

No sex please: we're British aphids

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Aphids are amongst the most important groups of insect pests and few crop plants escape the ravages of at least one species. Aphids which specialize on one species or group of plants are described as monophagous. When they reproduce both sexually and asexually on the same plant type, they are referred to as monoecious. The European large raspberry aphid, *Amphorophora idaei*, is categorized as

monophagous and monoecious. The life cycle of *A. idaei* is shown in Fig. 1A. Eggs are laid on the canes of the European raspberry, *Rubus idaeus*, they hatch in the spring and, as in all aphids, the population expands as a series of asexually reproducing clones. Using genetic markers it is possible to examine the relatedness of neighbouring aphids within and between fields¹. Fig. 1B shows an example from one of SCRI's experimental fields. Most of the *A. idaei* individuals were genetically different even from those collected from the same part of the same plant. However, one fingerprint did appear at more than one place, suggesting clonal expansion of this genotype. This could have occurred by chance if, for example, the egg of this genotype hatched earlier than others. Overall there were seven genotypes amongst nine individuals collected and tested. This is typical of the genetic variation expected from a sexual population.

At the opposite end of plant colonizing ability is *Myzus persicae*, the peach potato aphid. This is a polyphagous aphid that can colonize hundreds of secondary host plants. Many of these plants are important agricultural crops. However, like other polyphagous aphid species, the sexual stages of *M. persicae* can only reproduce on one primary host species, in this case peach. The life cycle of *M. persicae* is shown in Fig. 2. Like *A. idaei*, the movement between secondary and primary hosts requires specialized stages, or morphs. *M. persicae* genotypes, which can complete the life cycle by laying viable eggs, are known as holocyclic and those that cannot produce sexual forms as anholocyclic. The males produced by *M. persicae* are winged and can therefore fly from the secondary to the primary host; however, the egg laying females (ovipara) are not winged. To provide egg laying females on the primary host, a specialized migratory winged morph, the gynopara, is generated from aptera on secondary hosts in the autumn and its descendants are the egg laying females. Such an aphid life-cycle which alternates between different summer hosts and the primary winter host is described as diœcious. Restriction of polyphagous aphids to a single primary host has been taken as evidence that their ability to colonize many hosts is a derived characteristic and ancestral aphids were originally specialized.

Eggs are an essential part of aphid overwintering and survival from season to season. Therefore, *M. persicae*

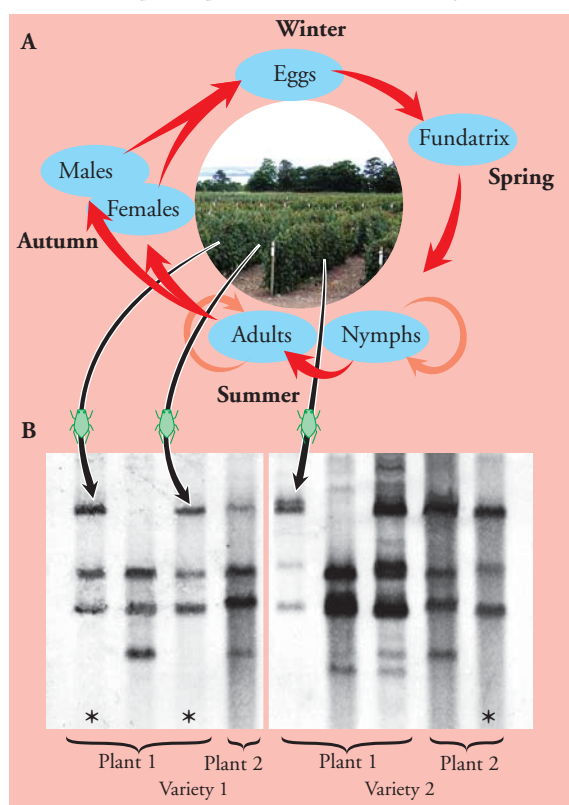


Figure 1 A. *A. idaei* reproduction starts with an egg laid on a raspberry cane. In the spring this hatches to give the first generation of asexually reproducing individuals. Asexual reproduction continues on the raspberry but winged forms (alatae) are also produced and these migrate to other raspberry plants allowing expansion of a clones. In autumn the shortening day length and decreasing temperatures induces the production of specialised sexual forms. These complete the life cycle on the raspberry. B. Using genetic markers it is possible to investigate the number of different genotypes in a population. Aphids collected from an experimental field were examined. These came from two different plants on two different varieties. There are clearly many different fingerprints, but one genotype (marked *) was found in more than one place and is probably the result of clonal expansion.

