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Source: Journal of Insect Science, 5(27) : 1-7

Published By: Entomological Society of America

URL: https://doi.org/10.1673/1536-2442(2005)5[1:EOSROW]2.0.CO;2

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Evidence of sexual reproduction of woolly apple aphid, *Eriosoma lanigerum*, in New Zealand

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Abstract

Reproduction of the woolly apple aphid, *Eriosoma lanigerum* (Hausmann), can take place parthenogenetically or sexually when both host plants, apple (*Malus domestica* Borkh.) and elm (*Ulmus americana* L.) are available. Since elm is not commonly grown in New Zealand, *E. lanigerum* , a major pest of apple, is thought to reproduce only parthenogenetically here. During our studies between 1999 and 2003, different morphs of *E. lanigerum* have been observed on apple trees, which were studied in more detail in 2003 and 2004. In the laboratory, alates reproduced mainly sexual morphs with degenerated mouthparts. Oviparous females lived for 8.95 ± 0.17 days (n = 20) and males lived for 7.1 ± 0.12 days (n = 20). Both went through 4 moults, without feeding or changing body size. Oviparous female laid a single egg and died soon after oviposition. In addition to sexual morphs, shiny brown, oblong eggs were seen on apple leaves grown outside as well as in the glasshouse. As the numbers of eggs and sexual morphs on trees grown outside were less than on those grown in the glasshouse, we suggest that alates disperse into the natural environment searching for an apple or elm tree to continue the sexual reproduction while spreading the population.

Cite this paper as:
Sandanayaka, W.R.M., Bus V.G.M. 2005. Evidence of sexual reproduction of woolly apple aphid, *Eriosoma lanigerum*, in New Zealand. 7pp. *Journal of Insect Science* 5:27, available online: insectscience.org/5.27

Keywords: *Eriosoma lanigerum*, apple, alate, sexupara, sexual morph, oviparous female, male, egg
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Received 09 September 2004 | Accepted 19 February 2005 | Published 03 November 2005
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Introduction

The woolly apple aphid, *Eriosoma Lanigerum*, is a pest in many apple-growing countries. In New Zealand, it is considered a serious pest, causing reduced tree growth and contamination of fruit. Insects infest both shoots and roots of trees, while 1st instar nymphs can enter through the calyx and establish colonies inside the fruit (Essig, 1942). Aphid colonies start to appear in spring on the branches of apple trees and spread through the entire summer, inducing galls in the tissue on which they feed.

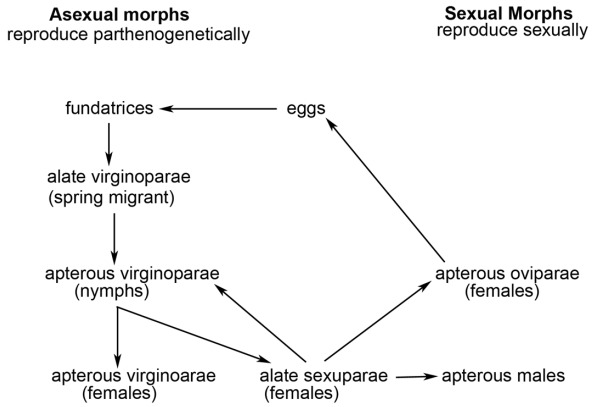
E. lanigerum is a North American insect where their primary host is the American elm tree (*Ulmus americana* L). Over-wintering eggs are laid on elm by apterous oviparous females that are produced by alate sexuparae in the fall that consist of reproducing males and oviparous females (Fig. 1). Fundatrices, which are a specialized apterous viviparous morph that can develop only on the primary host, hatch from the eggs, settle on the base of the bud, and produce the spring migrant alate aphids parthenogenetically. Spring migrants settle on apple trees, which are the secondary hosts, and spend the whole summer producing apterous virginoparae females (wingless females that reproduce parthenogenitically). In the fall the alate sexuparae develop from the colony and settle on the elm to produce apterous males and females (Baker, 1915). There are no records of sexual reproduction or natural dispersal by winged forms of *E. lanigerum* in countries where the elm is not present (Schoene et al., 1935; Pringle et al., 2001; Lal et al., 1947). However, in some countries where elm does not occur, winged forms produce males and females that lay eggs on apple (Theobald, 1921; Gautam et al., 1983). Schoene and Underhill (1935) reported that eggs hatch early in the spring.

