

BIOLOGICAL STUDIES OF APHIS RUMICIS, LINN.*

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This is the first of a series of papers based on results of breeding experiments and on observations in the field. It is hoped that a full investigation of the biology of this species will be of value in elucidating the many difficult biological problems of the APHIDIDAE.

The preliminary paper published by the author (1914) was to have been followed by further investigations, but owing to the outbreak of the European War there has been an unavoidable delay. However, experiments are now being continued, and the results of the researches will be published in parts from time to time.

As there is no complete description of *Aphis rumicis* in the literature, it is thought very desirable that a detailed illustrated description of all forms of this species should be given.

The following abbreviations are used in the text:—a.v. ♀ = apterous viviparous female; w.v. ♀ = winged viviparous female; 1st v. gen. = 1st, 2nd, etc., viviparous generation.

I. Description of *Aphis rumicis*, Linn.

1. FUNDATRIX (fig. 1). Average size, 1·8 mm. by 1·4 mm.†

Body oval to elongate, broadly rounded posteriorly, shorter and relatively stouter than the succeeding a.v. ♀♀; colour black to dark green; hairs scattered over the body.

Head: A few scattered hairs on dorsal surface. Eyes black; small tubercle-like accessory eyes‡ on posterior margin. Antennae§ about two-thirds length of body; black to dark brown, paler about the middle; five segments; seg. 3 the longest; 1 slightly broader than long; 2 slightly longer than broad, subequal in length; 4 shorter than 5; 5 almost as long as 3; a single subapical sensorium on seg. 4 and a compound sensorium on seg. 5; a few short hairs on each segment. Rostrum normal, with a few hairs on each segment.

Thorax: A pair of prominent lateral tubercles on prothorax. Legs black, with tibiae and proximal portions of femora paler; segments bearing many short hairs, especially the tibiae.

Abdomen with two prominent lateral tubercles on each side. Cornicles black to dark brown, imbricated, tubular, tapering very slightly distally, shorter than in succeeding a.v. ♀♀; about one and one-third times the length of cauda as seen from the dorsum. Cauda short, bluntly rounded, black on distal portion; bearing several long curved hairs. Anal plate black, roughly quadrangular as seen from venter, bearing a number of short hairs, anterior margin more or less straight. Genital plate black, somewhat crescentic in shape, with outer margins rounded; bearing a number of stout hairs and short spines.

* This species is the black aphid found in spring on the spindle tree (*Euonymus europaeus*), and later on beans, poppies, and many other plants. It has many synonyms, owing to its polyphagous habits, but the name given by Linnaeus in 1746 holds priority. The more important synonyms are *Aphis papaveris*, Fabr.; *Aphis euonymi*, Fabr.; and *Aphis fabae*, Scop. For other synonyms see Theobald, 1912.

† The measurements given are total length of body excluding the cauda, and the greatest width of the abdomen. The size is very variable, depending largely on food and temperature conditions.

‡ Accessory eyes (Berlese, "Gli Insetti"); ocular tubercles (Baker, 1920).

§ The "unguis" (Baker, 1920), or "processus terminalis" (Tullgren, 1909), of the terminal segment is here considered as being part of the distal segment.

First Larval Instar has 4-segmented antennae, with sensorium on segs. 4 and 5 ; tubercle-like cornicles ; small obtuse cauda and stout legs.

Second Larval Instar has 5-segmented antennae.

