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Predicting Evolutionary Change in Invasive, Exotic Plants and its Consequences for Plant–Herbivore Interactions

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Introduction

Invasion ecology, the study of the distribution and spread of organisms in habitats to which they are not native, has received considerable attention during past decades (Groves and Burdon, 1986; Drake *et al.*, 1989; Vitousek *et al.*, 1996; Williamson, 1996; Lonsdale, 1999; Walker, 1999; Alpert *et al.*, 2000; Mack *et al.*, 2000). This is mainly a consequence of the increased awareness of the major threats posed by invasions to biodiversity, ecosystem integrity, agriculture and human health (Lonsdale, 1999; Mack *et al.*, 2000). Two questions have dominated most of the studies in this context: which species are most likely to become invasive, and which habitats are most susceptible to invasion (Alpert *et al.*, 2000; Kolar and Lodge, 2001). Surprisingly, the evolutionary genetics of invasive species remained relatively unexplored despite the profound effect of genetic characteristics of populations on their capacity for range expansion (Ellstrand and Schierenbeck, 2000; Tsutsui *et al.*, 2000) and on species interactions (Carroll *et al.*, 2001; Siemann and Rogers, 2001). In fact, in a recent review on this topic, Lee (2002) concluded that 'the invasion success of many species might depend more heavily on their ability to respond to natural selection than on broad physiological tolerance or plasticity'. Natural selection and genetic drift can alter the genetic structure of invading populations, and hence affect not only the process of adaptation to the new physical environment, but also the plentiful biotic interaction encountered in the new habitat.

The invasion process is generally divided into two phases: the initial introduction and establishment, and the spread into the new environment. Many of

Genetics, Evolution and Biological Control (eds L.E. Ehler, R. Sforza and T. Mateille)

the species that become successful invaders do so only after a long lag time (Sakai *et al.*, 2001, and references therein). Some of the most frequently suggested explanations for this time lag are listed in Table 7.1. Several evolutionary explanations have been put forward, but few empirical data yet exist to test these hypotheses. Populations may be poorly adapted initially, but after a period of selection they may be able to expand. This assumption is confirmed by a recent review of published studies on the conditions that promote rapid adaptive evolution (Reznick and Ghalambor, 2001). Most of the studies cited show examples of species colonizing new habitats. In addition, a common feature of many studies given in this review is the combination of directional selection, the presence of genetic variation, and at least a short-term opportunity for population increase. The opportunity for population growth, together with availability of genetic variation, may be a key factor that promotes rapid evolution, since directional selection might otherwise be expected to cause population decline and lead to an extinction vortex (Silvertown and Charlesworth, 2001). Unfortunately, time series data on recently introduced plant populations do not exist (Bone and Farres, 2001).

Table 7.1. Explanations for a time lag between establishment and population increase during an invasion process.

- Ecological explanations
  - density-dependent forces and Allee effects (propagule pressure, pollen limitation)
  - lag phase of an exponential growth curve
  - lag phase varies with the detection threshold
- Evolutionary explanations
  - purging of genetic load responsible for inbreeding depression
  - accumulation of additive genetic variation
  - hybridization and polyploidization
  - recovery from loss of genetic diversity and fitness
  - adaptation to a new environment (including absence of antagonists)
- Sociological explanation
  - public awareness follows an exponential growth curve (multiplication of news)

Adaptation to local conditions is a particularly important form of evolution in plant populations, as plants are sessile. This makes plants ideal organisms for the study of local adaptations, as we know the environment they are exposed to. Indeed, many of the best examples of rapid evolution involve invasive plant species (Reznick and Ghalambor, 2001). This may be due to the generation of genetic variation (on which selection can act), such as through hybridization (e.g. Ellstrand and Schierenbeck, 2000), and/or strong directional selection exerted by abiotic, but particularly also by biotic, factors. Indeed, interactions with competitors and antagonists may differ strongly between the native and introduced range (Thompson, 1998; Bone and Farres, 2001).

