

Phenotypic plasticity in aphids (Homoptera: Insecta): Components of variation and causative factors

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Natural populations experience variable environment in space and time. The phenotypes that organisms express are the product of the genes that they carry and the environment that they experience. Diversity in populations of a species can be said to be the manifestation of diversity of environmental variations. A large number of aphid species are host-plant specific, but several species that are economically important are extremely polyphagous. The great success with which this insect has exploited a wide diversity of ecosystems can be attributed to its broad phenotypic plasticity and complex life cycle. For most of the known species, the life cycle of an aphid potentially consists of several clones which are endowed with a remarkable ability to adapt to a heterogeneous environment accompanied by phenotypic changes. Each clone goes through a seasonal life cycle made of a sequence of morphs or phenotypes that differ in their morphology, behaviour and physiology, but have identical genotype. The different phenotypes of a genotype provide the species ample scope to seek and exploit food resources under wide conditions. This article presents an account of the phenotypic plasticity, also known as polyphenism, in aphids in the context of their life cycles, production of different phenotypes, changes in phenotypes and their causative factors.

Keywords: Aphids, causative factors, life cycle, phenotypic plasticity.

APHIDS are sap-sucking insects of garden plants, in agriculture and horticulture, and also in forests. Known by 4702 valid species around the world¹, 637 of these belonging to the family Aphididae, order Hemiptera have been recorded from India². The mouths of aphids are in the form of minute hypodermic needles, with which they pierce the mesophyll cells of leaves or translocating vessels, the phloem of trees and suck their juices. Many of them are serious pests on the farm and garden. Polymorphism, i.e. occurrence of two or more morphologically distinct morphs in a population having the same genotype and each morph performing different ecological roles in the life

history, is characteristic of aphids³ (Figure 1). This trait coupled with the ability to breed by means of diploid parthenogenesis and viviparity for a major part of the life cycle in aphids has enabled them to produce a large number of clones in different kinds of plants even under adverse conditions. Each clone consists of offspring that are genetically identical to its parent and produced mitotically or asexually. Genetically identical individuals living in different environments may be different in form, physiology or behaviour. Such individuals demonstrate phenotypic plasticity in response to environmental factors like seasonality of their host plants, food quality, climate and natural enemy association, etc. that vary in space and time. Knowledge of the origin, cause, regulation, morphology, behaviour and fitness of the individual is vital to deal with the problems associated with phenotypic plasticity that prevail in aphids^{4,5}. The aim of this article is to present a review of phenotypic plasticity in aphids with particular reference to their life cycles, and roles of different environmental factors.



Figure 1. Polymorphism in aphids showing a colony consisting of winged and unwinged phenotypes (400×).

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Types of life cycle

Aphids exhibit a remarkable complexity in their life cycles. In areas having long and cold winter, majority of aphids show holocyclic life cycle, which is the alternation of a single sexual generation and laying of hibernating eggs under adverse weather conditions by several asexual generations of parthenogenetic reproduction in spring and summer during favourable periods on the same or different species of host plants⁶. In periods of parthenogenetic reproduction, host-alternating species can produce phenotypes as different as fundatrigeniae, emigrants, unwinged (apterous) and winged (alate) virginoparae, as well as alate males, alate gynoparae and sexual females^{7,8} (Figure 2a). In comparison, majority of aphids occurring in warmer areas live by asexual generations alone and produce unwinged and winged morphs (Figure 2b). A number of aphid species known by cosmopolitan distribution exhibit holocyclic and anholocyclic life cycles, both at the same time in different areas of their occurrence⁹ (Figure 3).

