

# ECOLOGY OF BIOLOGICAL INVASIONS: An Australian Perspective

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## GENETIC ATTRIBUTES OF INVADING SPECIES

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A consideration of the genetic attributes of invading species, and the genetic consequences of colonisation, depends on the concept of colonisation that is used. Clearly the process of colonisation is an integral component of the population biology of all plants and animals. In this volume, however, we are concerned with biological invasions and hence colonisation on a grand scale. We therefore define an invasion as the successful founding of a colony in a region where none previously existed followed by rapid expansion of the range of the invading species. Biological invasions may occur on various geographical scales from simple extension of range to intercontinental migration. The effects of such movement may involve the entry into a new physical or biological environment, sharp reductions in population size, restricted gene flow, and difficulty in finding mates. These influences can have major effects on colonisation; the ability of a species to cope with them may determine the likelihood of a successful biological invasion. In this chapter we examine the importance of these influences and whether successful invading species as a group share similar genetic characteristics.

Several detailed works on the genetics of colonising species are available (e.g. Baker and Stebbins 1965; Parsons 1983) and therefore there is no need for an exhaustive treatment of the subject. Instead we organise this chapter by posing a number of inter-related questions regarding the genetic aspects of biological invasions:

- 1) What is the effect of the invasion process on the amount of genetic variation in populations?
- 2) What levels of genetic variation are found in species that are successful invaders?
- 3) What genetic systems are associated with colonising success?
- 4) What are the relative contributions of inherited and environmentally controlled variation in life history traits of colonising species?
- 5) What evidence exists for local genetic differentiation following invasions?

Where possible we answer the above questions using examples of plant and animal invasions of Australia.

### WHAT IS THE EFFECT OF THE INVASION PROCESS ON THE AMOUNT OF GENETIC VARIATION IN POPULATIONS?

A new colony is usually, but not always, established by a small number of immigrants. In theory this could lead to a loss of genetic variation through sampling effects during the population bottleneck as a small random sample of individuals may not contain all the variation present in the parent population. Nei, Maruyama and Chakraborty (1975) studied the theoretical consequences of this process and concluded that the level of variability does in fact decline but that this depends not only on the size of the founder population, but also on the speed of recovery of large population size (i.e. for how many generations the population remains small). The theoretical effect of founder population size and speed of recovery are shown in Table 1. Nei, Maruyama and Chakraborty (1975) also point out that the effect of a bottleneck in population size on average heterozygosity (i.e. proportion of loci in an individual present in the heterozygous state) is smaller than on the average number of alleles at each locus. Most additional alleles are at very low frequency and contribute little to heterozygosity. These alleles are most easily lost by sampling effects.

An example of the effect of the colonisation process on the level of genetic variation was reported by Richardson, Rogers and Hewitt (1980) for the rabbit (*Oryctolagus cuniculus*) which occurs naturally in Spain.

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After domestication it was taken to England by the Normans and later to Australia in the mid 19th century. From the twenty or so animals released in Victoria the species increased rapidly in number and range until it reached Western Australia. During this latter phase of range expansion the 'rabbit front' apparently moved at a rate of 100 km/year (Myers 1971). The colonisation process in Australia therefore consisted of several stages. As well as the original colonisation event there was a sequence of founder events of local populations as the rabbit spread westward continuously over a period of 60 years and 3000 km. From the changes in allele frequencies of electrophoretic loci that accompanied this series of events (Table 2) it can be seen that domestication apparently led to significant changes in allele frequencies, the move to Australia little change, and the spread to Western Australia no change in frequency of common alleles but the apparent loss of a rare carbonic anhydrase allele. These results are in accord with the theoretical expectations and show that long-distance migration involving relatively few immigrants may have little effect on the amount of genetic variation if rapid population increase follows the initial establishment.

Marked reductions in genetic variation accompanying continental migration can occur in selfing species if propagules originate from a limited sampling of populations in the native range. Surveys of isozyme variation in native North American populations of barnyard grass (*Echinochloa microstachya*) reveal considerable variation among populations but little variation within populations (S.C.H. Barrett and A.H.D. Brown, unpublished data). Most populations surveyed were composed of a single homozygous genotype. The species was introduced this century to rice fields in New South Wales, probably as a contaminant of imported rice stocks from California (McIntyre and Barrett 1985). Since introduction, *E. microstachya* has spread throughout the rice-growing area as a weed of rice. The amount of genetic variation in Australian rice field populations is very restricted compared with the native range, although individual populations in the two regions are equally depauperate in variation. Brown and Marshall (1981) reviewed other comparisons of genetic variation in the native and introduced range of weeds. Where the reproductive system of weeds involves predominant selfing or apomixis (see below) we may expect marked reduction of genetic variation in the introduced range. In contrast, in outbreeding species relatively small differences may be evident if large population sizes are maintained following introduction.

