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CHARACTERISTICS OF PARTHENOGENESIS IN APHIDS

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ABSTRACT

In different habitats, several species of aphid with worldwide distribution portray both cyclic parthenogenesis (CP) alternating asexual and sexual reproduction and obligate parthenogenesis (OP) of only asexual reproduction, but no only sexual reproduction. The occurrence of CP and OP is respectively widespread and exceptional and influenced mostly by environmental factors which set survival status of aphids through mutation decay and genetic changes, thereby delineating tripartite association among gene, environment and evolution with the significance of reproductive polymorphism.

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INTRODUCTION

Aphids and scale insects, as pests, are economically important for their serious attack on a number of indoor and outdoor plants of most of the places. The biological relevance of both the insects is that they naturally show parthenogenesis in which eggs hatch and embryos develop within a female without fertilization and it is also found in other invertebrates and vertebrates. In the pineapple mealybug (scale insect), *Dysmicoccus brevipes*, asexual reproduction by parthenogenesis and sexual reproduction coexisted in Okinawa, a south-western region of Japan, but only asexual lineage exhibiting obligate apomictic thelytoky was discovered in Ishigaki another region (Tabata *et al.* 2016). Thus, two patterns of reproductions were found in two Japanese regions of mealybugs.

Sexual reproduction largely predominates in animals and indicates that this is outweighed by the genetic and ecological consequences of sexuality, including both the acquisition of advantageous mutations and the elimination of deleterious mutations occurring in different individuals.

The evolution of sexual reproduction becomes dominant and successful in the face of competition from asexual lineages in the same environment. In the present review paper, the characteristics of plasticity in asexual mode of reproduction are discussed to explore how parthenogenesis is successful in aphids.

Characters of parthenogenesis

Types: Cyclical and Obligate Parthenogenesis

Puterka *et al.* (2012) reported that in 1986, the Russian wheat aphid, *Diuraphis noxia* (Hemiptera: Aphididae), became an invasive species of USA. Nearly 20 yr later, new biotypes appeared that were capable of overcoming most sources of resistance and became a renewed threat to wheat, *Triticum aestivum*. This is due to the fact that Cyclical (CP) and Obligate (OP) Parthenogenesis enable aphids to both adapt to changing environments and exploit host resources. Puterka *et al.* (2012) documented these forms of reproduction for Russian wheat aphid in wheat and wild grasses in the Central Great Plains and Rocky Mountain regions during falls 2004-2009. Colonies from sample sites also were held under unheated greenhouse conditions and observed for the presence of sexual morphs and eggs through the winter. Russian wheat aphid populations were mainly OP and attempted to overwinter as adults, regardless of

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region sampled. A few populations contained oviparae but no males (gynocyclic) and were not specific to any particular region. Observation of the Russian wheat aphid colonies under greenhouse conditions failed to produce males or eggs. In spring 2007, CP was confirmed in a small population of Russian wheat aphid that enclosed from eggs (fundatrices) on wild grasses and wheat in the Colorado Plateau region where other aphid species undergo CP.

It is found that melon aphid population underwent anholocyclic, androcyclic, and intermediate reproductive modes on different host plants, when Liu and Gao (2010) prepared the aphid life tables. Further, it is indicated that the anholocyclic and androcyclic strains could become adults and produce offspring on cotton *Gossypium hirsutum L.*, whereas the intermediate strain could not. The abilities of the three strains to use a host plant were flexible, because their increase of rate of feeding on pumpkin or zucchini became equal after rearing for four successive generations. Furthermore, the intermediate strain attained the ability to use cotton, and the performance of anholocyclic and intermediate strains to use cotton also significantly increased after feeding on pumpkin or zucchini for one or three generations. It was concluded that the reproductive mode and feeding experience affected the performance of melon aphid to use a host plant.

Apomictic & obligatory parthenogenesis

Nokkala *et al.* (2013) surveyed *Cacopsylla myrtilli* (Wagner, 1947) (Hemiptera, Psyllidae) in Norway, Sweden, Finland and northwest Russia and found that all populations were highly female-biased and males being very rare from 0.1% to 9.1% were so-called spanandric males. Males in northern Norway, Finland and northwest Russia showed normal chiasmata meiosis, while in Norway and northern Sweden no chiasmata due to asynapsis. Due to asynaptic meiosis of all univalent chromosomes dividing during the first meiotic division and incomplete division in the second meiotic division for formation of diploid sperms, the males of these populations are nonfunctional without genetic contribution to the population.

