

The Role of Phenotypic Plasticity in Host Race Formation and Sympatric Speciation in Phytophagous Insects, Particularly in Aphids

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Abstract: The genetic structure of aphid populations has received increasing attention as a result of the evolution of insecticide resistance, the appearance of biotypes overcoming plant resistance and the increasing spread of aphid-born viruses. How can they manage to use different hosts and overcome insecticide and plants' morphological barriers? Recently, plasticity has been given more attention in ecological and evolutionary contexts as a specific adaptation to environmental variability. Phenotypic variation is crucial to a comprehension of evolutionary mechanisms, especially phenotypic host race formation and sympatric speciation in aphids. It is becoming clear that phenotypic plasticity is a fundamental component of evolutionary change and is one solution to the problem of adaptation to heterogeneous environments.

Key Words: Aphids, phenotypic plasticity, host race formation, sympatric speciation.

Böceklerde, Özellikle Aphidlerde Konakçı Irklarının Simpatrik Türlerin Oluşmasında "Fenotipik Plastisity" nin Önemi

Özet: Son yıllarda aphidlerin farklı insektisitlere dayanıklılık kazanmaları, farklı bitkilere uyum sağlayan biyotiplerin ortaya çıkması ve aphidlerce taşınan virüslerin artması aphidlere olan ilgiyi artırmıştır. Bunun sonucunda aphidlerin hangi mekanizmalarla bunları başardığı sorusu ortaya çıkmıştır. Son zamanlarda "Fenotipik plastisity", ekolojik ve evrimsel açıdan önem kazanmaya başlamıştır. Fenotipik plastisity sonucunda ortaya çıkan fenotipik değişikliklerin, aphidlerde yeni evrimsel yapılanmalara, özellikle yeni konakçı türlerin ortaya çıkmasına ve sonuçta simpatrik türlerin oluşmasına sebep olduğu gözlenmiştir. Gittikçede "Fenotipik plastisity" nin evrimsel değişimin önemli faktörlerinden biri olduğu ve değişen çevre koşullarına uyumda önemli rol oynadığı düşüncesi ağırlık kazanmaktadır.

Anahtar Sözcükler: Aphid, Fenotipik plastisity, Konakçı ırk oluşumu, Simpatrik türleşme.

1. Phenotypic plasticity and Reaction Norms

The organism's ability to express an alternative morphology, physiology and behaviour in response to environmental changes is called phenotypic plasticity that may or may not to be adaptive (1). The term phenotypic plasticity refers to the general effect of environment on phenotypic expression. A reaction norm is a property of genotype, summarising the direction and amount of plasticity that it is able to express in response to environmental changes (2). The degree of plasticity of herbivores can be defined, in an ecological context, by their capacity for making physiological, morphological and behavioural adjustments in response to the nutritional, chemical and physical structure of the host plant. There commonly are differences among genotypes within a species in their ability to phenotypically adjust to environmental changes, in other words there is often genetic variation for phenotypic plasticity. Genetic variation in phenotypic plasticity (genotype-environment

interaction) results in cross reaction norms. In contrast, parallel reaction norms indicate a lack of genetic variation in phenotypic plasticity (2). The actual shape of a reaction norm presumably depends on a complex and environmentally sensitive genetic regulatory control (3). Obviously, evolutionary change in phenotypic plasticity is not possible without genetic variation in phenotypic plasticity (2). The plasticity of an insect in response to its environment might allow the production of a better phenotype (increased fitness) without major (or indeed any) genetic changes. To demonstrate that the plasticity of a trait is adaptive, it is necessary to measure the correlation between the plasticity of a trait and fitness averaged across environments (4).