#### WHAT LEVELS OF GENETIC VARIATION ARE FOUND IN SPECIES THAT ARE SUCCESSFUL INVADERS?

The level of genetic variation within a population largely determines its capacity to respond, in an evolutionary sense, to changes in environment. Skibinski and Ward (1982) showed, for example, using

**TABLE 1.** *The effect of size of the founder population and the speed of recovery of large population size on the loss of heterozygosity (H).*  
Calculated from Nei *et al.* (1975).

Size of founder population	After one generation	Proportion of H remaining				
		200%	When large population size recovered*			10%
		100%	50%	20%	10%	
1	0.50	0.41	0.31	0.18	0.03	0.02
2	0.75	0.66	0.58	0.45	0.20	0.05
5	0.90	0.86	0.81	0.73	0.54	0.32
10	0.95	0.93	0.90	0.86	0.74	0.57
100	0.99	0.99	0.99	0.99	0.97	0.95
1000	1.00	1.00	1.00	1.00	1.00	0.99

\* (% population increase/generation).

**TABLE 2.** *Allele frequencies in rabbit populations from Europe and Australia.*  
After Richardson *et al.* (1980).

Location	<i>Ada</i> <sup>1</sup>	<i>Ada</i> <sup>2</sup>	<i>Pgd</i> <sup>1</sup>	<i>Est</i> <sup>1</sup>	<i>Ca</i> <sup>1</sup>	<i>Dia</i> <sup>1</sup>
s. France	0.75	0.01	0.01	0.69	0.66	1.00
Britain	0.42	0.20	0	0.64	0.16	—
Victoria	0.56	0.02	0	0.77	—	—
w. N.S.W.	0.54	0.03	0.07	0.55	0.11	0.76
s. W.A.	0.52	0.09	0.03	0.64	0	0.71

*Ada*, adenosine deaminase; *Pgd*, phosphoglucose dehydrogenase; *Est*, esterase; *Ca*, carbonic anhydrase; *Dia*, diaphorase.

electrophoretic and amino acid sequence data drawn from vertebrates, that the rate of evolutionary change in amino acid sequence is correlated with the average heterozygosity of the protein. Of prime importance is variation underlying characters of ecological significance. The genetic basis of these traits is often difficult to establish, however, and population geneticists have resorted to other measurements that are presumed to reflect the overall level of variation in populations. The simplest of these is 'H', the proportion of loci that are carried in the heterozygous condition in an average individual. An estimate of 'H' can be obtained from measurements of the amount of genetic polymorphism in enzymes and other proteins detected using electrophoresis. These estimates assume that the electrophoretically detectable proteins coded by structural genes vary in populations in a fashion similar to other classes of genes, such as those involved with gene regulation. Zouros, Singh and Miles (1980) studied the effect of average heterozygosity of seven enzyme loci on growth rates of individual oysters in a natural population. They found growth rate to be related linearly to average heterozygosity, thereby supporting the contention that 'H' is a biologically meaningful measurement.

Information from electrophoretic studies of isozyme variation in natural populations of 228 animal species has been summarised by Nevo (1978). He found significant differences in the amount of genetic variation for subsets of the data subdivided using different biological criteria. Cosmopolitan species exhibited higher levels of genetic variation than temperate species, but were not necessarily more variable than tropical species. This indicates that cosmopolitan species, which are frequently successful invaders, do have, on average, high levels of variation, but a wide range of heterozygosity values was found and successful animal invaders with little variation are known.

Successful colonists are frequently considered to be generalists and Nevo's analysis showed that generalists on average carry significantly more variation than specialists. However, some specialists harbour high levels of variation, e.g., the curculionid beetle *Otiorrhynchus scaber* has an 'H' value of 0.31 (Suomalainen and Saura 1973), which is 25% more than the next highest species reported by Nevo (1978), whilst some generalists carry little or no variation.

Nevo's analysis involves comparison of a large number of unrelated species and it would be useful to test his proposals in a closely related group of species where phylogenetic variation is restricted. Lewis (1981) examined the relationship between heterozygosity and a number of biological variables using data for tuna and other scombrid fishes. He found that the level of heterozygosity was correlated with size, vagility and geographical range of the species in the group. Species with high vagility, wide distribution and large size could be considered equivalent to the generalists or cosmopolitan species groups examined by Nevo (1978) and a similar result was obtained. Again, however, the range of heterozygosities observed by Lewis was very large in each class and it is clear that there is no necessary relationship between level of inherited variation and success as a coloniser in the animals surveyed to date.

A similar analysis involving exclusively plant data from 113 taxa revealed somewhat different patterns (Hamrick, Linhart and Mitton 1979). Mean levels of genetic variation were lowest in species with restricted distributions (endemics), increased for the regional category but declined in species with widespread distributions. The decrease was attributed to the large number of weedy, predominantly selfing species whose population variability was relatively low (see below). In a separate analysis of genetic variation in species of contrasting stages of succession, Hamrick, Linhart and Mitton (1979) found that weed species, which predominate in early successional stages, were significantly less variable than species of middle and late successional stages.

