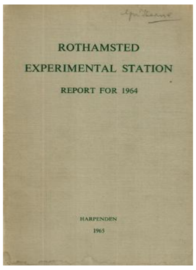
ROTHAMSTED
RESEARCH

Report for 1964

Full Table of Content


ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1964

HARPENDEN
1965

Aphid Nutrition and Reproduction

C. J. Banks

C. J. Banks (1965) *Aphid Nutrition and Reproduction ;* Report For 1964, pp 299 - 309 **- DOI: https://doi.org/10.23637/ERADOC-1-57**

APHID NUTRITION AND REPRODUCTION

C. J. BANKS

Aphids owe much of their success as plant parasites to a special method of feeding on plant sap, combined with an extraordinary method of reproduction that enables them to multiply and exploit their host plants rapidly (Kennedy and Stroyan, 1959). They have also evolved an efficient method of dispersal that enables them to move rapidly from one temporary host to another. Dispersal has been intensively studied at Rothamsted, but less attention has been paid to the food requirements of aphids, and their nutritional needs are very imperfectly understood. However, a proper understanding of such problems as host-plant selection, the basis of resistance by plant varieties to infestation and perhaps the transmission of plant viruses by aphids, may well depend on better information about aphid nutrition.

Aphids multiply faster on some host species than on others; for example, *Myzus persicae* increases faster on *Brassica* spp. than on sugar beet, spinach or lettuce (Heathcote, 1962), and *Aphis fabae* faster on beans than on sugar beet (Banks and Macaulay, unpublished results). They also grow faster and reproduce more on some varieties of plant than others, for example of pea (Auclair, 1959), wheat and barley (Painter and Pathak, 1962), raspberry (Hill, 1957) and beans (Davidson, 1922; Müller, 1951; Tambs-Lyche and Kennedy, 1958). They reproduce faster on young parts of plants than on older parts (Kennedy and Booth, 1951; Banks, 1958; Heathcote, 1962) and more on senescing parts than on mature parts (Kennedy and Booth, 1951). These different rates of increase might indicate differences in the nutritive quality of the sap, but might depend on different rates of feeding or assimilation.

Before the amount of food ingested could be related to the aphid's growth, reproductive rate and fecundity, a satisfactory method of studying the insect's feeding rate throughout its lifetime had to be developed. Much of this article deals with recent developments at Rothamsted on the feeding and reproduction of *Aphis fabae*, the bean and sugar-beet aphid, about whose anatomy and biology so much is already known (Davidson, 1925; Weber, 1928).

Method of feeding. Aphids were thought to suck plant sap in the way the Heteroptera or bugs do, until Kennedy and Mittler (1953) showed that when the stylets of *Aphis fabae* (feeding on bean plants) and of *Tuberolachnus salignus* (feeding on willow stems) were severed, sap continued to exude from the stylet stumps still embedded in the plants. Mittler (1957) found that sap exuded from the stumps at about the same rate as intact *T. salignus* excreted honeydew while feeding on the same willow plants, and that it sometimes continued to exude for days. Kennedy and Mittler suggested that the pressure of sap within the phloem sieve tubes, where these aphids usually feed, was responsible for forcing the sap into the feeding aphid. This advance in knowledge, confirmed by von Dehn (1961) with several other aphid species feeding on herbaceous plants, led to the assumption that the aphid feeds continuously and passively once its stylets have tapped a sieve tube element, and that the sap is forced through the gut of the insect by the pressure within the plant.

Banks and Nixon (1958), following a suggestion of Herzig (1937), advanced the subject further by showing that *Aphis fabae* feeding on fully turgid bean plants excreted and fed faster when attended by the ant *Lasius niger* and that excretion slowed to its initial rate when the ants were removed. They suggested that the so-called "sucking pump" in the aphid's head probably acts as a valve that opens periodically and allows some sap under pressure to enter the insect's gut; the relaxation of the muscles of the pump attached to the head wall would close it, and their contraction would open it again when another meal of sap was to be ingested. When attended by an ant the aphid could open the valve more often and thus increase the rate of feeding. To feed continuously, however, the muscles opening the valve would have to remain continuously contracted, something no muscle does. Whatever the mechanism whereby the aphid controls its rate of feeding and excretion, this work showed that the aphid does not feed continuously, and does not depend solely on pressures within the plant while feeding on a turgid plant.

