

The biotype concept and its application to insect pests of agriculture

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ABSTRACT. The use of the term biotype of insect pests of agriculture is discussed in the broad context of species, populations and individuals. There have generally been two quite distinct usages and thus two different concepts. The first is a general concept which applies, confusingly, both to individuals and to populations of a species which share certain biological characteristics, usually concerning virulence on different host varieties, with little or no knowledge of their genetic bases. This is generally synonymous with the term host race, used by many authors. The second is a very specific concept in which a particular gene or genotype for virulence in a pest is known to correspond with a particular gene for resistance in a host plant—the gene-for-gene relationship. We argue that the first concept is so general as to be of little value, and in some examples, such as the brown planthopper of rice, is potentially misleading. The specific concept depends on detailed genetic analyses which are available for very few examples and is thus of limited applicability. We conclude that the confusion of the two distinct concepts is dangerous. It is not possible to argue from the general to the specific. The term biotype has often been used to cover our ignorance of the detail of any particular insect/plant interaction.

Introduction

In recent years the importance of resistant plant varieties in integrated control strategies used to combat insect pests of agriculture, has served to emphasize the need for basic understanding of variation in the responses of such insects to crop cultivars. Some insect pests have developed virulence and cause significant damage to cultivars which previously showed field resistance to them. Such apparently new forms of pests have often been termed host races or biotypes. These terms usually cloak our ignorance of the exact nature of variation in the pest populations. As Eastop (1973) has remarked, 'biotype is a taxonomic concept mostly used by nontaxonomists!' It therefore tends to mean different things to different workers. Maxwell and Jennings (1980), in the glossary to their valuable compendium on breeding plants resistant to insects, define the term biotype in entomology as 'an individual or population that is distinguished from the rest of its species by criteria other than morphology, for example, a difference in parasite ability'. If we take this

very broad definition as a starting point, then it is clear that the concept is being used both of *individuals* and of *populations* within one *species* of insect. It is important, then, to give some consideration to the meaning of these subsidiary terms.

The species concept

First we may take the more inclusive species concept which for animals has been discussed at great length by many authors, among the most important of whom are Cain (1954), Mayr (1942, 1963), and Dobzhansky (1957). Despite much disagreement (*see*, for example Sokal and Crovello, 1970), biological definitions are generally accepted by field entomologists as the most useful ones. In these, emphasis is placed on the sharing of a common gene pool by individuals grouped into interbreeding populations. For sexually reproducing (biparental) insects there should be no problem about determining whether or not sympatric forms (those which occur together naturally in the field and have the possibility of freely interbreeding) regularly interbreed and contribute genetically to succeeding generations. In practice such decisions may be difficult and require considerable experimental work, especially in examples where morphological differences between species are either apparently lacking (sibling species), or very variable. Nevertheless, in applied problems such decisions may be important. For example, among mosquito and blackfly vectors of human diseases, many variants, showing little or no morphological differentiation and previously known as 'races', have been shown to be distinct and separate biological species (*see* Wright and Pal, 1967). Similar undetected sibling species undoubtedly remain to be discovered among agricultural pests. For example, Jaenike and Selander (1980) recently showed that forms of the fall webworm, *Hyphantria cunea* (Drury), previously known as host races, are in reality genetically distinct sibling species. Thus, when studying variable pests, it is important first to investigate the possibility that more than one species may be involved. This is not simply of academic interest, but may have practical implications. Different biological species do not interbreed regularly and therefore will evolve separately under natural selection, whether it be imposed by natural ecological factors or by man-made changes in ecosystems, such as the planting of new varieties of host plants with different resistance characteristics, or the widespread use of particular insecticides.

Intraspecific categories

For bisexually reproducing insects, the criterion of interbreeding under natural conditions ('crossability' of Mayr, 1942) is the essential one for differentiating between interspecific and intraspecific variation. Within local populations genetic variation may be either continuous or discontinuous, and may be inherited either by a complex system of polygenes or by a simpler system of major genes, or by a combination of both. The terminology which has evolved to account for the resulting genetic and environmentally induced phenotypic variation is enormous and includes such terms as race (geographic, host, biological, physiological, etc.), biotype, ecotype, pathotype, form, morph, strain, variety, subspecies, semispecies, etc. Much of the controversy surrounding particular cases, such as the variation in virulence of *Nilaparvata lugens* on different varieties of rice (Claridge and Den Hollander, 1980), is largely a result of lack of agreement on the definitions of such

terms and concepts. It is appropriate, then, briefly to discuss some of these terms in order particularly to understand what is meant by biotype in insect/plant interactions. It is essential to eliminate problems merely of terminology from the interpretation of real biological phenomena.