1.1. Importance of phenotypic plasticity in speciation and evolution

Many animals including aphids live in a fluctuating, seasonal environment and are exposed regularly to a

variety of conditions. An important question about individual survival in such heterogeneous environments is how an organism copes with these different conditions (5). There are two ideas about adaptation to fluctuating environments. If the period of a single environmental condition is more or less equal to the generation time, adaptation may take place by genetic polymorphism. The particular morph that is adapted in any one generation becomes the most prevalent, the others being reduced in numbers. This situation leads to considerable elimination of individuals. If the mean duration of the environmental fluctuation is much less than the generation time, and fluctuations are unpredictable and irregular there will be strong selection favouring the evolution of the ability to produce different phenotypes in response to changing conditions, that is phenotypic plasticity. Paradoxically, plasticity may either buffer the population from natural selection or maintain genetic variability within the population or both (6). Callahan et al. (3) proposed that selection for appropriate responses to environmental fluctuations may produce a diversity of genetic and developmental solutions to environmental challenges. An additional importance of plasticity as a diversifying factor in evolution is as a factor contributing to the origin of novel traits and to altered direction of change (7). Two aspects of phenotypic plasticity facilitate phenotypic change: (i) the capacity for immediate correlated shifts in related traits, (ii) the occurrence of environment-sensitive expression of phenotypes.

Organisms may be able to show different kind of phenotypic plasticities namely morphological plasticity, behavioural plasticity and plasticity in life history traits (performance). Plasticity in life history traits is explained in the host race formation section.

1.2. Morphological Plasticity

The host plant's features affect phytophagous insects' morphology. The leaves of many plants are covered by short hairs or trichomes, which are characteristics of the plant surface and influence the feeding success of phytophagous insects, which may thus produce adaptive morphologies (8). Several studies suggest that variation between species or populations in response to selection by diversity of plant surfaces has resulted in morphological specialisation for grasping and locomotion (8) and easily probing and penetrating plant surfaces for food or oviposition (9). The mean value of any morphological character expressed on two host plants might be expected to reach an optimum, as a result of stabilizing selection (10). This might result in host-dependent allometric growth, resulting in shape

changes that adjust morphology to the contemporary host plant (11). Phenotypic plasticity in morphological characters in response to different host plants may allow the insect to feed on these host plants more effectively and may play a role in phenotypic host race formation. Morphological characters of aphids have important roles in the adaptation to different host plants. Moran (8) showed that *Uroleucon* species have longer hind tarsi when using hairy plant species and shorter hind tarsi when using smooth plant species. She suggests that short tarsi help prevent entanglement in trichomes whereas long tarsi provide a better grasp. In contrast, Eastop (12) noted that aphids on hosts with sticky exudates had short tarsi, and as an extreme, a species described on *Grindelia squarrosa* has no tarsi (13). Bernays (14) suggested that walking on "tip toe" may reduce work and allows fast movement. Also aphids specialized on *Tilia spp.* with dense stellate hairs had an elongate rostrum. Host specific morphology has been described for a specialist oak aphid, *Myzocallis schreiberi* (15), which possesses a terminal tarsal pair of claws and a pair of flexible spatulate empodia, which allow a good grasp on the hairs of the densely pubescent leaves of *Quercus ilex*. Shaposhnikov (16) reared *Dysaphis anthrisci majkopica* genotypes on a less suitable host, *Chaerophyllum bulbosum*, and an unsuitable host plant, *Chaerophyllum maculatum*, for many asexual generations and he found that morphological changes, particularly in rostrum length and body size occurred in a proportion of aphids on this previously unacceptable host plant between the 4th and 8th generations. Phytophagous insects do not manage to feed on new host plants unless they show suitable morphological changes in addition to physiological changes. There are several studies showing that aphids express different sizes in response to environmental conditions, such as temperature, crowded conditions, age, quality of host plants and even seasonal change in plants (17). Individuals are smaller when they develop at higher temperatures and on poor host plants (18). Size is strongly correlated with the length of proboscis which is determined by the depth to which the aphid has to probe plant tissues in order to feed. The depth of phloem varies with plant species and the position of the aphids on the host. Thus the depth of the phloem element results in a particular optimum aphid size. Moran (8) mentioned that the length of aphids ultimate rostral segment (URS) responds rapidly to selection arising from host features. Via and Shaw (11) mentioned that different host plants act as agents of natural selection, therefore morphology may reflect host-specific behavioural adaptations.

