

Figure 4. Aphid (top right) as illustrated in a bookplate dating from 1805. These insects have been known to be pests of agriculture (more especially cereals) for at least 200 years. Their asexual spring and summer mode of reproduction, leading to their prodigious reproductive capabilities as noted in Part 1 of this article, *Antenna* (2007) Vol. 31(3), 152-158), was first shown by the Swiss naturalist and philosophical writer Charles Bonnet (1720-93) in 1740. However, the ability of particular aphid species to transmit pathogenic viruses to plants of economic importance (agricultural, horticultural and forestry) was only determined in the early years of the 20th century.

# Big issues in population biology: lessons from a greenfly

## Presidential Address

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### The Myth of the Clone

#### *Evidence for variation within the clonal genotype*

Some modern molecular evidence gives credence to clonal fidelity, other evidence does not. The use of microsatellite markers (Goldstein & Schlötterer, 1999) has shown that aphids (Fig. 4) can have multilocus genotypes which remain consistent in terms of genotypic expression over a range of loci (12 tested; Haack *et al.*, 2000). This suggests that such multilocus genotypes have descended from a common stem mother (Haack *et al.*, 2000; Miller, 2000). However, this may be an illusion of constancy. Mini- and microsatellites, essentially selectively neutral (but see Li *et al.*, 2002), are known to be notoriously fast mutating and evolving, with mutation rates typically of the order  $10^{-6}$  to  $10^{-3}$  per locus per generation (Hancock, 1999). There are thousands of such loci, perhaps tens of thousands, scattered throughout the genome (Loxdale & Lushai, 2003a). In addition, even sampling 12

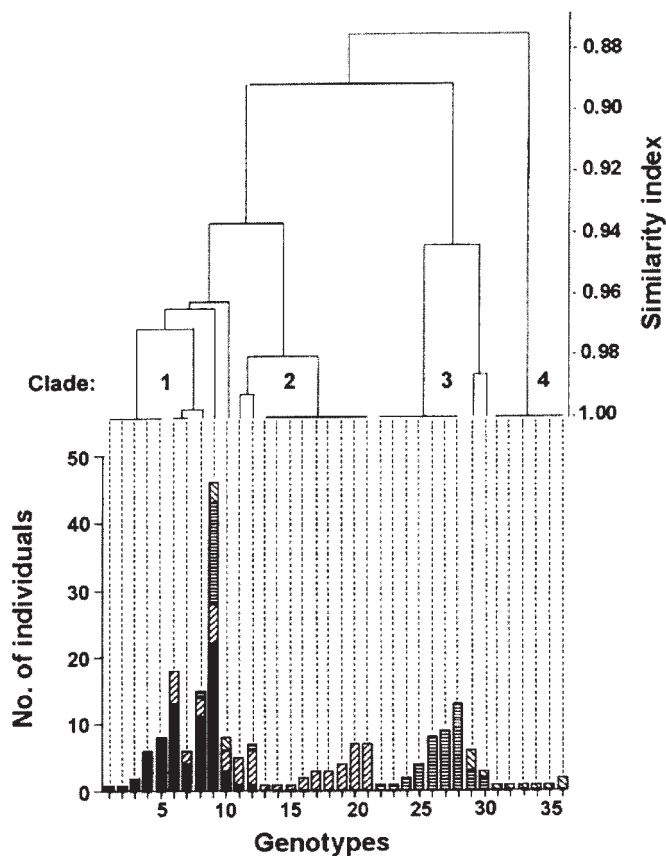


Figure 5. Stack-bar graph (lower) and cladogram (upper) showing host preference of winged asexual foundresses of the Grain aphid, *Sitobion avenae* attracted to four main Poaceous hosts in a Latin-square arranged field experiment (36 aphid genotypes resolved using RAPD molecular markers; hosts, from 1 to 4 = black (wheat); right-hand diagonal bars, (barley); horizontal bars (cock's-foot); left-hand diagonal bars (Yorkshire fog) (From: Lushai et al., 2002).

loci is but a tiny proportion of the total genome and it is not known with any certainty what particular regions are stable and which are fast mutating, hence what the rest of the genome is undergoing in terms of mutational changes.