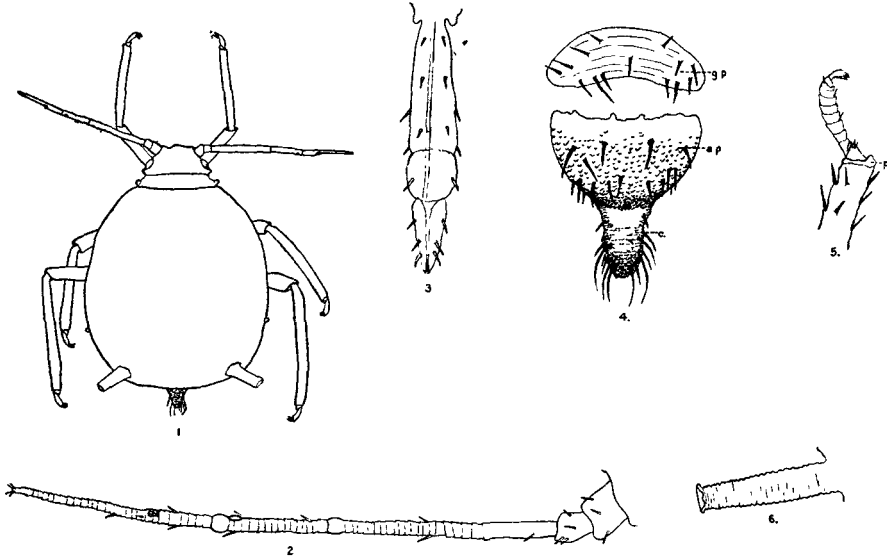


Fig. 1. *Aphis rumicis*, Linn., fundatrix : (1) dorsal view ; (2) antenna ; (3) rostrum ; (4) posterior end of venter, *a.p.*, anal plate, *g.p.*, genital plate, *c.*, cauda ; (5) tarsus of third leg, *p*, empodium or pad ; (6) cornicle.

2. **APTEROUS VIVIPAROUS FEMALE** (fig. 2). Average size 2.5 mm. by 1.6 mm.

Body elongate oval ; colour variable, black to olive-green, often with irregular darker pigmented areas over the abdomen ; small hairs scattered over the body.

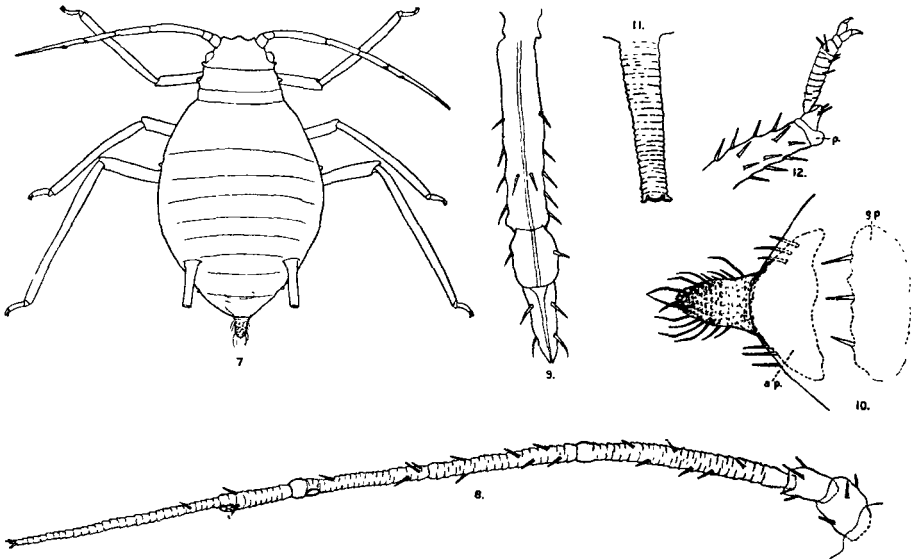


Fig. 2. *Aphis rumicis*, Linn., apterous viviparous ♀ : (7) dorsal view ; (8) antenna ; (9) rostrum ; (10) cauda, dorsal view, *a.p.*, anal plate, *g.p.*, genital plate ; (11) cornicle ; (12) tarsus of third leg, *p*, empodium.

Head: Eyes black, with prominent accessory eyes. Antennae six-jointed; seg. 1, apical portion of seg. 5 and proximal portion of seg. 6 black, remainder of a paler colour; seg. 6 (including processus terminalis) the longest, about equal to 4 and 5 together; 3 about three-fourths the length of 6, longer than 4; 4 slightly longer than 5; 1 and 2 subequal in length; a single subapical sensorium on seg. 5; a compound sensorium on seg. 6; a few hairs on all segments. Rostrum normal, with a few hairs on the segments.

Thorax with a prominent prothoracic tubercle on each side. Legs black; tibiae and proximal portion of femora paler; segments bearing stout hairs, especially the tibiae.

Abdomen with two lateral tubercles on each side and sometimes one or two small indefinite tubercles. Cornicles black, tubular, imbricated, slightly tapering distally, varying in length, but usually about one and one-third to one and one-half times the length of the cauda as viewed from dorsum. Cauda with distal half slightly spoon-shaped, black, clothed with short stout bristles and several long curved hairs. Anal and genital plates as in fundatrix.

