PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Do Invading Species have Definable Genetic Characteristics? [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1986 **314**, 655-674
doi: 10.1098/rstb.1986.0079

Phil. Trans. R. Soc. Lond. B **314**, 655–674 (1986)
Printed in Great Britain

Do invading species have definable genetic characteristics?

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The search for general answers to this question dates at least from the seminal conference at Asilomar in 1964. It has included comparative surveys of a wide range of taxa, investigations within congeneric groups of why some species are successful invaders and others are not, and, at the intraspecific level, comparisons of genetic variability in colonist *versus* source populations.

The relevant data are reviewed. They suggest that successful invading species have genetic characteristics (defined here as the set of attributes that collectively determine the form in which, and frequency with which, genetic information is passed from one generation to the next), which need only be sufficiently protean to ensure rapid expansion in the new environment. Generalizations attempting to relate colonizing ability to polyploidy, to levels of genetic variability, heterozygosity, or phenotypic plasticity, or to mating system types, ignore the interaction in individuals of these components of the genetic system, and rarely consider chromosomal and genic controls of recombination. The poor predictive power of such generalizations is emphasized by considering invaders into the British flora, which are drawn from a wide spectrum of families and life forms. They include only a few 'colonizing species', those that habitually invade and occupy transient habitats and from which most models of invaders have been derived. Analysis of the origin and spread of *Spartina anglica* emphasizes that serendipity is often an important element in successful invasions.

Studies of the genetic consequences of invading, especially those that take an experimental approach, are more likely to throw light on current problems in evolutionary theory than those that analyse the shared attributes of past invaders.

Introduction

In defining the terms of my title, I shall adopt a recent and conveniently broad prescription of an invading species as one that 'enters a territory in which it has never before occurred, regardless of circumstances' (Mack 1985). A successful invader is one that rapidly expands from its founding colony or colonies. Such a species may or may not belong to the class of organisms that habitually invade and occupy transient habitats, and to which the term 'colonizing species' is usually applied. This is an important distinction, to which we will return. 'Genetic characteristics' are here defined as the set of attributes that collectively determine the form in which, and the frequency with which, genetic information is passed from one generation to the next. My remarks are confined to eukaryotes and are biased towards examples taken from the plant kingdom.

A landmark in the search for generalities in this field was the seminal conference at Asilomar, California, in 1964 (Baker & Stebbins 1965), a useful source for several other concepts in ecology. The first part of this paper considers attempts that have been made since Asilomar to characterize invading species at three different levels: comparative surveys of a wide range of taxa, comparisons within groups of closely related species, and, at the intraspecific level, comparisons between colonist and source populations. These data are collected under three heads, which examine whether invaders have genomes that differ consistently from other species:

(i) quantitatively (in features such as ploidy level and genome size);
(ii) qualitatively (for example in levels of heterozygosity);
(iii) in their levels of recombination (principally as affected by the mating system).

These categories are, of course, entirely artificial and hopelessly confounded, but correspond to the different ways in which the subject has been approached. The importance of considering the entire genetic system is emphasized in the fourth section.

The second part of the paper comments on some plant species that have invaded Britain, and includes an analysis of the origin and spread of *Spartina anglica*. Finally, I address the question: Why do biological invasions continue to interest geneticists and evolutionary biologists, despite what turns out to be the rather poor predictive value of general theory derived from studies of colonizing species?

Genetic attributes of invading species

Quantitative differences in the genome

Polyploidy

Since Manton first suggested, more than 50 years ago (Manton 1934), that polyploid plants have greater colonizing potential than their diploid progenitors, the link between polyploidy and colonizing ability has become widely accepted. Stebbins asserts, basing this on a study of Californian weeds reported at Asilomar (Stebbins 1965), that, although diploid annual plants may become weedy, 'if related diploids and polyploids exist in the same group of annuals, the polyploids have a greater chance of becoming widespread as weeds than their diploid relatives' (Stebbins 1971). This idea is extended by the observation that, of weedy species introduced into eastern North America from Europe, in only 10 out of 74 genera containing diploid and polyploid species did diploids invade whereas their polyploid relatives did not (Stebbins 1970). A more ecological dimension is provided by Ehrendorfer's data from Austrian vegetation types, which indicate a significantly higher frequency of neopolyploids in disturbed, early-successional biotopes (Ehrendorfer 1980). The presumed greater ability than their diploid relatives to colonize open habitats has been advanced as a major reason why polyploids make up a large proportion of north temperate floras. The repeated advances and retreats of the Pleistocene ice sheets would have created new habitats into which polyploids could spread. A similar explanation has been provided for the more northerly distribution of polyploid races of certain insects, including the wingless moth *Solenobia triquetrella* and several species of weevils, mainly in the genera *Otiorhynchus* and *Trachyphloeus* (Lokki & Saura 1980).

Studies of field distributions have also led to the suggestion that polyploids are frequently more widespread than their diploid relatives because they can successfully invade and occupy a wider range of environments, i.e. polyploids have broader niches. There are many examples of such distribution patterns in the European flora: among congeners, the tetraploid *Polygala vulgaris* ($2n = 68$) compared with the diploids *P. serpyllifolia* ($2n = 32, 34$) and *P. calcarea* ($2n = 34$) (Lack & Kay 1986); among subspecies, the ssp. *hederifolia* ($2n = 54$) of *Veronica* *hederifolia* compared with its progenitors ssp. *triloba* ($2n = 18$) and ssp. *lucorum* ($2n = 36$) (Tutin *et al.* 1972); and, at the species level, the tetraploid ($2n = 28$) compared with the diploid ($2n = 14$) cytotype of *Hippocrepis comosa* (Fearn 1972). There are also several exceptions (for example, specialist tetraploids and widespread diploids).

If we turn to modern invasive floras, it should be noted that all 18 of the species designated by Holm *et al.* (1977) as 'the world's worst weeds' are polyploids (Brown & Marshall 1981). By contrast, Crawley's list of the 20 most successful British aliens (Crawley 1987) contains nine known diploids, including species such as *Senecio squalidus* and *Veronica filiformis*, which belong to genera that have undergone extensive polyploidization (table 1).