Meanwhile, other regions are seemingly changing within clonal lineages, including ribosomal DNA (rDNA) regions. Thus for example, Fenton et al. (1998a) showed that certain clonal Peach-potato aphid, *Myzus persicae* (Sulzer), lineages had two ITS (internal transcribed spacer) haplotypes, suggestive of an introgression event between *M. persicae sensu stricto* (s.s.) and another close relative, *M. certus* (Walker). Similarly, other clonal *M. persicae* lineages examined showed intra- and inter-clonal polymorphism for the number of IGS (intergenic spacer) repeats (Fenton et al., 2003, 2005), whilst persistent selection with chemical pesticides (disulfoton) over 200 generations (four years) has been demonstrated to alter the IGS genotype of Greenbug, *Schizaphis graminum* (Rondani) clones, involving the loss of specific bands (Shufran et al., 2003). Blackman et al. (2000), using fluorescent *in-situ* hybridisation (FISH) techniques, showed

interclonal variation in the number and position of rDNA arrays in the chromosomes of aphids belonging to the genus *Trama*, of which males are unknown, although there is other molecular evidence for sexual recombination events having occurred (Normark, 1999).

With regard to genotypic banding patterns as seen on gels using predominantly dominant markers (markers which usually do not provide heterozygous genotypes but are nevertheless useful in clonal studies; Loxdale & Lushai, 1998), new mutated bands have been seen using synthetic oligonucleotide probes [(GATA)<sub>4</sub>]<sub>n</sub>, RAPDs (random amplified polymorphic DNA; De Barro et al., 1994; Lushai et al., 1998) and especially using AFLPs (amplified fragment length polymorphism; Forneck et al., 2001a,b; Vorwerk & Forneck, 2007, in press). Furthermore, such random (somatic) mutations were seen within 1-14 generations (*S. avenae* and Phylloxera), and in one case (*S. avenae*) in the germ line (Lushai et al., 1998). Most extraordinary of all, Lushai et al. (1997) revealed using RAPDs both intraclonal as well as intermorph banding pattern differences in some *S. avenae* asexual lineages. As yet, the mechanism for such changes remains unknown, but may involve transposons, so called 'jumping genes'.

In terms of physiology, reference has already been made to genetically-based intermorph lineage differences in colour and life cycle. Large variations have also been recorded in the number of males produced between clones of different life cycle forms of *S. avenae*, especially androcyclic clones (Helden & Dixon, 2002). Lastly, highly insecticide-resistant *M. persicae* clones (R<sub>2</sub> and R<sub>3</sub>) which show amplification of the esterase-4 (E4) gene (which confers resistance and to some degree cross-resistance in this species), are known to undergo a

decline of gene expression, but not gene number, when chemical selection ceases. I will allude to this phenomenon at the end of the article (see section 'Was Lamarck partially right all along?'). Loxdale & Lushai (2003a) overview general mutational changes in aphids whilst, more specifically, Field & Blackman (2003) discuss the changes seen in the highly resistant strains of *M. persicae* in relation to E4.

#### Evidence for variation between clonal lineages

Using microsatellite and mtDNA markers, evidence for introgression events between different lifecycle morphs within species as well as between closely-related species has been demonstrated. Thus for example, the two species *S. avenae* (predominantly anholocyclic) and *S. fragariae* (predominantly holocyclic), both of chromosome number 2n = 18 (Blackman & Eastop, 2000), clearly cross breed. Using microsatellites, Sunnucks et al. (1997) showed there to be high levels of allelic/genotype variation in *Sitobion avenae sensu lato* collected from wheat and *Dactylis glomerata* (cock's-foot grass). There were found to be three apparently almost non-interbreeding genotypic groups, with high levels of sexual recombination within each. Host specialisation was apparent: thus there were wheat-specific lineages, lineages common to both wheat and *D. glomerata*, and lineages from *D. glomerata* only which were found to bear many alleles from *S. fragariae*; furthermore, the genotype class with *S. avenae*-like and *S. fragariae*-like alleles also carried *S. fragariae*-like mtDNA in 80% of cases. Such asymmetry suggests that *S. avenae* males are attracted via similar/identical sex pheromones (Goldansaz, 2003) to *S. fragariae* females (see Sunnucks et al., 1997 for further details and also Vialatte et al., 2005).