1.3. Phenotypic plasticity in host choice behaviour

It has been recognised that habitat choice has an important role in evolution (19), host race formation and speciation. Walsh (20) first mentioned the influence of host plant choice on the development of insect herbivore races and species. A common response to exposure to a particular host is increased preference for that host plant and often an increased preference for a closely related species, a phenomenon known as “Hopkin’s host selection principle”. Evolutionary change in host selection behaviour is very important in both diet breadth and host race formation. Individual insects display a considerable degree of plasticity in host choice behaviour and this may have a significant effect on evolutionary change in host use (20). The relationship between preference and performance has played an important role in studies of the evolution of host specificity and host shifts in allopatric and sympatric insect populations and evolutionary maintenance of diet breadth. The existence of genetic correlations between feeding preference for different hosts and performance on these hosts has been given prominence in models of the evolution of diet breadth, host race formation and sympatric speciation and the maintenance of genetic variation (21, 22). Bush (21) has argued that sympatric host shifts onto a new host, may involve separate loci affecting host recognition and offspring survival.

The question needed to be answered here is: does phenotypic plasticity play any role in host race formation and subsequent sympatric speciation in phytophagous insects, particularly in aphids?

2. Aphid–host plant relationships

Scientists have long been interested in aphids, because of their complex life style in close association with their host plants (especially crops), their capability of polyphenism and ability to reproduce both asexually and sexually. Aphids are an important group of phytophagous insects in temperate ecosystems due to their pest status and virus transmission (22). There are about 4150 described species of aphids (15). The highest species diversity in aphids occurs in temperate regions, unlike most insects groups, possibly due to their limited host location abilities (23) and cyclical parthenogenetic reproduction (15). Aphids have some of the highest population growth rates in insects (23). They reproduce parthenogenetically and have telescoping generations in which parthenogenetic females carry not only the embryos of their daughters but also their granddaughters. In periods of parthenogenetic reproduction different phenotypes are produced by the

same genotype (23), the diversity of forms in aphids being due to phenotypic plasticity (24). A key example of phenotypic plasticity in many aphids is the ability of parthenogenetic females to produce either winged “alatae” or wingless “apterae” forms in response to host plant quality changes and other factors. For example, during the summer the apterous form of the English grain aphid, *Sitobion avenae*, feeds on the flower heads of several species of grasses that provide high quality nutrition for only a short period. Subsequently, the alatae form develops in response to crowding and decrease in host quality (25). Similar results were shown for the pea aphid, *Acyrtosiphon pisum* (16) and the rosy apple aphid, *Dysaphis devectora* (26). Weisser and Stadler (24) proposed that the optimal decision on which morph to produce depends not only on the current quality of the plant where the aphid feeds but also on the predicted future quality of this plant. There is a degree of specificity in host plant usage with certain genotypes living only on certain species of host plants. The pattern of host use thus defines some biotypes (27). Intraspecific variations in host use have been recorded in *Aphis fabae*, *Myzus persicae* and *Acyrtosiphon pisum* (27, 28) and these forms have been proposed as a subspecies based on host plant affinities. Considerable host breadth within a subspecies indicates that genotypes are able to use many plant species and families (27).

3. Host race formation in phytophagous insects

Walsh (20) proposed that in phytophagous insects a host shift caused by changing host preference may give rise to new host races. He reasoned that there is sufficient “phytophagic isolation” (host induced specificity) to allow the adaptive evolution of new species. Several researchers have argued that host race formation represents the initial stages of sympatric speciation, in which the incipient species are isolated not by geographic barriers but by the choice of host plants on which mating occurs (20, 21). If a herbivore species exhibits a plasticity in host plant choice and displays induced performance on a novel host plant, colonization of this host plant may give rise to offspring which prefer that host plant over others (29). Furthermore, phenotypic plasticity does not only allow the colonisation of a new host plant, but it is also a mechanism which may reinforce differences in the ecological context of the ancestral and new host as individuals on the new host plant faced with a different set of interactions (30) which may result in new genomic organization (31). During the colonisation of a new host, larvae of phytophagous insects are faced with a new ecological scenario generated by the new host and new genomic organization allows phenotypic variability to