The amount of genetic variation in weed populations may also be associated with the life history strategy and ecological characteristics of the species. Some weeds have broad ecological tolerances and colonise a wide range of environments whereas others are highly specialised in their habitat requirements (Baker 1974). Among the world's most successful colonising species are members of the barnyard grass genus *Echinochloa* (Holm *et al.* 1977). *Echinochloa crus-galli* and *E. oryzoides* are both annual, self-fertilising hexaploid weeds of world-wide distribution. *Echinochloa crus-galli* invades a broad spectrum of disturbed habitats and agricultural crops whereas *E. oryzoides* is a satellite weed of cultivated rice restricted to flooded rice fields (Barrett 1983). A study of genetic variation at enzyme loci and quantitative characters in Californian and Australian populations of the two taxa (S.C.H. Barrett and A.H.D. Brown, unpublished data) found that the generalist *E. crus-galli* was more variable both within and between populations than *E. oryzoides* (Table 3).

Of particular interest was the contrast in patterns of variation exhibited by loci controlling the enzyme alcohol dehydrogenase (*Adh*). In *E. crus-galli* a total of 12 homozygous *Adh* multilocus genotypes were evident among populations as a result of polymorphism at 2 or 3 loci. Virtually all populations which were surveyed in both regions contained several *Adh* genotypes. In contrast all *E. oryzoides* populations, except one in California, were composed of individuals with the same multilocus genotype. The exceptional population was monomorphic for a variant *Adh* genotype. Although populations of *E. oryzoides* were monomorphic for *Adh* loci, polymorphism for other enzyme loci (e.g. aconitase, diaphorase, phosphoglucomutase) was apparent but the level of polymorphism was reduced in comparison with *E. crus-galli*.

Whilst historical factors associated with plant introduction obviously influence the variation exhibited by the two *Echinochloa* species it is also possible that the absence of *Adh* variation in populations of the obligate rice

**TABLE 3.** Genetic variation in Californian populations of *Echinochloa crus-galli* and *E. oryzoides*.

Species	X Coefficient of variation (%) of between family variation within populations		Percentage loci polymorphic (n = loci surveyed)	Total <i>Adh</i> genotypes
	Time to flowering	Fecundity		
<i>E. crus-galli</i>	13.84	29.74	51.6 (31)	12
<i>E. oryzoides</i>	6.85	23.46	15.6 (32)	2

Quantitative traits based on 15 families from each of 10 populations grown under uniform glasshouse conditions. Electrophoretic analysis on 15 families from 12 populations (S C H. Barrett and A H.D. Brown, unpublished data).

weed may reflect selection of an 'optimum' *Adh* genotype adapted to the relatively uniform and predictable conditions of flooded rice fields. In contrast, the polymorphism at *Adh* genes in *E. crus-galli* may be maintained by the heterogeneous nature of the disturbed habitats it occupies. Elsewhere it has been demonstrated that *Adh* enzymes may function to enable plants to tolerate the anaerobic conditions associated with flooded environments (Crawford 1967; Marshall, Broué and Pryor 1973).

A significant number of surveys of isozyme variation in weed species document depauperate amounts of genetic diversity both within and between populations, particularly following continental migration. Weed groups for which recent surveys have revealed highly homozygous populations or populations composed of a few genotypes include the examples reviewed in Brown and Marshall (1981) and Barrett (1982) and, in addition, *Amaranthus* spp. (Hauptli and Jain 1978), *Polygonum pensylvanicum* (Kubetin and Schaal 1979), *Capsella bursa-pastoris* (Bosbach and Hurka 1981), *Senecio viscosus* (Koniuszek and Verkeij 1982), *Lolium temulentum* (Hayward and Zaruk 1982), *Hordeum murinum* (Giles 1983) and *Echinochloa* spp. (S.C.H. Barrett and A.H.D. Brown, unpublished data). All these findings clearly indicate that high levels of genetic diversity are not a prerequisite for a successful invading species.

It is important to note, however, that populations of weeds that are genetically uniform for isozyme variation at single loci may in fact carry more genetic variation than may be appreciated if they are polyploid, through the presence of fixed heterozygosity (different alleles at homoeologous loci). Many cosmopolitan weeds are, in fact, inbreeding, polyploid annuals and the genetic systems of these plants may maintain high biochemical versatility contributing towards individual buffering in the varying environments they encounter (Roose and Gottlieb 1976; Babbel and Wain 1977; Allard, Miller and Kahler 1978). The role of polyploidy *per se* in colonising success is considered below.

Another reason for not assuming that weeds exhibiting uniformity for enzyme loci are entirely devoid of genetic variation comes from parallel studies involving both quantitative characters and isozymes. Where these have been undertaken it has often been shown that populations apparently monomorphic for enzyme loci contain significant genetically-based variation for important life history traits. An example of the disparity between the two classes of loci involves one of the most widespread and successful weeds, the inbreeding annual *Xanthium strumarium* noogoora burr. Moran and Marshall (1978) surveyed 12 populations of this species complex in Australia, comprising four taxonomic races, for isozyme variation at 13 loci. They found that within three of the four races, all populations were composed of the same homozygous multilocus isozyme genotype. However, a study of 15 quantitative characters revealed significant genetic variation within and between populations (Moran, Marshall and Muller 1981). Since the patterns of genetic variation were uncorrelated with differences in the distribution of the four races in Australia, it appears that the amount of genetic variation *per se* may be unimportant in explaining racial differences in colonising success within the group. Moran, Marshall and Muller (1981) suggest that differences in reproductive output and photoperiodic requirements for flowering may be more important attributes in accounting for the contrasting distributional patterns of the four races in Australia.

