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Evolution and speciation under conditions of type r and K selection on the example of the insect – host plant system

Plants growing in forests may be classified to two groups. To the first belong plants difficult to find on account of their inconspicuous appearance as for instance herbaceous plants. Plants of the second group are well noticeable and easy to find, for instance trees and shrubs /Feeny 1975/. Herbaceous plants, because of their short life period, are unable to meet the metabolic costs connected with the production of defence substances in high concentrations. They defend themselves from attacks of insects by producing numerous substances acting toxically in low concentrations. Such defence is referred to as "qualitative" and is easy to overcome. Brassicaceae for instance defend themselves by producing glucosinolates in concentrations of 0.02-1.00 per cent of dry weight.

Trees and shrubs are characterized by "quantitative" defence, that is they produce one or two compounds acting in high concentrations. Such defence is difficult to overcome. The oak for instance defends itself by producing tannins which reduce the accessibility of nitrogen by forming indigestible complexes with the leaf proteins. Tannins are present in concentrations of 2-10 per cent of dry weight /Feeny 1976/.

Insects feeding on ephemeral plants become readily adapted to their toxins and gradually extend the range of host plants becoming polyphages. Insects feeding on perennial plants cannot easily become adapted to the toxins contained in the host plant, therefore, their preferred strategy of feeding is monophagy.

Ephemeral plants produce new toxic substances as defence against the attack of insects and some /other plants/ increase the concentration of earlier produced ones. A large amount of toxic

compounds requires a large energy expending by the polyphage. When
there is a great diversity of toxins, the insects are obliged to
restrict the number of host plants, thus, diversified ways of defence
of the particular plant species lead to a specialisation of insects
in feeding.

Very high concentrations of quantitatively acting compounds
require from the monophage too high an energy expenditure. Then
a change of the host plant is beneficial. Thus, the defence
divergence of plants leads to the extension of the range of hosts
by insects /Rhoades, Cates 1976/. These relations are shown in
Figure 1. In general, specialisation makes the insect dependent
on the given plant, but it reduces competition and the metabolic
costs of detoxication of noxious compounds /Table 1/. Monophagy
is a rewarding strategy as long as the probability of mistake in
finding a host is not large.

TABLE 1. List of advantages resulting from various feeding
strategies of insects

Parametres	Feeding strategy	
	general	specialised
Niche	broad	narrow
Reproduction	independent on host	dependent on host
Feeding	wide nutritional spectrum	limited to definite host
Advantages	increased probability of survival in spite of changes in environment; independence on host population	reduced metabolic costs of defence; reduction of inter-specific competition; preservation of polymorphism

Polyphages and monophages choose their host plant differently.
The latter are dependent on only one plant and are obliged to feed
on it, notwithstanding the toxic compounds contained in it. They
mainly choose the plant on the basis of presence of positive
evoking chemical stimuli, especially phagostimulants of feeding
/sugars, nitrogen compounds/. Polyphages can feed on many plants.
Their selectivity is low. Sensory discrimination of the accepted
plants is relatively little specialised. The choice is determined by

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              ── cycle I ──                        ── cycle II ──
         ┌──────────────────┐              ┌──────────────────────┐
         │                  ↓              │                      ↓  predators
    plants           herbivores                                     parasites
       ↑ 4          5 ↑                                             pathogens
       └──────────────┘
     2                    3
    ↑ ╲_____↗
  1  physical environment + plant/plant interactions
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Position in cycle	Trait of plant or tissue undergoing selection	Trait of phytophage undergoing selection	Trait of plant or tissue undergoing selection
5		specialism /limitation of number of hosts/	generalism /increase of number of hosts/	
4	divergence of defence /increase of number of toxic compounds/			convergence of defence /increase of toxic compounds concentration/
3		generalism /polyphagy/	specialism /monophagy/	
2	ephemerality /large number of toxins but in low concentration/			predictability /low number of toxins but in high concentration/
1		spatial and temporal		