TABLE 1. THE WORLD'S WORST 18 WEEDS OF CROPS AND BRITAIN'S 20 MOST SUCCESSFUL ALIENS

(Weeds, after Holm *et al.* (1977); aliens, after Crawley (1987).)

weeds	aliens
Cyperus rotundus	*Acer pseudoplatanus*
Cynodon dactylon	*Aegopodium podagraria*
Echinochloa crusgalli	*Avena fatua*
Echinochloa colonum	*Buddleja davidii*
Eleusine indica	*Centranthus ruber*
Sorghum halepense	*Crepis vesicaria*
Imperata cylindrica	*Elodea canadensis*
Eichhornia crassipes	*Epilobium brunnescens*
Portulaca oleracea	*Epilobium ciliatum*
Chenopodium oleracea	*Erigeron canadensis*
Digitaria sanguinalis	*Impatiens glandulifera*
Convolvulus arvensis	*Matricaria suaveolens*
Avena fatua	*Mimulus guttatus*
Amaranthus hybridus	*Reynoutria japonica*
Amaranthus spinosus	*Rhododendron ponticum*
Cyperus esculentus	*Senecio squalidus*
Paspalum conjugatum	*Smyrnium olusatrum*
Rottboellia exaltata	*Symphoricarpos albus*
	Veronica filiformis
	Veronica persica

If polyploids are better colonizers of new or disturbed environments (this would enable them to escape from their progenitor's site of origin), and if they can invade and occupy a wider range of environments (giving them ecological separation when newly arisen), it is not clear where such abilities reside. This is for three main sorts of reason.

First, the pre-eminence of polyploidy among the flowering plants and ferns makes broad comparisons dangerous. Earlier estimates that 30–47 % of angiosperms may be of polyploid origin (Stebbins 1950; Grant 1963) have recently been revised upwards to around 70 % or even 80 % (Goldblatt 1980; Lewis 1980). Moreover, it is now believed that polyploidy with chromosomal rearrangements and sequence changes in the genome during subsequent diploidization may have been an important process in animal evolution (Ohno 1970; Leipoldt & Schmidtke 1982).

Second, and related, is the multifarious nature of polyploidy and its variable, often fundamental, biological consequences. At the very least, true polyploidy (eupolyploidy) implies the presence in the somatic cell nucleus of three or more haploid sets of chromosomes. Beyond that basic definition, the term embraces a very wide range of conditions from autoploids with essentially similar genomes to alloploids completely lacking in homology. It is extremely difficult to separate the effects of genome multiplication *per se* from those of hybridity, except in artificially produced, homozygous autoploids. Experiments comparing induced autoploids with their diploid progenitors (Stebbins 1949; Sakai & Suzuki 1955; Garbutt & Bazzaz 1983; Dewey 1980), and also naturally occurring polyploids (Smith 1946; Roose & Gottlieb 1976), have produced somewhat equivocal results and are frequently dogged, in the latter case, by rapid ecological divergence from the ancestral species. However, they tend to support theoretical conclusions (Levin 1975) that newly arisen polyploids must either be competitively superior to, or escape from, their progenitors. The possible importance in this respect of the various and manifold effects of autopolyploidy in flowering plants have been recently reviewed by Levin (1983) and need not be repeated here. Suffice it to note that recent treatments of the subject emphasize a wide range of likely beneficial genetic, physiological and biochemical consequences of polyploidy (see also Jackson (1976) and various papers in Lewis (1980)). Perhaps the most germane of these consequences for present purposes are the wider ecological tolerances bestowed by gene duplication and subsequent diversification, and the buffering against inbreeding depression in founder populations that is afforded by the presence of several genomes (figure 1).

A third reason why it is difficult to relate polyploidy to colonizing ability is the frequent association of polyploidy with specific breeding systems and life-history types. For example, all known insect polyploids are parthenogenetic (Lokki & Saura 1980). The only known reptilian polyploids are all female triploid lizards, which are thought to reproduce parthenogenetically (Bogart 1980). The association between polyploidy and apomixis, or extensive vegetative propagation, in flowering plants and ferns is well known. Among annual or monocarpic plants, where it is rare, polyploidy is found predominantly in self-fertilizing species. These various forms of uniparental reproduction have profound significance, both for the establishment of founding colonies from one or a few individuals and for subsequent rates of population growth. They also confound direct ecological comparsions with diploid, but bisexual, relatives (but see below). At a more general level, as Stebbins points out, comparisons of the proportion of polyploids among successful weeds, as opposed to the flora as a whole, either at a national (e.g. Canada (Mulligan & Findlay 1970)) or regional (e.g. Indiana (Heiser 1950)) level, should take account of the fact that 'most weeds are annuals and that annuals have a consistently lower percentage of polyploids than herbaceous perennials' (Stebbins 1970).

Genome size

The enormous variation in the amounts of nuclear DNA in eukaryotes has aroused considerable speculation as to its function and evolutionary significance (Dover & Flavell 1982). For example, the nuclear DNA content in the haploid genome of flowering plants varies from 0.2 pg (1 picogram = 10^{-12} g) in *Arabidopsis thaliana* to 127.4 pg in *Fritillaria assyriaca*, a more than 600-fold difference (Bennett *et al.* 1982). Nuclear DNA content appears to have effects on the phenotype that are independent of the encoded informational content (termed 'nucleotypic' effects by Bennett (1971)), being correlated, for example, with cell size, minimum cell cycle time, meiotic duration, and minimum generation time.