Bisexually reproducing organisms exist in nature as groups of individuals which occur in a sufficiently small area to have a high chance of interbreeding among themselves (the size of the area will vary greatly with different species and will depend on mobility and powers of dispersal); these groups of potentially interbreeding individuals form the Mendelian populations described by geneticists. The term *population* is best restricted to such a usage. Similar populations distributed over a wide geographical range together form the taxonomic species, but it is often local populations which are of most concern to economic entomologists. Intraspecific variation may occur either within populations or groups of neighbouring populations, or between geographically defined and separate groups of populations. It is important to recognize this differentiation between geographic (allopatric) variation and local (sympatric) variation. Within populations some degree of continuous variation will always be found. The range of this variation may be great or small, but, provided that it is under genetic control, it will be susceptible to evolutionary change, particularly by environmentally induced selection pressures. Equally susceptible to selection will be genetically determined discontinuous variation, in which distinct classes of variation, with few intermediates, are found. Such discontinuous variation is termed *polymorphism* and is also common: the distinct forms in the polymorphism may be referred to as *morphs*, whether they are recognized by morphological, physiological, behavioural, ecological or other features. It may sometimes be useful to prefix the term, as for example in *electromorph*—commonly used for biochemical polymorphisms recognized by techniques of electrophoresis. Thus *morph* is a term used for individuals and not for populations, although populations may be characterized by patterns of polymorphisms.

Discrete populations will be definable in terms of their own variation which may differ from that of other allopatric populations of the same species. Thus a number of terms have come into use which refer to population variation rather than to individual variation. Confusion between these two types of variation may lead to many misunderstandings and should be avoided. The most widely accepted system for describing the geographical variation of populations, which may be anything from very slight to very great, consists of a continuous series of arbitrarily separated categories—from geographically defined *population* to *race* to *subspecies* to *species* to *superspecies* (after Mayr, 1942). Other categories such as *semispecies* may also be inserted. Although geographical variation is usually very complex, for example making the use of the term *subspecies* difficult (Wilson and Brown, 1953), the conceptual differentiation between variation within and variation between populations is very important and relevant to many pest problems.

Perhaps the greatest difficulties have arisen in the use of the terms *race* and *biotype* when applied to plant-feeding insects with respect to their host-plant preferences or abilities to survive and flourish on different plant species, varieties or cultivars. As already stated, the term *race* refers to a geographically defined population or group of populations of a species which may be differentiated from other such populations of the same species. The differentiation between such races may be morphological, physiological, behavioural, etc. Thus, *race* implies some geographical or spatial

separation from other races (Gonzalez, Gordh, Thompson and Adler, 1979). Individual variation and variation between populations frequently have been confused. This is a major weakness of the definition of biotype by Maxwell and Jennings (1980), cited above, because it does purposely confuse these two biologically very different phenomena.

So far we have assumed that insect pests are bisexually reproducing or biparental organisms, in which fusion of male and female gametes results in great genetic variability among the progeny. This is certainly not always true. Many insects reproduce by obligate systems of parthenogenesis and therefore fall outside the scope of the biological species concept because individuals reproduce without the exchange of genetic material with another individual. Such forms may be expected to show relatively little genetic variation from generation to generation, forming clones of genetically similar individuals. From time to time new mutants may arise, resulting in new forms which may differ in important attributes, such as host or other habitat requirements. These new forms may be expected to reproduce clones with the new mutant characteristics which may flourish, and either replace the original forms or coexist with them. There is no doubt that some of the biotypes of aphid pests represent such clones (Eastop, 1973). Indeed, in some species, such as the pea aphid, *Acyrtosiphon pisum* (Harris), it has been suggested that new biotypes arise annually by adaptation of parthenogenetic clones to different species of host plant (Frazer, 1972).

Species in parthenogenetic organisms are different in kind to those in bisexual organisms. In the past they usually have been recognized on the basis of arbitrary morphological differences: Cain (1954) called them agamospecies. DeBach (1969) proposed the term uniparental species, to contrast with biparental species, and stressed that it was useful to recognize such species on a basis of behavioural or ecological differences rather than on morphological ones only. This is especially significant for plant-feeding insect pests and also for their parasites and predators which may be important in biological control and many of which are parthenogenetic. Gonzalez *et al.* (1979) have recently developed a similar conceptual framework for parthenogenetic species.