That some aphids can suck when they have to, is shown also by work of Mittler and Dadd (1962) and of Auclair and Cartier (1963), who reared *Myzus persicae* and *Acyrthosiphon pisum* that fed through stretched Parafilm membranes on liquid diets under negligible pressure. Nevertheless, many if not most aphids probably use the pressure of the sap for normal feeding, and only under unusual conditions, perhaps when the plant wilts, are they forced to suck. Some aphids feeding in galls and pseudo galls may feed by sucking, but little is known about their feeding behaviour.

It is generally thought that an aphid's stylets usually penetrate a sieve tube element in the phloem, where they reach sap under continuous pressure; so the aphid feeds with a minimum of effort and at the same time obtains a food rich with the plant's own nutrients. There is abundant evidence that aphid stylets penetrate to the region of the phloem but little to show that they habitually end in sieve elements. Phloem sap, still under pressure, may pass from sieve elements into nearby parenchyma cells where the stylet tips have penetrated, but the movement of phloem sap is imperfectly understood.

Feeding and excretory behaviour. The feeding and excretory behaviour differs in different species. *Myzus persicae* is said to be a restless aphid that often changes its feeding site, whereas *Aphis fabae* stays and feeds at the same spot for days, and when disturbed often has great difficulty in withdrawing its stylets. Other species, for example, *Acyrthosiphon pisum*, *Megoura viciae* and *Microlophium evansii* to mention a few, immediately withdraw their stylets and fall off the plants when disturbed. Such a different response suggests that these aphids might differ in their feeding habits.

Broadbent (1951) described the different ways in which aphids excrete. Larvae of 'free-living' forms (those that feed on the leaves and stems of plants and not in galls or pseudogalls) kick the honeydew droplet from the anus with a hind leg; the adults flick the droplet off with the cauda (tail). But the behaviour of aphids of this kind also differs; for example, *Aphis fabae* adults flick the droplet vertically downwards (Banks, 1958), whereas adult *Megoura viciae* flick the droplet downwards but to one side. The details of feeding and excretory behaviour of various aphid species deserve further study. The adult apterous virginopara is usually regarded as a neotinic, that is, a morph that retains many larval characters in the adult stage; the "metamorphosis" of the larval alata at its final moult is suppressed in the aptera, and morphological changes at the final moult are therefore extremely slight (Lees, 1961, p. 75). However, the conclusion seems to overlook the fact that the acquisition of a large cauda by the adult aptera and alata is a very prominent morphological change, which is also accompanied by a dramatic change in excretory behaviour.

Measurement of the feeding rate of *Aphis fabae*. Feeding rates of aphids have been measured hitherto usually for short periods and by various methods, some of them unsatisfactory. Watson and Nixon (1953), Day and Irzykiewicz (1953) and Banks and Nixon (1959), for example, estimated the feeding rates of aphids for periods of a few hours by measuring the radioactivity of insects that had fed on radioactive plants, but the measurement may not be valid because the concentration of the radioisotope of the sap actually ingested was unknown. The rates of feeding of various aphids obtained by different workers differ very greatly (Auclair, 1963), and many results imply that the rate rises to a maximum and then stays constant.

Before any attempt could be made to link the rate of ingestion with reproductive capacity it was essential to have a method of recording the feeding rate continuously over long periods, if possible for the whole of the insect's lifetime, and at the same time record its reproductive rate and fecundity. The only satisfactory method is that of Auclair (1959) who estimated the sap ingested by the larva of *Acyrthosiphon pisum* from pea plants by adding up the increase in body weight, the loss of water by evaporation, the weight of the cast skins and the weight of the honeydew excreted during 71 hours. Banks and Macaulay (1964) extended this method to estimate the sap ingested during the whole lifetime of *Aphis fabae* from two varieties of field bean, and recorded the growth, reproductive rate and fecundity of the same insects. They used the fact that most of the sap ingested is excreted and that the rate of excretion is a good index of the feeding rate so long as the environment is reasonably constant (Mittler, 1957). Excretion is affected, among other factors, by changes in temperature, air humidity, wind and the turgor pressure of the plant (Mittler, 1962), so Banks and Macaulay made their experiments under as constant conditions as they could maintain, and they used aphids of one kind only: the apterous progeny of alate virginoparae produced from a clone.