A general ecological interpretation of these data has been advanced by Grime & Mowforth (1982), who relate genome size to selection under different climatic régimes. Their list of 162 flowering plants occurring in the British Isles (which incorporates data from Bennett & Smith

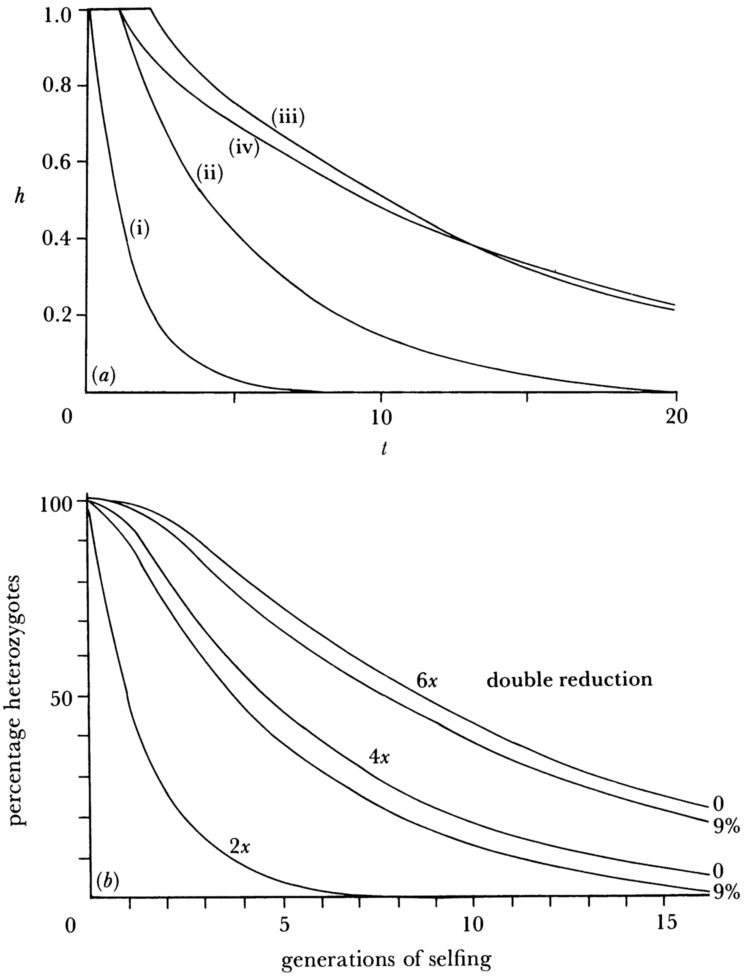

Figure 1. Loss of heterozygosity under various mating systems and ploidy levels. (*a*): Loss of heterozygosity on inbreeding in diploids with (i) self-fertilization, (ii) sib-mating, (iii) double first-cousin mating, and (iv) circular half-sib mating. The ordinate is the heterozygosity relative to the starting population, the abscissa is the time in generations. (*b*): Loss of heterozygosity on selfing in diploids, tetraploids and hexaploids. Note, by comparing (*a*) and (*b*), that selfing in tetraploids is equivalent to sib-mating in diploids.

(1976)) includes 17 introduced species, which are now well established. The average DNA content of the introduced species (2*C* DNA value = 13.37 pg) is not significantly different from that of the native species (11.92 pg), and includes species with large (*Lilium pyrenaicum*: 65.5 pg) and small (*Impatiens glandulifera*: 2.2 pg) genomes. Among congeners, *Avena fatua*, a successful invader, has a genome size among the largest in the genus (28.3 pg, compared with a mean of 16.9 pg for 20 *Avena* species in Bennett & Smith (1976)), whereas *Senecio squalidus* (1.8 pg) is the smallest in the genus (a mean of 4.8 pg for 14 species). The finding that nuclear DNA content may vary with-in species, and that in the ubiquitous grass *Poa annua* the variation is related to relative growth rate of seedlings in warm conditions (Mowforth & Grime 1983), offers the possibility of investigating more directly the effects on fitness of the nucleotype. However, there is insufficient evidence in general to relate genome size to either colonizing or invading ability (but see Grime, this symposium).

B chromosomes

Chromosomes that are additional to the basic complement occur very widely in both plant and animal populations. They are known from more than 1000 plant species and occur in more than 200 species in both the Gramineae and Compositae, families that have produced many weedy species (Jones & Rees 1982). Despite this, there is no general agreement about their adaptive significance or the forces controlling their transmission (Jones 1985). Although effects on plant performance (the odd/even effect in rye and other species), correlations with environment (in *Festuca pratensis*; Bosemark (1956)), and apparent selective advantage (in *Allium schoenoprasum* along the River Wye (Holmes & Bougourd, unpublished data)) have all been associated with B chromosome polymorphisms, no general patterns emerge relating such polymorphisms to invading species.

Qualitative differences in the genome

Among the questions that concerned those gathered at Asilomar were: Are successful colonizing species genetically more variable than non-colonizers? and, relatedly, Are their wide environmental tolerances characterized by genetic polymorphisms or individual phenotypic plasticity (then seen as alternative conditions)? A year after the conference proceedings were published, the reports by Hubby & Lewontin (1966) and Harris (1966), on electrophoretically detectable variation in *Drosophila* and man respectively, heralded two decades (at least!) of burgeoning research on protein variation, which should have helped to answer these questions. It has, if anything, served mainly to clarify the problems.

Several reviews of the extensive literature on isoenzyme variation in natural populations have compared different groups of species by using estimates of genetic variation such as the number of polymorphic loci per population, the number of alleles per locus, or the average number of heterozygous loci per individual. Although none of these reviews specifically considers colonizing or invading species as a group, and, for reasons advanced below, their conclusions should not be regarded uncritically, some interesting generalizations emerge.

First, among animal species, Nevo (1978, 1983) finds that cosmopolitan and widespread species are more variable than narrow-ranging and endemic species, and that habitat generalists are significantly more polymorphic than habitat specialists. We might imagine that invading species are more likely to be drawn from the first category in both of these comparisons (but see below).

Among plants, with their greater diversity of mating systems and ploidy levels, more recent reviews have emphasized not only the general level of genetic variation but its distribution within and between populations (Brown 1979; Gottlieb 1981; Hamrick 1983; Loveless & Hamrick 1984). Two generalizations are relevent to present considerations. First, widespread species have greater total allelic diversity than endemic or regional species but hold less of this variation between their populations. Second, and somewhat at variance, there seems to be little difference in overall diversity between species from different successional stages, yet late-successional species vary more within populations than do early and 'weedy' species (Hamrick 1983; contrast with Hamrick *et al.* (1979)). Studies of closely related species do not always support these generalizations. Babbel & Selander (1975) found greater genetic variability in the widespread *Lupinus texensis* than in the edaphically restricted *Lupinus subcarnosus*, but two *Hymenopappus* species of contrasting amplitude had similar levels of variability. Similar levels of variability have also been found in species of *Clarkia* (Gottlieb 1973) and *Gaura* (Gottlieb

& Pilz 1976) with contrasting ranges. Early-successional species of *Pinus* have less within-population variation than late-successional species (see Hamrick 1983). However, at the intraspecific level, colonist populations of the perennial outbreeding grass *Puccinellia maritima* are more variable, in terms of quantitative, metric, genetic variation, than those in later successional stages (Gray *et al.* 1979; Gray 1986).

