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Rates of Change in Introduced Organisms

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Abstract

Biological control workers have long been familiar with arguments concerning the importance, or lack thereof, of genetic variation in the successful establishment of a weed or a biocontrol agent. However, theories that deal with the genetic events accompanying the introduction of organisms have developed substantially in recent years. In particular, there have been studies of both natural and experimental examples of the interactions between chance events and the genetic systems determining characters that are selected for the new environment. These have led to clearer ideas of the nature of genetic 'transiliences', and the circumstances under which they are most likely to occur. Here I review the evidence from my own work and from the literature on the extent to which these circumstances have accompanied successful introductions of biocontrol agents. Probable cases are pointed out, and implications for rearing and release strategies are outlined.

Vitesses de Mutation Chez les Organismes Introduits

Les responsables de la lutte biologique connaissaient depuis longtemps les raisonnements concernant l'importance, ou le manque d'importance de variations génétiques lorsqu'il s'agit de l'établissement d'une mauvaise herbe ou d'un agent de lutte biologique. Cependent, on a developé d'une manière significative, avec les années récentes, les théories à propos des événements génétiques qui accompagnent l'introduction d'organismes. En particulier, on a étudié des exemples naturels et experimentaux des interactions entre des événements produit par le hasard et les systemes génétiques qui determinent les caractères appropriés aux environnements nouveaux. Ces études ont clarifié la nature de 'transiliances' génétiques et des circonstances les plus susceptibles de les produire. Ici on passe en revue les observations, tiré de mon travail et de la litterature, concernant le dégré auquel ces circonstances ont accompagné les cas d'introduction reussie d'agents de lutte biologique. J'indique des cas probables et esquisse leurs implications pour les stratégies d'élevage et d'élargissement des agents de biocontrôle.

Introduction

It is a familiar empirical observation in biological control literature that introduced populations of biocontrol agents can exhibit differences from source populations relatively soon after they are established. Examples of apparently adaptive phenotypic changes are those in the shelter-seeking behaviour of the St. John's wort beetle *Chrysolina quadrigemina* (Suffrian) (Coleoptera: Chrysomelidae) in British Columbian populations exposed to extremely low winter temperatures (Peschken 1972), and in the temperature threshold for adult emergence of the Californian population of cinnabar moth *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae) (Myers 1978). In addition, some species remain in low but detectable numbers, or enter an 'eclipse phase' during which they are undetectable for a number of generations after release, and then expand rapidly. This has been interpreted by some authors (e.g. DeBach 1965; Wilson 1965) as further evidence for 'post-colonization adaptation'.

An awareness of this need for organisms to adapt to new environments, together with observations from the population genetics literature on the distribution of kinds and amounts of genetic variation, led in the 1960s to a variety of ideas on strategies to maximize genetic variation, and hence subsequent adaptation, in the released population. These ideas are reviewed by Myers and Sabath (1981) in the light of available evidence on electrophoretic variation, phenotypic plasticity, and the genetic variance for quantitative characters. They concluded that there was little evidence that genetic variance was eroded by being passed through the sizes of bottlenecks usually involved in biocontrol introduction, although directional selection imposed during laboratory rearing could have a deleterious effect on subsequent establishment in the field. Recent developments in two areas of evolutionary genetics bear directly on these questions: studies aimed at the management of genetic variation in rare and endangered species, and investigations of the genetic phenomena associated with adaptation following very small bottlenecks.

The first of these areas has led to conclusions generally supporting those of Myers and Sabath (1981), in particular that single bottlenecks have very little effect on either heterozygosity or genetic variance (Frankel and Soule 1981). Moreover, quantitative guidelines for the minimum genetically effective population size (N_e) required to maintain variation have also been derived: to avoid inbreeding depression and maintain genetic variance in the short-term $N_e > 50$, and to maintain long-term adaptability $N_e > 100$–500 (Franklin 1980; Lande 1976 and pers. comm.). These values are probably in accord with most (successful) biocontrol practice (P. Harris, pers. comm.). As well, there is additional evidence that genetic variation is eroded through adaptation to artificial environments and that this presents a problem for attempted release programmes (Frankham *et al.*, *in press*).

