

Evolutionary models of heterogonic cycles of Aphids.

INTRODUCTION

The heterogonic cycles of aphids are extremely plastic and have adopted different adaptive strategies during the evolution of the taxon. Heterogonic cycle, per se, is a very efficient reproductive model, which takes full advantage of trophic availability by the rapid crowding of parthenogenetic generations during spring and summer, when peak plant metabolism is reached. On the other hand, autumnal amphigonic generation enables the species to survive by the production of overwintering eggs. Moreover, amphigonic generation is to be regarded as a source of genetic variability. These fundamental adaptive mechanisms have led to worldwide distribution of aphids, particularly abundant in temperate climates having mild to severe winters.

Besides the evident advantages of heterogonic cycles, many aphid species demonstrate extraordinary capability for life cycle modification to adapt widely to most variable environmental conditions. This paper evidences and discusses the adaptive potential of aphids and the possible evolutionary trend followed by individual species or/and groups of species.

APHID CHROMOSOMES AND KARYOTYPE EVOLUTION

The peculiar chromosome structure of aphids, with a diffuse centromere, like other Hemiptera (Schrader, 1947) allows all or large part of chromosome portion originating from fragmentation to be retained in the chromosomal settlement; this favours both evolution of the karyotype and differentiation of viable polysomic forms within the species. *Myzus persicae*, for example, exhibits a chromosomal polymorphism with $2n = 12, 13, 14$ chromosomes (Makino, 1931; Cognetti & Cognetti Varriale, 1961; Blackman, 1971a; Bonvicini Pagliai et al., 1971) related to modifications of the life cycle and of migratory tendencies.

Caryotype studies of aphids were based, at first, exclusively on chromosome number and size, since the diffuse centromere does not give the chromosomes an own peculiar shape. This fact is restrictive, the size of the single chromosome pairs varying within significant ranges in relation to the degree of contraction. However this problem can be solved by referring to the relative length of the chromosome, expressed as percentage of the total complement length (TCL) instead of the actual size (Harper & Mc Donald, 1966). Another interesting method for performing karyotype analysis is to measure the ratio between the total length of the autosomes and length of the sex chromosomes, which tends to be constant in very similar species (Kuznetzova, 1968). Researches performed on numerous aphid species has provided interesting, though still insufficient findings on the effective usefulness of cytotaxonomic studies on aphid species. The limit of these studies, probably, lies in the methodological approach. Indeed, except in a few cases, all researches were performed on numerous species not bearing a systematic likeness (Gut, 1976; Kurl, 1980; Misra & Kurl, 1980; Khuda-Bukhsh, 1980; Pal, 1982). Sun & Robinson (1966) analyzed 50 species belonging to 31 genera of both viviparous and oviparous aphids and recognized 24 karyotypes, of which 4 were common to several genera. In particular the genus *Aphis* has the same chromosome number ($2n=8$) arranged as a similar karyotype in all the investigated species. Kuznetzova performed a methodologically more correct research examining 28 species of the subtribe *Anuraphis*, belonging to 9 genera. She found that also karyotypes with different chromosome number have a very similar ratio between the total length of autosomes and the length of sex chromosomes. Blackman (1980) lists the chromosome number of 180 aphid species and evidences important evolutionary aspects of chromosome polymorphism among the species. Usually the karyotype is particularly stable among the genus. but exceptions are not unusual. Of particular interest is the finding of a relationship between chromosome polymorphism and life cycle changes. In fact, most of the within species karyotype variations have been found in anholocyclic populations. Indeed, loss of sexual reproduction favours retention of chromosome rearrangements which would be otherwise eliminated by the meiotic process.

It is known that some species of aphids with low chromosome number have rod-shaped chromosomes of similar length, whereas species with high chromosome number tend to have small chromosome pairs, with the exception of sex chromosomes, which are always longer than the others. This fact has an important evolutionary significance: supposing an evolution of the karyotype from a few modal karyotypes having low chromosome number ($2n = 4, 6, 8$) we can advance the hypothesis

that karyotypes with large chromosome numbers derived from the former, through chromosome fragmentation. Notably fragmentation did not affect the pair of sex chromosomes. Indeed, if sex chromosome fragments are transmitted to the progeny, an unbalance of sex factors would occur at amphigonic generation, with the probable production of sexual abnormalities, by the random segregation of the sex chromosome fractions. For this reason sex chromosomes must maintain their integrity to guarantee equilibrated sexual determination. On the contrary it seems that autosome fragments can be easily inherited, as experimentally demonstrated, for several cellular generations, in *Limotettix* (Halkka, 1965). This hypothesis is supported by the observation that species with high chromosome number, such as *Amphorophora stolonis* ($2n = 48$), have all very short autosomes and only one pair of much longer chromosomes, identifiable as sex chromosomes.

