previously presented pods, divided by the total number of attacks, was significant ($t = 4.70$, df = 9, $P < 0.05$). Ovipositing female weevils prefer to attack clean pods when previously attacked pods from another female are presented simultaneously. Oviposition marks did not increase in number on pods that had eggs laid in them ($n = 6$) or on the surface ($n = 4$). Only single egg batches were recorded in pods that had been oviposited in. This indicates only one oviposition event had occurred. Pods that were scarred, but contained no eggs, occasionally had an increase in oviposition marks (16.43%).

DISCUSSION

Ovipositing gorse seed weevils supply their progeny with a limiting resource to feed on, as larvae are granivorous, feeding within the confines of the gorse pod. To maximise reproductive fitness and optimise the level of larval competition, this study shows that several factors influence oviposition behaviour.

Female weevils preferentially lay eggs in susceptible gorse pods of a particular age (c. 3 weeks old). This strategy ensures soft green seeds for the hatching larvae to penetrate and feed on, while allowing adequate time for development to adulthood before the pod dehisces, releasing its contents.

Female weevils avoid attacking susceptible pods bearing conspecific oviposition marks when clean pods are available for attack. This would lead to a uniformity in egg dispersion among susceptible pods in the field, thereby reducing the number of occasions on which there is a deleterious effect on fitness caused by larval competition (Prokopy et al. 1984).

This is seen in several of the Curculionoidea: the bean weevil, *Callosobruchus maculatus* (Mitchell 1975; Messina & Renwick 1985; Wilson 1988), the dry bean weevil, *Acanthoscelides obtectus* (Szentesi 1981), the boll weevil, *Anthonomus grandis grandis* (McKibben et al. 1982), and the cabbage seed weevil, *Ceutorrhynchus assimilis* (Kozlowski et al. 1983). In these weevils, this effect is mediated by substances termed epideictic pheromones. They are chemical markers that deter conspecific females from laying eggs into the same substrate provided alternative egg laying sites are available (Szentesi 1981). These pheromones may be deposited during egglaying (Kozlowski et al. 1983), defecation, or adult walking (Messina & Renwick 1985). It is not known whether epideictic pheromones are used by *Apion ulicis*.

It is not known whether the decision to lay on a particular pod is based on a "relative" rule which compares the number of oviposi-tion marks on the present pod with that on previously encountered pods, or on an "absolute" rule which takes into account the current number of oviposition marks on the pod. Mitchell (1975), Messina & Renwick (1985), and Wilson (1988) have detailed the decision-making process should ovipositing weevils encounter conspecific oviposition marks.

Larval competition can be further minimised as *Apion* can oviposit in pods that have a varying age range (10–35 days). For example, should there be no

Table 1 The number of attacks by *A. ulicis* on three different ages of gorse pods .

Pod Age (Days)				
Pod attacked	14	21	28	Total
Yes	11	26	7	44
No	87	72	91	250
Total	98	98	98	294

Table 2 The frequency and number of eggs laid by *A. ulicis* in gorse pods of different ages.

Pod age (Days)		
	14	21	28
No. eggs laid	0	55	9
	$n = 49$	$n = 11$	$n = 1$
		$\bar{x} = 5$	
		SE = 1.1832	

virgin 3-week old pods to oviposit in, other pod ages can be used, although conditions in these pods such as seed chamber size and seed hardness may not be ideal for larval development.

Under intense egglaying pressure because of a shortage of available oviposition sites, these regulatory mechanisms are assumed to break down. This is seen in *Anthonomus grandis grandis* (McKibben et al. 1982). Tentative evidence for this in *Apion* is seen when more than one batch of eggs is deposited in a gorse pod. These batches have resulted from seperate oviposition activities, possibly from different females. In New Zealand, egglaying by *Apion* is poorly synchronised with the development of susceptible pods in the field (Hill et al. 1991), thus leading to a shortage of oviposition sites. However, Ofuya & Agele (1989) have shown that *C. maculatus* will lay eggs on seeds bearing their own eggs rather than on seeds bearing the eggs of other females, when there are no more available oviposition sites. This maybe caused by an Allee effect (Allee et al. 1949), whereby larval survival increases up to a certain larval density before decreasing because of competition (Hoddle 1991). Ovipositing gorse seed weevils may preferentially lay again in pods bearing their own oviposition marks when there is a scarcity of virgin pods.

Apion exhibits a univoltine lifecycle in New Zealand, attacking the spring crop of gorse pods only. The results of this study confirm that seed set in autumn escapes predation by *Apion*, as pods carried through the winter are not suitable for weevil oviposition in spring because of their age.

Seed colour can be used as an indicator of pod age in the field for the autumn and spring set of seed. It is a reliable indicator of the approximate age and developmental stage of pods at a given site. Cowley (1983) has shown that the number of immature (green) and mature (yellow and black) seeds do not significantly differ in number, indicating differential mortality of developing seeds does not occur.

CONCLUSION

Selection of a suitable site for oviposition by *Apion* appears to be a complex process with very little known about it. Several factors appear to influence *Apion*'s ability to successfully control gorse in New Zealand.

Apion will attack pods without ovipositing in them, as the female is unable to orientate her ovipositor into the hole (Davies 1928). When these uninfected pods are preferentially attacked. Consequently, uninfected pods that have been attacked bear deterrents that inhibit further oviposition attack and egglaying, reducing the level of successful pod infection. To some extent, this may be compensated for by the ability of *Apion* to attack and lay eggs in a varying range of pod ages.

There may be a hierarchy of stimuli influencing oviposition attack by *Apion*. For example, the desire to lay in a 3-week old pod that has already been attacked may override the response to look for another pod of a different age that has not been attacked. From this it is not known whether *Apion* can discriminate between pods bearing different oviposition mark loads and preferentially lay on pods bearing lower densities of these marks, or, whether *Apion* can assess the seed load of a gorse pod and lay eggs accordingly. These points warrant further research if the effectiveness of *Apion* as a biological control agent on gorse is to be fully understood. It would also assist in the assessment of the possible benefits arising from the release of other gorse seed-feeding invertebrates.

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