In *R. padi*, studies have shown that the anholocyclic and holocyclic lineages are very divergent in terms of their mtDNA (by some 0.4 -1.4 million years: Martinez-Torres, 1994 cited in Simon et al., 1996). Newer evidence suggests that a hybridisation event may have occurred in recent historical times between *R. padi* s.s. and a closely-related unknown species, causing asexuality (Delmotte et al., 2003). Other evidence points



to there being 'sexual leakage' (gene flow) between lifecycle morphs and that asexuals derive from sexuals, probably by three main mechanisms, including hybridisation (Delmotte *et al.*, 2001). As mentioned earlier, whilst microsatellites reveal multi-locus genotypes to be identical at a range of loci (Haack *et al.*, 2000), the rest of the genome is untested and may conceal widespread variations, both within and between asexual lineages. Hence at the present time it is not possible to say definitively that a given aphid species asexual lineage has identity in any strict genetic sense, without, that is, sequencing the entire nuclear and mitochondrial genomes and directly comparing the sequences of such lineages (Caillaud *et al.*, 2004; Sabater-Muñoz *et al.*, 2006).

#### *Evidence of higher level lineage evolution, especially in relation to host plant*

Apparently 'good' taxonomic species can show a range of polymorphisms related to the host plant and this implies the beginnings of sympatric speciation. Such changes are seen in both the chromosomal karyotype as well as in terms of molecular DNA differences. As an example of the first, clear chromosomal differences have been observed in the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), in relation to whether the insect feeds on barley or sorghum and maize in the northern hemisphere ( $2n = 10$  and usually 8, respectively; Brown & Blackman, 1988; Blackman & Eastop, 2000). Biotypes are well known in the Aphididae (Eastop, 1973). In the case of the greenbug, *S. graminum*, host-adapted forms almost leading to the point of incipient speciation have been detected using mtDNA COI sequence analysis (Anstead *et al.*, 2002). The three main clades found involve many wild species of Poaceae strongly suggesting that the evolution of such host-based differences in this species pre-dates the development of agriculture in historical times (i.e. last 5,000 years).

Using nuclear DNA markers, the existence of host-based stratification was first demonstrated in *Sitobion* species by Paul De Barro *et al.* (1995) employing RAPDs, a phenomenon that has been further explored by a number of researchers since (see Loxdale & Lushai, 2007 for details and references therein). Clear evidence for host preference in *S.*

*avenae* infesting wheat, wheat volunteers, barley and maize was also found in French populations using microsatellites (Haack *et al.* 2000). Thus many genotypes were detected, some with apparent host preferences, whilst two genotypes from maize were also found on all the other hosts. The data suggest specialist (s) and generalist (g) clones, 'g' clones seemingly being able to colonise large geographical areas and persist for several years. Such a scenario could be favoured by agricultural practice. Besides these two 'g' clones, a continual replacement of rare 's' genotypes was observed in maize in both years of the study. It was hypothesised by the authors that selection occurs via aphid-plant genotype interactions and natural enemies.

Other field experiments involving the application of molecular markers (RAPDs) have revealed that host preference is shown by early immigrants into the crop. Thus winged *S. avenae* foundresses showed such host preferences when landing on spring cereal and grass hosts and genotypes could be split into four main clades (Lushai *et al.*, 2002; Fig. 5).