Biological invasions by higher plants have increased in importance, with increasing human activities affecting both dispersal (trade and travel) and habitat availability (environmental change). Exotic plants constitute one of the most serious threats to biodiversity (Lonsdale, 1999, and references therein) and it seems that there is now no nature reserve in the world outside Antarctica that is without introduced plant species (Usher, 1988). The classical approach of biological control, referring to the introduction of a specialist enemy to control an invasive exotic species, has been the most successful control strategy against exotic plant invaders (Julien and Griffiths, 1999), and will probably remain the curative control measure of choice against environmental weeds in the near future, due to its effectiveness, low cost and relative environmental safety (Cronk and Fuller, 1995; Crutwell-McFadyen, 1998; van Klinken and Edwards, 2002; but see Louda *et al.*, 1997; Callaway *et al.*, 1999; Pearson *et al.*, 2000).

Two contrasting hypotheses dominate the literature on plant invasions; one assumes that trait combinations pre-adapt species to become good invaders ('pre-adaptation hypothesis'), whereas the other view postulates successful invasion as the outcome of rapid evolutionary change in the new habitat ('post-invasion evolution hypothesis'). If evolutionary change occurs, knowledge of its pace and direction is important to predict the impact of subsequent biological control attempts. The fact that certain correlates of invasion success have been identified, and that invasions can sometimes be reversed by biological control, support the view of pre-adapted invaders and the simple release from their natural enemies, respectively. However, recent theories (e.g. Blossey and Nötzold, 1995) and empirical evidence (e.g. Ellstrand and Schierenbeck, 2000) indicate that invasiveness can evolve. In this chapter, we will explore potential changes in plant traits and how this might influence species interactions, specifically subsequent biological control attempts by introducing specialist insect herbivores.

Framework and scope of our study

In this review, we adopt a quantitative-genetic framework to explore microevolutionary processes in invasive plants. We chose this approach because most of the plant traits relevant to our study are known to be quantitative (polygenic), as opposed to traits such as herbicide and pathogen resistance, where often only a few major genes are involved (Burdon and Thompson, 1992). Adaptation can be understood by studying how the interplay between natural selection and genetic variability translates into evolutionary change. According to a basic model of quantitative-genetic theory, adaptive evolutionary change (R) in quantitative traits can be predicted from knowledge of the selection differential (S) and the heritability (h^2), through $R = S \times h^2$ (Falconer and Mackay, 1996).

We will start by examining the direction and magnitude of expected selection pressures, and explore what phenotypic traits may be favoured by selection acting on invasive plants (S in the above equation). In a second part, we will examine processes that affect the amount of additive genetic variation (h^2 in the above equation) in invading plant populations and, therefore, their ability to evolve, and discuss consequences for plant–herbivore interactions and biocontrol success. Thirdly, we will compare these predictions with observed evolutionary responses (R in the above equation) and, again, explore how this might affect interactions with herbivorous insects, such as potential biological control agents. Finally, new studies will be proposed that link biocontrol with invasion ecology, an approach that might result in synergies contributing to the advance of both disciplines.

Selection Pressure in Invaded Habitats and Expected Selection on Plant Traits

Traits favoured by selection can be studied in several ways, including: (i) looking at the invaded habitats and the selection regime they impose, and (ii) adopting a comparative approach that contrasts invasive with non-invasive plant species, to predict traits associated with invasion.

Properties of invaded habitats

It has proven easier to identify habitat types prone to invasion than to identify traits associated with invasiveness (Lonsdale, 1999). There is a general agreement that disturbance can strongly affect habitat invasibility, mainly through changes due to fire, grazing or creation of gaps. D'Antonio *et al.* (2000) recently proposed that not only does increased disturbance affect invasibility, but that there has been a general departure from natural disturbance regimes, which facilitates invasion. Furthermore, low levels of environmental stress have been identified as a factor promoting invasions by plants (Alpert *et al.*, 2000). Absence of environmental stress might shift the competitive balance between invasives and natives. For instance, low abiotic stress may favour invasive plants because they are better able than natives to take advantage of high resource availability (Alpert *et al.*, 2000; Keane and Crawley, 2002). It was hypothesized that these factors probably interact, and it is mainly the combination of altered disturbance with high resource availability that renders habitats invasible (Alpert *et al.*, 2000). Besides low levels of nutrients and water, high levels of environmental stress also includes factors that limit resource acquisition (Alpert *et al.*, 2000, and references therein), such as competition and herbivory. Thus, low levels of competition and reduced levels of herbivory in a novel habitat might favour its colonization, but will also be of importance in view of a subsequent introduction of biological control agents. These habitats should, therefore, initially strongly select for 'ruderals' with short generation time, high growth rate, high fecundity and good dispersal (Grime, 1977, 2001; Stearns, 1992).