Temperature and lighting were kept constant; air was kept humid to lessen evaporation from the insects, and air movements were eliminated.

As the honeydew clocks used by other workers are bulky and expensive, a compact, inexpensive machine was made to collect simultaneously all the honeydew excreted by ten individual aphids feeding each on its bean plant, to record their daily total excreta continuously from birth to death. Two steel rods rotating slowly and continuously wound up ten long strips of chromatography paper stained with an indicator to reveal the honeydew droplets that fell on them as they passed under the aphids. The papers, which were long enough to last for 24 hours, were replaced each day; thus, all the honeydew droplets from each of the ten aphids was collected and counted throughout the insects' lives, and an estimate of variability obtained.

Honeydew was also collected daily in mineral oil from other aphids of the same age on similar plants to measure the size of the droplets. The average excretion rate was estimated from the product of the mean frequency of excretion and the mean size of the droplets, and this volume of liquid, when multiplied by the specific gravity of honeydew, separately determined, gave the total weight of the excreta. The sum of the weight of the honeydew, water lost by evaporation, the increase in body weight of the insects and the total weight of their larvae born estimated the total weight of the sap ingested. The reproductive rate, fecundity and the length of the reproductive and post-reproductive life of the same aphids were also recorded.

The larval aphid ingested 3·5–4·5 mg sap in a life of 7 days and the adult about 30 mg sap during a reproductive life of 21 days; only 10% of the ingested sap was used for growth and reproduction and 90% was excreted. The excretion rate of the adult increased to a maximum of 30–40 drops per day on the third day of adult life and then started to decrease. This decrease was apparently because of changes within the insect itself, for although the aphids were transferred to fresh plants every 5 days, the excretion continued to decrease.

The rate of feeding therefore also declined as the aphid aged. We can but speculate as to the cause; muscle degeneration or a gradual blocking of the stylet canal or gut (see also below) or, less likely, a progressively more efficient use of sap with increasing age, may be explanations; but whatever the reason, it is important to recognise that the rate *Aphis fabae* feeds is far from constant and that it rises quickly to a maximum and then declines with age. Other species probably have their own patterns of excretion and feeding, and comparisons of the feeding and excretion rates of different species or of the same species on various host plants should be based on complete records throughout the insects' lives. The large variations in rates of feeding listed by Auclair (1963) can probably be explained partly by differences in age of aphids and in their patterns of feeding; feeding rates will also probably be affected by differences in size of insect and the kind of host plant. So far as I am aware, feeding patterns of other aphid species have not yet been established, but if other aphids behave as *Aphis fabae* does, the loss of ability of older aphids to transmit plant viruses, reported for some species, may be associated with a decline in the feeding rate and what seems to be a change in the physiological state of the insect as it ages (Bawden, 1964, p. 130).

Reproduction. Adult insects usually need to ingest food to reproduce. The female in particular needs food to make materials to form yolk. In some species the reserves are built up during the larval stage, especially in those species whose adult insects have only vestigial mouth parts. In others, the reserves accumulated during larval life are supplemented by a carbohydrate diet during adult life, and some adult insects need a special protein meal before they can reproduce (Wigglesworth, 1960).

Aphids are, however, unusual insects because they reproduce parthenogenetically and viviparously over many generations, and some species reproduce in no other way. In the parthenogenetic aphid, therefore, the relationship between reproduction and food ingested is more complicated than in oviparous species of insects. The parthenogenetic adult contains embryos in all stages of development from eggs to mature larvae, and the more mature of these also contain embryos in an early stage of development (see below); an aphid larva is in effect starting to reproduce before it is born. Thus, an adult parthenogenetic aphid nourishes not only her daughter embryos but also some of her granddaughter embryos (Lees, 1959; Kennedy and Stroyan, 1959). It is the telescoping of the generations in one individual, as Kennedy and Stroyan have aptly put it, combined with the specialised method of feeding, that enables aphids rapidly to multiply and exploit their host plants.