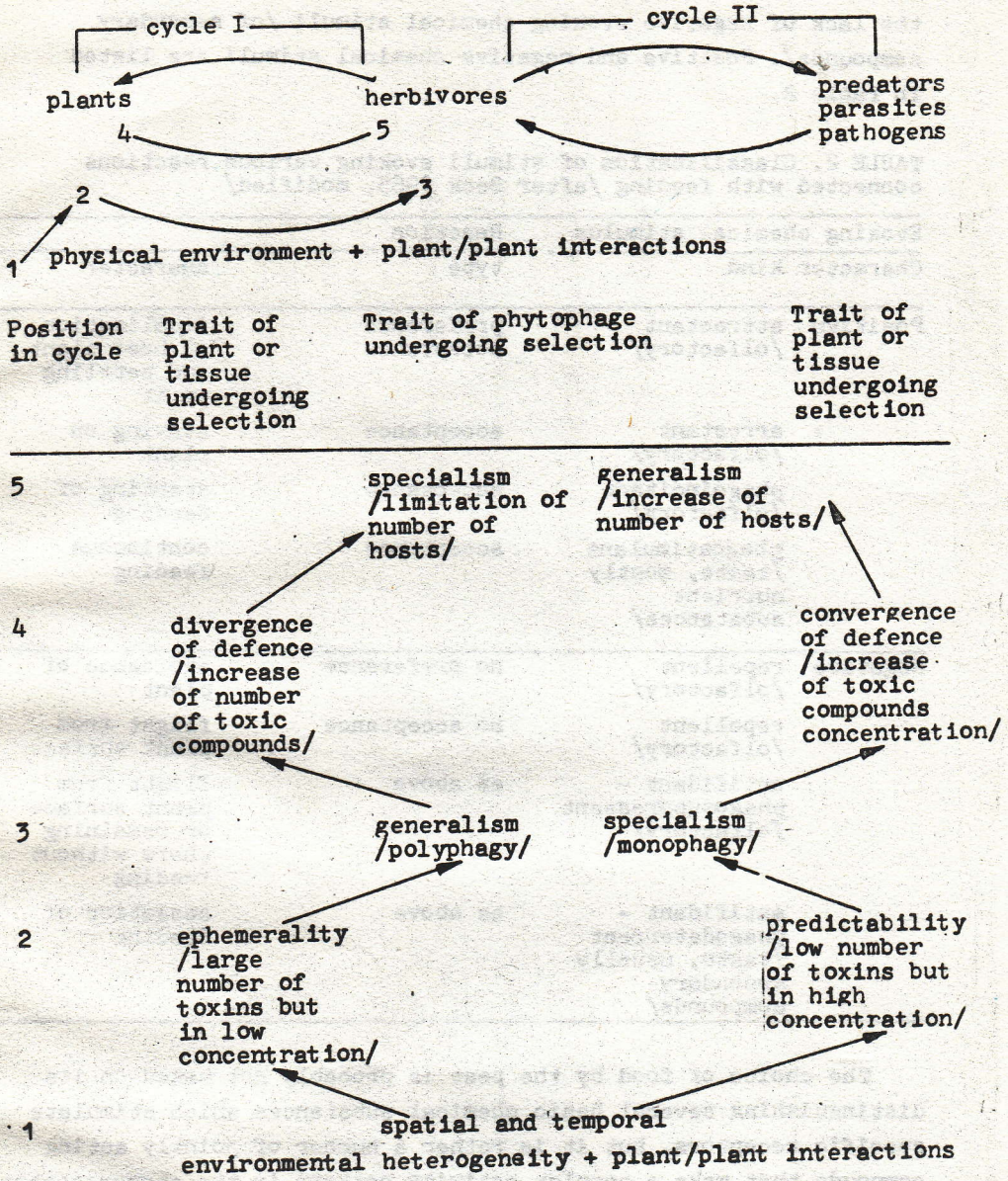environmental heterogeneity + plant/plant interactions

FIG. 1. Coevolution between plants and insects /after Rhoades, Cates 1976, modified/

the lack of negative evoking chemical stimuli /of secondary
compounds/. Positive and negative chemical stimuli are listed
in Table 2.