General traits associated with plant invaders

Traits found to be associated with invaders, based on interspecific studies, can also be used to infer expected selection at the intraspecific level, occurring during the invasion process. Such traits that are relevant for our study are listed in Table 7.2. Besides native range (species that occur more widely), rapid dispersal was found to be a good predictor of the first phase of the invasion process, i.e. during pick-up and initial introduction (see, for example, reviews by Alpert *et al*., 2000; Sakai *et al*., 2001). However, these traits are not good predictors of a species' invasiveness. This may be because the second phase of invasion, spread into the habitat, is habitat specific (Alpert *et al*., 2000). Table 7.2 lists traits of the second phase that might be of special importance for the habitat types described above. Flowering time is an important trait for colonization, as it directly affects fitness in different habitats (Neuffer and Hurka, 1999). Time at first reproduction is a further important life-history trait, with early reproduction being favoured when colonizing habitats that are characterized by low levels of environmental stress (Rejmanek and Richardson, 1996; Crawley, 1997). High relative growth rate (RGR) of seedlings was found to be the most significant life-history trait separating invasive from non-invasive *Pinus* species, and specific leaf area (SLA) was the main component responsible for differences in RGR (Grotkopp *et al*., 2002). Finally, several hypotheses have been put forward with regard to species interactions that provide mechanisms for invasions by an exotic plant species (see below).

Table 7.2. Expected selection on plant traits at two stages of the invasion process into novel habitats (based on interspecific studies).

During establishment (including probability of initial introduction)
- rapid dispersal (short generation time, long fruiting period, small seed size, prolonged seed viability, transport by wind)

Spread into the new habitat
- flowering phenology (latitudinal and altitudinal gradient)
- life cycle (annual/perennial; mono-/polycarpic)
- relative growth rate (RGR) and its components (mainly specific leaf area, SLA)
- response to resident competitors and antagonists

Traits related to competitors and antagonists

Human disturbance of native communities can create new habitats to which natives are not yet adapted (e.g. increased grazing regime, nutrient enrichment), decreasing their competitive ability towards potentially pre-adapted exotic species (see above). On the other hand, exotics might have a greater inherent competitive ability than native species, as a result of their different evolutionary history (e.g. faster uptake of limiting resources) (Lonsdale, 1999; Callaway and Aschehoug, 2000; Keane and Crawley, 2002).

Besides these plant–plant interactions, the release from antagonists in the new habitat has been proposed as one of the most important factors contributing to the success of exotics as invaders (Williamson, 1996). In this benign environment, resources normally lost to antagonists may be allocated to growth and/or reproduction by a plastic phenotypic response. The assumptions and predictions of the enemy release hypothesis, also referred to as herbivore escape or ecological release hypothesis, has recently been explored in considerable detail by Keane and Crawley (2002).

Based on optimal defence theory (reviews by Herms and Mattson, 1992; Zangerl and Bazzaz, 1992), an alternative and evolutionary mechanism has been proposed by Blossey and Nötzold (1995), by which well-defended exotic plants might benefit indirectly from a lack of specialist antagonists and become invasive. The EICA (evolution of increased competitive ability) hypothesis states that, because a plant has limited resources to partition to enemy defence and competitive ability, an exotic in an antagonist-free environment will, over time, evolve to invest less in defence. This evolutionary trade-off will allow exotics to invest more in fitness components other than defence, such as increase in size, biomass and/or reproductive effort (Story *et al.*, 2000). Thus, for a common environment, the EICA hypothesis predicts that, compared with genotypes from its native range, genotypes from a plant's introduced range will: (i) grow faster and/or produce more seeds; and (ii) be less well defended, and thus specialized herbivores (i.e. potential biological control agents) will show improved performance (Blossey and Nötzold, 1995).