During the first 2 weeks of reproductive life, adult *Aphis fabae* gave birth to 5 or 6 larvae daily, but only about 2 during the following week. Reproduction then ceased fairly abruptly, although excretion, which was also decreasing, continued intermittently for a few more days. The decline in the reproductive rate as the insect ages is more apparent when the number of larvae born in successive 5-day periods is considered rather than the numbers born daily (Banks and Macaulay, 1964). It then appears that the numbers of larvae born increases to a maximum of about 30 in the first 5–10 days of adult life and thereafter decreases. The maximum of the reproductive rate lags behind the maximum of the feeding rate, which occurs on the third day of adult life.

Reproductive life was followed by an almost equally long post-reproductive period. During this time the aphids remained with their stylets inserted into the leaves, the abdomen swelled and the insects increased in live weight and especially in dry weight (Banks and Macaulay, 1965), showing that, although excretion had stopped, small quantities of sap were still ingested. The comparatively large increase in dry weight in early post-reproductive life was not accompanied by a pronounced increase in fat content (Banks and Macaulay, unpublished results), although many oil globules occur in the body cavity once occupied by the tightly packed embryos. Sugars may accumulate during this period, probably because the aphid continues to feed but not to excrete. *Myzus persicae* and *Aphis fabae* have much larger crops when they feed on plants of the Chenopodiaceae (which includes sugar beet) (Moericke, 1960) than when feeding on other plants. Edwards (1965) examined the gut of *Aphis fabae* feeding on chenopods and discovered solid, insoluble polysaccharides in the crop, formed apparently as a secretion from the crop epithelium. It seems that aphids, feeding on plants containing an excess of sugar in the sap, and being unable to excrete faster to dispose of it, convert soluble sucrose from the sap into insoluble forms that are retained in the crop. Such a process perhaps also occurs in aged *Aphis fabae* that continue to feed on beans but not to excrete, and an accumulation of sugars might account for the increase in dryweight. Unlike *Aphis fabae*, the willow aphid, *Tuberolachnus salignus*, excretes large quantities of honeydew during post-reproductive life (Mittler, 1958), but this lachnid possesses a so-called filter chamber, one of whose functions could be to transfer unwanted excess sugar rapidly from the fore gut to the hind gut. *Aphis fabae*, like most other aphids, has no filter chamber, and excretion in old age may stop if the gut is gradually blocked with solids.

Banks and Macaulay (1964) found that the fecundity (total larvae born) of apterous *Aphis fabae* was remarkably constant, no doubt because they used a clone of aphids in a constant environment. Because reproducible results were obtained in this way, fecundity and reproductive rate are considered to be better criteria of the aphid's performance on a particular host plant than the multiplication rate of groups of aphids. On one batch of field beans (called variety A) the aphids consistently produced 89 ± 1·3 larvae and only 85 ± 1·3 larvae on another batch (variety B) in a reproductive life of 3 weeks. The difference, although small, is statistically significant. Taylor (1959) showed that on a variety of broad bean apterous adults of *Aphis fabae* produced an average of 96 ± 2·0 larvae during their lifetime, although his experimental conditions differed somewhat from those of Banks and Macaulay. Yet from the varieties A and B the aphids ingested the same amounts of sap; the difference in fecundity was not caused by the ingestion of different amounts of sap but probably by a difference in nutritiousness of the sap of the varieties.

Influence on fecundity of quantity and quality of nutrients ingested. The main component of the solid matter of the sap of plants is sugar (sucrose), much of which the aphid cannot use; nitrogen, dissolved in the sap as free amino acids and amides (Mittler, 1958; Zimmermann, 1960), is especially important for the synthesis of the protein essential for the aphid to grow and reproduce. Results of Auclair, Maltais and Cartier (1957) suggested that varieties of pea resistant to *Acyrthosiphon pisum* contained less free and total amino acids than susceptible varieties. The nitrogen in the plant sap could thus be a limiting factor in aphid development.

The differences in fecundity of *Aphis fabae* feeding on the field bean varieties A and B could have depended more on differences in the quantity and quality of the nutrients dissolved in the sap than on the total quantity of sap ingested. Differences in quality of sap rather than in rates of feeding were suggested earlier as the cause of differences in reproductive rate. For example, although larvae of *Aphis fabae* excreted and fed faster when attended by the ant *Lasius niger* (Banks and Nixon, 1958), as adults they did not reproduce faster than ant-free aphids (Banks, 1958). The greater multiplication rate of ant-attended aphids was attributed to the fact that they stayed longer on the young parts of the bean plants, where they reproduced faster, than on the old parts, where they reproduced more slowly. The reproduction of the ant-attended aphids was increased, it was suggested, because they benefited from a more nutritious sap on young parts of plants rather than from an increased flow of sap from which they could not assimilate nutrients faster.