Current controversy concerning modes of speciation among bisexually reproducing parasitic insects, including plant feeders, centres on the suggestion that sympatric host-race formation is relatively common in nature (Bush, 1975a,b; White, 1978; Price, 1980). It has been suggested, especially by Bush, that some relatively specific insect herbivores may transfer occasionally to new and previously unsuitable host plants. At the same time such insects might develop barriers to mating with the parental population. Such 'host-races' (Bush, 1969) might then evolve separately until they were genetically isolated from the original species on the old host plant, while retaining a sympatric relationship. Despite Bush's own work on *Rhagoletis* fruit flies, this intuitively attractive hypothesis seems to have little strong evidence in its favour. For example, Futuyma and Mayer (1980) and Jaenike (1981) have recently independently questioned whether such sympatric host races really do occur in the field. This is not the place to pursue such arguments, but if truly sympatric host races do exist among plant-feeding insects, then the term race would not be appropriate; it is now widely agreed that it is best restricted to allopatric populations (*see above*). Thus, both Berlocher (1979) and Gonzalez *et al.* (1979) recommend that biotype, rather than host race, should be used of such host-plant-associated and genetically differentiated populations. This area is one of consider-

able current discussion and disagreement. Detailed field studies are urgently required to demonstrate conclusively whether such sympatric host-plant-associated biotypes (host races) are common among plant-feeding insects. It is also particularly important that some such studies be made on insects and plants in relatively natural communities in which the genetic variation of both has not been modified by artificial selective breeding and agricultural practice.

The biotype in practice

It is now possible to discuss the practical usage of the term biotype, which has come into prominence in recent years particularly to describe the responses of insect pests of agriculture to cultivars and other variants of their food plants (Painter, 1951). Russell (1978) has recently reviewed the use of the term more widely in breeding plants for both pest and disease resistance. Pathak (1975) listed seven species of insect pests in which biotypes had then been identified. Of these, five were aphids with at least a parthenogenetic phase of reproduction in their life cycles. The remaining two species were the Hessian fly of wheat, *Mayetiola destructor* (Say), and the brown planthopper of rice, *Nilaparvata lugens* (Stål). Eastop (1973) reviewed the concept of biotype with particular reference to aphids and suggested that the term was usually synonymous with clone and referred to individuals of the same genotype. The most significant biological characteristic of such biotypes is their ability to feed on, and damage, plants resistant to all or some other biotypes (clones). Here the term definitely refers to individuals of the same genotype, at least with reference to virulence (*see above*). For parthenogenetic clones such a concept may be useful, but in sexually reproducing organisms it is impossible to imagine the existence of natural populations consisting only of genetically identical individuals. The use of the biotype concept in such examples is very confused (*see recent discussions by Berlocher, 1979; Gonzalez et al., 1979; Mackenzie, 1980; Maxwell and Jennings, 1980*), but generally it is agreed that genetic homogeneity, at least for virulence characters, is important.

The association of virulence in a pest with resistance in a plant to that pest, whether it be insect, fungus, or micro-organism, is widely assumed to be characterized by a gene-for-gene relationship (*see, for example, Day, 1974; Gallun and Khush, 1980; MacKenzie, 1980; Price, 1980*). This was first noted by Flor (1956) for the rust disease caused by the fungus, *Melampsora lini*, of flax, *Linum usitatissimum*, and later developed by van der Plank (1963). The essence of the hypothesis is that a single gene in the pathogen matches a corresponding gene in the host. This idea was extended to insect pests, especially by the work of Gallun and others on the Hessian fly (e.g. Gallun, 1977; Gallun and Khush, 1980). Here up to nine different biotypes of the insect have been recognized, with virulence genes which correspond to resistance genes in the wheat plants (Everson and Gallun, 1980; Gallun and Khush, 1980). Thus each biotype of the fly is genetically homogeneous for a particular single major gene or group of major genes. Field populations appear to be mixtures of different biotypes and thus the biotypes represent different morphs of polymorphic populations (Hatchett and Gallun, 1968). The cultivation of large areas of land with just one variety of wheat with a single gene for resistance would be expected then to select populations of flies of one dominating biotype. It appears that here the term biotype is being used in a similar manner to the aphid and fungus examples, that is for individuals genetically identical for virulence genes. Where

there is a gene-for-gene relationship the biotype concept may be useful, because a particular biotype may be defined as those individuals in a population which possess a particular gene for virulence. However, if the same phenomenon were produced by a polygenic system, or even by a complex group of major genes, it would be difficult to define a biotype other than by its phenotypic effects. The Hessian fly example is the only biparental species of insect in which it has been clearly established that a gene-for-gene relationship exists. There are some unusual features in the genetic system of these flies (Gallun, 1977), but nevertheless they are bisexually reproducing. There is little evidence to suggest that such a gene-for-gene relationship is usual or indeed common for insect/plant feeding relationships generally.