On the other hand, special genetic events can accompany introductions based on a small number of founding genomes. Since these events lead to rapid adaptation to new environments and since the necessary conditions appear to have accompanied at least one classically successful biocontrol introduction, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) in Australia (Murray 1982), it seems worth exploring in more detail their relevance to past and future introductions.

The Nature of Founder Effects and Genetic Transiliences

Population bottlenecks occur when a large population is temporarily reduced to a small size or when a geographically separate new population is founded by a small number of individuals. When a population experiences such a bottleneck the frequencies of alleles at polymorphic loci are subjected to random shifts through sampling error. At such a time, rare alleles may be lost, or occasionally fixed, but reductions in heterozygosity and the additive genetic variance for quantitative characters are not great (Nei *et al.* 1975; Franklin 1980). More variability is lost if the population remains small for a number of generations, or if it is subjected to repeated bottlenecks.

These random effects would be of little interest in natural populations but for the fact that they can strongly influence the outcome of subsequent selection. Mayr (1954) pointed out the potential interplay of random and selective forces. He noted in particular that random effects on allele frequencies at one of a number of loci that interact in the determination of a character subject to selection, will be followed by rapid selective readjustments in the frequencies of alleles at the other interacting loci. He termed this the 'founder principle' and used it to account for rapid, phenotypic changes (genetic revolutions) in geographic isolates of tropical birds.

More recently, detailed genetic analysis of the rapid speciation undergone by flies of the genus *Drosophila* (Diptera: Drosophilidae) in the Hawaiian Islands has led to a clarification of these ideas. Speciation in this group appears to have accompanied the founding of new populations by a small number of individuals followed by a rapid expansion of population size in the new environment: the 'founder-flush' cycle (Carson 1968). Carson (1975) noted that the genetic consequences of these cycles are different for different parts of the genome: morphological evolution and speciation have been rapid, but electrophoretic and karyotypic evolution have been much slower in spite of much within-species polymorphism. He suggests that the genome can be regarded as having a 'closed' and an 'open' component. The open component consists of additive genetic variance and most electrophoretic variation, and responds to selection and random influences in accord with general 'bean-bag' theoretical expectations. The closed component, on the other hand, consists of special inter-locus epistatic interactions underlying directionally selected morphological and developmental characters, and is therefore resistant to all but the extremely strong forces for change that accompany a founder-flush cycle. Random shifts are seen as generating novel genetic combinations, particularly homozygotes for rare alleles at these closed-system loci. The subsequent flush is mainly necessary for the population to retain sufficient variability to adapt to this new genetic environment. Since mate-recognition characters are part of the closed system in Hawaiian *Drosophila*, mating isolation is a frequent outcome of these cycles.

This theory has led to attempts to generate and analyse founder-flush speciation in laboratory populations of *Drosophila*. Powell (1978) and Templeton (1979) have been successful. More importantly, not all founder-flush cycles lead to a genetic revolution, and Templeton (1980) has described in detail the conditions under which such rapid genetic readjustments are most likely to occur. These will now be considered in detail. Because of ambiguities surrounding earlier terminology, Templeton (1980) has referred to these phenomena as 'genetic transiliences'.

Conditions Favouring Genetic Transiliences: What Sorts of Organisms, Characters, and Environments?

Both genetic and ecological characteristics are crucial in predisposing an organism to such events. So are the characteristics of the new environment. Table 1 summarizes the factors noted by Templeton (1980) as affecting the chance of a transilience when a population is established by a very small number of founders. These factors influence first, the chances of a bottleneck generating a novel homozygous genotype and second, the chances of maintaining that genotype while restoring linkage equilibrium in the remainder of the genome during the population flush.