As with most theories on the evolution of plant defences, these proposed changes in the evolutionary trajectory hinge on the presence of fitness costs of defence. Strauss *et al.* (2002), who recently updated the seminal review paper by Bergelson and Purrington (1996) on resistance costs, found significant fitness reductions associated with herbivore resistance in 82% of the studies in which genetic background was controlled. The magnitude of direct costs ranged from 6 to 15%, and 40% of the studies investigated ecological costs (= indirect costs expressed as altered species interactions), with costs ranging from –20 to 58%. These magnitudes are generally greater than those reported by Bergelson and Purrington (1996) and indicate a strong selective disadvantage to resistance in herbivore-free environments, given that the relative fitness of the resistant genotype in the absence of the selective agent is [1 – (cost/100)]. The same conclusion can be drawn by comparing selection gradients, a measure of the selection intensity, for resistance traits, given in the review by Strauss *et al.* (2002), with 393 selection gradient estimates from 19 plant studies published in a recent review on the strength of phenotypic selection in natural populations (Kingsolver *et al.*, 2001). Selection gradients of resistance traits generally lay in the uppermost quartile (Fig. 7.1), thus greatly influencing fitness. In their review, Bergelson and Purrington (1996) have found costs of pathogen resistance to be nearly twice as high as those for herbivore resistance, indicating even stronger overall selection

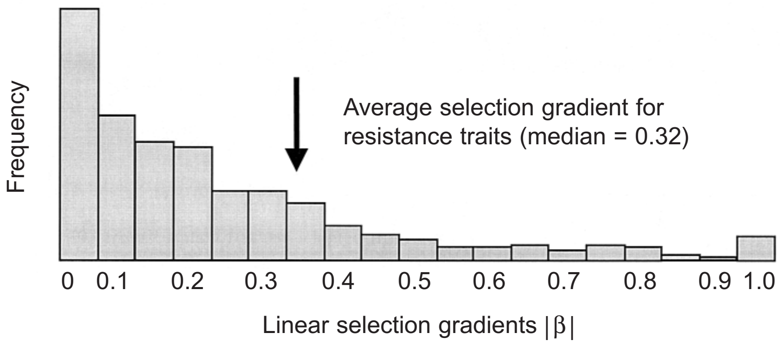

Fig. 7.1. Frequency distribution of the absolute values of the linear selection gradient estimates |β| (*N* = 393 from 19 plant studies; adapted from the database of Kingsolver *et al.*, 2001), in relation to the average selection gradient for resistance traits (trichomes, furanocoumarins and glucosinolates; *N* = 4) (from Strauss *et al.*, 2002).

towards reduced defence in the novel antagonist-free habitat. However, these general considerations have to be taken with some caution, as discussed in the following.

Caveats

Tolerance, the neglected defence strategy

Tolerance, i.e. the ability of plants to buffer the negative effects of antagonists on fitness through compensatory growth and reproduction after damage, constitutes an alternative to resistance as an evolutionary response to selection imposed by consumers. Heritable variation in tolerance has been widely documented, but with mixed support for fitness costs (reviewed by Strauss and Agrawal, 1999). Thus, in a novel, antagonist-free environment, evolution of increased competitive ability may also be expected at the expense of tolerance. If tolerance instead of resistance is involved in defence, then relaxed defence in the novel habitat (as hypothesized in the EICA hypothesis) cannot be detected by measuring insect performance, although invasive plants are assumed to be less able to tolerate herbivory. As tolerance does not impose selection on the consumers, the dynamics of plant–herbivore relationships are expected to be more stable (Roy and Kirchner, 2000; Tiffin, 2000).

Tolerance traits, such as compensatory growth, might also directly increase a plant's competitive ability. Lennartsson *et al.* (1997) recently compared life histories and morphologies of populations with consistently different histories of attack from antagonists. They showed that overcompensation occurred only in historically grazed or mown populations of field gentians (*Gentianella campestris*). Overcompensation was largely associated with changes in flowering phenology in these populations, as well as axillary branching. Most interestingly, such selection by herbivores may have resulted in a higher overall plant fitness in these environments, even in the absence of herbivory (Strauss and Agrawal, 1999). Thus, plants introduced from areas with a long selection history might be more competitive in the novel habitat as compared with plants introduced from regions with little herbivore pressure. If these plant traits are maintained in the novel habitat, subsequent biological control will be more difficult.