adjust to different environments so as to increase its fitness (30). Genetic loci might undergo adaptive changes over a period of time following the initial colonisation that could allow the insect to better exploit the new host. Such changes may increase the degree of reproductive isolation between the old and new population over time and may lead to formation of new sympatric host races. Moreover, selection may eventually lead to reorganization of at least a portion of the genome in the new host races and it has been suggested that during the formation of a new host race 10% of the insect genome is altered (21). The most widely acclaimed example of sympatric host race formation is that in *Rhagoletis pomonella*, which has apple and hawthorn races. Adult individuals reared from hawthorn have slightly longer ovipositors than those associated with apple (32). Host races also exist in a range of insect groups (reviewed in 33). Although sympatric speciation via host race formation is still controversial, recent studies support the idea that many organisms such as aphids with a parasitic life style speciate sympatrically through host race formation (34, 35). In contrast, some researchers insist that the conditions for sympatric speciation are too stringent for the process to be important in nature and support the allopatric speciation (36).

3.1. Host race formation in aphids

Aphids show variation in performance on their various hosts and host preference varies among biotypes, host races or subspecies (37, 38). Shaposhnikov (14) showed that after eight parthenogenetic generations the aphid *Dysaphis anthrisci* was able to survive and reproduce on *Chaerophyllum maculatum* which previously had caused 100% mortality. Mackenzie (39) reported that the black bean aphid, *Aphis fabae* showed increased performance on *Tropaeolum majus* after exploiting 3 generations which caused high mortality when they had used it initially. Some species of aphids are composed of a number of host races, adapted to and preferring different host plants, and these races may occur sympatrically (22, 15, 34). Such races may arise suddenly on cultivated fields and rapidly cause crop damage (21). The pea aphid, *Acyrtosiphon pisum* consists of a number of sympatric forms, which have specialized on certain species of papilionaceous (Leguminosae: Papilionidae) plants (34).

For example, *Acyrtosiphon pisum* on *Aulacorthum solani* are isolated from *Acyrtosiphon pisum* on *Aulacorthum solani lange*. Müller (34) defined them as sympatric races isolated from each other mainly by strict host preference and by hybrid inferiority. Guldmond (40) showed that two host races exhibited in *Cryptomyzus galeopsidis* are restricted to *Ribes rubrum* and *R. nigrum*. In aphids, host race formation is strongly promoted by their reproductive biology, i.e. cyclical parthenogenesis, and host plant specificity (34). Parthenogenesis allows the telescoping of generations and the development of higher rates of increase, which are important in colonising on new host plants. Cyclical parthenogenesis thus aids the use of different resources and facilitates rapid colonisation. Therefore it can be considered that, particularly in aphids, phenotypic plasticity is potentially important in giving rise to "phenotypic host races" and hence facilitating sympatric speciation. There are different factors such as trade-offs and polymorphism which play a role in the occurrence of host races. Recently phenotypic plasticity was also accepted as another important factor.

Conclusion

Phenotypic plasticity in phytophagous insects particularly in aphids, in terms of having ability to express alternative performance, morphology and behaviour is considered to be crucial to the comprehension of evolutionary mechanisms, especially host race formation and sympatric speciation (21, 32, 34). Aphids genotypes show substantial genetic variation within an aphid species for this plasticity. The differential response of one genotype to different hosts and the variation in this response between genotypes provide the best evidence available to date that phenotypic plasticity may facilitate aphid host race formation. Indeed phenotypic plasticity in a novel environment may be a major determinant of the evolutionary trajectory of a parasitic species. It is crucial to know the significance of phenotypic plasticity in aphids for using different host plants, overcoming plant resistance and insecticide in Turkey where many economically important agricultural crops are grown. There are not enough detailed studies in Turkey.

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