3. WINGED VIVIPAROUS FEMALE (fig. 3). Average size, 2.4 mm. by 1.3 mm.

Body: Head and thorax black to brownish black; the abdomen varying from dirty brownish black to olive-green, usually with irregular darker pigmented areas on the abdomen. Small hairs scattered over the body.

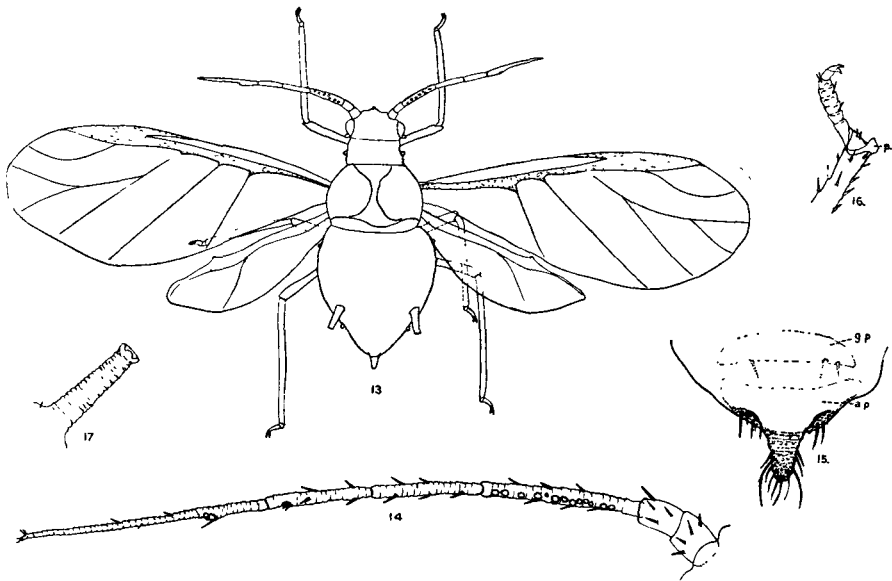


Fig. 3. *Aphis rumicis*, winged viviparous ♀: (13) dorsal view; (14) antenna; (15) cauda, dorsal view, *a.p.*, anal plate, *g.p.*, genital plate; (16) tarsus of third leg, *p*, empodium or pad; (17) cornicle.

Head black. Eyes black, with prominent accessory eyes. Antennae dirty brown to black, varying in length, about two-third length of body; seg. 3 slightly longer than 4; seg. 4 slightly longer than 5; 1 and 2 subequal; subapical sensorium on seg. 5, and a compound sensorium on seg. 6; a varying number of about 12-18 subcircular sensoria distributed over seg. 3 and none or 1-4 over seg. 4; segments 3 to 6 imbricated. Rostrum dark towards distal end; normal.

Thorax with two prominent lateral tubercles on prothorax. Wings normal. Legs somewhat longer than in a.v. ♀, otherwise similar.

Abdomen varying in colour from dark velvet-black to olive-green, usually with five irregular pigmented areas along the lateral dorsal area and irregular transverse areas segmentally arranged; lateral tubercles prominent. Cornicles black, varying in length, usually about one and one-half times length of cauda as viewed from dorsum, imbricate, tubular, slightly tapering distally. Gauda not so large as in a.v. ♀, otherwise similar. Anal and genital plates as in a.v. ♀.

4. SEXUPARAE.

(a). Male-producing sexuparae, apterous, resembling apterous viviparous female.

(b). Female-producing sexuparae, winged, resembling winged viviparous female, but somewhat larger in size.

5. MALE (fig. 4). Average size, 1.4 mm. by 0.7 mm.

Body smaller than in w.v. ♀, narrower and more tapering distally; seen from dorsum it appears to be shining black, but the abdomen is often very dark green; small hairs scattered over the body.