In the eastern United States, woolly apple aphid alates were important in spreading the species over long distances. In some other areas in the world, their importance is limited since any sexual forms deposited by alates rarely mated (Hoyt et al., 1960).

Dumbleton (1934) found no evidence of *E. lanigerum* migration to elm in New Zealand, therefore continuous existence of the aphid on apple depended solely on the wingless females. It is believed to be anholocyclic (developing without eggs) on apple spending the winter either aerially or on roots. Crawlers (1st instar virginoparae) are regarded as migrants, and close tree spacing or wind favours their dispersal. Laboratory studies in New Zealand and Australia revealed that the main progeny of alate *E. lanigerum* were apterous sexual morphs with degenerate mouthparts (Asante et al., 1990; Dumbleton et al., 1938). Different records of varying progenies have been reported by many researchers in several countries (Table 1).

In this paper observations are described of sexuparae and sexual morphs of *E. lanigerum* in

Figure 1. Life cycle of the woolly apple aphid



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the laboratory as well as on apple trees grown outside the laboratory in Auckland, New Zealand.

Materials and Methods

This research was carried out in late summer-autumn (February-April) in two consecutive years (2003 and 2004) in Mount Albert, Auckland. Ten potted apple trees (variety 'Royal Gala') infested with *E. lanigerum* and grown outside were used to collect the aphids. *E. lanigerum* colonies on another 10 apple trees of the same variety were maintained in a glasshouse at 25 ± 3° C. All laboratory tests were carried out in controlled environmental conditions at 24 ± 1° C, 65 ± 10% relative humidity, and 16:8 hours light:dark cycle.

Measurements on sexual morphs

One hundred alate aphids collected from colonies on apple trees outside using a fine brush, were placed individually in covered Petri dishes (1.2 cm high and 5.5 cm diameter). Every 24 hours, offspring were checked and the total number of males and oviparous females reproduced recorded. Morphological differences between male, oviparous female, and 1st instar virginoparae were studied under the microscope (10 x). Body measurements on each of 30 newly emerged oviparous females, males, and 1st instar virginoparae were made. Body length was measured from the front of the head to the base of the cauda, and the body width was measured across the abdomen.

Development of sexual morphs

Development of the males and oviparous females was studied in the laboratory using clean apple leaves. Mature leaves collected from uninfected apple trees were washed with water to remove possible predators. The leaf was placed with the abaxial surface upwards in a Petri dish (1.2 cm high and 8.5 cm diameter) that was glued to a rectangular Perspex board (10 x 20 cm). A small hole (0.5 cm diameter) was drilled in the side of the Petri dish through which the stem of the leaf protruded into a plastic vial (5 cm long, 1.2 cm diameter) filled with water, which was also glued to the same board of Perspex. The vial was refilled with water every day to keep the apple leaf alive. Five males and five oviparous females were placed on the abaxial side of the leaf in the Petri dish. Each aphid was observed daily until dead and exuviae (indicating ecdysis) around each sexupara were counted.

Oviposition by oviparous females

When eggs were present next to dead oviparous females, the bodies were removed and eggs were left on the leaves for further observations. Apple trees both outside and in the glasshouse were also checked for presence of sexual morphs and eggs. When the *E. lanigerum* colonies on the trees became overpopulated and more alates were visible, 10 leaves were randomly picked from each tree and checked under the microscope for oviparous females, males and eggs. The number of sexual morphs and eggs found were compared between the trees grown under different environmental conditions. The eggs were separated

Table 1. Comparison of reproduction of alates of woolly apple aphid reported by various authors.