Templeton's (1980) discussions concentrate on changes in the epistatic interactions underlying characters involved in sexual recognition, and hence pre-mating isolation. However, such interactions also occur in the genetic control of other characters, and these too should be subject to transiliences, although premating isolation may not be a direct result. Mather (1973) reviews evidence that strongly epistatic genetic architectures characterize responses to strong directional or disruptive selection. These include the natural genetic architectures of such 'fitness' characters as viability and fertility, and of naturally polymorphic complex phenotypes such as sex differences, host races or other phenotypes controlled by complex supergenes. We should therefore expect that transiliences influencing these characters will occur, and that some will lead to incipient post-mating isolation between parent and daughter populations, especially where, for example, viability in a novel biological or physical environment is selected for in the daughter population.

These considerations also point to particular groups of organisms as being more susceptible to transiliences than others. In Lepidoptera, strong epistatic interactions between X-linked and autosomal loci are common (e.g. Grula and Taylor 1979, 1980*a*, *b*) in spite of the small genetic size of the X-chromosome. Pearse and Murray (1982) have pointed out that this is expected to be a general state of affairs given the lack of dosage compensation of X-linked genes in Lepidoptera (Johnson and Turner 1979), the amount of any X-linked gene product serving as a potentially interactive signal to autosomal genes with different optimal levels of expression in males and females. The predominance of these interactions should make Lepidoptera particularly susceptible to transiliences, especially in sex-limited or sex-influenced traits. A similar argument should apply to birds, which also lack dosage compensation of X-linked genes (Baverstock *et al.* 1982).

Table 1. Attributes of the ancestral population, the founding sample, and the introduced population, that affect the probability of a genetic revolution.

	Probability of Genetic Revolution	
Ancestral Population	High	Low
Size	Large	Small
Mating structure	Panmictic	Inbred
Genetic variability	High	Low
Founding Sample		
Size	Small	Large
Source	Single population	Mixed populations
Introduced Population		
Average No. offspring	Large	Small
Reproductive value of founders	High	Low
Capacity to expand rapidly in new environment	High	Low
Initial density	Low	High
Initial population structure	Subdivided	Panmictic
Generations	Overlapping	Discrete
Mating	Assortative	Disassortative
Chromosome number	Large	Small
Total genomic map length	Large	Small
Crossover suppressors	Few, easily lost	Many, not easily lost
[1] Selection on mate recognition system	Directional	Stabilizing
[1] Sexual behaviour	Partially learned	Totally Genetic

[1] Characters leading to pre-mating isolation between introduced and ancestral populations.

Are There Examples of Transiliences in Biocontrol Introductions?

Whilst there is an obvious demographic parallel between a founder-flush cycle and a successful biocontrol introduction, the combination of conditions described in Table 1 as maximizing the chances of a genetic revolution during such a cycle are met with more rarely. Ideally, candidates for biocontrol agents have all the listed ecological attributes centering on the capacity for rapid increase in the new environment. However, current strategies for maintaining existing genetic variability by introducing large representative samples from ancestral populations would work against the possibility of a transilience. As well, it is difficult to assess the probability that transiliences have occurred because we often know very little about the genetics and ecology of the populations from which previous introductions have been derived. In spite of this, there is good circumstantial evidence that they have occurred in some cases, whilst in others they almost certainly have not. Some examples are described below.

Cactoblastis cactorum

Murray (1982) described evidence for genetic differentiation in life-history traits between Australian populations of *C. cactorum*, and suggested that transiliences could have occurred during and subsequent to the moth's introduction to Australia. Although we are ignorant of many features of the moth's population structure and genetics in both Argentina and Australia, the following more detailed comparison with the attributes listed in Table 1 is possible.