should be restricted to areas where peach trees are available for egg deposition, with numbers rapidly declining further away from peach trees. However, this is not what happens and *M. persicae* is a prevalent pest in temperate and colder regions, such as Scotland, where peach trees are very rare and can only be cultivated under glass. In these latitudes it has become clear that *M. persicae* can overwinter through continuation of parthenogenetic asexual summer generations

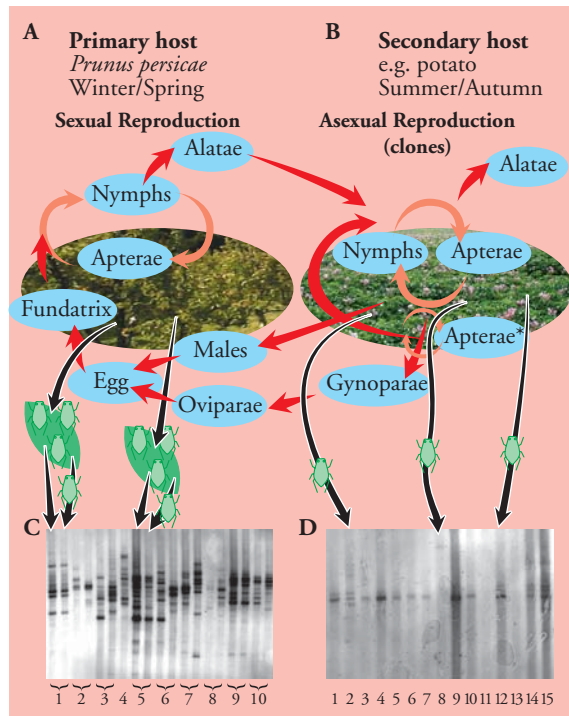


Figure 2 **A.** *M. persicae* reproduction starts with an egg laid on a peach tree. In the spring this hatches to give the first generation of asexually reproducing individuals. Asexual reproduction continues on the peach tree but winged forms (alatae) are also produced. These migrate to summer crops continuing the expansion of a clone. **B.** On summer crops asexual reproduction reaches its full potential and numbers build up. In autumn the shortening day length and decreasing temperatures induces the production of specialised winged forms. These migrate to peach trees where the complete life cycle. However, in the winter in Scotland *M. persicae* continues to reproduce using only the asexual parts of its life cycle. **C & D.** Using genetic markers it is possible to investigate the number of different genotypes in a population. In Panel C aphids collected from a single peach tree were examined. The first track contains an analysis of many individuals from a peach leaf and the second track an individual from the same leaf (sample 4 is from a single individual). There are clearly many different fingerprints. This contrasts to the situation in Scotland (Panel D) where there are very few fingerprints.

