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SHORT REVIEW

Wing Dimorphism in Aphids

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Many species of insects display dispersing and nondispersing morphs. Among these, aphids are one of the best examples of taxa that have evolved specialized morphs for dispersal versus reproduction. The dispersing morphs typically possess a full set of wings as well as a sensory and reproductive physiology that is adapted to flight and reproducing in a new location. In contrast, the nondispersing morphs are wingless and show adaptations to maximize fecundity. In this review, we provide an overview of the major features of the aphid wing dimorphism. We first provide a description of the dimorphism and an overview of its phylogenetic distribution. We then review what is known about the mechanisms underlying the dimorphism and end by discussing its evolutionary aspects.

Keywords: alternative phenotypes; aphids; phenotypic plasticity; wing polyphenism; wing polymorphism

Aphid biology

Aphids are small, soft-bodied insects of the order Hemiptera that feed on the fluid in plant phloem. Aphids exhibit complex life cycles. Approximately 10% of species alternate between a primary (usually woody) host plant and a secondary (herbaceous) host plant. Nonhost-alternating species are usually monophagous but may feed on a range of related host plants (Blackman and Eastop, 1994). Aphids display a high reproductive rate due to three peculiarities of their reproductive biology. First, during the spring and summer months, female aphids reproduce parthenogenetically, obviating the need for males. Second, during these parthenogenetic generations, the embryos initiate development immediately after the budding of the oocyte from the germarium and are born as fully developed first-instar nymphs (ie, they are viviparous). Finally, the oldest embryos also contain embryos, so that adult parthenogenetic aphids carry not only their daughters but also some of their granddaughters within them. During the fall, declining daily photoperiod and temperature induce the development of sexual females and males. These sexual aphids mate and females produce yolk-rich eggs that undergo diapause to survive the winter (ie, they are oviparous).

Different species of aphid may exhibit wing dimorphism at various stages of the life cycle. Here, we distinguish between environmentally induced dimorphism, known as polyphenism, and genetically determined dimorphism, known as polymorphism. Wing polyphenism occurs primarily among parthenogenetic females, while wing polymorphism has been found only in males. While the bulk of the discussion that follows concerns the female polyphenism, we end with a consideration of its relationship to the male polymorphism (Figure 1).

Differences between winged and wingless aphid morphs

The winged and wingless phenotypes in aphids differ in a range of morphological, physiological, life history and behavioural features. Besides having wings and functional flight muscles, the fully winged morph exhibits heavier sclerotization of head and thorax, more fully developed compound eyes, ocelli, longer antennae, more rhinaria, and sometimes larger siphunculi and cauda (Kalmus, 1945; Kring, 1977; Kawada, 1987; Miyazaki, 1987). Most of these differences reflect the different life styles of the two phenotypes, as the winged morphs are equipped with an elaborate sensory system for flight and host plant location. Consistent with this theme, winged forms are also more resistant to starvation (Tsuji and Kawada, 1987b; Hazell *et al.*, 2005).

The morphological differences between winged and wingless phenotypes usually correlate with differences in life history. In general, the winged phenotype differs from the wingless phenotype by showing longer nymphal development, longer pre-reproductive adult period, longer reproductive period, lower offspring production, and prolonged longevity (Noda, 1960; MacKay and Wellington, 1975; Campbell and Mackauer, 1977; Tsuji and Kawada, 1987b; Tsumuki *et al.*, 1990). In addition, in response to shortened photoperiod, winged females tend to produce mainly sexual females whereas wingless females produce both sexual females and males (MacKay *et al.*, 1983; Nunes and Hardie, 1996).

Phylogenetic distribution of wing dimorphisms

Phylogenetic evidence indicates that the wingless form in aphids has been secondarily derived, as in most other insects. Within the Aphididae – comprising more than 95% of all 4,400 extant aphid species – there is extensive variation in the occurrence of winged and wingless morphs at different