As regards what constitutes a natural species population, early evidence using a single polymorphic allozyme locus (GOT, glutamate oxaloacetate transaminase) revealed that *S. fragariae* may even be a complex of species/forms (Loxdale & Brookes, 1990). Samples collected at various sites within a ~ 65 km radius around Rothamsted and tested for GOT variation showed that, at certain sites, high frequencies of a slow (S) allele occurred within large sub-samples from grass (*D. glomerata*). However, this allele was largely absent from samples collected from blackberry, *R. fruticosus*, as if such genotypes were not completing the holocycle by returning in the autumn to the primary host. Specimens bearing the 'S' GOT allele sent to Dr. Victor Eastop at the Natural History Museum, London, were morphologically-indistinguishable from *S. fragariae* s.s. These may constitute an anholocyclic strain or perhaps a cryptic species (Loxdale & Brookes, 1990), assuming that another common primary host on which the aphids regularly lay their eggs does not exist for the species in England (besides *Rosa* spp. and strawberry, *Fragaria* spp.), a

possible but unlikely event (Hille Ris Lambers, 1939; Dicker, 1940; Blackman & Eastop, 2000; see also Tatchell *et al.*, 1983).

The available evidence reveals convincingly that a 'Janzenian' superclonal population is unlikely to prove a reality, because of the clear molecular heterogeneity and levels of host adaptation shown to exist within and between natural aphid populations of given species (real or apparent). Even so, as shown using molecular genetic markers, some generalist clones of certain species (so-called 'Superclones') have a wide distribution and may persist for some years, e.g. the aforementioned 'g' clone of *S. avenae* (Haack *et al.*, 2000; see also Figueroa *et al.*, 2005) and *M. persicae* in Australia (Vorburger *et al.*, 2003) as well as in Scotland, notably the 'Braveheart' or 'J' clone (Fenton *et al.*, 1998, 2003, 2005; Kasproicz, 2006). Whether in the long term these clones or strains are successful has yet to be shown and perhaps never can be (but see 'Clonal Selection' section), whilst the ecological reasons for their success has yet to be fully understood (Kasproicz, 2006 discusses this issue in depth in relation to *M. persicae*). Undoubtedly ecological scenarios change, of which host switching is one, as demonstrated, for example, in the alfalfa and red clover-associated host races (subspecies) of the pea aphid, *A. pisum* (Via, 1999; Via *et al.*, 2000) and in other insect species, notably the tephritid fruit fly, *Rhagoletis pomonella* (Walsh), which has hawthorn and apple-preferring forms (Feder *et al.*, 1998). In the case of both *Acyrtosiphon pisum* (Harris) and *R. pomonella*, the level of sympatric speciation, whilst strong, is still only partial, i.e. with no fixed allelic differences between host-preferring forms. With many aphids, the level of such speciation may be greater and pre-date agriculture. Certainly when chromosome polymorphisms are also involved, especially differences in number, divergence is more likely, perhaps to the point of total differentiation (Blackman, 1980; Blackman *et al.*, 1989). Other examples of population divergence seem to have occurred between aphids on wild hosts and cultivated crops, such as cereals and wild grasses in the case of *Sitobion* aphids (Vialatte *et al.*, 2005). The theory of, and empirical evidence for, sympatric speciation in aphids has

#### Box 4 *Aphid development*

With regard to whether aphids are winged (alate) or wingless (apterous), this is governed mainly by the degree of crowding, short day conditions (8h light:16h dark) and starvation. Wing formation is possibly mediated via juvenile hormone (JH) titre when induced by short days, but probably not when crowd-induced in long day conditions (16h light: 8h dark) (Hardie, 1980; Hardie *et al.*, 1985; Lees, 1967, 1980, 1990; Lees & Hardie, 1981); however, the exact role of hormones in wing development is still not fully understood (see Braendle *et al.*, 2006). Generally, aphids show dimorphism in terms of 'wingedness', depending on lifecycle strategy and whether the insects need to fly to find new hosts. The production of wings in males and females is associated with a single sex-linked, bi-allelic locus (aphicarus, *api*), although only in females is the expression at the locus governed by environmental cues including crowding and starvation (Braendle *et al.*, 2005; see also Braendle *et al.*, 2006) and so-called 'transgenerational' predator effects (although these effects are no more, or less, transgenerational than the response to crowding in many species – i.e. crowding the mother produces winged offspring; see section 'Was Lamarck partially right all along?'). But as often found with aphids, various scenarios pertain; thus for example, Sycamore aphids also have winged asexual summer forms which undergo 'trivial' flights within the canopy (Dixon, 1969), whilst some species such as *A. svalbardicum* are obligately apterous, and members of the pea aphid, *A. pisum* subspecies complex have winged or wingless males depending on the subspecies concerned and its particular host association within the Leguminosae (Knäbe, 1999). Like so much in aphidology, to every 'rule' there often is an exception, and even when the rules seem more or less established, as with the holocyclic and anholocyclic lineages of *R. padi*, new information tends to supersede the previous accepted norms!