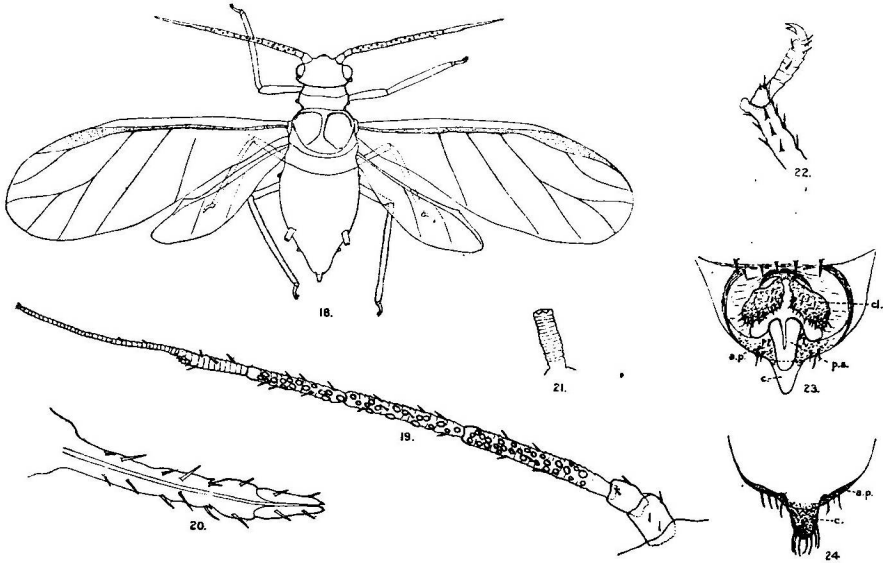


Fig. 4. *Aphis rumicis*, ♂: (18) dorsal view; (19) antenna; (20) rostrum; (21) cornicle; (22) tarsus of third leg; (23) posterior end of venter, showing genital armature, a.p., anal plate, c., cauda, cl., claspers, p.s., penis sheath; (24) cauda, dorsal view.

Head black. Eyes large, black; accessory eyes prominent. Antennae about two-third to three-quarters length of body, black, but sometimes paler; segments 1 and 2 subequal; 3 shorter than 6; 4 slightly shorter than 3; numerous subcircular sensoria on segments 3, 4 and 5, and a compound sensorium on 6; a few hairs on all segments. Rostrum normal.

Thorax black and shining; prothoracic tubercles prominent. Legs slender, black, with greater part of tibiae and femora paler; hairs on all segments, especially tibiae.

Abdomen varying, almost black to dark green, black along lateral margins, irregular patches of darker pigmented areas more or less segmentally arranged; two lateral

tubercles present on each side. Cornicles dark to black, short, small, tubular, imbricated, a little longer than the cauda viewed from the dorsum. Cauda smaller than in w.v. ♀; covered with short spines and several long hairs; distal portion black. Anal plate black. Genital plate black, bearing two dark claspers (gonapophyses) clothed with spines and stout hairs. Penis sheath paler.

6. OVIPAROUS FEMALE (fig. 5). Average size, 1–6 mm. by 0·9 mm.

Body small and narrow compared with the a.v. ♀, tapering posteriorly; dirty brownish black to dark green in colour, often of a dark green velvety appearance; short hairs distributed over the body.

Head black to dark green. Eyes small, black; accessory eyes small. Antennae about two-thirds length of body; pale dirty grey, segments 1 and 2 and distal portion of 4 and 5 darker; seg. 6 about equal in length to 3, 4 and 5 together; 3 longer than 4 or 5; 4 slightly shorter than 5; a compound sensorium on seg. 6 and a sub-apical sensorium on 5; a few hairs over each segment. Rostrum normal, dark on distal portion, with fewer hairs on the segments.

Thorax with lateral tubercles on prothorax prominent. Legs relatively short and stout; of a dirty greyish colour, with coxae, trochanters and tarsi darker; hairs on all segments, especially on tibiae; tibiae of third pair of legs much swollen, and possessing numerous irregular roundish light-coloured areas (? sensoria) over the whole length.

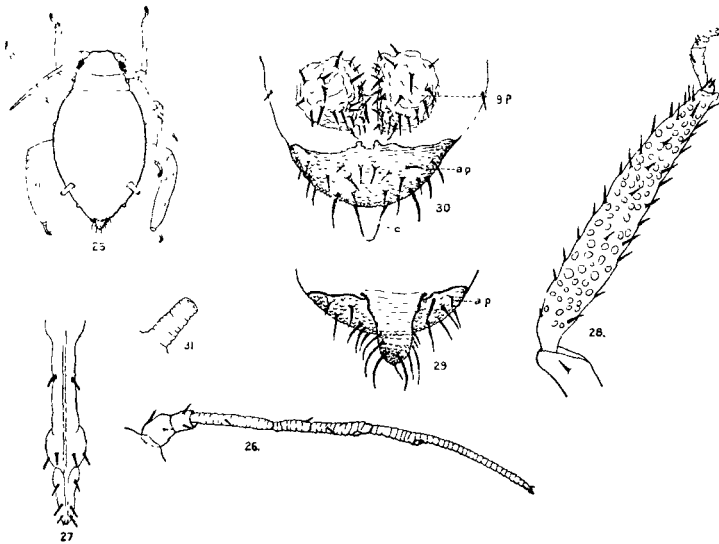


Fig. 5. *Aphis rumicis*, oviparous ♀: (25) dorsal view; (26) antenna; (27) rostrum; (28) tibia of third leg; (29) cauda, dorsal view; (30) posterior end of venter, a.p., anal plate, g.p., genital plate, c, cauda; (31) cornicle.