Therefore, Kuznetzova's method for karyotype analysis, which measures the ratio between total length of autosomes and sex chromosomes, appears particularly suitable. This method, in fact, groups together karyotypes with different chromosome number, but, probably, deriving from the same modal karyotype.

ADAPTIVE SIGNIFICANCE OF ENDOMEIOSIS

During parthenogenetic oogenesis pairing between homologues chromosomes, followed by endonuclear division (endomeiosis) takes place (Cognetti, 1961; 1962). This process is temperature sensitive (Bonvicini Pagliai, 1983a) and photoperiod-dependent (Orlando, 1983). Although some Authors (Von Baehr, 1920; Paspaleff, 1929; Blackman, 1978) have reported synaptic processes during parthenogenetic oogenesis in several aphid species, these had been considered casual and not-functional.

Indeed, researches on aphids have, generally, been performed during the summer months, a period when these insects are particularly abundant and high temperatures prevail. Under high temperature endomeiosis is suppressed (Boschetti & Pagliai, 1964). More recent researches carried out at low temperature on *Acyrtosiphon pisum*, *Megoura viciae* and *Macrosiphum rosae* have further emphasized the dependence of endomeiosis on temperature and photoperiod (Bonvicini Pagliai, 1983b). This process is fundamental for the holocycle, providing the male sex determination by the loss of an X chromosome. Under low temperatures it occurs also in paracyclic forms that have lost the capability to produce males. The last finding may be interpreted as a potential reversal towards the holocycle.

EVOLUTION OF HETEROGONIC CYCLES

The typical heterogonic cycles are, by assumption, the dioecious cycles, characterized by host alternation. The primary host plant is, generally, a woody perennial plant and represents the ideal shelter for latent forms of life as winter eggs. Instead, the secondary host plant is, usually, a leaf plant and represent the ideal *pabulum* for a rapid succession of parthenogenetic generations, as occurs in spring and summer. However, a variety of alternative solutions exists in nature, often occurring among populations of the same species living together in the same area: For example, *Myzus persicae*, a cosmopolitan dioecious species, shows a complex series of cycles in relation to chromosome polymorphism and high polyphagy (Muller, 1954, Waldhauer, 1957, Blackman, 1971, Bonvicini Pagliai et al. 1971, Blackman and Takada, 1977). Facultative migration from the primary to secondary host plant, and, hence, the capability to survive for several generations on the primary host plant, seems to be related to climatic conditions. During very rainy summers with weak sunlight irradiation the buds of the primary host plant can mantain the favourable physiological features for the development of aphids and these do not migrate, or do it later. This fact points out the adaptive significance of the host alternation, if we consider the secondary host plant as an optimal trophic supply during the hot and dry summertime. The dioecious heterogonic cycle thus represents the optimal adaptation to the trophic need of large aphid colonies showing rapid seasonal development, such as during parthenogenetic generations. However, under particulary favourable climatic conditions, such as mild winters in Mediterranean countries, many aphid species tend to produce anholocyclic strains, which reproduce parthenogenetically throughout all the year. These strains easily originated from holocyclic parents, are destined to disappear in regions having cold winters (Blackman, 1971b) whereas permanent anholocyclic strains or sexual races (Cognetti and Pagliai, 1963) which reproduce indefinitely by parthenogenesis, may be established in the warmer climates. Here is to search the possible origin of the paracyclic races and species. We have already seen that *Macrosiphon rosae* is known as a paracyclic species in the northern emisphere and only sporadic findings of sexuals on *Ilex* have been reported. In this species and in paracyclic strains of *Acurthosiphon nisum* and *Megoura viciae* we have evidenced the capability of survival at very low temperature by overwintering as parthenogenetic larvae with suppression of amphigonic generation (Bonvicini Pagliai, 1983a). Such a capability is due to diapause, which is shifted, in these forms, from winter egg stage to parthenogenetic larva. The resistance to low temperatures was investigated

(Bonvicini Pagliai, 1983b) in two strains of *Megoura viciae*, the first holocyclic and the second paracyclic. The developmental pattern of the ovarioles in the two strains was quite different: in the paracyclic strain a few days of exposure to low temperature induces resistance by larval diapause, while in the holocyclic one a very slow development occurs until necrotic degeneration takes place.