TABLE 2. Classification of stimuli evoking various reactions
connected with feeding /after Beck 1965, modified/

Evoking chemical stimulus		Reaction	
Character	kind	type	character
Positive	attractant /olfactory/	preference acceptance	localisation of host plant and settling on it
	arrestant /olfactory/	acceptance	staying on plant
	phagoincitant /olfactory/	acceptance	starting of feeding
	phagostimulant /taste, mostly nutrient substances/	acceptance	continuous feeding
Negative	repellent /olfactory/	no preference	avoidance of plant
	repellent /olfactory/	no acceptance	flight from plant surface
	antifidant - phagosuppressant /olfactory/	as above	flight from plant surface or remaining there without feeding
	antifidant - phagodeterrent /taste, usually secondary compounds/	as above	cessation of feeding

The choice of food by the pest is probably not based on its
distinguishing several basic chemical substances which stimulate
specific receptors, but it is rather a number of jointly acting
compouds that make a complex activity pattern in the chemoreceptors
/Jermy 1976/.

Phytophagous insects linked with "ephemeral" plants which defend
themselves "qualitatively" belong to species undergoing selection
of type r. Insects linked with "apparent" plants using "quantitative"

defence belong to species in which selection takes place according
to type K /MacArthur, Wilson 1967/. The traits of species undergoing
selection of r and K type are shown in Table 3.

TABLE 3. Characters of species undergoing selection of type r and K

Parametres	Selection of type	
	r	K
Environment	unstabilised	stabilised
Occurrence at stage of ecological succession	initial	final
Occurrence frequency	unfrequent	frequent
Distribution	wide	strictly local
Adaptation to types of environment	diverse	one
Host plants	"ephemeral" defending themselves "qualitatively"	"predictable" defending themselves "quantitatively"
Value of maximal growth rate r	high	low
Reproduction	early	late
Body size	small	large
Reproduction	single	repeated
Fertility	high	low
Mobility	high	low
Way of feeding	polyphagic	trophic specialisation
Development	rapid	slow
Type of species	eurytopic	stenotopic
	not many common species	many rare species characterised by capability of individual defence, competition and symbiosis

Insect species undergoing selection of r type are active in an
unstable environments, and those the selection of which occurs
according to type K in a stabilised environments. Sometimes species
may be found exhibiting adaptive selection both of type r and K.
The traits resulting from selection of both these types are extremes
of a continuous spectrum of trait changes connected with ecological
succession, ageing of plant associations and transition from a
variable to balanced climate /Mathews 1976/.

Evolution and speciation have a different course in environments
in which selection has a different course according to type r or
according to type K. Speciation, that is formation of species,
semispecies, host races, biotypes and other systematic units is
a strategy of adaptation of animals to a nonuniform environment.
Thus, speciation is a strategy of adaptation.

For the occurrence of speciation a formation of barriers of
gene flow is necessary between the forming species. Natural
selection controls the rate of speciation by controlling the range
of gene flow between populations. The more strictly is the population
adapted to the local conditions the less successful are its
individuals in neighbouring regions, that is environments of other
populations. Thus, selection counteracts gene flow. Under conditions
of high stability this process is self-accelerating and leads to
a high limitation of mobility. Speciation is, therefore most rapid
under stable conditions, that is under conditions specific for type
K selection /Mathews 1976/.

Thus when selection occurs according to type K, speciation is
quicke, but it does not mean that evolution also runs faster since
these two terms have completely different meanings. Evolution is
associated with wide genetic changes. Speciation may occur when
these changes are minimal, but wide genetic changes may take place
without speciation. For instance genetic differences between host
races in aphids are minimal and concern only the key loci connected
with host finding that is coding the complex pattern of activity
in the receptors.