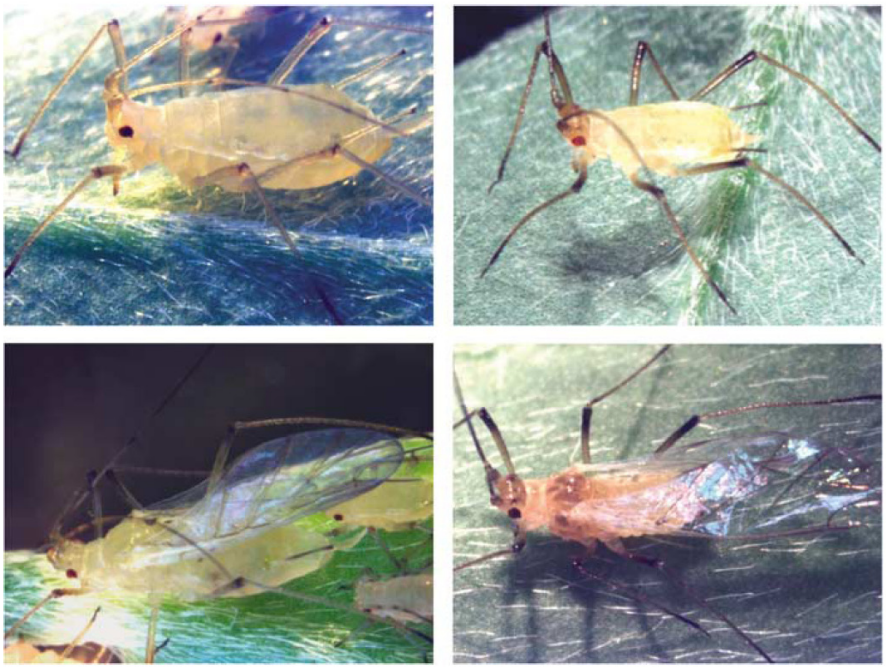

Figure 1 The female polyphenism (left) and male genetic polymorphism (right). In both cases, discrete alternative wingless (top) or winged (bottom) morphs are produced.

stages of the life cycle. Many species of the more primitive taxa, such as the Calaphidinae, produce only winged parthenogenetic females (Hille Ris Lambers, 1947, 1966; Heie, 1982). In some of these species, however, some winged females may differ in their flight capability or colonies may display variation in wing length (Hille Ris Lambers and van den Bosch, 1964; Hille Ris Lambers, 1966; Dixon, 1972; Heie, 1982; Heikinheimo, 1987). In Drepanosiphum dixoni, for example, all parthenogenetic females develop wings, yet some individuals lack indirect flight muscles and are therefore not capable of flight (Dixon, 1972). In other calaphidine species (*e.g.*, Symydobius oblongus) the parthenogenetic females show consistent differences in wing length, and the short-winged females do not fly (Heikinheimo, 1987). Most species of the Aphididae, however, produce both fully winged and completely wingless parthenogenetic females.

The diverse dispersal strategies of aphids appear to have evolved in association with two dominant ecological factors: host plant alternation and type of host plant. In host-alternating species, the morphs migrating between the primary and secondary hosts are always winged, whereas both winged and wingless females frequently occur during the parthenogenetic generations on the summer host for both host-alternating and nonhost-alternating species (Blackman and Eastop, 1994). Certain host plant characteristics, such as host plant persistence, may also correlate with the propensity to produce predominantly winged or wingless parthenogenetic females. Ephemeral host plants, including annual herbaceous hosts, can be exploited only temporarily and dispersal to new or more persistent hosts must take place at some point during the life cycle. Consistent with this idea, species feeding on large or perennial host plants may exhibit a lower incidence of winged morph production (Groeters, 1989). An exception are tree-dwelling aphid species, which often produce exclusively winged females compared to species feeding on herbaceous plants, possibly because flight allows aphids to find a suitable feeding location in architecturally complex trees (Waloff, 1983).

In most species the sexual females are wingless, with exceptions in more primitive taxa. Sexual males of Eriosomatinae, Anoeciinae, Hormaphidinae, and some Lachninae are wingless. In most other taxa males are winged; for example, the males of all host-alternating aphidines are winged (Blackman and Eastop, 1994, 2000). In about 10% of European species, however, both winged and wingless males have been recorded (Smith and MacKay, 1989). In the few species that have been examined in detail, this dimorphism is apparently caused by a genetic polymorphism (Hille Ris Lambers, 1966; Müller, 1969; Smith and MacKay, 1989).