It has been proposed to distinguish anholocyclic forms, capable of overwintering parthenogenetically in temperate regions, with mild winters, and paracyclic forms, which, on the contrary, can also overwinter in regions with severe winters. Clearly, the appearance of a paracyclic form from an holocyclic one represents an advanced step in the evolution of heterogonic cycles. *Megoura viciae* can, therefore, be considered in a dynamic stage of heterogonic cycle evolution, while *Macrosiphon rosae* is a specific example of successful evolution of paracycle at a specific level.

ADAPTIVE SIGNIFICANCE OF ALATA/APTERA POLYMORPHISM

Wingness is the primitive aphid state, analogously to all polymorphic Pterigotes insects. Thus apterism is a secondary adaptation that, in particularly favourable trophic conditions, induces a more rapid pullulation through parthenogenesis. Apterousness is an example of neoteny which, by suppression of complete metamorphosis and, thus *energy saving* favours fecundity which is, in fact, higher in apterous than in winged females. On the other hand, wingness favours a wide and rapid dispersion of populations when trophic conditions deteriorate both for overcrowding and senescence of the host plant.

Recent researches have shown a different determinism of the winged forms in relation to crowding and trophic factors and to back migration to the primary host plant (Bonvicini Pagliai et al., 1985).

In some aphid strains only excessive crowding and the state of leaf maturation exert a control on winged morph determination, while in other strains a photoperiodic control is also involved. A detailed research on this topic, performed on four aphid species with different features of the biological cycle showed a correlation between photoperiodic control of winged forms and the type of cycle in the examined strains. The dependence of the winged forms on photoperiod is marked in the dioecious cycles, where an host alternation is required, weaker in the monoecious ones and disappears at all in the paracycles.

SUMMARY

Aphids exhibit an extraordinary adaptability to different environments and climates that allowed the group to attain a worldwide distribution. Main factors involved in the great adaptability of aphids are:

- 1) The high probability of retention, within the populations, of any variation of the karyotype. This easy retention is determined, firstly, by the holocentric nature of aphid chromosomes which allows any fragment to move into the daughter cells during mitosis and, secondly, by the expansion of new karyotypes favoured by permanent telotoky.
- 2) The synaptic process which occurs during maturation of the parthenogenetic egg, and determines genetic variability in the parthenogenetic lines.
- 3) The variety of life cycles, which extend from the highly complex holocycle to the extremely simple paracycle, and which are differently adapted to the trophic and climatic conditions. Aphids can easily perform within species evolutive steps changing the type of their life cycle.
- 4) The polymorphism, which gives the most quick response to environment. Factors affecting morph determination may be different in strains exhibiting different life cycles. The alata/aptera polymorphism, e.g., is mainly controlled by trophic factors in the paracyclic and anholocyclic and by seasonal factors (mainly: photoperiod) in the holocyclic aphids.

Modelli evolutivi dei cicli eterogonici degli Afidi.

RIASSUNTO

Gli afidi posseggono una straordinaria capacità di adattamento a diversi ambienti e climi che ha consentito a questo gruppo di conseguire una vasta distribuzione in tutto il mondo. Il grande potenziale adattativo del gruppo è determinato principalmente da alcuni fattori.

- 1) La facilità con cui possono essere ritenute nelle popolazioni le modificazioni del cariotipo. Questa facilità è determinata, in primo luogo, dall'assenza di un cromosoma localizzato, con la conseguente possibilità di propagarsi per mitosi dei cariotipi che si originano per rottura dei cromosomi ed, in secondo luogo, dalla riproduzione paraciclica che, in assenza di riproduzione sessuale, può portare all'espansione dei nuovi cariotipi.
- 2) I fenomeni sinaptici che caratterizzano la maturazione dell'uovo e la conseguente variabilità genetica delle linee partenogenetiche.
- 3) La varietà dei cicli eterogonici, dall'olociclo fino all'estrema semplificazione del paraciclo, con molte situazioni intermedie variamente adattate alle diverse condizioni trofiche e climatiche dell'ambiente. A questa varietà si accompagna la facilità di passaggio, da un tipo di ciclo all'altro pur nell'ambito della stessa specie.
- 4) Il polimorfismo, che determina una risposta immediata all'ambiente e che appare controllato da fattori che possono essere differenti in ceppi con differenti cicli. Il polimorfismo alata/attera, ad esempio, appare controllato da fattori trofici nei paracicli e negli anolocicli e prevalentemente da fattori stagionali (fotoperiodo) negli olocicli.

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