Perhaps the most consistent and profound effect observed in reviews of plant allozyme data is that due to the mating system. The major dimension of variation is not in the general levels of genetic diversity, although there are consistent differences, but in the way in which it is shared between populations. Hamrick (1983), surveying a data set of 91 species, noted that 44% of the variation in self-pollinating species was distributed between populations, compared to only 6% for wind-pollinated outcrossing species. Gottlieb's review is particularly useful in this respect because it recognizes the overriding influence of polyploidy on levels of heterozygosity and compares inbreeders and outbreeders at the diploid level (Gottlieb 1981). It confirms the contrasting pattern of population genetic differentiation in relation to mating systems.

Comparison of patterns of population genetic structure and the way they are affected by the mating system brings into focus a central problem in the study of invasions: how representative of the genetic diversity within the species as a whole is that which is present in invading populations? (And, at the level of individual traits, does it represent selected colonizing ability?) Clearly, within self-fertilizing plant species, there is a much greater probability that a single invasion will carry less of the total variability than in outcrossing species. Even multiple introductions of 'selfers' may transmit only a small proportion of the species variability. This idea is largely confirmed by studies of self-pollinating species introduced into North America and Australia. Classic studies include those on *Avena barbata* (Clegg & Allard 1972) in America, and *Xanthium strumarium* (Moran & Marshall 1978) in Australia, but many examples of allozymically depauperate populations of such species are known (Brown & Marshall 1981; Barrett 1982; Jain 1983; Barrett & Richardson 1986). An exceptional species among introduced weeds, the genetic structure of which has been studied in detail, is *Echium plantagineum*, an Australian population of which contained high levels of multi-locus genotypes, and which, interestingly, is an outbreeder (Brown & Burdon 1983).

Irrespective of mating system effects, the invasion process itself will have a fundamental effect on the relative amounts of variability in the colonist and source populations. Considerations include the effects of a small number of founders (a population bottleneck), the frequency of founding events (repeated immigrations), and the distance over which the invasion occurs (determining whether the founder could have come equally well from a geographically central or peripheral population). These sorts of problem have particularly concerned animal geneticists, and two examples from the recent literature will serve to illustrate that, even in well-documented invasions, there are no hard-and-fast rules. The patterns of variation in allele frequency at ten polymorphic enzyme loci in the introduced giant toad *Bufo marinus* have been compared in local and national Australian populations by Easteal (1985), who concludes that genetic drift has been the most potent force generating the observed patterns, natural selection having played little, if any, rôle. By contrast, Prevosti *et al.* (1985) describe very rapid effects of natural selection in *Drosophila subobscura* populations that have recently (1978) invaded Chile. They attribute the rapid emergence of clines in chromosomal arrangements, which parallel those in Old World populations, to the effects of selection on a broad-niched species with high reproductive potential and few indigenous competitors.

In view of variation in the invasion process and its associated effects, it is perhaps not surprising that consistent differences in levels of genetic variation between colonizers and non-colonizers, or colonist and source populations, are hard to find. It is certainly not yet possible to translate into genotypic variation the 'general flexibility', 'greater physiological tolerance' and 'generalism for resource utilization' (Parsons 1983) displayed at the phenotypic level by the ideal colonizing species. There is a temptation to do so in terms of general models of buffered genetic systems incorporating high levels of genic heterozygosity. Speculations about heterozygosity based on protein electrophoresis seem premature for several reasons. These include the large standard errors associated with the measurement of average heterozygosity (Nei & Roychoudhury 1974), the relatively small effects that population bottlenecks have on average heterozygosity, compared with the average number of alleles at each locus (Nei *et al.* 1975), and the fact that allozyme variation represents an extremely small, and possibly unrepresentative, part of the genome. The few studies that have compared patterns of allozyme and polygenic variation in the same species have produced contrasting results. These range from a close relationship between enzyme and morphological variation (in *Avena barbata* (Jain & Marshall 1967) and *Liatris cylindracea* (Schaal & Levin 1978)) to complete contrasts between the two measures of genetic variation (*Xanthium strumarium* (Moran *et al.* 1981) and *Hordeum spontaneum* (Brown *et al.* 1978)).

A recurrent theme in discussions of colonizing ability in plants is the extent to which it is based on genetic variation or phenotypic plasticity. These are generally viewed as alternative pathways to colonizing success. Jain (1979) lists three pairs of species, *Avena fatua* and *A. barbata*, *Bromus mollis* and *B. rubens*, and *Limnanthes alba* and *L. floccosa*, in which the first-named has more or less ubiquitous genetic polymorphisms, whereas in the latter genetic monomorphism is coupled with high levels of phenotypic plasticity. These sorts of contrast among congeners support theoretical predictions that selection operates so as to favour either genetic or plastic variation (Thoday 1953; Levins 1968). However, if, as Bradshaw (1965) proposed, and later empirical evidence confirmed, phenotypic plasticity for specific characters is under genetic control (not necessarily related to heterozygosity (Schlichting & Levin 1984)), then the association between plastic and genetic variation need not be negative. In their trials of five populations of the grass *Danthonia spicata* across six environments, Scheiner & Goodnight (1984) found no relation between the amounts of genetic and plastic variation, none of the correlations for 12 traits being significant. Although many successful weeds are characterized by high levels of phenotypic plasticity (for example, *Rumex crispus* (Hume & Cavers 1982)), to invoke plasticity to account for their success in the absence of genetic variability amounts to 'adaptationist storytelling' (Gould & Lewontin 1979).

To escape the problem of correlation analysis of *post hoc* events, there is a clear need to test ideas about the importance of genetic variation and plasticity in colonizing species, either by controlled introductions or by careful comparison, within the same species, of several populations that are clearly colonizing or not colonizing (ideally by reciprocal transplants).