been discussed by several authors over the years, especially Guldmond & Mackenzie (1994), Mackenzie & Guldmond (1994) and Via (2001). In *A. pisum*, biotypic host preference has recently been shown to be associated with strain differences of the endosymbiotic bacteria of the aphid mycetome, comprising specialist cells (mycetocytes) in the aphid body cavity which they inhabit (Simon *et al.*, 2003).

The fact that aphids show host preferences means that such differences need to be taken into account during programmes to combat pests, especially when natural biological control agents are involved – entomopathogenic fungi and hymenopterous parasitoids in particular. This is due to genotypic differences of the aphid host and also its preference for particular plant hosts which is certainly very likely to enhance parasitoid specificity (Storeck *et al.*, 2000; Ferrari & Godfray, 2006). The evolution of

biotypes of *S. graminum*, which break the plant resistance of newly bred strains of cereals (e.g. Sorghum), is the bane of expensive plant breeding industries, especially in the U.S.A. (Puterka & Peters, 1990).

#### **Images of immortality: Does the asexual lineage show population longevity and is the so-called 'clone' immortal?**

These questions can only be answered – if they can yet at all – by providing a little of the background of sexual *vs.* asexual modes of reproduction, including the positive and negative aspects of both. Sexual reproduction increases variance within populations and eliminates deleterious alleles. However, negatively, there are costs involved: (i) two organisms are needed to produce one offspring, unlike asexuals where the ratio is 1:1 ('two-fold cost of sex'); (ii) maladapted genes may be incorporated into the genome ('cost of recombination');

(iii) an individual has to find a mate, which may be rare and widely dispersed and requires much effort to find ('cost of rarity'); and lastly (iv), there is an increased risk of infection by pathogens and transposons (Arkhipova & Meselson, 2000).

In the case of asexuals, a major benefit potentially includes a fast rate of reproduction and adaptation to favourable environmental conditions, involving *r*-type selection (Dixon, 1998). But negatively, there is great potential for the accumulation of deleterious alleles within clonal lineages leading to 'mutational meltdown' (Muller's ratchet; Muller, 1964; Lynch *et al.*, 1993), although recent molecular evidence (using AFLPs) of aphid (Phylloxera) asexual lineages seems to cast some doubt on this happening, since 'most polymorphisms were characterised as random mutations, which were not continuously detected in later generations' (Vorwerk & Forneck, 2007). Such asexual lineages might also still contract deleterious transposons (Nuzhdin & Petrov, 2003) by horizontal gene transmission, e.g. inter-aphid infection via parasitic hymenoptera, as is thought possibly to occur with *Wolbachia* infections (Cook & Butcher, 1999).

With aphids, it may be asked why is sex retained in so many species, even rare sex? Indeed, even those species that are apparently totally obligately asexual may have males and oviparae, but as a consequence of inadequate sampling, they have yet to be found. For aphids, even finding the right host and a mate is difficult and there is certainly much more than a two-fold cost involved. Ward *et al.* (1998) estimated that only around 0.6% of *R. padi* winged forms (gynoparae) were able to locate the widely-dispersed primary woody host, *Prunus padus*, and thereafter produce oviparae (which mate with the winged males) and hence reproduce sexually – assuming that is, the males are successful in 'homing in' on the ovipara's sex pheromone trail in order to find her. In addition, some aphid lineages have seemingly persisted asexually for long periods. For example, the so-called 'Kennedy clone' of the Black Bean aphid, *Aphis fabae* Scopoli, founded at Cambridge in 1946 and which came to Imperial College, Silwood Park in 1968, has persisted for over 60 years (> 1000 generations). Similarly, *M. persicae*