Normally, genetic variation at different loci within populations is distributed independently and all possible combinations of alleles at different loci may be found. However, self-fertilisation and population bottlenecks during the early stages of colonisation can produce linkage disequilibrium between loci. Such effects can generate a limited number of multilocus associations within populations; they have been documented in Californian populations of slender wild oat, *Avena barbata* (Allard *et al.* 1972) and Israeli populations of wild barley, *Hordeum spontaneum* (Brown, Feldman and Nevo 1980). Both of these weed species are highly self-pollinating. In Australia only three distinct multilocus genotypes are evident in introduced populations of skeleton weed, *Chondrilla juncea* (Burdon, Marshall and Groves 1980). Here triploidy in association with the apomictic mode of reproduction prevents recombination and the three genotypes presumably result from separate introductions from Europe.

At the other extreme, in terms of multilocus structure, is the annual outbreeding weed *Echium plantagineum* (Paterson's curse), one of the most successful invaders of temperate Australia. In a survey of the genetic

structure of a population at Gundagai, New South Wales. Brown and Burdon (1983) revealed remarkably high levels of genetic diversity. A vast array of multilocus genotypes was present, with no detectable non-random association among the 11 polymorphic enzyme loci which were assayed. The organisation of genetic variation within the population suggests that the outcrossed mating system of *E. plantagineum* encourages sufficient recombination to overcome the effects of bottlenecks on multilocus structure.

To date, the population of *E. plantagineum* at Gundagai not only represents the most isozymically variable weed population which has been assayed but is also among the most diverse of any plant population which has been studied electrophoretically (Hamrick, Linhart and Mitton 1979). Brown and Burdon's findings raise several interesting questions concerning the invasive properties of the species in Australia. Are other *E. plantagineum* populations in Australia as diverse as the one they studied? How variable are populations in the native European range and to what extent has the dramatic spread of *E. plantagineum* been aided by high levels of genetic variation? Further comparative ecogenetic studies of the species in Australia and Europe would seem warranted. If high genetic diversity is a general feature of Australian populations of *E. plantagineum*, the rapid evolution of races locally adapted to Australian conditions would be anticipated.

Together these surveys suggest that the patterns of genetic variation in colonising plants and animals of widespread distribution may often differ. Where differences are evident they are most likely associated with the contrasting genetic systems found in the two groups.

## WHAT GENETIC SYSTEMS ARE ASSOCIATED WITH COLONISING SUCCESS?

### *Mating systems*

Colonisation of unoccupied territory is often associated with periods of low population density. The difficulties of mating under these circumstances may be expected to impose severe restrictions on the colonising potential of non-motile, outbreeding organisms. In plants an association between unsaturated habitats and self-fertilisation was first noted by Henslow (1879) who reported that most weeds in Britain were selfers. More recently the search for correlations between colonising ability and uniparental modes of reproduction, either by selfing or apomixis, has been a repeated theme in studies of weed groups (Stebbins 1957, 1965; Allard 1965; Baker 1965; Mulligan and Findlay 1970). Two main advantages have been proposed to explain why plants capable of uniparental reproduction should be more effective colonisers. The first, originally proposed by Baker (1955, 1967), concerns the ability of selfing or apomictic colonists to start reproducing colonies following long-distance dispersal of a single individual. In addition, Stebbins (1957) and Allard (1965), among others, have argued that following successful establishment selfing allows the rapid fixation and multiplication of adapted genotypes. Two recent surveys of colonising plants support the general association first observed by Henslow. Price and Jain (1981) surveyed 400 species from 43 plant families from the flora of the British Isles in an attempt to see whether plants capable of uniparental reproduction were better colonisers than outcrossers. They found that predominant selfing or apomixis was significantly more common among plants they classified as colonisers than was outbreeding. However, as Price and Jain (1981) note, many cases occur, particularly among perennial weeds, where both obligate outbreeding, through self-incompatibility or dioecism, and clonal propagation are associated. Among the plants judged to be the world's most successful invaders (see Holm *et al.* 1977) Brown and Marshall (1981) found that about half reproduced predominantly by selfing and most of the remainder multiplied primarily by asexual means.

With their diversity of reproductive systems, it is not unexpected that both inbreeding and outbreeding weeds should occur. What is required, however, are experimental ecological studies of successful, outbreeding invaders to examine how they overcome the constraints imposed by the requirement for mates during colonisation. Temporary reversals to self-compatibility in multilocus incompatibility systems (Pandey 1980), 'leaky' dioecism (Baker and Cox 1984), multiseeded diaspores, individual longevity and extended reproductive periods can all reduce in different ways the likelihood of reproductive failure during the establishment phase in outbreeding colonising plants.