Both these approaches have been taken in a rare empirical study of colonizing ability, involving the annual, largely inbreeding, legume *Trifolium hirtum*, introduced into California in 1946. Experimental introductions to roadside sites were made of populations classified on the basis of four morphological and four allozymic markers as being of high, medium or low genetic variation (Martins & Jain 1979). Unfortunately, only two years' results are reported, but there is some evidence that the more variable populations were the more successful colonizers. In a complementary study, roadside (colonist) *T. hirtum* populations displayed differences from older range (non-colonist) populations in a number of phenotypic features that could explain their success as colonizers, including consistently (but not statistically significant) higher outcrossing rates and genetic variability (Jain & Martins 1979).

Finally, a link with the next section is provided by studies on Drosphilidae, notably those of Carson and his colleagues on Hawaiian species (Parsons (1983), Carson & Templeton (1984) and Carson (1987) provide recent summaries). These studies indicate that widespread colonizing species are, in general, characterized by chromosomal monomorphisms or inversion polymorphisms, which change relatively little throughout the species' range. Whatever the levels of genic heterozygosity, and colonizers may have substantially higher levels, such structural heterozygosity provides, in a diploid, cross-fertilizing species, a genetic system not easily perturbed by inbreeding. Thus, successful invaders may go through repeated colonizing episodes and preserve the essential integrity of the genome.

Patterns of recombination

Setting aside the types of genome rearrangement and alterations that are now known to occur outside the orbit of classical Mendelian genetics (for plants, for example, see Walbot & Cullis (1985)), the only major factor that exerts control on genetic recombination, and which has been considered in relation to colonizing species, is the mating system. Coupled with this, the longevity of individual genotypes affects the frequency with which recombination events occur, and is also of direct interest to colonizing ability. Rarely considered, but vitally important, is meiotic control of recombination (see later).

Recent reviews of the plant literature have emphasized the link between colonizing success and uniparental modes of reproduction, either self-fertilization, apomixis (agamospermy) or clonal propagation (Brown & Marshall 1981; Brown & Burdon 1987). Indeed, this rather general observation has generated that rare specimen in ecology, a rule (Baker 1967). Baker's rule states that weedy annuals will be either self-fertilizing or agamospermous, or if outcrossing they will tend to be wind-pollinated, and that weedy perennials, which may be self-compatible, will display extensive 'vegetative reproduction' '...which here achieves the same end, i.e. rapid multiplication of individuals with appropriate genotypes' (Baker 1974).

Broad surveys support the association between selfing and weediness. Mulligan & Findlay (1970) bagged the flowerheads of 65 Canadian weed species to see if external pollinators were needed. They noted that all 33 annuals, and 21 out of 23 biennials and caespitose perennials, set seed (but that no stoloniferous or rhizomatous perennials set seed). Price & Jain (1981) classified 400 randomly selected species from 43 plant families according to their occupancy of habitat types ranging in 'stability; from woods, bogs and swamps to highly disturbed, man-made habitats. They found that predominant selfing or apomixis was significantly more common in species from the more disturbed habitats.

Interestingly, only half of the 18 'world's worst weeds' are self-pollinated, but Brown & Marshall (1981) emphasize that the remaining outbreeders 'invest massive resources in vegetative propagules'. A similar pattern is seen in the 20 most successful British invaders (Crawly 1987) and is typified by the contrast between the self-incompatible, but vegetatively vigorous, *Veronica filiformis* and its congener, the annual, autogamous *V. persica*.

Whereas most species of invading animals are outbreeding, several examples of self-fertilizing hermaphrodites or parthenogenetic species are known. In the terrestrial slug families Arionidae and Limacidae, those European species that have invaded North America are predominantly drawn from self-fertilizing forms (Selander *et al.*, quoted in Barrett & Richardson (1986)). To the success of parthenogenetic insects, noted earlier, can be added that of several colonizing parthenogenetic lizards (Bogart 1980; White 1970). Parthenogenesis is particularly common among parasitic insects, which may constitute about half the known animals on earth (Price 1980).

The profound effect of breeding systems on the genetic structure of plant populations has been emphasized earlier. Autogamy and breeding among close relatives increases correlations between uniting gametes, reduces recombination, and maintains gametic phase disequilibrium (Loveless & Hamrick 1984). Outcrossing generally decreases correlations between uniting gametes and, by increasing the effective population size, reduces the subdivision between populations.

The generally damaging effects of inbreeding on normally outbreeding species, inbreeding depression, are well known and operate (presumably) via reduced heterozygosity and the exposure of deleterious recessive alleles. Reduced fitness due to inbreeding of normally outbred plants has been demonstrated in natural populations (e.g. net reproductive rate in *Gilia achilleifolia*; Schoen (1982)), and, in a recent review, Mitton & Grant (1984) have emphasised the overriding influence of heterozygosity on growth and developmental stability. These considerations militate against outcrossing species establishing populations from single founders. However, factors such as the buffering effect of polyploidy on loss of heterozygosity (figure 1), and of meiotic controls on recombination (below), should be taken in account.

Furthermore, the prediction that autogamous species, or apomicts, are devoid of heterozygosity is not borne out. Indeed, contrary to expectation, parthenogenetic animal species have significantly higher levels of heterozygosity than do sexual species (Nevo *et al.* 1984). Although confounded by polyploidy, even diploid parthenogenetic races may have higher heterozygosity than bisexuals, as demonstrated by the insect *Polydrosus mollis* (Lokki *et al.* 1976). There is evidence among *Taraxacum* species that the greater heterozygosity in the agamospecies reflects not only their hybrid origin but that most loci that are polymorphic in diploid species are found fixed as heterozygotes in agamosperms (Hughes & Richards 1985; J. Hughes & A. Richards, personal communication). The generally higher than predicted levels of heterozygosity in natural populations of autogamous plants, and lower levels than predicted in outbreeders, have been termed 'the heterozygosity paradox' (Brown 1979).

In addition, plant mating systems are especially flexible. Rare increases in outcrossing rate among habitually self-pollinating species may have a fundamental effect on the provision of new recombinant genotypes. In *Festuca microstachys*, for example, outcrossing rates of less than 1% were, in one year, elevated to 6.7% (Adams & Allard 1982). Shifts in mating system towards higher outcrossing in introduced weedy species have been documented in Australian populations of *Bromus mollis* (Brown & Marshall 1981) and *Trifolium subterraneum* (Cocks & Phillips 1979). The apparently higher outcrossing rate in colonist *Trifolium hirtum* populations, reported above, provides a further example.