The amounts of total nutrients ingested and assimilated by *Aphis fabae* from the two bean varieties was therefore measured throughout the whole life of the insect, to see if they were used in different ways (Banks and Macaulay, 1965). The indirect method of Auclair and Maltais (1961), who estimated the total nitrogen taken by *Acyrthosiphon pisum* larvae from varieties of pea during 72 hours, was extended to estimate the total solids (total nutrients) and total nitrogen taken by *Aphis fabae* from bean plants of varieties A and B throughout the whole larval and adult reproductive life. The total solids ingested approximately equal the increase in dry weight of the larva during development plus the weight of its four exuviae and of the solid matter of all the honeydew. Similarly, the total weight of solids ingested by the adult equal the sum of its increase in body dry weight, the dry matter of the total larvae it bears and the dry weight of the honeydew it excretes during its lifetime. Gases exchanged during respiration can be neglected. The total nitrogen ingested can be similarly determined by summing the nitrogen contents of these various components.

The larvae reared on variety B assimilated and excreted significantly more nitrogen than those on variety A, but this had no effect on reproduction for, as adults, they did not reproduce faster or produce more larvae, and those larvae did not contain more nitrogen than those born on variety A. The adults on variety A assimilated more total nitrogen because they were more fecund on it and they did not excrete more nitrogen in their honeydew. It seems that, although the aphids used the nutrients, particularly nitrogen, from the two varieties in somewhat different ways, this did not cause the difference in fecundity. The concentration of the nutrients, particularly nitrogen, in the sap of both varieties was apparently more than enough for reproduction, and did not determine the aphids' fecundity. The composition of the nutrients provided by variety A was possibly such that more larvae could be matured on it than on variety B.

The number of embryos in adult apterae. Because of the telescoping of the generations in the parthenogenetic aphid, nutrition during larval life affects the development of the embryos and the embryos within them to some extent. Good nutrition during larval life could allow more embryos to develop or to be matured faster, and thus could affect the early reproductive rate of the adult insect. But adult reproductive life is much longer than larval life, and the adult feeds more than the larva, so the nutrition of the adult would be expected to affect reproduction more than the nutrition of the larva.

According to Lees (1959), the newly born larva of the vetch aphid, *Megoura viciae*, has two differentiated embryos in each ovariole, and at the end of larval development there are six embryos in each of the 18 ovarioles, so that a newly moulted adult carries a potential of 108 larvae that it can bear during its lifetime; few further eggs are produced during adult life. Some embryos are resorbed and the usual number of larvae born is 97. In *Megoura viciae*, therefore, larval nutrition sustains the production of most of the eggs and the partial development of the embryos; adult feeding produces a few more eggs, but is mainly needed to complete the maturation of the embryos already differentiated.

By contrast, the newly moulted, unfed, apterous adult virginoparae of *Aphis fabae*, reared from alate virginoparae on field beans (variety B) under conditions outlined above, contain only an average of 36 embryos and egg cells, and such adult apterae produce an average of 85 larvae during their lifetime. Therefore, on the average, 49 more eggs and embryos (58% of the total) are developed and nourished to maturity entirely on nutrients ingested by the adult. We suppose, therefore, that the nutritiousness of the sap determines how many more than 36 embryos will be developed by the adult.

Linti (1960) counted the embryos and egg cells in apterous, alate and intermediate forms of *Aphis fabae* fed on mature detached leaves of *Phaseolus vulgaris* in damp petri dishes. Adult apterae contained an average of 54 egg cells and embryos, but many of the insects he dissected were not newly moulted and had fed and reproduced for an unspecified time, so could have had more egg cells and embryos than they contained when newly moulted; nevertheless, his adult apterous aphids contained many more embryos than Banks and Macaulay found in theirs. Linti did not say from what kind of parent (alata or aptera) his aphids came. The numbers of embryos differentiated and developed during larval life (depending on the state of larval nutrition) may depend, among other factors, on the parentage of the aphid; for example, adult apterae developed from alate virginoparae (like those of Banks and Macaulay) might contain fewer embryos initially than aphids born to apterous virginoparae; that is, the number of embryos may differ from generation to generation and even from morph to morph, and thus reproductive rate and fecundity could also vary. Aphid morphs differ mainly in structure but also differ in physiology (Lees, 1961), and the initial number of embryos contained in the newly moulted adult may be a characteristic of the morph, and thus an example of "physiological polymorphism" (Richards, 1961; Johnson, 1963). Larvae born to alate virginoparae are smaller and weigh less than those born to apterous parents (Banks and Macaulay, 1965) and might develop fewer embryos. The reproductive rates and fecundities of aphids of different generations are at present being examined further.