Defend and compete

The growth differentiation balance hypothesis (Herms and Mattson, 1992) and similar hypotheses predict that plants will evolve to 'grow *or* defend', by either investing resources in defence against herbivory and growing more slowly, or investing in growth to outcompete neighbours and relax defence against antagonists. Empirical evidence of the assumed underlying physiological trade-off between growth and differentiation is based on growth responses of single plant individuals. In a recent experimental study, Siemens *et al.* (2002) used *Brassica rapa* lines genetically divergent in constitutive levels of both glucosinolates and myrosinase (which breaks down glucosinolates into toxic compounds), which are known to affect herbivory on plants in the *Brassica* family. Defence costs (measured as growth rates) were significant in the absence of competition, but, in contrast to theoretical predictions (Bergelson and Purrington, 1996; Weis and Hochberg, 2000) and empirical evidence (Baldwin, 1998), costs of defence were not detectable in the more stressful competitive environment. This was explained by the fact that these secondary compounds also functioned as allelopathic agents against interspecific competitors, such that allelopathic benefits outweighed costs (Siemens *et al.*, 2002). Thus, 'grow and defend' might be possible because of the dual function of some secondary metabolites (Herms and Mattson, 1992; Inderjit and Moral, 1997).

The generalist–specialist dilemma

Up to now, we have assumed an antagonist-free situation in the novel, invaded habitat. However, generalist herbivores may always be present and continue to impose selection on plant defence traits. Surprisingly, little information is available on generalist enemy impact on introduced plants as compared with their native range, or as compared with co-occurring natives (Maron and Vila, 2001; Keane and Crawley, 2002). Several studies indicate a genetic basis for variation in secondary plant compounds, leading to variation in plant susceptibility to herbivores (Van der Meijden, 1996, and references therein). Van der Meijden (1996) specifically addressed the generalist–specialist dilemma for plant defence: high concentrations of the same plant chemical, such as glucosinolates or pyrrolizidine alkaloids, may deter generalist herbivores, while at the same time attracting specialist herbivores that use these chemicals as cues to find or identify their food plant. A theoretical model predicts that when attacked by specialist and generalist herbivores, plants should produce neither very low nor very high levels of defence substances, and that intraspecific variation in defence concentrations can be maintained by a shifting balance between selection pressure exerted by generalists and by specialists (Van der Meijden, 1996). Thus, a novel specialist-free environment may allow an invading plant species to defend optimally against generalists by increasing its concentrations of secondary plant metabolites. In addition, specific chemicals that only deter specialist herbivores (Shinoda *et al.*, 2002) will become redundant in these habitats. Both these mechanisms will lead to increased attractiveness and reduced resistance to specialist herbivores. Biocontrol impact is therefore expected to be higher on these introduced plant populations than on populations in the native habitat.

Genetic Variation in Invasive Plants

Quantitative-genetic theory predicts that the evolutionary response to directional selection is proportional to the magnitude of additive genetic variation in a population (Falconer and Mackay, 1996; Lynch and Walsh, 1998). An analysis of the ecological and genetic processes determining genetic diversity of invasive populations is therefore pivotal to an understanding of the role of adaptive changes for invasion success.

Reduced genetic variation in invasive plant populations?

The process of invasion into a new territory generally involves one or several successive episodes during which population size is highly reduced. Theory on the genetic consequences of small population size is well developed and predicts a loss of genetic diversity in proportion to the effective size of a population (Nei *et al.*, 1975; Brown and Marshall, 1981; Barrett and Husband, 1990). This is because founders of a colonizing population carry only a small subset of the genetic information in the source population (founder effect). If a population remains small for several generations after initial establishment, then genetic drift will become strong enough to lead to an additional loss of allelic diversity through the fixation of alleles at polymorphic loci. In addition, the frequency of heterozygotes will decrease in small populations as a result of increased mating among relatives (inbreeding).

A number of models have been proposed to describe the population-genetic consequences of colonization (Barrett and Husband, 1990). Among the simplest is the continent–island model, which assumes unidirectional dispersal of propagules from a large source population to small, isolated sink populations. Although simple, this model may nevertheless be adequate to describe the genetic effects of many examples of invasions in which a long-distance dispersal event has led to population establishment on a new continent or island. The continent–island model predicts a reduction in within-population diversity and increased differentiation from the source, depending on number of founding individuals, their total genetic diversity, and the rate of increase in population size after founding. The effects of genetic bottlenecks will be particularly strong when migration, and therefore gene flow, from the native range is restricted after initial establishment, e.g. by geographic barriers. In contrast, multiple introductions from different source populations will counteract the effect of genetic bottlenecks, especially when source populations are genetically highly structured.