Known factors favouring the occurrence of a transilience are: whilst the characteristics of the ancestral *C. cactorum* population are not recorded, on the basis of its biology in Australia it must have had high levels of genetic variability and was probably wide-ranging as an adult; the founding sample was small, although not extremely so (between 14 and 55 females), but came from a single population representing only one of a number of apparent host-races in South America (McFadyen 1984); the species has a high r_m and underwent a spectacular population flush after release; it was adapting to a new species of host cactus, *Opuntia stricta* (Haworth) Haworth (Cactaceae); natural colonization would have resulted in further local founder-flush events in a peripherally subdivided population structure, as would the major oscillations of cactus and moth populations that followed in the early 1930s (Dodd 1940), and that still take place in some isolated populations today (Murray, unpubl. data). Lepidoptera have high chromosome numbers and a genetic architecture favouring epistatic interactions.

Known factors working against transiliences are the non-overlapping generation pattern, the artificial spread of large batches of eggs and larvae, and the lack of crossing over in female Lepidoptera.

Subsequent introductions of *C. cactorum* to other countries for cactus biocontrol were generally carried out with large samples. However, in Hawaii and the West Indies, natural inter-island colonizations have apparently produced further opportunities for rapid genetic change (Murray 1982). Preliminary observations in the Hawaiian Islands reveal that Oahu moths differ from Maui and Hawaii moths in their phenology and their capacity to feed on different forms of *O. megacantha* Salm-Dyck.

Species Known to have Undergone Very Small Bottlenecks During their Establishment

Cochineal insects, *Dactylopius* spp. (Hemiptera: Dactylopiidae), provide some of the most spectacular examples of biocontrol successes. Many of these introductions have involved a very small number of founders (Moran and Zimmermann, pers. comm.). Notable examples are the introduction of *D. opuntiae* (Cockerell) to Mauritius from Ceylon, which was based on a single fertilized female, while *D. austrinus* De Lotto in South Africa is derived from five females.

The successful release of *Hypogeococcus festerianus* (Lizer y Trelles) (Hemiptera: Pseudococcidae) in Australia was based on the progeny of six females. Interestingly, these were maintained during rearing as single-female lines to remove a parasite

(McFadyen, pers. comm.), a procedure shown in Table 1 as contributing to the probability of a genetic transilience.

Comperiella bifasciata How. (Hymenoptera: Encyrtidae) is a parasite of California red scale *Aonidiella aurantii* (Mask.) (Hemiptera: Diaspididae). DeBach (1965) notes that the release stock of over two million individuals was based on only five females. As well, the stock entered an eclipse phase for 5–6 years before spreading rapidly through southern California.

Chrysolina spp.

The chrysomelid beetles *C. hyperici* (Forster) and *C. quadrigemina* have mostly been spread both within and between continental areas as mass introductions (Clausen 1978), and they would therefore seem unlikely candidates for the sort of genetic reorganization being considered. However, two phenomena suggest that they could be of interest. First, an 'eclipse phase' has occurred during several introductions of these species. When *C. hyperici* was introduced to Australia from England, many separate releases were made, with the animals appearing to become extinct each time. After four years of apparent extinction, a single population erupted and was the base for all subsequent introductions both within and outside Australia (Clausen 1978). A long period of low numbers has also characterized *C. quadrigemina*'s establishment in British Columbia, where its recent spread has been accompanied by changes in phenology that adapt it to survival in non-Mediterranean climates (Harris and Maw 1984; Williams *et al.*, pers. comm.).

Second, in *C. quadrigemina* there is an example of epistatic genetic control in a character associated with fitness differences. In this species there is a colour polymorphism, individuals being bronze or some colour in the green-blue-purple range. Genetic analysis of colour differences in Australian populations (Tomasov, unpubl. data) suggest that a single gene is responsible for the bronze *vs.* coloured difference, bronze being homozygous recessive. A second unlinked locus determines whether coloured individuals will be green or blue/purple. This model has also been found to accommodate the unpublished results of Garthside (1934–36), obtained when he was rearing French *C. quadrigemina* for food tests and for release in Australia. Moreover, the colours are known to be associated with fitness differences and their frequencies vary between populations (Peschken 1972; Williams, Myers and Edwards, unpubl. data; Tomasov, unpubl. data). The ecological genetics of this system deserves far more attention, especially with regard to the ways that the interacting loci influence physiology and development in populations with different phenologies.