Author	Year	Country	Progeny of alate		Progency per alate		
			Season	Progeny	Virginoparae	Oviparae	Males
Asante	1994	Australia	spring	virginoparae only	6.30±0.76		
			summer	virginoparae & sexuals	2.77 ± 0.1	1.92 ± 0.1	2.38 ± 0.1
			late summer-autumn	sexuals only		3.47 ± 0.1	3.76 ± 0.1
Baker	1915	North America		virginoparae & sexuals			
Cottier	1953	New Zealand		virginoparae & sexuals			
Dumbleton & Jeffreys	1938	New Zealand	summer	virginoparae & sexuals			
			autumn	sexuals only		2.8 - 3.5 mean total	
Fluiter de	1931	The Netherlands		virginoparae & sexuals		4 - 8 total	
Gautham & Verma	1983	India		sexuals only			
Hely et al.	1982	Australia		sexuals only			
Hoyt & Madsen	1960	North America		sexuals only			
Lal & Singh	1947	India		virginoparae only			
Mols	1996	The Netherlands		virginoparae only			
Monzon	1925	Japan	autumn	sexuals only		3.1 ± 1.7	3.2 ± 1.0
Pringle & Heunis	2001	South Africa		virginoparae only			
Sandanayaka & Bus	2004	New Zealand	late summer-autumn	mainly sexuals		3.52 ± 0.13	3.94 ± 0.11
Schoene & Underhill	1935	North America		virginoparae & sexuals			
Thakur & Dogra	1980	India		virginoparae & sexuals			

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carefully from the leaves and kept individually on a layer of moist tissues in small plastic Petri dishes (3.5 x 1 cm). They were kept under three different environmental conditions for further observations to simulate seasonal variation: a) 24 ± 1° C and L:D 16:8 (summer); b) 18 ± 1° C and L:D 12:12 (spring); c) 12 ± 1° C and L:D 10:14 (winter).

Results and Discussion

All alate aphids tested in the laboratory produced sexual morphs mainly parthenogenetically. Seven out of 100 alates produced 1 or 2 viviparous nymphs as well as males and females, which agrees with the findings of Asante and Danthanarayana (1990) who reported that some alate individuals in New Zealand could give birth to a mixture of sexual morphs and nymphs with fully developed mouthparts. Asante (Asante, 1994) further described that alates produced a mixure of virginoparae and sexual morphs only in summer (Table 1). Dumbleton and Jeffreys (1938) tested autumn alates in glass tubes and found that their progeny were exclusively sexual morphs, but they also reported that summer alates reproduce both virginoparae and sexual progenies.

In New Zealand, reproduction of *E. lanigerum* in the field was believed to be totally parthenogenetic by apterous viviparous females. In this study, virginoparae, sexuparae (alates reproducing males and oviparous females) and sexual morphs (males and oviparous females) were observed on apple, both in laboratory and natural populations in the absence of elm trees. Alates were produced mostly in autumn or when the colonies become overpopulated.

Varied observations have been reported of the reproduction of alate *E. lanigerum* from different parts of the world (Table 1). Our findings of sexual reproduction on apple differ with those by Schoene and Underhill (1935); Pringle and Heunis (2001); and Lal and Singh (1947), who stated that sexual reproduction by the winged forms of *E. lanigerum* could not take place if elm was absent as occurs in many parts of the world. For example, in South Africa, although winged forms are produced, they remain on apple trees and reproduce parthenogenetically (Pringle et al., 2001). In Turkestan, where elm does not occur, the winged forms produce males and females that lay eggs, which hatch into parthenogenetic females. Furthermore it was recorded that *E. lanigerum* reproduced for 10 years on apple without sexual revival from elm (Theobald, 1921). No eggs were observed by Schoene and Underhill (1935) in aerial colonies on apple during their study of 14 seasons in the United States, but they assumed that sexual forms might be born on apple and on rare occasions an over-wintering egg might occur. They also reported that natural spread of *E. lanigerum* by flight would not take place if elm trees were absent. Although the dispersal behavior of alates was not covered in this study, from our observations we assume they move out from the colonies and settle on the same or a different apple tree. As far as we know, the elm , *U. americana,* is not present in Auckland, however it is possible that the lifecycle could adapt to the secondary host. As some alates are produced young virginoparae in addition to sexual morphs, both asexual and sexual reproduction may happen on apple. Similar adaptation of the life cycle has been recorded by Theobald (1921).