Mechanisms

Environmental cues: The environmental conditions affecting the production of winged versus wingless morphs have been studied intensively (Hille Ris Lambers, 1966; Lees, 1966; Mittler and Sutherland, 1969; Kunkel and Kloft, 1974; Müller *et al.*, 2001). Here, we briefly summarize the conditions known to cue production of the winged morph, focusing on parthenogenetic females.

Density (tactile stimulation): Density-dependent regulation of alternative dispersal phenotypes is common in aphids and other insects. Increased aphid density triggers wing formation in many species and in some species a small increase in density is sufficient (Bonnemaison, 1951; Johnson, 1965; Lees,

1967; Sutherland, 1969a, b; Shaw, 1970a). The proximate mechanism mediating these environmental conditions appears to be increased tactile stimulation between individual aphids (Johnson, 1965). However, it is possible that chemical cues play an additional minor role (Kunert and Weisser, 2005). While the location of the tactile receptors is not known, in some species perception is mediated mainly by the antennae (Johnson, 1965; Lees, 1967; Sutherland, 1969a).

Host plant quality (nutrition): For a given aphid clone, variation in winged morph production correlates with variation in host plant species (Vereschagina and Shaposhnikov, 1998) and with changes in host plant quality or host plant age (Sutherland, 1969b). However, a review by Müller *et al.* (2001) showed that more than half of 38 examined studies in 12 different aphid species did not confirm the hypothesis that poor nutrition is responsible for an increase in winged morph production. In many of the earlier studies, the reported host plant effect on winged morph production was likely due to the effect of the host plant on the number of physical contacts between aphids (Müller *et al.*, 2001). Nevertheless, a decrease in plant quality alone can trigger wing induction in some species (Müller *et al.*, 2001).

Interspecific interactions: Interactions among different aphid species that aggregate on the same host plant can cause increased production of winged individuals (Lamb and MacKay, 1987), but this is likely to reflect a density-dependent response. In contrast, the mere presence of particular natural enemies may elicit an increase in winged morph production in the pea aphid, *Acyrthosiphon pisum* (Dixon and Agarwala, 1999; Weisser *et al.*, 1999; Sloggett and Weisser, 2002; Kunert and Weisser, 2003) (parasitization may also directly affect wing development, see below). The induction of winged morphs seems to result from increased tactile stimulation triggered by either predator avoidance behavior or from the release of aphid alarm pheromone (Kunert *et al.*, 2005). The presence of ants (which provide some protection for aphids against predators) seems to inhibit the production of winged individuals (El-Ziady and Kennedy, 1956; Kleinjan and Mittler, 1975). Aphid or plant pathogens (*e.g.*, fungi or viruses) and the facultative aphid endosymbionts may also affect wing induction (Müller *et al.*, 2001; Leonardo and Mondor, 2006).

Abiotic factors: Several other factors, in particular temperature, may influence wing production either directly or indirectly via the host plant (White, 1946; Kenten, 1955; Johnson and Birks, 1960; Schaefers and Judge, 1971; Liu, 1994). Most studies have reported a decline in winged morph production as temperature increases (Müller *et al.*, 2001). Photoperiod may be responsible for wing induction of parthenogenetic females in clones that do not undergo sexual reproduction (Lees, 1966).

Maternal effects

In addition to environmental factors, several maternal and transgenerational influences affect winged morph determination. In many species where wing determination occurs prenatally (in parthenogenetic embryos carried within adults), winged adults rarely or never produce winged offspring (Lees, 1961; Sutherland, 1970). Similarly, early born progeny descended from winged mothers exhibit a decreased production of winged morphs (Mackay and Wellington, 1977). In contrast, early born (wingless) progeny derived from wingless mothers respond strongly to wing-inducing stimuli (Mackay and Wellington, 1977; MacKay and Lamb, 1979). Grand-maternal phenotype, maternal phenotype, and age therefore all affect and modulate the response to wing-inducing environmental conditions.