Abdomen dark green, with occasional lighter-coloured areas; two tubercles on each side. Cornicles quite small, black, imbricated, tubular, a little longer than the cauda as viewed from the dorsum. Cauda small but stout, black on distal portion. Anal plate black. Genital plate bilobed, black, and covered with long hairs.

Ova, when first laid, somewhat greenish, but rapidly becoming black and shiny on exposure to the air. Average size, 0·5 mm.

II. Life-History of *Aphis rumicis*.

The following account of the life-history of this species is based upon extensive breeding experiments and observations in the field. Experiments were carried on during 1913 and the early part of 1914, and continued during 1920.

The Aphids were reared from eggs on *Euonymus*, and transferred to broad beans as the summer host, the winged remigrantes or sexuparae of the later generations being transferred back to *Euonymus*. The plants were grown in pots in a large open glasshouse and kept covered with muslin bags, and observations on the different generations of the Aphids were periodically recorded. It is hardly practicable, for reasons of economy, to publish the observations made on the long series of plants infected, but the records of certain plants will be given in later sections of these biological studies. It is from the data derived from these observations, together with contemporary observations in the field, that the life-cycle has been worked out.

The ova hatch out in spring (March and April) on the winter host, *Euonymus europaeus*,* giving rise to the larvae of the fundatrices. In 8-10 days after birth, in favourable temperature conditions, the fundatrices become adult and begin to produce parthenogenetic viviparous young, which become adult about 10 days after birth. This is the first viviparous generation, and it may consist of a mixed progeny of both alate and apterous viviparous females, or of the latter only. The a.v. ♀♀ produce on *Euonymus* the second viviparous generation, which may consist of w.v. ♀♀ and a.v. ♀♀, the former being generally in the majority. The a.v. ♀♀ produce a further generation, consisting either entirely of w.v. ♀♀, or of a mixed progeny of w.v. ♀♀ and a.v. ♀♀, the w.v. ♀♀ being in the majority.

There is a tendency for the a.v. ♀♀ of these early generations on *Euonymus* to produce w.v. ♀♀ in the majority. These w.v. ♀♀ are the winged migrants from the winter host to the intermediate or summer hosts, such as beans, poppies, etc. It is owing to this tendency that the a.v. ♀♀ on *Euonymus* eventually die out, and as the season advances the tree becomes free from the aphid. Some of the w.v. ♀♀ may in some cases remain a short time on *Euonymus* and produce young on it, but owing to the innate desire of the winged forms to migrate (a marked feature of the winged forms when the Aphids are reared in captivity), they soon leave the *Euonymus* and fly to the intermediate hosts.

The generations of individuals from the fundatrices on *Euonymus* are the fundatrigeniae, the a.v. ♀♀ being the fundatrigeniae apterae and the w.v. ♀♀ the fundatrigeniae alatae. These latter are the winged migrants (migrantes), which fly to the intermediate hosts, being the mothers of the succeeding viviparous generations. The generations of individuals from the migrantes on the intermediate hosts are called the alienicolae, the a.v. ♀♀ being the alienicolae apterae, and the w.v. ♀♀ the alienicolae alatae.