Eggs were kept in three different laboratory conditions to investigate the relationship between temperature and development of the eggs. However, they did not hatch during the 3 months observation period. Dumbleton and Jeffrerys (1938) and Asante (1994) also found that eggs did not hatch in the laboratory, but they did not test the viability of eggs in the field. Although we were unable to prove the eggs hatch on apple, we suggest the eggs that females lay on apple could develop into young virginoparae, with well-formed mouthparts for feeding.

The fecundity and longevity of alate sexuparae are much lower than those of apterous virginoparae (Gautam et al., 1983; Sandanayaka et al, 2003). The smaller number of offspring produced by alates appears to have no significant effect on increasing the population and infestation. However, alates may enable dispersal over greater distances and provide increased genetic diversity through sexual reproduction.

An alate reproduced an average total of 7.46 ± 0.15 (range 4-10) sexual morphs, including 3.52 ± 0.13 (1-6) females and 3.94 ± 0.11 (2-7) males, during their lifetime of 2.06 ± 0.05 (1-3) days in the Petri dish. Most of the alates started reproduction on the first day and reproduced the highest number of nymphs on the second day. There was no difference between female and male numbers reproduced ($P<0.05$) (Fig. 2). Asante and Danthanarayana

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Figure 2. Mean reproduction of alate woolly apple aphids in a Petri dish during day 1-3 of their lifetime.

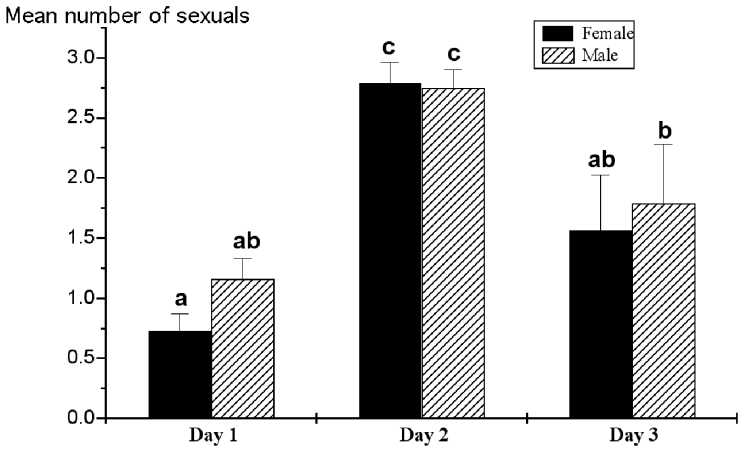


Table 2. Different characteristics of oviparous female, male, and the first instar virginoparae of *Eriosoma lanigerum*.

Characteristics	Oviparous female	Male	Virginoparae (1st instar)
Color	reddish brown	dark green	brown with white wax
Body length (mm) Mean ± SE	0.85 ± 0.01 (n = 30)	0.55 ± 0.01 (n = 30)	0.64 ± 0.01 (n = 30)
Body width (mm) Mean ± SE	0.45 ± 0.01 (n = 30)	0.27 ± 0.00 (n = 30)	0.25 ± 0.00 (n = 30)
Mouth parts	not developed for feeding	not developed for feeding	well developed mouth parts, proboscis longer than the body
Antennae	5 segments, ca. 1/5 of the body size	5 segments, ca. 1/4 of the body size	5 segments, ca. 1/3 of the body size
Leg color	lighter than the body color	lighter than the body color	darker than the body color
Feeding	no feeding during the life time	no feeding during the life time	start feeding soon after emergence
Mobility	not very mobile, mostly stay at the same place	mobile, faster than oviparous females	fast moving