For studying meiosis in males, large samples of *Cacopsylla myrtilli* (Wagner, 1947) (Hemiptera, Psyllidae) were collected in Norway, Sweden, Finland and northwest Russia. It is found that all populations were highly female-biased, the proportion of males varying from 0.1% to 9.1%. These males are rare, so they are called spanandric males. Males in northern Norway, Finland and northwest Russia showed normal chiasmata meiosis, while complete absence of chiasmata due to asynapsis was found in males collected in Norway and northern Sweden. In asynaptic meiosis, all univalent chromosomes divided during the first meiotic division resulting in incomplete second meiotic division and formation of diploid sperms. Hence, non functional males do not contribute to the genetic constitution of the population, but appear in every generation as reversals from apomictic parthenogenesis and mode of parthenogenesis is of obligatory type.

Ploidy

Using cytological and molecular approaches, Nokkala *et al.* (2017) reported ploidy of parthenogenesis in *Cacopsylla led.* In all three populations studied from Finland, i.e. Turku, Kustavi and Siikajoki, males were present at a low frequency but were

absent from a population from Vorkuta, Russia. In a follow-up study conducted in the Turku population during 2010-2016, the initial frequency of males was 10 % and showed no intraseasonal variation, but then dramatically decreased down to approximately 1-2 % level in seasons 2015-2016. Male meiosis was chiasmata with some traces of chromosomal fragmentation and subsequent fusions. In most females, metaphase in mature eggs included 39 univalent chromosomes which indicated apomictic triploidy. Only a small fraction of females was diploid with 13 chiasmata bivalents. The frequency of diploid females approximately equaled that of males. Mitochondrial cytochrome oxidase subunit I (COI) barcode analyses showed that triploid females (N = 57) and diploids (7 females and 5 males) displayed different haplotypes, demonstrating that triploid females reproduced via obligate parthenogenesis. The rarity of diploids, along with the lack of males' preference towards diploid females, suggested that most likely diploids were produced by rare triploid females which shared the same haplotype with the diploids (not found in the present analysis). Minimum haplotype diversity was detected in the Turku population, but it was much higher in Vorkuta with some indication for the mixed origin of the population.

Reproductive polymorphism in aphid *Rhopalosiphum padi*

Nespolo *et al.* (2008) found OP and CP in aphid *Rhopalosiphum padi*. When the quantitative genetics of life histories (the structure of the genetic variance-covariance matrix (G)) were found in these two lineage types, they viewed that the elements and the whole structure of the resulting G matrices differ in the very short term, between lineage types. This would involve the evolution toward different evolutionary optima in the same population, depending on whether sexual or asexual lineages predominate with reproductive polymorphism.

Sex pheromone's role

Tabata *et al.* (2017) reported in a pineapple mealybug, *Dysmicoccus brevipes* that an asexual lineage reproducing by parthenogenesis coexists with its ancestral sexually producing lineage. They found a role of a pheromone compound of monoterpene, [(-)-(anti-1,2-dimethyl-3-methylenecyclopentyl) acetaldehyde], differentiating the mealy bug either sexually or asexually reproducing individuals. It is found that sexual females (ancestral lineage) of *D. brevipes* produced this pheromone compound that is needed in attracting males. If not produced by asexual females that have lost capacity of producing the pheromone long back, parthenogenetic reproduction exists. Thus they suggested that sex pheromones play an essential role of reproduction through intersexual communication and reproductive isolation leading to speciation is caused by alteration of pheromone secretion.

Roles of Juvenile Hormone

Most aphids show reproductive polyphenism, i.e. they alternate their reproductive modes from parthenogenesis to sexual reproduction in response to short photoperiods. Although juvenile hormone (JH) has been considered a likely candidate for regulating the transition from asexual to sexual reproduction after photoperiod sensing, there are few studies investigating the direct relationship between JH titres and the

reproductive-mode change. In addition, Ishikawa *et al.* (2012) used the sequencing of the pea aphid genome to identify the genes involved in the JH pathway. It was found that the expression level of JH esterase, which is responsible for JH degradation, was significantly higher in aphids reared under short-day conditions and that the up regulation of the JH degradation pathway may be responsible for the lower JH titre in aphids exposed to short-days, leading to the production of sexual morphs.