Although the majority of animal invaders reproduce exclusively by outbreeding, a growing number of examples involving parthenogenesis or self-fertilisation in hermaphrodite species are coming to light. For example, the parthenogenetic gecko, *Lepidodactylus lugubris*, is an extremely successful coloniser of new islands and is now found in Australia and widely throughout the Indo-Pacific region from India to Tahiti (Cuellar and Kluge 1972). Recent work by Selander and his colleagues (McCracken and Selander 1980; Foltz *et al.* 1982; Selander 1983) on the breeding systems of two families of terrestrial slugs (Arionidae and Limacidae) demonstrates that selfing is a major mode of reproduction in this group. Most of the selfing species consist entirely of homozygous genotypes throughout much of their range. In *Arion circumscriptus* and *A. silvaticus* both native (Europe) and introduced (North America) populations are composed of a single monogenic strain. Among the European species which have invaded North America self-fertilising forms are disproportionately represented. Of the 10 such species so far identified in Europe only two have failed to invade North America. In contrast nine of the 13 outcrossing species have not become established. Among the introduced species in North America the selfers apparently occupy a wider range of habitats than the

outcrossers. It appears that, in common with many weeds, colonising success in these slugs may be relatively independent of the amount of genetic variation carried by populations and be more strongly influenced by the problem of finding mates in new areas.

Whilst many successful plant invaders reproduce primarily by selfing or asexual means there is some evidence that increased outcrossing in selfing species can follow continental migration (Brown and Marshall 1981). In the Mediterranean grasses *Avena barbata* (wild oat) and *Bromus mollis* (soft brome) estimates of outcrossing, based on isozyme markers, in populations from the native and alien range indicate significantly higher outcrossing in the latter (Kahler *et al.* 1980; Brown and Marshall 1981). In both studies increased outcrossing was also associated with greater heterozygosity in the introduced region. Since colonisation of new territory may be associated with altered selection pressures it seems plausible that such modifications in mating systems are adaptive. Where novel environments are encountered there may be selection for genetical innovation through increased recombination. In contrast, where pre-adapted gene combinations are favoured, high selfing may be maintained to restrict the disruptive effects of outcrossing.

Modifications of the mating system of wind-pollinated plant species, such as the grasses mentioned above, usually involve small alterations in floral structure and reproductive timing. However, in animal-pollinated species the mating system will be strongly influenced by the abundance and type of pollen vectors in the introduced region. Where colonisation of new territory is associated with a loss of specialised pollinators, modifications favouring autogamy may be selected (Baker 1967; Barrett 1979; Lloyd 1980). In such cases ensuring the production of offspring (by selfing) may outweigh any requirement for developing new gene combinations. It is notable that among the most successful insect-pollinated invaders most have unspecialised floral structures and are fed upon by generalist flower visitors (e.g. the combination of *Echium plantagineum* and *Apis mellifera* in Australia).

Although selfing variants of normally outcrossing plant species are often found at the margins of their range (Lloyd 1980), in some cases the presence of suitable pollinator guilds and the advantages of increased recombination may result in the development of new floral traits favouring outcrossing in selfing colonists. The geographical patterns of breeding system distribution in the neotropical weed complex *Turnera ulmifolia* suggest that this process has taken place (S.C.H. Barrett and J.S. Shore, unpublished data). Populations from continental South and Central America are primarily distylous and self-incompatible (Barrett 1978). However, on many of the Caribbean Islands autogamous homostyles replace the outcrossers probably because the selfing habit was favoured during colonisation of these islands. On some of the larger islands which are more complex ecologically, such as Jamaica, selection for herkogamy (separation of anthers and stigmas) has resulted in the re-establishment of outcrossing in the homostylous colonists. These changes emphasise the lability of plant mating systems and cast doubt on the commonly held view (reviewed by Jain 1976) that the evolution of selfing from outcrossing is a 'one way street'.

#### *Asexual reproduction*

Among plant invaders with perennial growth most possess some means of vegetative multiplication. This can be by stolons, runners, rhizomes etc. or by the production of viable seeds without fertilisation (apomixis). In plants, asexual reproduction, particularly clonal propagation, is often associated with long generation times and large size, whereas among animal groups it is more frequently found in small organisms with short generation times (e.g. parthenogenesis in *Daphnia* and *Aphis*). The adaptive features of parthenogenesis in invading species are numerous and include high reproductive rates, the ability of single isolated females to establish colonies, and the fixation of adaptive heterotic gene combinations (White 1973; Williams 1975). In some animal groups a mixed strategy, consisting of an alternation of sexual and asexual generations is found (e.g. in coelenterates and in protozoan and platyhelminth parasites).

The evolution of parthenogenetic races among insect groups is often associated with the invasion of areas unoccupied by the ancestral bisexual forms (Vandel 1928; Suomalainen 1962; White 1973; Lokki and Saura 1980). An example involves the parthenogenetic cockroach *Pycnoscelus surinamensis* which has a pan-tropical distribution. Examination of enzyme polymorphisms at five loci in diploid and triploid races of this widespread species indicate multiple origins from the restricted bisexual diploid *P. indicus* (Parker *et al.* 1977). Similar patterns are evident among the numerous apomictic plant taxa where interspecific hybridisation and polyploidy are often also involved.