Development

The development of alternative phenotypes has been examined in several aphid species using histological methods (Shull, 1938; White, 1946; Kitzmiller, 1951; Johnson and Birks, 1960; Tsuji and Kawada, 1987a; Ganassi *et al.*, 2005). Wing development appears to be the default developmental pathway and the wingless phenotype develops by diversion from this developmental pathway during prenatal or postnatal development. For example, Johnson and Birks (1960) examined a large number of fully developed embryos and first instar nymphs of Aphis craccivora and found wing anlagen in all of them, irrespective of whether or not they were destined to develop into winged adults. In this species, wing anlagen first appear as hypodermal thickenings shortly before the embryonic moult (Johnson, 1958a), which takes place about one day before birth. The wing buds increase in size until the embryo hatches from the mother. In nymphs destined to be wingless, the anlagen cease development at this stage. A similar scenario has been described in the pea aphid where all embryos, first-instar nymphs and second-instar nymphs exhibit wing buds, which subsequently degenerate in the developing wingless morph (Tsuji and Kawada, 1987a).

Intermediates between winged and wingless phenotypes also occur rarely. Such intermediates may be wingless but show some morphological features of the winged morph or they may be winged without having flight muscles and show morphological characteristics of the wingless morph. In the case of Aphis fabae and other species, these intermediates can be induced when wing-inducing stimuli are removed at different time points of nymphal development (Shaw, 1970b). Furthermore, parasitoids that lay their eggs in adult aphids affect the wing development of offspring. Such offspring very frequently show an intermediate winged-wingless phenotype and wing development is inhibited in presumptive winged individuals (Johnson, 1958b, 1959; Christiansen-Weniger and Hardie, 1998, 2000).

The role of hormones in the expression of the wing polyphenism

Juvenile hormone

The observation that wingless adults and nymphs are morphologically similar led early workers to suggest that high titers of juvenile hormone (JH) induce the wingless state by promoting the retention of juvenile features in adults (Lamb, 1956; Johnson, 1959; Kennedy and Stroyan, 1959). Naturally occurring JHs, as well as crude JH-containing extracts, JH precursors, and JH analogs have all been tested for their ability to inhibit the induction of winged morphs when administered to mothers carrying parthenogenetic embryos and to nymphs.

These studies have yielded disparate and sometimes conflicting results (Hardie and Lees, 1985), in part due to mistaking mere juvenilization by JH for authentic apterization (Lees, 1977), but also because of differences in species, dosages, means of administration, and experimental design. One clear result concerns the migratory winged morphs that produce sexual females, which in certain species (*e.g.*, A. fabae) can be induced by short days. Both long days and natural JHs administered to first-and early second-instar nymphs of these individuals cause them to develop as wingless morphs (Hardie, 1980, 1981). This appears, however, to be a special case – unrelated to the summer wing polyphenisms – in which JH is able to mimic the effect of long days. Indeed, the effects of both long days and JH can be cancelled out by crowding, suggesting that something other than or in addition to JH mediates the density-cued wing polyphenism (Hardie, 1980).

Attempts to correlate the activity of the organ that secretes JH, the corpus allatum, with the production of wingless morphs have also yielded equivocal results. Several studies showed that third-and fourth-instar nymphs without wing buds possess larger corpora allata, either by volume or nuclei diameter (White, 1965, 1968, 1971; Lamb and White, 1971; Elliot, 1975). In at least one other species, however, this correlation does not hold (Leckstein and Llewellyn, 1975; Leckstein, 1976) and the working assumption that volume or nuclei diameter are suitable proxies for either corpus allatum secretory activity or JH titer may be invalid (Hardie and Lees, 1985). Attempts to measure JH directly have detected JH III at very low levels in *Megoura viciae* (Hardie *et al.*, 1985), but no study has successfully correlated JH titers with the production of wingless morphs.

Precocenes

The failure to unequivocally induce or correlate winglessness with JH led to the proposal that the use of anti-JH compounds or experimental destruction of the corpus allatum might break the experimental impasse (Hales, 1976). Cells of the corpus allatum are selectively destroyed by the plant-derived precocenes, Precocene I (PI) and Precocene II (PII), as well as the more potent synthetic precocene, Precocene III (PIII) (Ohta and Bowers, 1977). In sensitive species, precocene treatment thus prevents JH synthesis and results in the precocious appearance of adult characteristics in nymphal instars (Brooks and McCaffery, 1990). Consistent with a predicted role for JH in mediating the aphid wing polyphenism, PII applied to mothers can induce the entire suite of characteristics found in the winged morph in her parthenogenetic offspring (Mackauer *et al.*, 1979; Delisle *et al.*, 1983; Hardie, 1986; Rup and Sohal, 1989; Hardie *et al.*, 1995, 1996; Gao and Hardie, 1996). However, PIII is capable of inhibiting the production of winged morphs, at least in the pea aphid (Hardie *et al.*, 1995; Gao and Hardie, 1996).