Although mating systems have received considerable attention in respect of colonizing ability, the importance of chromosomal and genic controls of recombination should not be forgotten. In fact, these may interact further to preserve combinations of favourable genes in inbreeding plants. Callow (table 2) has collated data from 71 natural polyploid flowering plant species where meiotic and breeding behaviour are known (57 tetraploids, 10 hexaploids and 4 octoploids) (R. S. Callow, personal communication). All 23 inbreeding species (from 9 genera) formed only bivalents at meiosis, whereas 37 of the 48 outbreeding species exhibited multivalent formation. This argues for balance in the breeding system and indicates that, whether diploidized or amphiploid, pairing behaviour can further stem the loss of heterozygosity on inbreeding.

TABLE 2. THE RELATION BETWEEN THE MEIOTIC AND BREEDING BEHAVIOUR OF 71 NATURAL POLYPLOIDS

(57 tetraploids, 10 hexaploids and 4 octoploids; of these 71 angiosperm species, 48 are grasses, and of the 37 genera, 23 are grasses. Data provided by R. S. Callow. $\chi^2[1] = 37.13$ ($P < 0.01$).)

	inbreeding	outbreeding	total species
form bivalents at meiosis	23 (9 genera)	11 (7 genera)	34
form multivalents at meiosis	0	37 (21 genera)	37
total species	23	48	71

Genetic systems

Discussion of the genetic attributes of colonizing species has attempted to deal separately with the component parts of the genetic system. It is quite clear – indeed, it is the patent straw man in this essay – that this separation is difficult, and probably misleading. Asking simply whether inbreeders or polyploids, or heterozygotes, are better colonizers than outbreeders, diploids or homozygotes is to make a (literally) elementary mistake. Many of the interconnections in the elements of genetic systems have emerged above, such as links between polyploidy and heterozygosity. Other aspects are fundamental tenets of genetics, e.g. the relations between inbreeding and heterozygosity. Yet others are trends perceived only at a general level and not mentioned above, for example, a general relation between levels of heterozygosity and amount of nuclear DNA (Pierce & Mitton 1980; Nevo *et al.* 1984).

The rhetoric regarding the dangers of approaches that fragment systems, and of the problems of correlation analysis, need not be repeated here, except to say that important factors are easily omitted. For example, few surveys consider the meiotic or genic control of recombination, yet, as mentioned earlier, these add an important dimension to individual genetic systems. They can suggest not only why species are widespread but why they may be rare. This can be illustrated by *Mibora minima*, a diminutive grass rare in Britain, which appears to combine an annual life history, diploidy ($2n = 14$), and (although self-compatible) marked protogyny with the ecologically precarious habitat of temporarily open areas in sand dunes. In terms of the above discussion, its rarity seems assured! Recent examination of meiosis (C. Ferris, R. S. Callow & A. J. Gray, unpublished data) reveals that the majority of chiasmata are proximal (close to the centromere), itself a rare phenomenon but one that indicates a restricted pattern of recombination. Proximal chiasmata are known in *Allium porium* and *A. fistulosum*, and in males of the grasshopper *Stethophyma grossum*, which is also a rare species once believed to have been widespread. Limited recombination, which protects normal outbreeders from the effects of inbreeding and may preserve favourable combinations of non-allelic genes, in both *Mibora* and *Stethophyma* probably arose in favourable habitats, which now have largely vanished.

Mention of the historical element raises a second, and more serious, pitfall that accompanies the fragmenting of integrated genetic systems from the biological entities of which they are a part: the seductive, but well-publicized, 'adaptationist programme' (Gould & Lewontin 1979; Harper 1982). This may be illustrated by dandelions. Of more than 2000 species so far described in the genus *Taraxacum*, around 90% are obligate agamosperms (Richards 1973). These agamosperms are polyploids or aneuploids and contain many highly successful weeds. They are more widespread than the primitive sexuals, which are almost always diploid (rare triploid mutants occur), and the two types have a distribution that suggests that, in common with cases discussed above, the polyploids were able to exploit the disturbed habitats left by the retreating Pleistocene ice. The high levels of heterozygosity fixed by the breeding system in the agamospecies have been mentioned earlier, and it has also recently been established that genetic variation occurs between siblings (Mogie 1985; Ford & Richards 1985; van Oostrum *et al.* 1985), possibly by somatic recombination in the genome by transposable genetic elements (Mogie 1985). The temptation to ascribe the success of the agamospecies as weeds to these perfectly adapted features of their genetic system is overwhelming. However, the story is incomplete without, and spoiled by, knowledge of the ecology of the primitive sexual species, many of which, although restricted geographically (in Europe to the south and Mediterranean), have distinctly 'weedy' habitats. Even high alpine species tend to be found associated with paths and disturbed areas and rarely in closed vegetation (A. J. Richards, personal communication). It appears there is something in the biology of *Taraxacum*, possibly the rosette growth habit with a well-developed tap root, that makes it a poor competitor, and which confers the escapist, and therefore weedy, characteristics. Dandelions, it seems, were 'preadapted' to become weedy.

Invaders in the British flora

It is immediately clear, from examining any list of the most successful invasions in the British flora, that the considerations in the first part of this paper must be set aside in favour of a series of anecdotes. This is partly because our ideas about the genetic attributes of colonizing plants, as conceived at Asilomar, have been biased by the extensive studies of those European, and especially Mediterranean, species introduced to North America and Australia. The influence of man on the British flora since the Middle Ages has resulted in introductions which have been drawn from a wide and largely unpredictably spectrum of families and life forms. They include escaped ornamental shrubs, such as *Rhododendron ponticum*, *Buddleia davidii*, *Reynoutria japonica* and *Symphoricarpos albus*, as well as aquatic and wetland species, such as *Impatiens glandulifera* and species of *Elodea*. The introduction and spread of several of these species has been well documented; for example, the spread of *Elodea canadensis* that was associated with the extensive network of canals and waterways in the 19th century (Simpson 1984). The invaders in the British flora have little cohesion as a group because they are not all colonizing species, i.e. they are not drawn exclusively from the subset of species which habitually invades disturbed or transient environments (although a few are, e.g. *Avena fatua* and *Matricaria suavolens*). In this respect, it is clear that not all colonizers become invaders (although all invaders colonize, and in doing so may sometimes enter stable communities and replace existing species).