Effects of larval and adult nutrition on reproduction. The reproductive rates (numbers of larvae born per 5-day period) of the aphids reared on the field bean varieties A and B were nearly identical during the whole reproductive life. The small but significantly greater fecundity of the aphids on variety A was caused by a few more larvae being born *late* in reproductive life, which suggested that the adult aphids were somewhat better nourished on variety A and could mature more larvae than those feeding on variety B. However, more recent work suggests that the adult aphid's fecundity may also be affected primarily by larval nutrition. In any batch of larvae, all born to winged aphids on bean plants of variety B at the same time or within a few hours of each other, some develop and become adult sooner than others. The fecundities and reproductive rates of a batch of adult aphids that had developed quickly (fast developers) were compared with those of a late-developed group (slow developers). The fast developers produced significantly more larvae than slow developers, and the difference was double the difference between the fecundities of aphids reared on the two bean varieties. Further, differences in the reproductive rate were much greater during the first 5 days of adult life than during the next 5 days; thereafter the rates were identical. The difference in reproductive rate accounted for the difference in fecundity. The greater fecundity and reproductive rate of the fast developers was caused by events during *early* adult life and suggests a better nutrition during the larval life of the parent insects. Newly moulted fast and slow developers contained the same number of embryos, so fast developers must have matured their embryos more quickly during larval life and delivered them faster when they became adult. Fast developers were also heavier and larger than slow ones; they did not feed faster in the adult stage, but they must have assimilated food faster. When comparing the fecundities and reproductive rates of aphids it is important, therefore, to use aphids with similar rates of larval development. The causes of the greater fecundity of fast developers are not yet understood, but larval nutrition may affect fecundity by increasing the early reproductive rate of the adult. The difference in fecundity between aphids on the two bean varieties differs from that between fast and slow developers, and for another cause.

We have also recently discovered that the fecundity of aphids reared on variety B can be greatly increased by changing the conditions of growing plants. The mean fecundity of aphids on variety B was 85 ± 1·3 larvae, but it was 94 ± 1·5 larvae when aphids (born, as before, to alate virginoparae) were reared and kept under the standardised conditions described earlier, but on plants that had previously been grown in daylight with supplementary light from mercury fluorescent lamps. The aphids apparently received a still more nutritious sap from plants irradiated in this way, and had been under-nourished under the previous lighting régime.

There is, presumably, an upper limit to the number of larvae that an aphid can produce, and this maximum could be genetically determined and characteristic of the species or race. But reproductive rate and fecundity can depend on the conditions of rearing of aphids and plants, so it is essential to know the conditions that achieve maximum fecundity; also to adopt standardised conditions when testing host plants for ‘resistance’ and ‘susceptibility’ to aphid growth and reproduction, for a variety ‘resistant’ under one set of conditions may be ‘susceptible’ under others.

Thus, the apterous aphid’s fecundity seems to depend primarily on its nutrition, that is, on the quality of the nutrients it gets from its host. The feeding rate and quantity of sap ingested are not basically important in deciding reproductive rate and fecundity of *Aphis fabae* on a suitable host plant such as the bean, although under some conditions or on other host plants the inability to feed at an optimal rate might well impair the assimilation of nutrients. The quantity of nutrients ingested from the two bean varieties did not determine differences in fecundity. It is the quality of the sap in the plant that seems primarily to affect the rate embryos develop

https://doi.org/10.23637/ERADOC-1-57

during larval life, the rate of reproduction (especially during early adult life) and the numbers of larvae that the adult can mature; these features in turn affect the rate a colony of aphids will increase and the degree to which the aphid exploits its host plant. A great reproductive capacity is the aphid's main defence against natural enemies, and anything that decreases it makes the aphid more vulnerable to them.