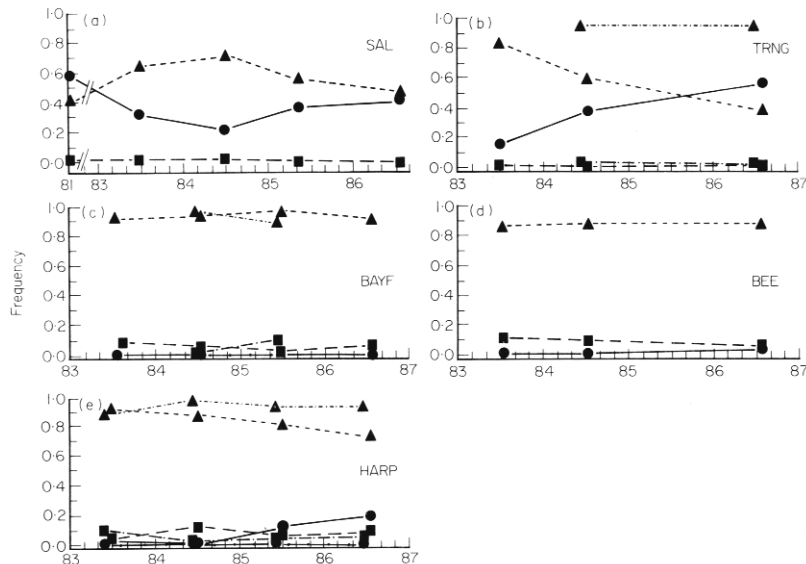


Figure 6. Graphs showing temporal stability of allele frequencies (y-axis; GOT, glutamate oxaloacetate transaminase) in local sub-populations of the Blackberry-grain aphid, *Sitobion fragariae*, infesting cock's-foot grass (straight or broken lines) or blackberry (lines interrupted with dots) at a number of sites within a 65 km radius of Harpenden, UK; 1981/3-86 (x-axis). This, along with the discovery of clear spatial genetic heterogeneity between local sub-populations, suggests the species to be not very migratory, leading to a restriction of inter-population gene flow (HARP = Harpenden; BEE = Bee Department, Rothamsted Estate; BAYF = Bayfordbury Estate, Hertfordshire; TRNG, Tring, Hertfordshire; SAL, Salcey Forest, Northamptonshire). Alleles ●, slow; ■, medium; ▲, fast. From: Loxdale & Brookes, 1990)

lineages have been reared at Reading University on artificial diets for over 30 years (van Emden, 1988). Lastly, some species appear to be truly obligate asexual, e.g. the Shallot aphid, *M. ascalonicus* (Blackman & Eastop, 2000), although males and oviparae may yet be found one day, as they were eventually for *R. maidis* in Pakistan (Blackman & Eastop, 2000).

Sex therefore appears not to be *that* useful in aphids at a population level for either *ridging the germ line of mildly deleterious mutations* or for *increasing population genetic variation*, although these mechanisms clearly have some longer-term importance. Why is it maintained then? Part of the reason could certainly be to produce cold-hardy overwintering eggs (Blackman, 1980), although holocyclic aphids may still go through a sexual phase if the primary host is present and even if conditions are relatively mild, e.g. southern France in the case of *M. persicae* (Guillemaud *et al.*, 2003). Another idea is that sex has to occur to reset chromosomal telomere length, telomeres being nucleotide repeats, (TTAGG)*n* in insects, where *n* can be many thousands. These repeats, associated with various proteins, protect the ends of the chromosomes and decline in terms of repeat number in an apparently stochastic manner per cell division throughout the life of an individual organism. Periodic resetting may be necessary to rejuvenate asexual lineages over the course of many generations (see

Loxdale & Lushai, 2003c and references therein). In this way, such rejuvenation may have a profound effect on natural populations such that, over the longer term, only those lineages which had periodic recombination and rejuvenation would persist, whilst other clones would senesce and die out, much like cells within the body (Lushai & Loxdale, 2007).