The intermediate hosts are numerous, but of the cultivated plants beans are specially favourable, and afford the best stimulus to rapid reproduction. The migrantes give rise to the first viviparous generation on the intermediate host, the individuals of which are a.v. ♀♀. These produce a further generation, which may consist of a.v. ♀♀ or a mixed progeny of w.v. ♀♀ and a.v. ♀♀. The former may remain a little time on the same plant and produce young, or may fly to other plants, either of the same kind or other hosts, and produce a further generation. My experiments show that the tendency is for w.v. ♀♀ to produce a.v. ♀♀, and for a.v. ♀♀ to produce either a.v. ♀♀ or a mixed progeny with a varying percentage of w.v. ♀♀. This would

* The spindle-tree is undoubtedly a winter host of *Aphis rumicis*, but considering the local distribution of *Euonymus* in Britain, it is highly probable that there are other winter hosts. Gaumont (1913) found all stages on *E. japonicus*. Mordwilko (1907) found *Aphis euonymi* in spring on *Viburnum opulus* at Bjelovesch. It was also found on *Viburnum opulus* by Kaltenbach (*Aphis euonymi*) and by Passerini (*Aphis papaveris*). It is evident that further research is greatly needed in order to ascertain the common winter hosts of this abundant Aphid.

appear to be an adaptation of the species to its polyphagous habits. Thus when the w.v. ♀♀ alight on a new plant a good colony is established on that plant by a.v. ♀♀ being produced. On the other hand, the liability to overcrowding as the plant becomes heavily infested is overcome, and the wider distribution of the species to other host-plants is ensured by the production of winged forms in due course.

Towards the end of summer, after a number of agamic generations have been passed through on the intermediate hosts and at a time when suitable intermediate hosts are becoming scarce, there are produced winged viviparous females, which are physiologically specialised, but morphologically resemble the other alienicolae alatae. These are the sexuparae alatae or remigrantes. They fly back to the winter host, on which they produce true oviparous ♀♀.

At about the same period winged ♂♂ are produced from certain of the alienicolae apterae (sexuparae apterae) on the intermediate hosts and fly to the winter host, where the sexual ♀♀ are fertilised. Fertilised eggs are then laid on the winter host, near the buds, or in crevices in the bark of the older branches. These over-winter and hatch out in spring, producing the fundatrices.

The alienicolae apterae on the intermediate hosts gradually die out, owing partly to the tendency to produce w.v. ♀♀ or winged sexuparae and ♂♂, and partly to unfavourable conditions.* By confining the Aphids to broad bean plants, sexual forms were produced on these plants in due course.†

In my experiments it was found that the alienicolae alatae of any generation could be transferred back to *Euonymus*, on which plant they produced young, and eventually in succeeding generations both sexual ♂♂ and sexual ♀♀ appeared. Further, it was found that even if the Aphids are bred in successive generations on *Euonymus*, sexual ♂♂ and ♀♀ will appear in due course. It should be noted, however, that young growth was ensured on the *Euonymus* bushes by cutting them back. Males were first noted on 10th August 1920.

Similarly on beans, on which intermediate host the Aphids were bred continuously from May, several ♂♂ appeared in due course, and in some cases oviparous ♀♀ were also found. The ♂♂ are produced by alienicolae apterae toward the end of summer on the intermediate host-plants, and the oviparous ♀♀ by the physiologically specialised alienicolae alatae (sexuparae alatae) on the winter host, at about the same time. The male-producing sexuparae are thus a.v. ♀♀. One and the same mother may produce sexual males and sexuparae alatae, but the sexuparae alatae only produce sexual females.

It seems evident that in the adventures of migration the alienicolae alatae of any generation may alight on the winter host (*Euonymus*) and produce young, resulting eventually in colonies consisting of all stages, namely, a.v. ♀♀, w.v. ♀♀, ♂♂ and ♀♀. Mordwilko (1907) found all stages on *Euonymus* in Warsaw at end of September 1894. He also found a colony of a.v. ♀♀ on *Viburnum opulus* in Warsaw at the end of September.

Similarly, sexuparae alatae alighting on intermediate host-plants may give rise to sexual ♀♀, which might thus be found together with colonies of agamic forms and sexual males. This would explain the finding by Theobald (1912) of sexual ♀♀ ovipositing on *Rumex*, by Gaumont (1913) on sugar-beet in October 1913, and by Malaguin and Moitié (1914) on haricot beans in October 1913.

* It seems probable that during a mild winter agamic forms may persist throughout on certain plants and carry on agamic reproduction normally in the following year. Davidson (1914) found a colony of apterous agamic females on 30th January 1913 on *Euonymus* at Richmond. The tree was taken into a greenhouse, and agamic reproduction was carried on normally throughout 1913. Several cases of long-continued parthenogenetic reproduction have been observed. The question will be discussed in a later section dealing with the appearance of sexual forms. It may be stated here that I have carried on a parthenogenetic strain throughout winter in a warm greenhouse, winged sexuparae (which produce sexual ♀♀), sexual ♂♂ and parthenogenetic a.v. ♀♀ being produced in each generation from September to May.