Despite what is generally understood about the targets of precocenes, their contradictory effects on winged morph induction are probably not mediated by JH. Although PII is able to induce winged progeny in several species, the majority of studies suggest that it fails to induce precocious development, the classic JH-mediated hallmark of precocenes (Mackauer *et al.*, 1979; Delisle *et al.*, 1983; Hardie, 1986; Hardie *et al.*, 1995, 1996). Consistent with this result, JH generally fails to reverse the winged morph-inducing effects of PII (Hardie, 1986; Hardie *et al.*, 1995; Gao and Hardie, 1996). Moreover, although the inhibition of winged morph production caused by PIII is accompanied by precocious development and destruction of the corpus allatum (Hales and Mittler, 1981; Kambhampati *et al.*, 1984; Hardie, 1986; Hardie *et al.*, 1995, 1996), the application of JH is capable of rescuing precocious development without reversing the inhibition of winged morphs (Gao and Hardie, 1996). Together, these observations suggest that PII and PIII exert their effects on the wing polyphenism independently of JH, and that the target mediating the effect of precocene on winged morph production remains unknown.

These results for precocenes, as well as a dearth of clear positive evidence for regulation by JH, leave the question of hormonal regulation of wing induction unanswered. Other than one study reporting a negative result for ecdysterone (Applebaum *et al.*, 1975), no other hormonal candidates for mediating the wing polyphenism have been investigated. This despite the likely requirement, for species showing prenatal induction, that the morph-determining signal must be able to cross the haemolymph. In seeking other candidates, it is perhaps worth keeping in mind one old but telling result for both *Aphis craccivora* and *Megoura viciae*; decapitation of females that have been cued to produce winged offspring leads to the almost immediate and exclusive production of wingless morphs. This suggests that signals either from the brain or the corpus allatum of the mother are likely to induce winged characteristics and not to suppress them as the JH model suggests (Johnson and Birks, 1960; Lees, 1966).

Evolution

Origin and maintenance of alternative phenotypes

For most organisms displaying alternative phenotypes, neither phenotype exhibits higher fitness overall. Rather, there is a trade-off, with the relative fitness of the different phenotypes being contingent upon environmental conditions. The evolution and maintenance of alternative phenotypes therefore requires variation in the environment. In aphids and many other wing-dimorphic insects, the winged morph usually has a lower individual fecundity than the wingless morph. In the face of deteriorating conditions, however, the ability to disperse may grant the winged morph an advantage. The wing polyphenism and other alternative phenotypes enable aphid clones to specialize for different environments and functions. As aphids produce alternative phenotypes within a genetic clone, there is no genetic conflict among individuals and selection should act to optimize investment in alternative phenotypes.

The evolution of polyphenism requires several conditions. First, environmental conditions must influence development to generate different phenotypes. Second, the resulting phenotypes must exhibit higher than average fitness in their respective environments. The factors acting as cues may be the same as the selective agents or may be different. As the developmental environment precedes the selective environ-

ment, an environmental cue must at least be correlated with future selective factors. Environmental control of alternative phenotypes can therefore evolve in organisms living in spatially or temporally variable environments in which cues can be used to reliably predict the future selective environment (Moran, 1992). It is possible that polyphenisms originated as polymorphisms that accumulated environmental influences (West-Eberhard, 2003). Aphids are particularly well suited for addressing this question because in some species the male wing dimorphism is genetically determined.

Male wing polymorphism in the pea aphid

Winged and wingless males of the pea aphid are found both in the ancestral range of Europe and in introduced populations of North America (Meier, 1958; Müller, 1962; Cartier, 1963; Hille Ris Lambers, 1966; Blackman and Eastop, 1994, 2000). The male polymorphism is controlled by a single locus on the X chromosome called aphicarus (*api*) (Smith and MacKay, 1989; Caillaud *et al.*, 2002; Braendle *et al.*, 2005a). In aphids, males are haploid for the X chromosome, so one allele of *api* causes winged males and the other causes wingless males. Given that males are produced only for a short period of time in the autumn, a lack of available environmental cues might explain why the male polymorphism relies upon a genetic switch.