In few insect examples where biotypes have been identified, have allopatric biotypes been differentiated from sympatric ones, despite the fundamental differences between the two concepts (Bush, 1975a). Allopatric (that is geographically or spatially isolated) populations of plant-feeding insects may be expected to adapt to local conditions so that the existence of local races with distinctive patterns of host-plant preference and virulence should be expected. It is probable that some forms which have been described as distinct biotypes are indeed such geographical races, e.g. the European corn borer, *Ostrinia nubilalis* (Hübner) in North America (Chiang, Keaster and Read, 1968; Chiang, Kim and Brown, 1970; Kim, Chiang and Brown, 1967); the rice gall midge, *Orseola oryzae* (Wood-Mason) in India, Indonesia and Thailand (Heinrichs and Pathak, 1981); and the rice green leafhopper, *Nephotettix cincticeps* (Uhler), in different parts of Japan (Sato and Sogawa, 1981).

The rice brown planthopper—an example

The brown planthopper, *Nilaparvata lugens* (Stål), is currently one of the most important pests of rice in Asia where it kills plants directly by feeding on them and also by transmitting the virus diseases, ragged stunt and grassy stunt (IRRI, 1979). It has come to prominence as a pest only in the last fifteen years or so, with the widespread cultivation of high-yielding and rapidly maturing rice cultivars. A major strategy for control has been the search for resistant varieties of rice and the incorporation of resistance factors into modern varieties. This work was pioneered, and continues actively and very successfully, at the International Rice Research Institute (IRRI), Philippines. Results have been summarized recently by Pathak and Khush (1979). Three isolated laboratory cultures of *N. lugens* from Luzon have been maintained at IRRI for many generations on three different rice varieties characterized by different genes for resistance. These populations were early termed biotypes 1, 2 and 3, with the ability to survive, respectively, on cultivars with no known gene for resistance (for example cv. TN1), gene *Bph 1* (cv. Mudgo), and gene *bph 2* (cv. ASD 7) (IRRI, 1975). Field populations also have been collected in the Philippines with the same patterns of virulence as biotypes 1 and 2. The assumption has been widely made with some experimental evidence (IRRI, 1978), that these biotypes represent a further example of the gene-for-gene relationship, with major genes for resistance in rice corresponding with major genes for virulence against them in the insect biotypes, as in the flax rust and the Hessian fly.

We have studied individual variation within the inbred IRRI biotype populations with respect to virulence/resistance relationships and found great variation within each (Claridge and Den Hollander, 1980). Sogawa (1981a) independently obtained similar results. In addition, there is strong evidence to suggest that virulence in the

IRRI biotypes is inherited in a complex polygenic manner (Den Hollander and Pathak, 1981; Sogawa, 1981b). Thus there can be no simple gene-for-gene relationship between insect and host plant.

Recently we have shown that the virulence characteristics of each of IRRI biotypes 1, 2 and 3 may be changed towards those of one of the others by selection for only about ten generations on an appropriate cultivar (Claridge and Den Hollander, 1982). It was thus possible effectively to convert one biotype into another. Other selection experiments point to the same conclusions (Kaneda and Kisimoto, 1979; Den Hollander and Pathak, 1981; Pathak and Heinrichs, 1982).

Thus we concluded that the term biotype and especially the specific labelling of biotypes, either by numbering or naming, is not appropriate in this species (Claridge and Den Hollander, 1980; 1982). The reasons for this conclusion are (1) the biotype populations are very variable and show great individual variation for virulence—the only characteristics by which they may be recognized; (2) there is clearly little genetic homogeneity where virulence characteristics are inherited by many genes with small effects. Particular virulence patterns then may be achieved by many different combinations of polygenes, as demonstrated in the selection experiments. Virulence characters are thus highly labile. It is therefore positively misleading to name or number such populations without any clear genetic basis for this. At most, the term biotype might be used of these populations in a general non-specific sense to denote similar phenotypic patterns of virulence.

The problems of naming, or otherwise specifically identifying, biotypes in *N. lugens* are greatly increased when comparing allopatric, or probably allopatric, populations. Different gross patterns of virulence have been described in different parts of Asia. Many of these have been summarized recently by Seshu and Kauffman (1980). For example, biotypes 1 and 2 have been identified in Indonesia and 1, 2 and 3 in Taiwan, but detailed analysis shows that those at least from Taiwan clearly are not identical to those in the Philippines (Cheng and Chang, 1979). This is not surprising as we should expect them to have evolved separately by adaptation of local populations, so that they may be genetically quite different.