Several of the classic cases of plant invasion on the Australian continent involve apomictic groups, including *Opuntia* spp., *Rubus* spp., *Chondrilla juncea* and *Hypericum perforatum*. Several of these taxa have been successful targets in biological control schemes. Burdon and Marshall (1981) have argued that this largely results from the restricted recombination and low levels of genetic diversity which characterise populations in the introduced range. Unfortunately in comparison with sexually-reproducing weeds there have been relatively few electrophoretic analyses of populations of apomictic species (Solbrig and Simpson 1974; Usberti and Jain 1978; Burdon, Marshall and Groves 1980) and despite the development of theoretical models for estimating the degree of sexuality in facultative apomicts (Marshall and Brown 1974) relatively little is known of their reproductive behaviour in natural populations.

Of particular interest for studies of genetic systems in invading species are closely related groups, with diverse reproductive systems, where a single species has become a successful weed whilst close relatives are relatively innocuous (Baker 1965). An outstanding example is the aquatic plant genus *Eichhornia* comprised of seven species, one of which, *E. crassipes* (water hyacinth), is perhaps the world's most successful weed of natural and artificial water bodies (Sculthorpe 1967; Holm *et al.* 1977). The remaining species of *Eichhornia* all have widespread distributions in their native regions and colonise, to varying degrees, a range of wetland habitats including lakeshores, rivers, seasonal pools, drainage canals and rice fields. However, none has shown the dramatic world-wide spread exhibited by *E. crassipes* during the past century.

Examination of the breeding systems of *Eichhornia* species provides few clues to account for this difference in behaviour (Table 4). Although selfing has evolved on a number of occasions in the genus in association with the breakdown of trimorphic incompatibility (Barrett 1979, 1985), the selfers have shown no tendency to become aggressive weeds, despite the increased colonising potential selfing may give. Selfing variants of the normally outbreeding *E. paniculata* have colonised Jamaica and the successful establishment of *E. natans* on the African continent was no doubt aided by its selfing habit (Table 4).

TABLE 4. Genetic systems and colonising ability in *Eichhornia* species. Data of S.C.H. Barrett.

Taxon	Ploidy level	Breeding system	Asexual reproduction	Distribution	Weed status
<i>E. paniculata</i>	2x	tristylous	none	N. Brazil & Caribbean	occasional in rice fields
<i>E. paradoxa</i>	2x	S. homostylous	none	neotropics rare disjunct	no reports
<i>E. azurea</i>	4x	tristylous	moderate	neotropics widespread	local problem
<i>E. crassipes</i>	4x	tristylous	highly developed	worldwide	noxious aquatic weed
<i>E. heterosperma</i>	4x	S. homostylous	moderate	neotropics local	no reports
<i>E. diversifolia</i>	4x	S. homostylous	moderate	neotropics widespread	occasional in rice fields
<i>E. natans</i>	—	S. homostylous	moderate	Africa widespread	occasional in rice fields

Water hyacinth's aggressive behaviour is principally the result of its prolific powers of asexual reproduction by stolons and possession of the free-floating life form. Under favourable conditions it has been estimated that 10 plants of *E. crassipes* can produce 0.4 ha of plants in 8 months by clonal propagation (Penfound and Earle 1948). No other member of the genus possesses the clonal architecture and free-floating habit which are adaptations to the periodic water-level fluctuations and temporary aquatic habitats that *E. crassipes* inhabits in its native Amazon Basin (Barrett 1977). In many parts of its adventive range water hyacinth is represented by relatively few asexually-reproducing clones and the development of genetic diversity is restricted because of the failure of seeds to germinate and establish (Barrett 1980). However, limited sexual reproduction in these areas has little effect on its invasive power which results from its rapid powers of clonal multiplication and water dispersal of vegetative fragments.

#### Polyploidy

Polyploidy is a widespread and common condition among eukaryotes, particularly flowering plants and ferns. Today it is recognised that 70–80% of the Angiosperms are of polyploid origin (Goldblatt 1980; Lewis 1980). Accordingly, attempts to demonstrate a general relationship between polyploidy and colonising success are fraught with difficulty. This theme has been examined in numerous biosystematic studies (reviewed by Ehrendorfer 1980) with the distinction usually being made between the differences in ecological behaviour of autopolyploids and allopolyploids (Stebbins 1942; Love and Love 1943; Lewis 1980; Levin 1983). In particular it has often been stressed that neopolyploids of hybrid origin will usually surpass their ancestors in genetic variation, heterosis, adaptability and potential to invade novel environments. Among diploid-polyploid complexes there is often a greater likelihood of the polyploids exhibiting weediness and in some cases this tendency increases with ploidy level. It is noteworthy in this connection that of the 18 most widespread and successful weeds all are believed to be of polyploid origin (Brown and Marshall 1981; Clegg and Brown 1983). Despite these patterns many successful colonisers are diploid and polyploids of restricted distribution are also known.