(1990) found that an alate produced on average 6.88 0.34 (2-11) mainly sexual morphs, in a ratio of 1: 1.69 males to females, during their lifetime of 3-6 days. Gautam and Verma (1983) observed that an alate lived for 4-7 days and produced an average number of 5.3 (4-8) of sexual morphs. Dumbleton and Jeffreys (1938) found that the maximum number of sexual morphs produced by an alate was 7. Schoene and Underhill (1935) observed twice as many females as males produced by alates. Table 1 shows the previous records of *E. lanigerum* sexual reproduction in many parts of the world. Our findings disagree with those of Lal & Singh (1947), Mols (1996), and Pringle and Heunis (2001), who reported that alate *E. lanigerum* produced only virginoparae.

The oviparous female is bigger (0.85 ± 0.01 mm in length and 0.45 ± 0.01 mm in width) than the male (0.55 ± 0.01 mm in length and 0.27 mm in width). The male is similar to the size of first instar virginoparae (0.64 ± 0.01 mm in length and 0.25 ± 0.01 mm in width) (Fig. 3, Table 2). Asante and Danthanarayana (1990) reported that the length and the width of an average oviparous female were 0.93 ± 0.01 mm and 0.50 ± 0.01mm respectively. They also found that males were smaller (0.70 ± 0.01 mm in length and 0.30 ± 0.01 mm in width) than oviparous females.

Oviparous females live for 8.95 ± 0.17 days (n = 20) and males live for 7.1 ±0.12 days (n = 20). Our observations show that both males and oviparous females undergo four molts, completing five instars without feeding with no change in body size. They have degenerated mouthparts, which are not suitable for feeding and become sexually mature after the last molt. Oviparous females usually stay in one place until oviposition whereas males become mobile after the third or fourth instar. Oviposition occurs only after successful mating, after which the oviparous female lays a single egg, which almost equals the size of her abdomen (Fig. 4). These findings agree with those of Gautam and Verma (1982) and Asante (1994).

The egg is shiny brown in color, oblong in shape (Fig. 4) and 0.64 ± 0.01 mm in length and 0.29 ± 0.01 mm in width (n = 20) and becomes darker with age. These measurements are similar to those

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Figure 4. Woolly apple aphid oviparous female; laying an egg on the abaxial surface of an apple leaf.



reported by others: Baker (1915) 0.64 mm x 0.288 mm; Monzen (1925) 0.55mm x 0.35 mm; Asante (1994) 0.58 ± 0.01mm x 0.33 ± 0.01 mm wide. Eggs are mostly laid on the abaxial surface of apple leaves and occasionally are found covered with wool secreted by the oviparous female. The female dies soon after laying the egg. More sexual morphs and eggs were found on leaves collected from apple trees grown in the glasshouse (7.6 ± 0.93 sexual morphs and 3.5 ± 0.60 eggs per tree) than from the trees grown outside (1.0 ± 0.39 sexual morphs and 1.3 ± 0.34 eggs per tree). In addition, more alates were seen on the leaves collected from the glasshouse.

Alates on the trees outside the glasshouse obviously have more opportunity to disperse and find another apple tree than those on the trees in the glasshouse. Since some alates produced young virginoparae before producing sexual morphs, both asexual and sexual reproduction may happen on the new host. Although sexual morphs may not be able to feed on the new host, oviparous females lay eggs, which develop into young viginoparae. It may be that alates from aphid colonies can spread long distances between apple trees, however, nothing has been published on the migratory behavior of alates. From our findings we suggest that they could have a considerable impact on spreading infestation among apple trees. Further research is required on the dispersal behavior of alate aphids and any other alternative host plants under different environmental conditions in New Zealand.

Figure 3. Progeny of an alate Woolly apple aphid. First instar apterous virginoparae (left), oviparous female carrying a single egg (middle) and male (right).



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Acknowledgements

We wish to thank Ms Philippa Stevens, Mr Dave Rogers and Dr Peter Dentener for their valuable comments on this paper.

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