Phenotypes of aphids

A phenotype or morph is considered to be the one which is distinguishable in certain morphological, biological

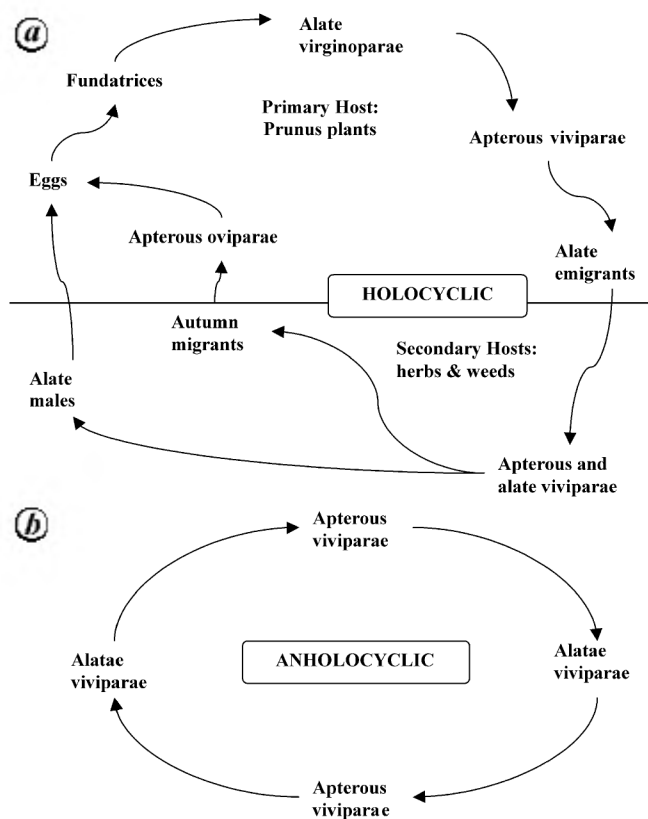


Figure 2. Phenotypes in aphid life cycle. *a*, Holocyclic, consisting of single sexual generation on a primary woody host plant and several viviparous asexual generations on secondary herbaceous host plants. *b*, Anholocyclic, on secondary host plants only.

and even physiological attributes from other phenotypes of the same genotype of a species. 'Form' is used to represent variation within a phenotype, which is often encountered in natural populations. For example, green and red forms of the unwinged or winged phenotype of the pea aphid, *Acyrtosiphon pisum* Harris or brown and green forms in the wheat aphid, *Sitobion avenae* (Fabricius)³.

Fundatrix: the stem mother or foundress

This phenotype is characteristic of egg-laying holocyclic aphids and is the first product of eggs. Each fundatrix represents a source of distinct genotype with a potential to produce a clone of different phenotypes. Morphologically, a fundatrix is a short and stout version of apterous or alate viviparous females.

Apterous viviparous female: the multiplier

In monoecious species, fundatrices usually produce unwinged morphs called apterous vivipara, also termed as 'virginoparae' due to their being virgin mothers, which are prolific breeders under favourable conditions. In heteroecious species where sexual and asexual generations are spent on plants of unrelated taxa, this morph is distinguishable into fundatrigeniae and alenicolae. The former phenotype is produced by fundatrices at the beginning of spring on the primary hosts, whereas the latter phenotype is produced by fundatrigeniae on the secondary hosts (Figure 4).

Alate viviparous female: the migrant or disperser

The winged morph, alate vivipara, of the parthenogenetic females differs from the apterous morph in the possession of two pairs of wings, sometimes incompletely developed

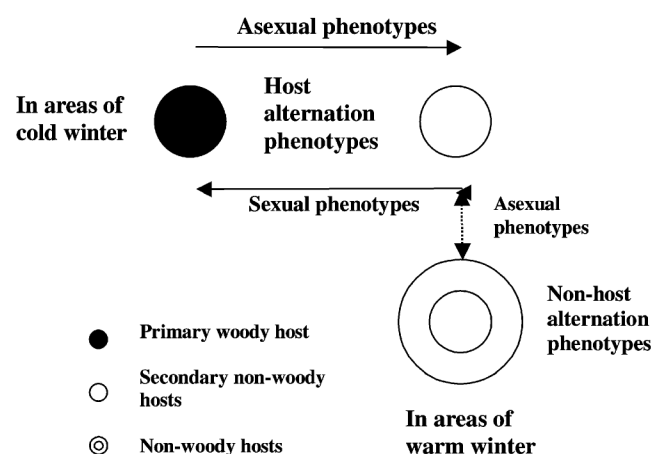


Figure 3. A hypothetical scheme of aphid species showing holocyclic and anholocyclic life cycles at the same time in different areas of their occurrence.