### Airborne aphids: Is there such a thing as the 'Aerial Plankton'?

In a 'Janzenian' sense, aphid aerial movement is important because it potentially spreads the genes, or genotypes, far and wide and allows asexual lineages to establish in lands anew (Taylor, 1965, 1986a,b; Loxdale *et al.*, 1993). However, on arrival at the new destination, lineages are usually untested by selection of one form or another (abiotic/biotic), including in the modern agro-ecosystem, pesticide treatment. More of this later. More prosaically, it is of course also essential in many species as hosts senesce, to enable them to find new or alternative hosts and thereby, at the same time, escape the effects of pathogens, predators and parasitoids - in effect, for them to move into 'enemy free space' (Jeffreys & Lawton, 1984; Loxdale & Lushai, 1999). Lastly, it is essential in other species for them to complete the holocycle by moving to an alternative primary or secondary host, including, in the case of the former, to find a mate and lay overwintering eggs.

In former times, ideas of the 'aerial plankton' abounded to describe the effectively passive transport of aphids borne on the wind above their air

### Box 5 Aphid flight

The generally small size and weak flight of aphids (see 'Airborne aphids' section) makes them seemingly 'prisoners of the wind' above the boundary layer so that flight speed and direction may then be largely out of their control (Taylor, 1965, 1974). However, they can control flight duration, being able to ascend and descend at will (including take off if the wind speed is favourable) so that they are by no means totally passive objects (Johnson, 1954; Taylor, 1965, 1986a). Indeed, they have species-specific flight behaviours, allowing them to locate hosts below the boundary layer of still air, as discussed later on. Having said that, these general features of migration and dispersal make tracking aphids a difficult task, although the advent of high resolution molecular population markers, especially DNA markers, has helped to elucidate migratory ambit to some degree, although rarely direction (Lushai & Loxdale, 2004). Unlike direct tags such as fluorescent markers, molecular markers usually only provide indirect measures of migratory range and gene flow (Loxdale, 2001). Furthermore, the parthenogenetic phase of reproduction of aphids (which conveniently provides large numbers of individuals of the same lineage for molecular studies) and their complex life cycles, often involving multiple routes of asexuality /sexuality (see Box 3 'Aphid life cycles'), make them ideal subjects for ecological and population genetic studies. Indeed, as a consequence of a plethora of such studies in recent years, much new, often very surprising, information has been gained on these fascinating insects.



speed, since they cannot make progress against a headwind of more than around 2 km per hour (Loxdale *et al.*, 1993). Drake and Farrow (1989) in an article entitled "The 'aerial plankton' and atmospheric convergence" discuss the current ideas concerning this plankton, analogous to that in the sea, but also detail why the analogy is not that good, highlighting the fact that flying insects are not feeding or developing in the aerial medium, but merely being transported by it (unlike the zooplankton in water). With aphids, usually only the teneral forms disperse, and besides showing a biphasic pattern of flight behaviour (Johnson, 1954), they settle on plant hosts in response to suitable visual and olfactory cues (Hardie, 1993; Niemeyer, 1990) as soon as possible in order to conserve fuel supplies (lipids) and maximise their potential for reproduction (see Loxdale *et al.*, 1993 and references therein).

The zooplankton – for example copepods (Crustacea) – do show behavioural changes as a function of daylight hours, descending and ascending to feed at different times of the day. In many respects, the population genetics of zooplankton, including *Daphnia* (Cladocera) in lakes, mirror that of aphids, including the fact that they sometime have widespread genotypes: these may be so-called 'general purposes genotypes' (GPGs; Lynch, 1984), but equally, they may represent the most ancient lineages (Weider *et al.*, 1999; see also Llewellyn, 2000). Taken as a group, aphids cannot be treated as a homogeneous whole. Rather, they have to be considered as individual species, like the zooplankton, with different lifecycles and forms, which greatly impinge on the population structures observed empirically. After all, even some morphs of particular aphid species (e.g. virginoparae *vs.* gynoparae of *R. padi*) are known to have different flight heights and behaviours, since their ultimate targets are different, the former morph seeking Poaceae, which is usually abundant and widespread, whereas the latter morph locates the much less common and more isolated primary host *P. padus* and hence, on average, tends to fly at a greater height (Tatchell *et al.*, 1988).