The wide adaptability of many polyploid species is believed to stem from extensive gene duplication and subsequent diversification, fixed heterozygosity, and the reduced effects of inbreeding depression. Whilst it would appear that heterosis is involved in the success of many polyploids of hybrid origin, clear experimental verification of their superior fitness under field conditions is still lacking. Detailed comparative measures of fitness components from natural populations of progenitor and derivative species are often complicated in polyploid groups owing to the rapid divergence in ecological preferences of polyploids following their origin. These ecological effects may not be limited solely to polyploids of hybrid origin, but may also arise from chromosome doubling alone (Levin 1983).

In plants with well developed powers of clonal propagation sterile polyploids arising from wide hybridisation can possess remarkable invasive powers as a result of the effects of heterosis on vegetative vigour. For example, the neotropical aquatic fern *Salvinia molesta* has become one of the world's most noxious aquatic weeds during the past century (Mitchell 1972). The plant is a sterile pentaploid in which spore production is largely abortive and spore germination does not occur (Loyal and Grewal 1966). In common with water hyacinth the multiplicative pattern of growth and free-floating habit of *S. molesta* results in rapid regeneration and wide dispersal of vegetative fragments by water. Clones in the two species, both of which occur in Australia, occupy large areas and may be near immortal. Another successful weed in Australia, which like *S. molesta* is also sterile, is the pentaploid *Oxalis pes-caprae* which reproduces vegetatively by means of underground bulbils (Baker 1965). Clearly the absence of genetical recombination in these plants has not been an impediment to colonising success, although the genetic uniformity of populations may make them more prone to natural or managed pest attack (Levin 1975; Burdon and Marshall 1981; Room *et al.* 1981).

Among insects polyploidy is rare and is reported from less than one hundred species. Of these, several have been examined in detail providing an opportunity to compare the colonising ability of diploid and polyploid forms (Suomalainen, Saura and Lokki 1976). All documented cases of polyploidy in the insects are associated with parthenogenesis and in several groups the polyploids have become highly successful at invading vast land areas (cases reviewed in Lokki and Saura 1980). Part of this success doubtless lies in the acquisition of uniparental reproduction (see above); however, it appears that in many cases parthenogenetic species are often only successful as invaders when they are polyploid, apparently indicating a direct advantage to chromosome increase. The benefits may arise from the greater genetic versatility engendered by gene duplication and heterozygosity. In a survey of the degree of heterozygosity per locus in various diploid and polyploid insect populations, Lokki and Saura (1980) found that a general increase in heterozygosity was associated with polyploidy. However, as yet there is only limited evidence available to test whether polyploid populations are more polymorphic intragenomically than related diploids, or whether intergenomic diversity is the basis of their success (Brown and Marshall 1981).

#### WHAT ARE THE RELATIVE CONTRIBUTIONS OF INHERITED AND ENVIRONMENTALLY CONTROLLED VARIATION IN LIFE HISTORY TRAITS OF COLONISING SPECIES?

Many invading species establish in a wide range of environments, some of which can be highly heterogeneous in space and time. Two contrasting modes of adaptation to variable environments have been proposed for colonising species. These involve either genetic polymorphism (population buffering) on the one hand or phenotypic plasticity (individual buffering) on the other (Thoday 1953; Lewontin 1957; Bradshaw 1965; Lande 1982). Whilst colonising plant species frequently exhibit marked inter-population genetic differentiation (Baker 1974; Brown and Marshall 1981) in many instances, as we have seen, populations may contain relatively low levels of genetic polymorphism. In such cases, and these frequently involve selfing annual weeds, it is probable that phenotypic plasticity plays a significant role in enabling populations to survive and reproduce in unpredictable environments. Nevertheless, how phenotypic plasticity is directly related to the fitness of individuals in natural populations has rarely been investigated.

An unresolved issue concerns the relationship between the degree of phenotypic plasticity exhibited by a species or population and its genetic variation and heterozygosity. Both positive (Wilken 1977) and negative associations have been demonstrated (Marshall and Jain 1968). One difficulty in investigating this relationship involves the choice of characters which are measured in experimental manipulations. Schlichting and Levin (1984) demonstrated markedly different patterns of response among 18 characters, measured over six environments, in three annual species of *Phlox*, with contrasting heterozygosities. The results provided few clear relationships and the authors concluded that whilst heterozygosity may influence the degree of plasticity exhibited by some characters, other features of the biology of organisms, such as their ecology and phylogeny, are likely to shape the response of others.

Another difficulty in studies of the relationship between plasticity and heterozygosity concerns the distinction between the adaptive and maladaptive features of phenotypic and developmental variation. Intra-organismal variation can take the form of developmental instability brought about by inbreeding and homozygosity (Lerner 1954). Here such variation is usually maladaptive, thereby reducing the fitness of individuals (Soulé 1973). However, under certain circumstances developmental instabilities may give rise to novel phenotypic expressions which are at a selective advantage (Levin 1970; Barrett 1985). Invading species may be particularly prone to these effects since colonisation is frequently associated with strong directional

selection, inbreeding, and genetic drift. These influences can result in the disruption of balanced gene complexes and developmental instability. Whether such variation, much of which can be modified by environmental stimuli, should be regarded as plasticity will depend on its effects on fitness.