Three *api* genotypes are present in natural populations: clones homozygous for the *api*-winged allele that produce all winged males, clones homozygous for the *api*-wingless allele that produce all wingless males and clones heterozygous for *api* that produce winged and wingless males in equal proportions. Although all three possible *api* genotypes may occur on the same host plant species, several studies suggest that male morph production may correlate with host plant range and persistence (Meier, 1958; Müller, 1962; Markkula, 1963; Eastop, 1971). The precise costs and benefits of producing winged versus wingless males are not known. Only winged males can move long distances to find mates on distant host plants. On the other hand, wingless males develop more quickly than winged males and may out-compete winged males born on the same host plant. There may therefore be specific advantages associated with each morph.

Genetic variation for the wing polyphenism

Different clones of the pea aphid, *Acyrthosiphon pisum* (Markkula, 1963; Lowe and Taylor, 1964; Weisser and Braendle, 2001; Hazell *et al.*, 2005; Braendle *et al.*, 2005b), and other species (MacGillivray and Anderson, 1958; Kvenberg and Jones, 1974; Blackman, 1979; Groeters, 1989) display variation in the propensity to produce winged females, even when exposed to the same environmental conditions. It is not yet known whether this genetic variation in the plastic response to environmental cues is adaptive. Some of this variation may be related to the host plant preferences of aphid clones (MacGillivray and Anderson, 1958; Weisser and Braendle, 2001), yet variation is also observed in clones collected from the same host plant species (Braendle *et al.*, 2005b).

Relationship between female wing polyphenism and male wing polymorphism

As the female wing polyphenism mimics phenotypes generated by the male wing polymorphism, one question is whether the genotype-environment interaction associated with the polyphenism involves the same loci that control the polymorphism. We have started to test this possibility by examining the wing-induction tendencies of the three possible *api* genotypes (Braendle *et al.*, 2005b). We derived F2 clones from a cross between parental clones homozygous for the two *api* alleles, which randomized alleles at loci that were not closely linked to *api*. In every case, clones homozygous for the *api*-winged allele produced few winged females. In contrast, clones heterozygous for *api* or homozygous for the *api*-wingless allele produced comparatively large numbers of winged females. In other words, alleles of the *api* locus producing the male winged morph and unknown loci influencing female wing plasticity are genetically linked in opposite phase. We do not know the extent of the linkage between *api* and the factors contributing to variation in wing polyphenism, but in the extreme they could represent pleiotropic effects of *api*. One important caveat of this work is that this linkage has been found in progeny derived from a single cross of two wild lines homozygous for the two *api* alleles. Without analyzing a larger sample of clones segregating for the different *api* alleles, we do not yet know if the genetic variation for the female polyphenism and *api* are in linkage disequilibrium in natural populations.

Future directions

The wing polyphenism in aphids provides a clear example of adaptive phenotypic plasticity. The coexpression of a wing polyphenism (females) and a wing polymorphism (males) in the pea aphid provides a rare opportunity to address the relationship between environmental and genetic induction of alternative phenotypes. This may also help to clarify how genetic and environmental factors interchangeably control the same developmental events, and how evolutionary transitions between polyphenisms and polymorphisms take place. From a practical point of view, the identification of genes involved in the polymorphic control of alternative phenotypes may facilitate the study of a polyphenism displaying a similar set of alternative phenotypes.

Aphid ecology and physiology have been studied intensively during the past few decades but little is known about the genetics and development underlying the expression of alternative phenotypes. Currently, aphids are becoming an increasingly important model system because a large community has begun to develop genomic resources for the pea aphid, *Acyrthosiphon pisum*. Perhaps most importantly, the genome of the pea aphid is currently being sequenced at the Human Genome Sequencing Center at Baylor College of Medicine with funds provided by the National Human Genome Research Institute (www.hgsc.bcm.tmc.edu/ projects/aphid/). These resources will provide novel opportunities for investigating the aphid wing dimorphism and many other features of aphid biology, such as aphid–plant interactions and the relationship between aphids and their endosymbiotic bacteria.

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