Of those species sufficiently common to appear in their distribution atlas, Perring and Walters (1962) designated 239 taxa as introductions and a further 363 as probable or certain natives whose distribution has been extended by man's activities. Not all have become invasive. One such introduction, that of *Spartina alterniflora*, gave rise to a well-known invasion by its derivative, *Spartina anglica*. The elements of this particular invasion are worth considering in the light of the first part of this paper.

The origin of *Spartina anglica* has been documented in detail by Marchant (1967, 1968), and its derivation via a sterile F_1 hybrid, designated *S. townsendii*, and subsequent chromosome doubling, has become a classic textbook example of a natural allopolyploid. Interestingly, it has not been possible either to repeat the cross or to induce an existing F_1 to double its chromosomes. Pairing behaviour was very difficult to observe, but low multivalent frequency, morphological and cytological evidence, and the presence of sterile polyhaploids and putative backcross hybrids with *S. alterniflora* point to the allopolyploid origin. The possibility of an autotetraploid origin is further reduced by preliminary evidence of variation in the pattern of electrophoretic phenotypes of phosphoglucose isomerase (PGI, EC 5.3.1.9) in the three species (A. J. Gray & P. E. M. Benham, unpublished results). The pattern of phenotypes on horizontal starch gels suggests that two loci, with non-overlapping parental bands with distinctly different mobilities, have been combined in the F_1 hybrid and amphidiploid.

The site of the original hybridization was believed to be Hythe in Southampton Water, where the North American *S. alterniflora*, probably introduced by shipping, came into contact with the European native *S. maritima*. Thus, the first element in this invasion was chance. The progenitor species may have been in contact for about 70 years near Hythe, but elsewhere *S. maritima*, native to southern Europe and Africa, had disappeared from the estuary by the late 1830s, and *S. alterniflora* was not recorded before about 1816. Both species have continued to recede, *S. maritima* now being restricted largely to saltmarshes in Essex and *S. alterniflora* to two or three known sites. The recession is inseparable from the spread of *S. anglica*, but is seems likely that the range of *S. maritima*, which is ecologically differentiated from the amphidiploid, was contracting independently; it is at its northern limits in Britain and rarely sets seed. The relatively brief contact between two species outside their centres of distribution was quite serendipitous.

A second element in the invasion of *S. anglica* is clearly the perennial nature of the species involved, enabling the hybrid to survive on its site of origin, possibly to overcome the initial deleterious effects of polyploidy (Stebbins 1971; but see Levin (1983)), and eventually to have its fertility restored by natural chromosome doubling. Beyond this stage the full complex of features associated with polyploidy will have come into play and it is not possible to disentangle these. Gigas effects, increases in cell size, higher rates of net photosynthesis, larger seeds, later flowering, more vigorous vegetative growth, greater resistance to pathogens because of enhanced levels of secondary products, greater biochemical diversity – all these, and other effects, have been associated with autoploids (Levin 1983), and to them may be added the effects of hybridity. One important, and perhaps overriding, element is the fact that the ecological area lower down the shore, into which *S. anglica* expanded, had formerly been occupied only by a few annual species of *Salicornia*, i.e. there was a vacant niche (unexploited space and resources, usually only recognized when it has been occupied!). The remarkable spread of *S. anglica*, both natural and aided by planting, has been well charted (Goodman *et al.* 1959; Hubbard & Stebbins 1968; Ranwell 1967; Doody 1982), as has its current decline along the south coast (Haynes & Coulson 1982; Gray & Pearson 1984). The species continues to spread elsewhere. In China, where it was introduced as recently as 1963 (from Essex and Dorset), there are now in excess of 33000 hectares (Chung 1983).

A description of other invasions in the British flora would serve only as a catalogue of similar combinations of chance and circumstance, of changes in human, and especially agricultural, activity and of the paramount importance of serendipity. Hindsight bestows perfectly acceptable explanations for all cases of successful invaders, but the predictive power of these explanations is low. A knowledge of genetic attributes may rule out some species as unlikely to become invaders, but this will be a small list. At the other end of the scale there are several potential invaders that have expanded little beyond their sites of introduction (e.g. *Acaena anserinifolia*, a serious weed in its native New Zealand) or origin (e.g. *Senecio cambrensis*, an amphidiploid with all the apparent genetic attributes of *Spartina anglica*). Crawley (1987) concludes that 'what little we do know tends to suggest that we shall never be able to predict which of a set of invaders is likely to establish and which, having become established, is likely to become abundant'.

Biological invasions and genetic change

Brown & Marshall (1981) conclude that colonizing species are interesting to geneticists 'not so much because they form a homogeneous group, but because they display a wide range of evolutionary pathways'. In the wider context of invading species, this can be extended to the assertion that studies of the shared attributes of successful invaders are unlikely to provide as many insights as those that focus on the genetic changes that invaders undergo, i.e. on the genetic consequences of invading. Particularly interesting is the idea that biological invasions may occasionally enable species to break their genetic moulds in the sense of escaping, to various degrees, from the many internal and external constraints on the genetic system.

This idea has many facets. It is embodied in current models of founder-induced speciation, such as founder-flush speciation (stochastic genetic effects in small founding populations followed by rapid expansion under a relaxed selection régime that allows genetic remodelling) and genetic transilience (disruptive effects through drift on major genes followed by strong selection in a new genetic milieu) as well as in the older model of 'genetic revolutions' in peripheral founding populations (Mayr 1954). The possible rôle of small founding populations in speciation has been extensively reviewed recently by Carson & Templeton (1984), who emphasize its potential importance, and by Barton & Charlesworth (1984), who find no support for a major rôle. This lively debate is part of a general evolutionary problem, that of defining the circumstances under which species, largely observed to be in some form of stasis, move from one adaptive peak to another (as envisioned in Wright's shifting balance theory of evolution (Wright 1955)). Founding events provide one circumstance in which rapid changes in the external and internal (genetic) environment might occur. These events provide a possible escape from the homogenizing effects of large populations, or perhaps alter the balance of advantages in pleiotropic genes such that one of the characters they control is no longer disadvantageous, or, by escaping from a predator or pathogen, change the rules governing frequency-dependent selection. All these imagined mechanisms essentially disrupt the genome and then change the circumstances under which it is reassembled.