REFERENCES

AUCLAIR, J. L. (1959) Feeding and excretion by the pea aphid, *Acyrthosiphon pisum* (Harr.) (Homoptera: Aphididae), reared on different varieties of peas. *Ent. exp. & appl.* **2**, 279–286.

AUCLAIR, J. L. (1963) Aphid nutrition. *A. Rev. Ent.* **8**, 439–490.

AUCLAIR, J. L. & CARTIER, J. J. (1963) Pea aphid: Rearing on a chemically defined diet. *Science* **142**, 1068–1069.

AUCLAIR, J. L. & MALTAIS, J. B. (1961) The nitrogen economy of the pea aphid, *Acyrthosiphon pisum* (Harr.), on susceptible and resistant varieties of peas, *Pisum sativum* L. *Proc. XI int. Congr. Ent., Vienna*, 1960, **I**, 740–743.

AUCLAIR, J. L., MALTAIS, J. B. & CARTIER, J. J. (1957) Factors in resistance of peas to the pea aphid, *Acyrthosiphon pisum* (Harr.) II. Amino acids. *Can. Ent.* **89**, 457–464.

BANKS, C. J. (1958) Effects of the ant, *Lasius niger* (L.), on the behaviour and reproduction of the black bean aphid, *Aphis fabae* Scop. *Bull. ent. Res.* **49**, 701–714.

BANKS, C. J. & MACAULAY, E. D. M. (1964) The feeding, growth and reproduction of *Aphis fabae* Scop. on *Vicia faba* under experimental conditions. *Ann. appl. Biol.* **53**, 229–242.

BANKS, C. J. & MACAULAY, E. D. M. (1965) The ingestion of nitrogen and solid matter from *Vicia faba* by *Aphis fabae* Scop. *Ann. appl. Biol.* (in the press).

BANKS, C. J. & NIXON, H. L. (1958) Effects of the ant, *Lasius niger* L., on the feeding and excretion of the bean aphid, *Aphis fabae* Scop. *J. exp. Biol.* **35**, 703–711.

BANKS, C. J. & NIXON, H. L. (1959) The feeding and excretion rates of *Aphis fabae* Scop. on *Vicia faba* L. *Ent. exp. & appl.* **2**, 77–81.

BAWDEN, F. C. (1964) *Plant viruses and virus diseases.* 4th ed. New York: The Ronald Press Company.

BROADBENT, L. (1951) Aphid excretion. *Proc. R. ent. Soc. Lond.* (A), **26**, 97–103.

DAVIDSON, J. (1922) Biological studies of *Aphis rumicis* Linn. Reproduction on varieties of *Vicia faba*. *Ann. appl. Biol.* **9**, 135–145.

DAVIDSON, J. (1925) Biological studies of *Aphis rumicis* Linn. Factors affecting the infestation of *Vicia faba* with *Aphis rumicis*. *Ann. appl. Biol.* **12**, 472–507.

DAY, M. F. & IRZYKIEWICZ, H. (1953) Feeding behaviour of the aphids *Myzus persicae* and *Brevicoryne brassicae*, studied with radiophosphorus. *Aust. J. biol. Sci.* **6**, 98–108.

VON DEHN, M. (1961) Untersuchungen zur Ernährungsphysiologie der Aphiden. Die Aminosäuren und Zucker in Siebröhrensaft einiger Krautgewächsarten und im Honigtau ihrer Schmarotzer. *Z. vergl. Physiol.* **45**, 88–108.

EDWARDS, J. S. (1965) Some observations on the solid components of the gut content of aphids. *Proc. XII int. Congr. Ent., Lond.* 1964 (In the press).

HEATHCOTE, G. D. (1962) The suitability of some plant hosts for the development of the peach–potato aphid, *Myzus persicae* (Sulzer). *Ent. exp. & appl.* **5**, 114–118.

HILL, A. R. (1957) Observations on the reproductive behaviour of *Amphorophora rubi* (Kalt.), with special reference to the phenomenon of insect resistance in raspberries. *Bull. ent. Res.* **48**, 467–476.

HERZIG, J. (1937) Ameisen und Blattläuse. (Ein beitrag zur Ökologie aphidophiler Ameisen.) *Z. angew. Ent.* **24**, 367–435.