We have studied a population from Queensland, Australia, which responds to the supposedly universally susceptible variety, TN1, as resistant (Claridge and Den Hollander, 1982). After ten generations of selection on TN1 we were able to produce a population with virulence characteristics similar to those of IRRI biotype 1. However, we know that the Philippine and Australian populations are in other respects genetically differentiated and could be regarded as distinct geographical races (Claridge, Den Hollander, Morgan, Furet and Vansnick, 1982).

In addition, in Sri Lanka we have shown that local populations of *N. lugens* separated by distances of no more than 100 km may show quite different patterns of virulence and close adaptation to the particular rice varieties from which they were collected (Claridge, Den Hollander and Furet, 1982). In such situations the use of a biotype nomenclature could only obscure both the nature of variation within and between populations, and the remarkable potential which they show for change in virulence.

Conclusions

The concept and usage of biotype as synonymous with race for insect pests derives directly from often much better understood examples of disease organisms (such as

fungi and bacteria) of crop plants, where often a gene-for-gene relationship is well established (e.g. van der Plank, 1963; Day, 1974). We contend that, for bisexually reproducing insects, where genetic variation is necessarily always great, such simple relationships are unlikely. The transfer of the concept of 'biotype' or 'race' from micro-organisms to insects serves only to conceal the true nature of variability in these animals and therefore to give a false impression of simple relationships between different populations.

The variability of insect pests, as described above, may be the result of at least three distinct, but easily confused, phenomena: (1) genetically isolated, but morphologically very similar biological (sibling) species; or (2) geographically separated (allopatric) races; or (3) variants within an interbreeding population, such as morphs in a polymorphism. Only detailed analyses will enable us to establish the true nature of variation for any particular pest. There can be no simple solution to these problems.

In practice, the term biotype is one which has been applied to insect pests of agriculture in two quite different ways: either (1) in a very general and broad manner, as in the definition of Maxwell and Jennings (1980); or (2) in a very precise and specific way to refer to particular genotypes of a pest, as in the Hessian fly (Gallun, 1977). The two are not strictly compatible and are certainly not interchangeable.

In the first the term is used both of individuals within a mixed population and also of whole populations which show particular phenotypic characteristics, such as virulence to a particular host-plant variety. This may be useful to refer to insects which have the ability to damage a particular crop variety and to differentiate them from other insects of the same species which do not. However, such clear-cut differentiation is seldom found in nature and pests are unlikely to show either no ability to survive and feed on a particular variety or conversely the ability totally to destroy it; almost always there will be a continuum between the two extremes. Certainly, agricultural entomologists do use the term biotype in this general sense and presumably find it useful. Difficult problems arise only when such very general biotypes are named, numbered or otherwise specified.

The second and more specific usage of the term biotype depends on the gene-for-gene relationship between crop and pest, as described above. Where there is such a relationship it is possible to define precisely the genes which must be present in a particular individual for it to belong to a particular biotype. However, among bisexual insect pests, so far only the Hessian fly has been shown to have such a system. The widespread assumption that such a gene-for-gene relationship is usual for insect/plant relationships is certainly premature and currently unwarranted. In the brown planthopper, evidence to date suggests a polygenic system for the inheritance of virulence. More studies on the genetics of virulence in insect pests are urgently required.

A system of nomenclature exists for describing allopatric populations of a species (*see above*) and there is no reason why it should not be used also for virulence characteristics, if they really are sufficiently consistent to differentiate such populations. This may be true, for example, for the South Asian (India, Sri Lanka etc.) and South East Asian (Indonesia, Philippines, etc.) populations of *N. lugens* (Seshu and Kauffman, 1980). These perhaps might then correctly be termed geographical races. However, we have already provided some evidence for very considerable virulence differences between different populations locally within Sri Lanka so that such supposed racial differences require further study. It is evident

that before different geographical races are recognized and named, data on other aspects of genetic differentiation, such as biochemical differences, for example (*see* Berlocher, 1979), are desirable.

It is clear that a precise biotype terminology for any insect pest should be used only when considerable information on genetic variation, both within and between populations, is available. Such information is not available for most pests, so that if the term biotype is to be used it should be restricted to the general sense of Maxwell and Jennings (1980). However, it can be argued that biotype in this general sense is a superfluous term and represents no distinct biological concept. In most examples where it has been used in this way it could be dropped without any loss of clarity and frequently with considerable gain in objectivity of description.

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