Unfortunately, there is little empirical evidence to test these speculations. Of those features described earlier, the shifts in mating system in some plant colonizations, the genetic differences between source and colonist populations, and the dramatic impact of *Spartina anglica* all attest to the fact that biological invasions may sometimes involve rapid genetic change. In addition, there is some evidence that the pattern of genetic correlations between fitness components may be disturbed by inbreeding (see, for example, Rose 1984) and by novel environments (Service & Rose 1985). Negative correlations, which are commonly observed between fitness components in natural populations, are believed to be a major constraint on evolutionary change (Antonovics 1976; Lande 1982; Rose 1982). A recent study of quantitative genetic variation in two natural populations of *Impatiens capensis* suggests that small population size and strong selection, as often occurs in plant species, may lead to very different patterns of genetic correlation and heritability between populations (Mitchell-Olds 1986).

To this circumstantial evidence there is the need to add data from field experiments. Experimental introductions of the type made with *Trifolium hirtum*, described above, where populations in which at least some parameters are known are introduced to a wide range of habitats, have considerable promise as a technique for helping us to understand the genetic consequences of invasions. Most invasions represent (successful) attempts at such introductions, but they frequently happened too far in the past to enable a characterization either of the event or of those individuals that were the first invaders. An experimental approach is likely to prove considerably more informative than comparisons of the genetic characteristics of those species that have been successful invaders.

I am grateful to C. Ferris and Dr R. S. Callow for permission to use unpublished data, to Dr R. S. Callow and Dr A. J. Richards for helpful discussions, and to Mrs P. E. M. Benham and Mrs M. K. Perkins for preparation of the manuscript.

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Discussion

R. N. Mack (*Washington State University*). I dispute the suggestion that *Mibora minima* is likely to become rarer. It has a successful strategy, flowering and setting seed before other annual species. I support the view that diversity in the gene picture facilitates colonization. *Bromus tectorum*, taken from a range of habitats, exhibits some 15 systems in one species.

A. J. Gray. *Mibora* seems to have an assured future in the places where it grows. The point is that its rarity might have been thought to be due, at least partly, to its outbreeding in disturbed habitats where a retention of characters would be an advantage. Actually the meiotic process retains certain gene combinations, showing how important it is to look in detail at the genetic processes. On *Bromus*: this illustrates well how there may be a range of solutions to the same evolutionary problem.

J. L. Harper, F.R.S. (*Unit of Plant Population Biology, School of Plant Biology, University College of North Wales, Bangor, Gwynedd, U.K.*). How far is the picture distorted by the habit of explaining how perfect organisms must be to have got where they are! Would it not be better to ask why they do not invade new habitats? Why not do translocation experiments with plants like *Mibora* to test hypotheses of the 'why not, where not?' variety?

A. J. Gray. I agree. Perhaps we should test *Mibora* in a field of winter wheat! My paper argues against looking at how well individuals or species fit where we find them and for an experimental approach, perhaps to seek alternative pathways of colonization.

M. B. Usher (*Department of Biology, University of York, U.K.*). I would like to comment on Professor Harper's remarks relating to *Mibora minima*. I collected about 10 cm^3 of the sand from the Aberffraw sand dunes in May, after *Mibora* has seeded. I scattered this sand in a small area of my garden in York, and three or four plants of *M. minima* developed from the seed bank in the following August/September, and flowered in May the following year. During the subsequent four years the population of *Mibora* in the garden soil has increased. *Mibora* can clearly survive in other kinds of soil apart from the sand-dune soils of Aberffraw, and it can also survive in what is probably the colder climate of the northeast of England.

A. J. Gray. *Mibora* has also been recorded as a weed of nurseries and garden centres in Dorset and elsewhere, as a result of transfer of seeds from the Channel Islands.

K. Joysey (*Department of Zoology, Downing Street, Cambridge*). I welcome your comments about genetic change. I am an evolutionist, not an ecologist, and I must stress that species should not be talked about as if they are entities. Speciation is associated with periods of rapid change, and this almost always also involves invasion. Only rarely has the genetic difference between a source population and that in the invaded region been quantified. For example, the gene frequencies in man in Africa were sculpted by diseases. In Guyana, there has been about 50% infant mortality in the first two years of life, exerting strong selection. We are now looking at the genetic bottlenecks in plant and animal colonizations, but it is hard to determine where source populations came from. Where, for example, did British *Elminius modestus* originate from?

Sir Hans Kornberg, F.R.S. (*Department of Biochemistry, University of Cambridge*). As a biochemist, I am increasingly worried by the lack of attention to causes. For example, the discussion of colonization by the collared dove seems to begin at the point where it appeared in Britain and then spread. But the key question may be why it failed to colonize before. If two microorganisms are tested in a medium novel to them, and one succeeds while the other fails, we should ask why. One may have acquired a plasmid, say, giving heavy-metal tolerance. We should look at the impact of the sudden development of such capacities. If a species apparently flourishes both on a lead-contaminated tip and in a woodland, are the individuals that appear in those different habitats really the same? Could their roles be reversed? If I had sickle cell anaemia, it would handicap me here, but help me in a area in which malaria was prevalent. We have to ask whether the successful organism is really the same as the unsuccessful.

A. J. Gray. Professor A. D. Bradshaw and his colleagues have looked at the genetic basis of metal tolerance in plants and demonstrated that those not on the contaminated soils are generally those that do not have the appropriate gene. In recent writings, Professor Bradshaw has used the word 'genostasis' to cover this type of concept, where species cannot move from their adaptive peak. Small populations subject to drastic changes in many factors may be the site of rapid evolutionary change because genetic variance–covariance patterns are disturbed. Certainly fitness components are not always negatively correlated genetically in such populations, removing one of the constraints widely believed to limit evolutionary change. Studies of such correlations and of the variation in heritabilites between populations of different size and ecology would be most instructive.