To date there are still few empirical studies comparing the genetic structure of plant populations in the introduced and native range, although the situation may change rapidly as a result of the widespread availability of molecular genetic marker technology. Available studies have focused mainly on the static description of spatial patterns of genetic variation, with the principal aim of reconstructing the historical process of migration and expansion (but see Saltonstall, 2002). Although valuable, there is a lack of more integral studies examining directly key processes of invasions (number of introductions, size of founder populations, levels of gene flow after introduction, identity and genetic structure of source populations) over more than one generation. The paucity of data on these processes currently restricts direct tests of theoretical models dealing with the genetics of migration and colonization.

A number of empirical studies confirmed the theoretical prediction of reduced genetic variation in invasive plant populations (reviews by Brown and Marshall, 1981; Barrett and Richardson, 1986). For example, invasive populations of the weed *Rubus alceifolius* were characterized by a single different genotype in three Indian Ocean islands, whereas great genetic variability was found in the native range in South-East Asia (Amsellem *et al.*, 2000). The spread of these genotypes after introduction seems to have been favoured by the switch towards an apomictic breeding system (Amsellem *et al.*, 1991). Indeed, a reduction of genetic variation in the introduced range may only be common in species that reproduce primarily by selfing, apomixis or clonal spread, whereas similar levels of genetic variation are often observed in outcrossing species, or when multiple introductions of propagules from different source populations have occurred (Novak and Mack, 1993; Schierenbeck *et al.*, 1995; Novak and Welfley, 1997; Meekins *et al.*, 2001).

Low levels of genetic variation may influence plant–antagonist dynamics, in both the short and the long term. Data from several agricultural studies comparing disease dynamics in crop monocultures and in multiline mixtures have demonstrated that low levels of genetic variation can accelerate the development of epidemics within the field (Finckh and Wolfe, 1997; Garrett and Mundt, 1999; Zhu *et al.*, 2000). Similarly, in their review on biological control and the reproductive mode of weeds, Burdon and Marshall (1981) found that apomictic and other asexually reproducing plants were effectively controlled more often than sexually reproducing plants (but see Chaboudez and Sheppard, 1995). This was explained by the lack of genetic variation in populations of the clonal weeds. Thus, genetic uniformity in introduced plant populations is expected to increase biocontrol efficacy.

Genetic diversity in invasive plant populations may not only reduce spread of the antagonists, but may also allow selection by biological control agents for less-susceptible target populations, which is well illustrated by the *Chondrilla juncea* programme in Australia. Successful control of the most widespread 'narrow-leaved' form of the rosette-forming apomict *C. juncea* was achieved by the 1971 release of the rust pathogen *Puccinia chondrillina* collected from natural populations in Italy – a spectacular biocontrol success. However, the reduction of populations of this genotype resulted in the spread of the more-resistant 'intermediate-leaved' form, previously suppressed by the competitive dominance of the narrow-leaved plants (Cullen and Groves, 1977; Burdon *et al.*, 1981, 1984). Genetic diversity (only three genotypes in the case of *C. juncea* in Australia!) in resistance towards a biocontrol agent may therefore reduce biocontrol sustainability in the long term.

Small population size during initial colonization will result in increased levels of inbreeding, due to both mating between close relatives and increased self-fertilization. The direct (negative) effects of inbreeding on plant fitness have been widely demonstrated, but surprisingly little is known about indirect effects mediated by altered interaction with plant antagonists. Carr and Eubanks (2002) found that the detrimental effects of selfing on plant biomass and flower production in *Mimulus guttatus* increased by up to three times when plants were attacked by an insect herbivore as compared with unattacked control plants. In a study with *Silene alba*, Ouborg *et al.* (2000) reported altered levels of resistance to a fungal pathogen due to inbreeding. Effects ranged from inbreeding depression to inbreeding enhancement, depending on the population studied. The general finding of large between-population variation in inbreeding effects demonstrates that the consequences of inbreeding at the population level will be largely dependent on the genotypic composition of the founder population.

Caveats

Low correlation between molecular- and quantitative-genetic variation

Although the recent spread of molecular marker techniques may boost studies on the population-genetic consequences of plant invasions, caution must be applied when one tries to use molecular data to infer the adaptive potential of populations. Adaptive changes in invasive plants will mostly depend on genetic variation in quantitative traits of ecological importance (e.g. growth rate, phenology, reproduction, herbivore resistance). These traits show complex, polygenic inheritance, and their expression is generally highly dependent on environmental conditions. Based on the results of a meta-analysis of published data, Reed and Frankham (2001) concluded that the correlation between molecular- and quantitative-genetic estimates of within-population variation is generally low, questioning the value of molecular marker data to predict a population's capacity for adaptive evolutionary change (see also Steinger *et al.*, 2002).