due to local adaptations called brachyptery, antennae possessing more sensoria, longer legs and eyes prominent, including ocelli. The phenotypes produced on the primary host in the beginning of spring, called spring migrants or emigrants, fly to secondary hosts. The return migrants or immigrants to the primary hosts are the sexuparae or sexuales³.

Sexuparae and sexuales: the genetic recombinants

The term Sexupara is applied to specialized phenotypes which would produce sexual phenotypes in the next generation in holocyclic species^{8,10}. Male phenotypes are usually produced directly and in ready-to-mate condition, except in Pemphigidae where a distinct phenotype called 'andropara' is produced as a preparation to alate males. Sexual males can be distinguished from viviparous phenotypes by sclerotized genital structure, abdomen being smaller and slender, and antennae bearing many prominent sensoria. Sexual females, also called oviparous females, are mostly apterous, and possess swollen hind tibia bearing scent plaques, genital plate more hairy and appendages stouter than in viviparous females.

Changes in phenotypes

Hibernating phenotypes

Most of the holocyclic aphids hibernate in egg stage during winter, but some species or their clones also do so by specialized phenotypes from the developing stages either on the primary or secondary hosts. In *Colophina arma* Aoki, some of the apterae viviparae continue to live on *Clematis*, the secondary host, and produce 'midget' larvae which take shelter in crevices in the bark and hibernate there without moulting until next spring. This phenotype

is easily distinguishable from the normal first-instar larvae by its smaller body, shorter rostrum and partly sclerotized terga¹¹. Similar instances of hibernating phenotypes have been reported in several other species^{3,8}.

In contrast, anholocyclic clones of aphids like *Elatobium abietinum* (Walker) and *Eriosoma lanigerum* (Hausmann) overwinter in larval or adult stages which are not morphologically distinguishable from viviparous females but are physiologically cold-tolerant phenotypes¹².

Aestivating phenotypes

Several aphids aestivate during summer to tide over the poor food quality and/or high temperature. Monoecious species of *Periphyllus* do so by producing dormant first-instar larvae, which remain glued to the leaves until autumn⁸. This phenotype has a flattened body covered with plates (Figure 5). Low temperature during autumn induces the species to produce normal first-instar nymphs, leading to the development of sexuparae. *Rhopalosiphum tiliae* (Matsumura), a heteroecious species, aestivates in the first instar stage on the secondary host. Many aphids like *Aphis gossypii* Glover, *Aphis ruborum* (Börner), *Aphis urticae* Gmelin, *Scizaphis graminum* (Rondani), and some species of *Sitobion* produce dwarf phenotypes during summer^{3,13}.

Soldier phenotype

Some aphids are known to produce extreme phenotypes that do not contribute to essential functions of the life cycle such as reproduction, dispersal, etc. but increase the survival value of parental colonies. The 'soldier' phenotypes in divergent taxa such as *Erisoma*, *Colopha*, *Paracolopha*, *Colophina*, *Astegopteryx*, *Pseudoregma* and *Ceratovacuna* have evolved to defend aphid colonies from attacks from



Figure 4. An aphid clone of the green peach aphid, *Myzus persicae* consisting of alenicolous offspring laid by fundatrigeniae on a secondary host plant (200×).