Use of molecular genetic markers has largely confirmed the above mentioned trend of species- and

morph-dependent flight behaviour, perhaps predictable from comparative examination of the peak abundance of aphids caught in 12.2 m high suction traps of the Rothamsted Insect Survey (RIS; Harrington *et al.*, 2004). Hence, for example, *S. avenae* is very abundant in June-July, whereas its congener, *S. fragariae*, is an order of magnitude rarer (Woiwod *et al.*, 1988), perhaps pointing towards a more restricted flight behaviour and concomitant aerial displacement. Molecular ecological studies using allozymes and/or DNA markers show *S. avenae* to display rather similar allele frequencies over a wide geographical area in Britain (i.e. allelic homogeneity; Loxdale *et al.*, 1985; Llewellyn *et al.*, 2003), whereas *S. fragariae* shows patterns of restricted gene flow (i.e. allelic heterogeneity), even over a relatively small geographic area, i.e. ~ 65 km radius of Rothamsted (Loxdale & Brookes, 1990). In addition, in the latter species and in further support of a lack of movement/gene flow, temporal samples collected over a number of years show somewhat stable gene and genotype frequencies (Loxdale & Brookes, 1990; Fig. 6).

In *S. avenae* in one year sampled, the distribution of genotypes appears clinal as a function of latitude, governed by climatic factors which influence the proportion of holocyclic genotypes successfully overwintering as eggs *vs.* obligate asexuals overwintering as live individuals (Llewellyn, 2000; Llewellyn *et al.*, 2003). Similar trends have also been documented in France (Simon *et al.*, 1999). Other aphids clearly display genetic population patterns in relation to flight behaviour: Sycamore aphids, *D. platanoidis*, very abundant in 12.2 m suction trap catches, display homogeneous gene/genotypic patterns at all spatial scales from leaf, tree to larger geographic scales (hundreds of kilometres; Wynne *et al.*, 1994). In contrast, the Damson-hop aphid, *Phorodon humuli* (Schrank), resistant to a range of pesticides and expressed as elevated carboxylesterase activity (Devonshire *et al.*, 1986), is much less migratory, its autumn migration probably being restricted to within 15-20 km of the main hop growing centres in the U.K., Herefordshire and Kent (Loxdale *et al.*, 1998), a conclusion drawn from the use of allozyme markers (insecticide resistance-

conferring esterase markers and a supposed more selectively neutral marker, 6-phosphogluconate dehydrogenase, 6-PGD), which broadly supports earlier suction traps findings (Taylor *et al.*, 1979). Several strands of molecular evidence suggest generally restricted gene flow in this species. These include the observation that esterase markers have significant heterogeneity in localised hop growing regions, whilst observed and expected genotype frequencies for aphids collected from *Prunus spinosa*/*P. domestica* (primary hosts) and hops (*Humulus lupulus*, secondary host) fall largely within Hardy-Weinberg (H-W) expectations, indicative of random mating. If insects landing on hops had come from very far away, significant deviations from H-W proportions would be expected (see Loxdale *et al.*, 1998 for further evidence and details). In the case of the Tansy aphid, *Macrosiphoniella tanacetaria* (Kaltenbach), molecular ecological evidence using microsatellite markers shows the aphid to display restricted gene flow (significant genetic heterogeneity at small spatial scales), with a metapopulation structure and no obvious isolation by distance (IBD) relationships until many hundreds of kilometres between populations (Massonnet *et al.*, 2002, Massonnet & Weisser, 2004; see also next issue of *Antenna*).

Such species-specific molecular evidence, especially as gained by Loxdale and co-workers in Britain and J.-C. Simon and co-workers in France, lends support to the flight chamber (wind tunnel) experiments by Jim Hardie and colleagues at Silwood Park that show that the attraction of winged aphids to white lights (sky) or green targets (plant hosts on which to land) varies depending on the apparent migratory tendencies of the species or morphs concerned (see Hardie, 1993 and Hardie & Campbell, 1998 for details). It seems certain that aphid migration has to be viewed in a case-specific manner, both in terms of the readiness of a given species to migrate and its ability to do so, a behaviour that is mirrored in population genetic patterns determined empirically using molecular markers.

*To be continued in the next issue...*

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