Environmental factors

Le Trionnaire *et al.* (2012) reported that during spring and summer aphids reproduce clonally and efficiently by parthenogenesis. At the end of summer, they perceive the shortening of day length, which triggers the production of sexual individuals - males and oviparous females - that will mate and lay overwintering cold-resistant eggs. Thus, the mode of reproduction, either CP or OP is determined by environmental conditions. Jedlička *et al.* (2015) reported that aphids, that have an intricate life cycle with seasonal polyphenism, show the physiological background of migration from unfavourable nutritional conditions to a new, intact host plant.

Harsh winters

Sandrock *et al.* (2011) carried out a Europe-wide sampling of black bean aphids, *Aphis fabae*, and combined population genetic analyses based on microsatellite data with an experimental determination of life cycle strategies. They found that aphids were collected from broad beans (*Vicia faba*) as well as some Chenopodiaceae, and detected no genetic differentiation between aphids from different host plants. It is further reported that life cycle variation was related to climate, with aphids from areas with cold winters investing more in sexual reproduction than aphids from areas with mild winters. Accordingly, only populations from mild areas exhibited a clear genetic signature of clonal reproduction. These differences arise despite substantial gene flow over large distances, which was evident from a very low geographic population structure and a lack of isolation-by-distance among 18 sites across distances of more than 1000 km. There was virtually no genetic differentiation between aphids with different reproductive modes, suggesting that new asexual lineages are formed continuously. Indeed, a surprising number of *A. fabae* genotypes even from colder climates produced some parthenogenetic offspring under simulated winter conditions.

Development and adaptation

Miura *et al.* (2003) described a detailed description of parthenogenetic, viviparous embryonic development in the pea aphid, *A. pisum*. The primary variation between the embryos is the scale on which development occurs: early parthenogenetic development occurs in a volume roughly 3 orders of magnitude smaller than the sexual egg, chiefly because of the apparent absence of yolk in the eggs of parthenogenesis. The eggs also develop on time scales that differ approximately by an order of magnitude and the timing of the embryonic movements, collectively called blastokinesis, have temporally shifted relative to growth of the embryo. Finally, the function of the serosa has diverged greatly in the two embryos: in the sexual

egg the serosa deposits a thick cuticle that protects the egg, whereas the serosa of the parthenogenetic embryo is greatly reduced and its function is unclear. Thus it is obvious that the winter eggs show adaptation in possessing more yolk and thick cuticle for longer duration of development with resistance during winter season.

Effects of host plants

By analysing the phenotypic and genetic variation of *Eriosoma lanigerum* in relation to the dry and wet season and plant phenology, Ruiz-Montoya *et al.* (2015) showed that the site and season has a significant effect on morphological variation of trait. The largest aphids were recorded during cold temperatures with low relative humidity and when the plant was at the end of the fruiting period. The mean genetic diversity was low and populations were genetically structured by season and site. Morphological and genetic variations appear to be associated with environmental factors that directly affect aphid development and indirectly by host plant phenology. Thus, Ruiz-Montoya *et al.* (2015) reported that *E. lanigerum* undergoes obligate parthenogenesis due to the unavailability of the host plants required for sexual reproduction.

Symbiotic association

Simon *et al.* 2011 delineated that some bacterial symbionts alter their host's reproduction through various mechanisms that enhance their transmission in the host population. In addition to its obligatory symbiont *Buchnera aphidicola*, the pea aphid *Acyrtosiphon pisum* harbours several facultative symbionts influencing several aspects of host ecology. Aphids reproduce by cyclical parthenogenesis whereby clonal and sexual reproduction alternate within the annual life cycle. While the role of facultative symbionts has been well studied during the parthenogenetic phase of their aphid hosts, Simon *et al.* (2011) found that most facultative symbionts exhibited detrimental effects on their host's fitness under sex-inducing conditions in comparison with the reference lines. Further, they observed that the loss of sexual phase in permanently parthenogenetic lineages of *A. pisum* was not explained by facultative symbionts and that Spiroplasma infection annihilated the production of males in the host progeny by inducing a male-killing phenotype, an unexpected result for organisms such as aphids that reproduce primarily through clonal reproduction.