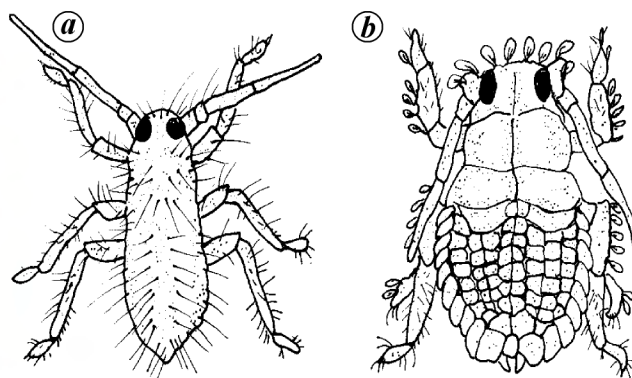


Figure 5. Phenotypic plasticity in *Periphyllus* species infesting aesculus or acer plants in the mountains of Himalayas. **a**, First instar normal phenotype produced in autumn. **b**, First instar aestivating phenotype produced in summer.

enemies and ants^{14,15}. Soldiers are non-moulting first-instar aphids characterized by sclerotized legs, prehensile forelegs, and long and pointed frontal horns (Figure 6).

Colour phenotypes

Several colour variants, both within a clone and between clones, have been documented in many aphids. A true colour phenotype is considered to be the one which retains colour over generations and can occur concomitantly with other variants within a species. Well-known examples include green and red phenotypes of *A. pisum*, *M. persicae*, *Metopolophium festucae* (Theobald), *Drepanosiphum platanoides* (Schr.) and various species of *Macrosiphum*^{3,8,16}.

Generation-specific phenotypes

There is a growing body of evidence to show that the life cycle of aphids has generation-specific plasticity in the expression of a genotype. The first three generations of the monoecious *Periphyllus* show striking changes in their proboscis length relative to a change in habitat quality of their monoecious host, either *Acer* or *Aesculus*, forcing aphids to shift sites of feeding in each generation on the same host³. Similarly, the first and third generations of the sycamore aphids which experience favourable habitat quality during spring and autumn respectively, produce phenotypes having fewer ovarioles, larger appendages and many sensorial in comparison to the second generation that faces poor food quality during summer and enters a reproductive diapause^{17,18}.

In contrast, heteroecious or host-alternating aphids show a more complicated life cycle. The black bean aphid, *A. fabae*, overwinters as an egg on spindle (*Euonymus*) trees, hatching in spring and giving rise to two generations of apterous individuals on the primary host before producing the third generation of alatae that colonizes

secondary herbaceous hosts. Alate males and gynoparae are produced in autumn, which migrate to the spindle trees to produce sexuales and complete the life cycle. Here phenotypes of the aphid life cycle show generation-specific variation in the number of ovarioles, body size and fecundity in response to specific needs of quality of food plants and climatic conditions, temperature and day length in particular³.

Factors triggering phenotype plasticity

Food quality

The growth and reproduction of aphids are dependent upon the state of growth, and level of soluble nitrogen in their host plants¹⁹. Cultivated plants exist as a large number of varieties and cultivars. Ecotypic variations are also common in natural plants in their distribution range. In addition, plants show seasonality in their growth and abundance. Thus, the food of aphids shows marked variation in quality in space, i.e. between different parts of a plant or different plants, and in time, i.e. between different stages in the seasonal growth cycle of a plant.

A. gossypii grown on poor quality or unsuitable hosts produces yellow dwarf phenotypes¹³. Apterous viviparous phenotype of *Lipaphis erysimi* (Kaltenbach) collected from radish, mustard and a wild cruciferous plant in fields and reared on the respective host plants in a greenhouse differed in morphometry, intrinsic rate of increase and mean relative growth rate²⁰ (Table 1), and showed isozyme variations²¹.