JOHNSON, C. G. (1963) Physiological factors in insect migration by flight. *Nature, Lond.* **198**, 423–427.

KENNEDY, J. S. & BOOTH, C. O. (1951) Host alternation in *Aphis fabae* Scop. I. Feeding preferences and fecundity in relation to the age and kind of leaves. *Ann. appl. Biol.* **38**, 25–64.

KENNEDY, J. S. & MITTLER, T. E. (1953) A method of obtaining phloem sap via the mouth-parts of aphids. *Nature, Lond.* **171**, 528.

KENNEDY, J. S. & STROYAN, H. L. G. (1959) Biology of aphids. *A. Rev. Ent.* **4**, 139–160.

LEES, A. D. (1959) The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton—I. The influence of these factors on apterous virginoparae and their progeny. *J. Insect Physiol.* **3**, 92–117.

LEES, A. D. (1961) Clonal polymorphism in aphids. In: *Insect polymorphism.* Symposium No. 1, Royal Entomological Society of London, pp. 68–79.

LINTI, H. (1960) Der Flügelploymorphismus der Schwarzen Bohnenlaus—*Doralis fabae* (Scopoli) im Zusammenhang mit der Ausbildung des Ovars und der Flugmuskulatur. Dissrt. Ludwig-Maximilians Universität, München.

MITTLER, T. E. (1957) Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae) I. The uptake of phloem sap. *J. exp. Biol.* **34**, 334–341.

MITTLER, T. E. (1958) Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin) (Homoptera, Aphididae) III. The nitrogen economy. *J. exp. Biol.* **35**, 626–638.

MITTLER, T. E. (1962) What affects the amount of honeydew excreted by aphids? *Proc. XI int. Cong. Ent., Vienna* 1960, **II**, 540–541.

MITTLER, T. E. & DADD, R. H. (1962) Artificial feeding and rearing of the aphid, *Myzus persicae* (Sulzer), on a completely defined synthetic diet. *Nature, Lond.* **195**, 404.

MOERICKE, V. (1960) Die Magengrösse von *Myzus persicae* (Sulz.) und *Doralis fabae* (Scop.) in Abhängigkeit von der Wirtspflanze. *Z. angew. Ent*, **47**, 137–142.

MÜLLER, H. J. (1951) Über die Ursachen der unterschiedlichen Resistenz von *Vicia faba* L. gegenüber der Bohnenblattlaus *Doralis fabae* Scop. III. Über das Wirtswahlvermögen der Schwarzen Bohnenlaus *Doralis fabae* Scop. *Züchter* **21**, 161–179.

PAINTER, R. H. & PATHAK, M. D. (1962) The distinguishing features and significance of the four biotypes of the corn leaf aphid, *Rhopalosiphum maidis* (Fitch). *Proc. XI int. Congr. Ent., Vienna* 1960, **II**, 110–115.

RICHARDS, O. W. (1961) An introduction to the study of polymorphism in insects. In: *Insect polymorphism.* Symposium No. 1. Royal Entomological Society of London, pp. 1–10.

TAMBS-LYCHE, H. & KENNEDY, J. S. (1958) Relation between growth pattern and resistance to *Aphis fabae* Scopoli in three varieties of field bean (*Vicia faba* L.). *Ent. exp. & appl.* **1**, 225–239.

TAYLOR, L. R. (1959) Abortive feeding behaviour in a black aphis of the *Aphis fabae* group. *Ent. exp. & appl.* **2**, 143–153.

WATSON, M. A. & NIXON, H. L. (1953) Studies on the feeding of *Myzus persicae* (Sulz.) on radioactive plants. *Ann. appl. Biol.* **40**, 537–545.

WEBER, H. (1928) Skelett, Muskulatur und Darm der schwarzen Blattlaus *Aphis fabae* Scop. Mit besonderer Berücksichtigung der Funktion der Mundwerkzeuge und des Darms. *Zoologica*, **76**, 1–120.

WIGGLESWORTH, V. B. (1960) Nutrition and reproduction in insects. *Proc. Nutr. Soc.* **19**, 18–23.

ZIMMERMANN, M. H. (1960) Transport in the phloem. *A. Rev. Pl. Physiol.* **11**, 167–190.