The phenomenon of transition of species from type r to type K
selection occurs in aphids. The decisive way of transition from one
type to the other is speciation by specialisation in feeding and
formation of new host races and biotypes. It is a frequent event

in aphids /Szelęgiewicz 1976/. Nutritional specificity acts at early stages of speciation as an isolating mechanism. The significance of nutritional specifity consists in the maintenance of a high variability and thereby a high evolutional potential since every polyphagous species consists of numerous sympatric and partly isolated populations with various nutritional selectivity. In these populations the complete range of initial variability of the species is preserved, and at the same time each of them is capable of feeding on a different host. The variability range becomes narrower when the changes occurring in the gene loci /coding choice of a new host plant/ become irreversible, because then such populations, as the result of specialisation, lose part of the initial variability of the species.

The process of genetic dismemberment of the population is self-accelerating if the conditions remain unchanged. In this way the species, under stable conditions may disintegrate to numerous host breeds and biotypes. It may, therefore, be stated that the specific aspects of bionomy of aphids predestinate these insects to the formation of host races and biotypes. Probably the aphid population on a given site is a mixture of biotypes changing its composition from year to year /Szelęgiewicz 1976/. A change of environmental conditions causes changes in the numeric proportion of abundance of the particular biotypes, and the biotype best adapted to the existing conditions attains the largest size.

The basic factors exerting an influence on speciation are therefore, the range of variability of characters in insects and the degree of stability of the environment. A complex system as for instance an ecosystem remains in a state of continuous dynamic equilibrium. The durability of the state of equilibrium is described by the term stability. Any system is the more stable the more it has parametres and the less variables. Parametres are permanent characters or slowly changing ones. By variables are meant rapidly occurring changes. The stability of forest ecosystems is ensured by the maintenance of the range of variability at a definite possibly stable level. The factors affecting this genetic variability level and protecting variability are shown in Table 4 /Mayr 1974/.

It has been found that there exists a developmental stability which makes possible survival of a favoured phenotype, in spite of

TABLE 4. Factors influencing the genetic variability level /after Mayr 1974, modified/

Factors	
Increasing variability	diminishing variability
Mutations	natural selection
Gene flow	random and accidental events
Recombinations	
Protecting variability	
Cytophysiological mechanisms	ecological factors
Higher adaptability of heterozygotes	opponent selective pressures change of selective pressure and of selection direction in time
Prevention of free recombination	mosaic pattern of local environment and geographical variability of environment heterogamy privileged selection of rare genes

wide changes in the genotype. The latter is buffered so that it would ensure preservation of pathways of development. Notwithstanding what genes meet in the gene pool, the existence of definite development pathways warrants the attainment of the standard end product. This stabilisation of development can cope not only with the variability of the gene pool, but also with environmental variability. The development of the aphid population runs along definite pathways /channels/ independently of the genotype as long as the variability of the external or genetic environment does not transgress a certain critical level. Each sudden change of the population size produces changes in the intensity of selection. Diminishing of the population increases its homozygosity, this favouring the appearance of nonstandard phenotypes with prevalence of adaptability. An increase of selective pressure or increased population size lead to a rapid elimination of the genes present in it.

Unidirectional selective pressure as for instance industrial pollution, choose a strong directional selection and tend to change the phenotype standard prevailing to this time. This change is the

more difficult /slower/ the larger is the number of interactions
/links/ entangling the given species. For instance, the greater
is the hierarchic complexity of the ecosystem the slower are the
changes in the prevailing phenotype standard of the given species.

Variations of the population size are particularly important
for species undergoing selection of type K. Those in which selection
occurs according to type r, tolerate well rapid changes occurring
in the environment or drastic changes in population size. Temporary
disturbance of environmental stability creates for species with
type K selection conditions of development specific for species
undergoing selection of type r. This causes a drastic increase
of the heterozygosity of the insects and an increase of their
numbers in the species. When the environment is very uniform
/e.g. plant monocultures/, frequently mass appearance occurs in
connection with the profuse availability of food and limited
competition. The presumable causes of mass appearance of aphids,
with particular reference to the genetic structure of forest
ecosystems have been presented by one of the authors at the XI
Symposium of the Forest Entomology Section of the Polish Entomologi-
cal Society at Lipusz in September of the foregoing year.

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