† Mordwilko (1907) was not able to obtain females on intermediate hosts.

During the autumn, when the intermediate hosts are mostly unfavourable for the Aphids, the winter hosts, such as *Euonymus*, offer the most favourable food conditions and the greatest chances of survival. From the nature of *Rumex* and other intermediate hosts under winter conditions and the difficulty in ensuring food for the young larvae immediately they hatch out from the eggs in spring, these cases, I think, must only be considered as casual winter hosts. The sexual forms may develop in several generations. In fact, in one series of experiments under favourable conditions of food and temperature, sexual forms appeared in five succeeding generations. Weather conditions and the dying down of the intermediate hosts are very important factors in limiting the length of period over which sexual forms are produced. These questions will be discussed more fully in a later section dealing with the appearance of the sexual forms.

The life-history of *Aphis rumicis* may be illustrated by the following diagram:—

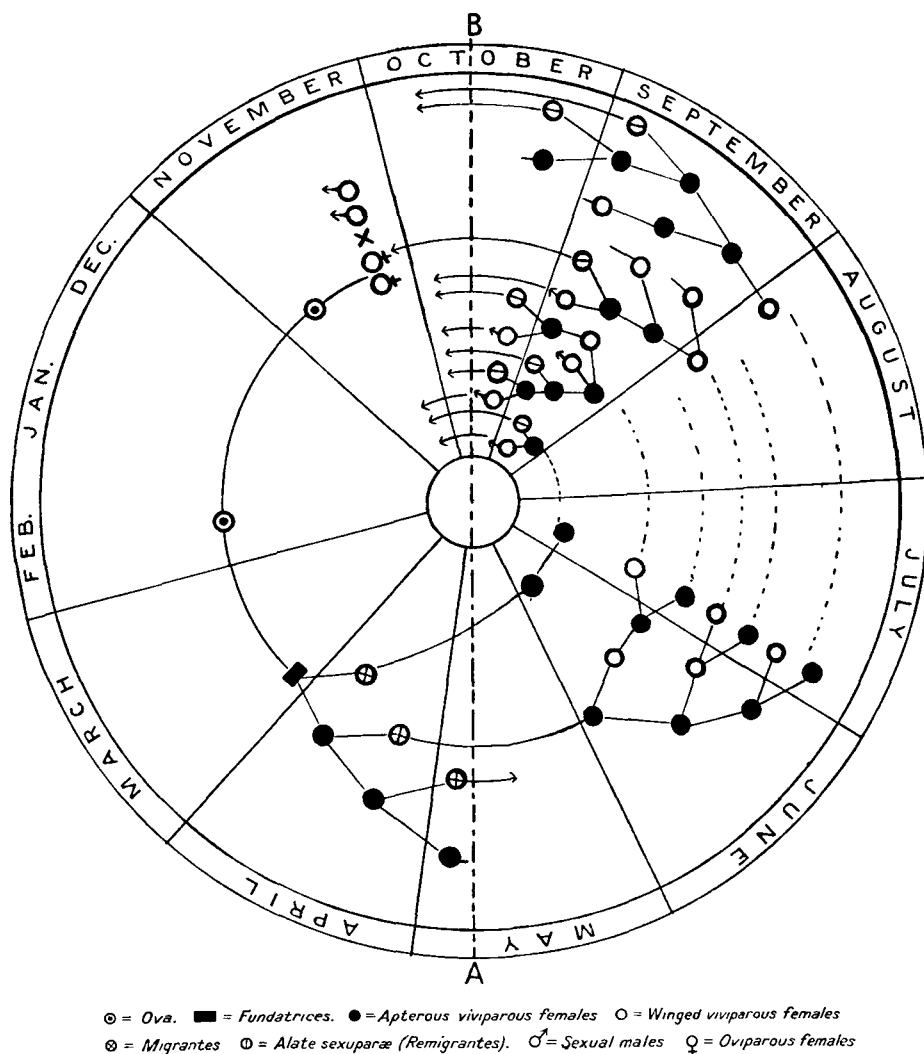


Fig. 6. Diagram illustrating the life-cycle of *Aphis rumicis*. The line AB divides the circle into two halves, the winter host being represented on the left and the summer hosts on the right; the sectors indicate the months, and the dotted concentric lines a varying number of generations occurring in July and August.

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