(see Fig. 2). This is not a general ability of all *M. persicae* clones, and in fact it appears to be restricted to a very small number of regionally specialized genotypes, which have remained dominant in this area for decades. One of the main characteristics of such clones is that they are anholocyclic, that is, they lack the ability to complete the life cycle through egg production. Induction of the latter process would result in resources being wasted in a generation that would require peach trees to continue the life cycle. The result is a paradox which has interested entomologists and evolutionary biologists alike: Why do species that can successfully maintain their populations without sex, continue to reproduce sexually? The reasoning is that sex is an energetically expensive process and any organisms that reproduce without sex should gain an advantage. In the case of aphids sex requires the production of two and sometimes three specialized forms which must colonize one plant species and, once there, they can only reproduce if a suitable mate has found the same location. Males and females have to spend energy in the process of mating and reproduction. In addition, each individual generated from mating will carry only half of the mother's genes. In contrast, asexual females can colonize and reproduce on any suitable plant immediately and their progeny will be, barring mutation, genetically identical to the mother. Therefore, at face value asexual aphid females have at least a double advantage over their sexual peers. The *M. persicae* asexual clones in Scotland support this hypothesis as they have persisted for 20 years although this is still very short on evolutionary timescales. It is possible that entirely asexual species, such as the morphologically distinguishable, *M. antirrhinii*, are long-term asexual derivatives of *M. persicae*, reflecting at least short-term evolution and success for asexual clones. However, it is also possible that asexual aphid populations can be derived in one step through hybridization and *M. antirrhinii* could be a hybrid between *M. persicae* and *M. certus* and there is some molecular and morphological evidence that this is the case.

Two fold cost of sex and advantages of not having sex are likely to be outweighed by the plasticity of an aphid's sexual population. The role of aphids as agricultural pests causing both direct damage and vectoring viruses is well documented and studies to prevent spread occurring continue. One of the biggest problems that applied biologists face when dealing with aphids is their capacity to adapt to new challenges. For example, plant breeding has successfully generated

raspberry plants with resistance to *A. idaei* using the single dominant gene A1 from European raspberry. However, within a relatively short time, in evolutionary terms, the population of *A. idaei* has adapted to this source of natural plant resistance. For *M. persicae* plant resistance genes are less important for control and insecticide application is used instead. Throughout the world and in many different crops *M. persicae* is the target of all classes of insecticide. Perhaps because of this, and its potentially large and diverse population, it is one of the most adaptable aphids in counteracting insecticides. There are at least four characterized insecticide resistance mechanisms. One of these involves the amplification of neutralizing enzymes and the remaining mechanisms are based on point mutations in insecticide target sites. Through time the resistance mechanisms have become incorporated into common genotypes.

The ability of sexual recombination to generate new combinations of genes incorporating the necessary local physiological adaptations with genes that overcome either plant resistance or confer immunity to the actions of insecticides is crucial. But, is this scenario the complete picture? In *A. idaei* the adaptive process seems to be repeating itself with the A10 gene, originally from the North American Black raspberry (*Rubus occidentalis*), and now widely used in the *Rubus* breeding programmes at SCRI and EMR. Recent field observations show that some *A. idaei* are able to survive and reproduce on some resistant raspberry genotypes. It is uncertain if these aphids are as

‘fit’ as those that have overcome the A1 resistance gene and the commercial implications are not fully understood. However, in *M. persicae* the population consists of sexual populations, between which gene flow is frequent, and fragmented local asexual populations such as those in Scotland. The latter populations cannot acquire genes from sexual populations. Thus, for locally adapted asexual populations of *M. persicae* insecticide resistance would require *de novo* mutations, recreating those found in the sexual populations. While the spontaneous mutation rates are likely to be the same in sexual and asexual populations, the spreading process will be much slower in asexual populations. Sexual populations can expand asexually and then different individuals of the same clone can interbreed and lay large numbers of overwintering eggs. Overwintering of asexual clones is likely to result in a decrease in the number of individuals, particularly in a severe winter. It only requires one or two survivors from millions of individuals to start a new season of asexual clones. There are additional problems for adaptation in asexual clones: firstly, the acquisition of multiple resistance mechanisms or physiological adaptations would be so slow that the clone’s genes may be subjected to natural turnover long before this is acquired. Secondly, while some mutations may eventually confer resistance, there are likely to be deleterious mutations in many other genes during the acquisition time. There are also likely to be fitness costs to insecticide resistance mutations. In conclusion, sex appears to be beneficial to aphid species, however some long-term asexual clones challenge this assumption. Current research is investigating the ecophysiology and adaptability of these clones.

References

- ¹Fenton, B., Birch, A.N.E., Malloch, G., Woodford, J.A.T., Jones, A.T., & Gonzalez, C. (1995) *Scottish Crop Research Institute Annual Report 1994*, 153-154