Ant-aphid interaction

In the figures 1 and 2 are shown red and black ants attending respectively scale insects and aphids to obtain honey dew from them which mutually get ant protection from its predators. Yao and Akimoto (2009) found relationship of mutual effects on the microgeographical genetic population structure between the aphid *Tuberculatus quercicola* (Matsumura) (Homoptera: Aphididae) and the attending ant *Formica yessensis* Forel (Hymenoptera: Formicidae). An analysis of molecular variance showed a significantly large genetic difference between spring and summer samples in *F. yessensis* but not in *T. quercicola*, indicating that changes in genetic composition occurred in the *F. yessensis* colony. It is proposed that the suitability of host trees for the aphid *T. quercicola* may have an effect on the genetic structure of the attending ant *F. yessensis*. Within a colony of aphids, clonal diversity decreased significantly as the

season progressed. The reduction in clonal diversity may be due to an increase in identical genotypes by parthenogenesis or selective pressure from host plant deterioration.



Legend: A nymph and B-adults of scale insect



Genetic basis of reproductive plasticity

The pea aphid (*Acyrtosiphon pisum*) can reproduce either sexually or asexually (parthenogenetically), giving rise, in each case, to almost identical adults and these two modes of reproduction are accompanied by differences in ovarian morphology and the developmental environment of the offspring, with sexual forms producing eggs that are laid, whereas asexual development occurs within the mother (Duncan *et al.*, 2013). The effect of each mode of reproduction has on the expression of key maternal and axis patterning genes; orthodenticle (*otd*), hunchback (*hb*), caudal (*cad*) and nanos (*nos*). Three of these genes, except (*nos*), are expressed remarkably between the asexually and sexually produced oocytes and embryos of the pea aphid.

While phenotypic plasticity in response to environmental change is a common phenomenon, the genetic basis of this reproductive plasticity is reported by assessing the meiosis and cell cycle gene repertoire in the genome of the pea aphid, *A. pisum* (Srinivasan *et al.* 2010). Aphids possess meiotic recombination genes and G1-to-S phase transition regulatory genes in gene copy numbers similar to other metazoans. However, mitotic and meiotic regulatory genes have

duplicated, and several paralogues exhibit differential expression between reproductive morphs. Further it is viewed that cell cycle plasticity may be important in the evolution and mechanism of aphid reproductive plasticity.

Genotypic diversity

Kanbe and Akimoto (2009) revealed that organisms reproducing asexually showed greater allelic diversity per locus but lesser genotypic diversity than organisms reproducing sexually. When genotypic and allelic diversities in the sexual and asexual populations of the pea aphid, *A. pisum* (Harris) were evaluated, microsatellite analysis revealed that populations in central Japan are asexual, whereas populations in northern Japan are obligatorily sexual. No mixed populations were detected in these sites. Phylogenetic analysis using microsatellite data and mitochondrial cytochrome oxidase subunit I (COI) gene sequences revealed a long history of asexuality in central Japan. Asexual populations exhibited much lower genotypic diversity but higher allelic richness per locus than did sexual populations. Asexual populations consisted of a few predominant clones that were considerably differentiated from one another.

Rarity of males and mutational decay

Brisson and Nuzhdin (2008) reported that if females can reproduce without males, males become an evolutionarily weaker sex whose genes experience mutational decay. They employed microarray analyses to identify male-biased, asexual female-biased, and neutral genes in aphids, whose reproduction alternates between parthenogenetic and sexual forms. Interspecific comparisons reveal accelerated evolution of male-biased genes, and intraspecific polymorphisms exhibited a significant excess of nonsynonymous coding variation in male-biased genes. Therefore, they concluded that the ability of females to reproduce asexually without males reduced selection constraints on male-based genes, resulting in their mutational decay

CONCLUSIONS

In aphids, clonal reproduction through parthenogenesis is found during favourable growing season allowing rapid population increase, whereas sexual reproduction is found during late summer leading to frost-resistant eggs that are capable of survival during unfavourable winter conditions (Simon *et al.* 2010). It is found that this alternating shift between these two extreme reproductive modes (CP & OP) occurs within the same genotype, i.e. within the same genetic clone, and is caused by photoperiodic changes controlled by aphid visual and brain system. Further, it is reported that besides reproductive mode of variation expressed at the genotypic level, aphid species also frequently include lineages which have lost the sexual phase and hence the alternating clonal and sexual reproductive phases of the life cycle is the trend set by the external factors. This coexistence of asexual and sexual reproduction within the same aphid species is the apparent evidence of its ecological and evolutionary significance.

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