Whilst many weeds display marked phenotypic plasticity this does not preclude populations from containing significant amounts of genetic variation for important life history traits such as development rate and reproductive output (Hamrick and Allard 1975; Law, Bradshaw and Putwain 1977). Earlier, Lewontin (1965) predicted that, based on theoretical studies of selection in colonising species, populations of colonisers should contain low amounts of additive genetic variance for development time but relatively high amounts for fecundity. Among animal groups Istock (1981) showed that in the mosquito *Wyeomyia smithii* there was considerable genetic variation for development rate. This led to adaptive local variation in development associated with seasonality and density-dependent effects. Dawson (1977) also reviewed evidence contradictory to Lewontin's prediction. At present it is clear that more studies of the quantitative genetics of life history traits in colonising species are required before we can confidently predict the responses to selection imposed by repeated colonising episodes.

### WHAT EVIDENCE EXISTS FOR LOCAL GENETIC DIFFERENTIATION FOLLOWING INVASION?

Whether local adaptation following invasion occurs will depend on the kinds of environments a colonist encounters, the range and distribution of genetic variation available to populations, and the inheritance patterns of traits conferring increased fitness. Where there is correlated variation among individual traits, selection for 'improvement' in one trait may result in deterioration of another (Lande 1982). For example, selection for more rapid development may result in reduced fecundity (Lewontin 1965). These effects, which have been demonstrated in numerous artificial selection experiments, have usually involved polygenic characters (Falconer 1960).

Where the genetic basis of traits important to colonising success are relatively simple then rapid changes in behaviour or ecology may occur. Carson and Ohta (1981) reported that an ecological shift from a specialist monophagous habit to a generalist polyphagous habit in the *Drosophila grimshawi* species complex of Hawaii is apparently under control of one gene and two alleles with the generalist behaviour dominant. In plants, Gottlieb (1984) recently detailed many cases of control, by one or two genes, of morphological traits many of which are of ecological significance. Notwithstanding such examples, although shifts in ecology may be initiated by mutation at major genes, it seems likely that selection operating on many genes with small effects is required to achieve a well integrated phenotype.

Several studies have examined adaptive changes following colonisation events. Myers and Sabath (1980) found that larval dispersal and the temperature threshold for adult emergence, in North American populations of the European cinnabar moth (*Tyria jacobaea*) had changed value significantly following colonisation. These changes appear to be in response to different food plant spacing and early spring temperatures in their new environment. Similarly, Cocks and Phillips (1979) were able to document strains of the introduced subterranean clover (*Trifolium subterraneum*) in Australia with divergent flowering times. The strains appear to have resulted from hybridisation between different introductions followed by local selection. Other cases of intraspecific and interspecific hybridisation among weeds giving rise to locally adapted as well as aggressive variants are reviewed in Barrett (1982).

Unfortunately few workers have artificially founded colonies with known genotypes and followed their survival. One attempt involved establishing colonies of rose clover (*Trifolium hirtum*) outside of the range of the species in California with low versus high levels of genetic variation (Martins and Jain 1978). Surveys of establishment over 2 years provided evidence that the more variable populations had the highest levels of colonising success. More studies of this sort are required before we can fully evaluate whether genetic variation plays an important role in successful colonising events. Similarly, to evaluate whether local genetic differentiation following invasion has occurred, detailed comparisons of populations from the native and introduced range are needed. Where the species in question has a widespread distribution in its native area problems of sampling will inevitably be involved unless historical information on the source of immigrants is available.

### CONCLUSION

One of the major difficulties in the study of the biology of invasions is the lack of information on the early stages of colonisation. For most successful invaders no genetic data are available from the founding populations. In the case of biological control programs, many of which are being carried out in Australia, this information could be readily obtained. However, for most introductions, retrospective analyses of contemporary populations are all we have. A particular deficiency is our ignorance of why some colonists fail to establish. Is this because of the absence of suitable genetic variation, lack of broad ecophysiological adaptation to the new environment, or merely chance?

The range of genetic attributes found in successful invaders suggests that there is no single optimal solution to the challenges facing the colonist. There is rather a series of ways to improve the chances of success. It is

clearly an advantage for a colonising population to contain much genetic variation, to be able to produce offspring even though mates are hard to find, and to be able to rapidly develop adaptive phenotypes in the face of new challenges. Whilst some invaders do indeed contain significant stores of genetic variation others are genetically uniform. Whilst many successful invaders are capable of uniparental reproduction some are obligate outbreeders. Colonising success may be achieved by relatively simple genetic changes in some species whereas in others more complex adaptations are involved. These contrasting patterns highlight the importance of comparative experimental studies of related groups containing both successful invaders and taxa of restricted distribution.

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