Species Unlikely to have Undergone a Genetic Transilience

There are few species for which we have the basic biological information necessary to decide this. However, the cinnabar moth, *T. jacobaeae*, has a low level of electrophoretic variability and has a naturally sub-divided population structure (Myers and Sabath 1981). Whilst these attributes are adequate to maintain quantitative genetic variance, they make *T. jacobeae* a less likely candidate for genetic transilience than other moth species.

Implications for Release Strategies

Most of the species described above have done what is theoretically necessary to undergo a genetic transilience and it would be surprising if they had all failed to achieve it. There is a clear need for work aimed at comparing source and derived populations of biocontrol agents. Such work necessarily involves controlled crosses that explore the genetics of complex characters rather than crude electrophoretic or molecular comparisons. They will therefore be difficult, but it is important to know the answers for two major practical reasons, quite apart from the theoretical interest of whether or not we are making new species. First, if different populations of the same initial species now differ substantially from one another, then care needs to be taken in mixing diverse materials in further introductions. As well, supplementary introductions into long-established populations are sometimes considered because of possible declines in effectiveness. These will probably be useless and may in fact do more harm than good by swamping existing local adaptations.

Second, if genetic revolutions in traits with epistatic genetic architectures have been important in the establishment of biocontrol agents, then strategies to maximize the chances of this can be devised.

Two alternative strategies for weed biocontrol releases are suggested by genetic considerations. First, if the aim of the release is to transplant an organism to an environment (climate, host plant) known to resemble that of the source population, then attempts to represent heterozygosity and genetic variance and to avoid inbreeding depression are desirable. This can best be achieved by: (1) mixing individuals from different source locations; (2) maintaining them as a large stock which is prevented from adapting to artificial rearing conditions (e.g. by rearing in field cages near the ultimate release site); and (3) making only a few releases composed of a large number of individuals. This procedure would allow adaptation based on the additive component of genetic variance.

The second strategy, which would maximize a response based on epistatic interactions between loci, would be more appropriate where the new environment is known to differ in some major way from that of the source population. This strategy would involve: (1) taking a small sample from a single source population; (2) expanding it rapidly in the new environment; and (3) either splitting it into many separate lines shortly after release, or establishing many lines from a number of separate small initial samples. This method would lead to extinction of most of these small release populations but the few surviving populations would be expected to be better adapted to the new environment than a population derived under the bulk-breeding programme described in Strategy 1. A similar idea was suggested by Lewontin in the discussion attached to DeBach (1965).

Interestingly, as pointed out earlier, some of the features of the multi-line strategy have occurred naturally in successful biocontrol releases. For example, splitting of the release stock into several single-female lines may occur, as with *H. festerianus*. The 'eclipse phase' may also represent a period in which a number of release populations are reduced to very small size, with only one undergoing an adaptive genetic revolution. If this population then serves as the basis for subsequent natural or artificial spread, as occurred with *C. hyperici*, then Strategy 2 will have been carried out.

Summary and Conclusions

(1) There is a class of rapid genetic change (a 'genetic transilience') that occurs in some populations subjected to a founder-flush cycle.

(2) The conditions accompanying some biocontrol introductions are such that some transiliences should have occurred.

(3) There is evidence from the comparison of derived populations of biocontrol agents that genetic differences have arisen, but more information is required to assess their nature and extent.

(4) Given the right sort of organism, release programmes can be planned to maximize the chance of generating novel adaptations to new environments.

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