Secondary plant substances

Many plants may differ in the nature and quantity of secondary plant substances that they possess, which are usually toxic to herbivores. *Brevicoryne brassicae* and *L. erysimi* which live on cruciferous plants rich in sinigrin, possess an enzyme, glucosinolase, in their tissues, which is capable of detoxifying sinigrin. *B. brassicae* will not settle on plants lacking sinigrin²². On the other hand, the rose aphid, *Macrosiphum rosae* (Linnaeus) is deterred from feeding on late buds and flowers of rose plants due to the presence of high concentration of flavenoids, catechin and epicatechin²³. The glucoside phlorizin, present in the leaves of apple and other plants of order Pomoidea, promotes colonization by the apple aphids, *Aphis pomi* de Geer and *Rhopalosiphum insertum* (Walker)³.

Plant structure

Plants also vary greatly in structure, both external and internal. External structures like hair, hook, waxy layer and texture can be the deciding factor in the selection of a host plant for an aphid. For some phenotypes within a

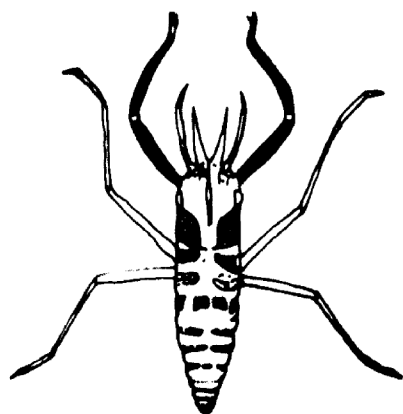
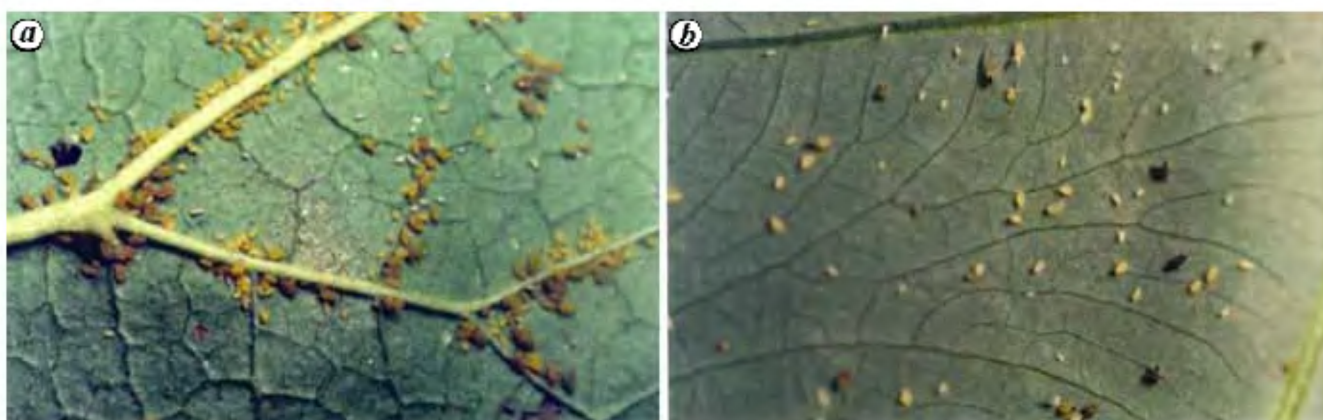


Figure 6. Sterile first-instar soldier phenotype of a bamboo-feeding aphid, *Ceratovacuna* sp. showing frontal horns in the head.

Table 1. Morphometrical and ecometrical variations (mean \pm SEM) recorded in unwinged viviparous phenotype of the mustard aphid, *Lipaphis erysimi* when reared in greenhouse on three different hosts of Cruciferae: *Brassica juncea* (1), *Rorippa indica indica* (2) and *Raphanus sativus* (3)

Character	Host plants			ANOVA (df = 2, 27)	
	(1)	(2)	(3)	F-ratio	P (<)
Morphometrical					
Body length	1.45 \pm 0.002 ^a	1.59 \pm 0.006 ^b	1.61 \pm 0.004 ^c	73.73	0.001
Antennae length	1.03 \pm 0.005 ^a	0.91 \pm 0.003 ^b	1.04 \pm 0.004 ^a	10.17	0.001
Siphuncus length	0.15 \pm 0.003 ^a	0.13 \pm 0.003 ^b	0.08 \pm 0.004 ^c	101.18	0.001
Ecometrical					
Mean relative growth rate ($\mu\text{g m } \mu\text{g}^{-1} \text{ d}^{-1}$)	0.39 \pm 0.009 ^a	0.29 \pm 0.015 ^b	0.31 \pm 0.015 ^b	16.77	0.001
Intrinsic rate of increase (per day)	0.29 \pm 0.009 ^a	0.18 \pm 0.009 ^b	0.21 \pm 0.009 ^c	41.24	0.001

Different alphabets following means in each row indicate significant difference by Duncan's multiple range test (modified after Agarwala and Das²⁰).

**Figure 7.** *a*, Normal yellow-unwinged phenotype of *Aphis gossypii* (20 \times) forming aggregated colony along bigger veins of egg plants. *b*, Dwarf yellow-unwinged phenotype of *A. gossypii* (20 \times) forming sparse colony along smaller veins of arum host.

species, any of these plant structures could be a barrier in colonization, whereas others might just overcome them. The lime aphid in Europe does not infest lime plants covered with stellate hairs, whereas a phenotype of the lime aphid having longer proboscis occurs on lime trees with stellate hairs in Turkey²⁴. Leaves of wild potato bearing glandular hairs are resistant to *A. gossypii* and *M. persicae*, which cannot negotiate the sticky secretions of glandular hairs. However, the same aphids colonize cultivated potatoes lacking such hairs²⁵.

Similarly, the size of phloem elements and their location within the tissues vary greatly between plants. Generally the smaller aphids feed on the smallest veins and the largest aphids on the largest veins, i.e. there is a positive relationship between the size of aphids and depth of phloem tissue. For example, in the northeastern parts of India, a yellow dwarf phenotype of *A. gossypii* feeds on smaller veins in the laminar areas of leaves of wild arums, but the greenish, bigger phenotype of this species, which infests egg plants copiously, feeds along bigger veins (Figure 7; Agarwala and Raychaudhuri, under preparation).

Temperature

Aphids are ideal insects to examine the effects of temperature on the development of phenotypes, as single genotypes can be studied in replicated experiments. In a study involving phenotypic response to a range of temperatures in morphs from different seasons, Helden *et al.*²⁶ reported a high degree of phenotypic plasticity both within and between morphs of *S. avenae*. Temperature often acts with other environmental variables like day length and food quality. Increased production of alate phenotype in response to longer day length and higher temperature has been reported for *M. persicae*²⁷ and *Cinara todocola* Inouye²⁸. The pea aphid, *A. pisum*, when reared at a range of temperatures on good quality food, resulted in an increase in embryonic growth rate and relative growth rate and a decline in developmental time³.

Predator-mediated plasticity

Kairomones (a kind of chemicals) produced by predators have been reported to cause plasticity in the morphology,

life history and behaviour of prey organisms in freshwater ecosystems and in aphids²⁹. Pea aphids, *A. pisum*, show facultative change in their development in response to the presence of predators. This species responded to the chemicals present in the tracks left by ladybird larvae or when kept with adult ladybirds for 27 days by producing a greater proportion of winged offspring, which avoid increased risk of predation by dispersing. The black bean and vetch aphids, which are afforded some protection by association with ants, did not respond in this way to the presence of ladybird larvae^{29,30}.

Thus, aphids have evolved a combination of sexual reproduction and a highly successful mechanism of parthenogenetic reproduction. This property enables this insect group to have the selective advantage of genetic recombination in the sexual phase and a high rate of population increase in the asexual phase. The clonal structure of aphid population has enabled them to produce a sequence of phenotypes, each of which shows plasticity in response to environmental variables.

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