Various factors may be responsible for this low correlation (Lynch, 1996; Reed and Frankham, 2001). For example, the effect of population bottlenecks on additive genetic variation of quantitative traits may deviate from a simple model of genetic drift when trait variation is influenced by non-additive effects of alleles (dominance, epistasis). Several theoretical studies have shown that epistasitic and/or dominance variance can be converted to additive genetic variance as populations pass through a bottleneck (Goodnight, 1987, 1988; Whitlock *et al.*, 1993; Cheverud and Routman, 1996). Thus, predicted reductions in additive genetic variance of bottlenecked, invading populations may be limited, or even reversed, allowing them to maintain their adaptive capacity during colonization. Several experimental studies have confirmed the predicted increase in additive genetic variation following one or several bottlenecks (Bryant *et al.*, 1986; Lopez-Fanjul and Villaverde, 1989; Ruano *et al.*, 1996), although the range of taxa studied is limited and plant studies are almost entirely missing (but see Waldmann, 2001).

An additional complication for the assessment of the evolutionary potential of invasive populations arises from the general observation that additive genetic variance in quantitative traits is not a fixed property of a population but may be strongly dependent on environmental conditions. Few generalizations seem currently possible that would allow prediction of the environmental influence on the expression of additive genetic variation. Hoffmann and Parsons (1996) proposed the hypothesis that environmental stress will tend to increase genetic variance and heritability, and there is some empirical support for this prediction (reviewed by Jenkins *et al.*, 1997), but other studies found the opposite (for plants see Sultan and Bazzaz, 1993; Bennington and McGraw, 1996).

Increased genetic variance through hybridization

Invasive populations can escape genetic impoverishment after bottlenecks not only through gene flow with native populations or co-introduced populations that were previously isolated, but also through introgression of genes from other plant species, both native and introduced. Interspecific hybridization is being increasingly recognized as an important mechanism stimulating the evolution of invasiveness. In their review, Ellstrand and Schierenbeck (2000) list 28 examples where invasiveness was preceded by hybridization. A number of hypotheses have been put forward to explain the superior competitive ability of hybrid taxa, which may contribute to invasion success. First, hybridization may generate genetic variation, that is, provide the raw material for rapid adaptation. This can involve the recombination of phenotypic traits from both parental taxa, or the generation of transgressive phenotypes that are extreme relative to either parent. Rieseberg *et al.* (1999) noted that transgressive segregation may be the rule rather than the exception, and is likely to contribute to the evolutionary success of hybrids, in particular when transgression involves tolerances to various biotic and abiotic factors. Secondly, hybrids may show heterosis, i.e. their fitness can surpass that of both parents. Although heterosis will be eroded quickly by sexual recombination, several mechanisms exist that maintain heterosis (vegetative propagation, apomixis, allopolyploidy, permanent translocation heterozygosity). Thirdly, hybridization may reduce the genetic load resulting from the accumulation of mildly deleterious alleles in small populations.

How will hybridization affect the interactions of plants with their antagonists? Fritz *et al.* (1999) recently reviewed published plant studies analysing the consequences of hybridization for herbivore and pathogen resistance. A surprising result was that, for cases where parental taxa differed in resistance levels to herbivores or pathogens, hybrids resembled the susceptible parent more often than the resistant parent. In quite a number of cases, hybrids exhibited transgressive phenotypes in the direction of increased susceptibility; that is, hybrids were less resistant than either parent. The generality of these results is not known, but because of the large implications for biological control programmes and the widespread occurrence of hybridization in invasive plants, a closer look at the genetics of resistance in intra- and interspecific hybrids would be valuable.

Observed Evolutionary Response

Far more predictions than experimental data are available on genetic changes in introduced plants, mainly as the genetics and evolution of invasive species have received far less attention than their ecology (Sakai *et al.*, 2001). Bone and Farres (2001) estimated rates of evolution in plants from previously published studies, and found widespread evidence for rapid evolutionary change in response to changing environmental conditions. Although estimated rates of evolution of invasive plants were, in general, relatively low, most interestingly, exceptionally high rates (>0.5 haldanes) were found for traits associated with loss of herbivore resistance, indicating the potential for rapid evolution associated with the presence or absence of the plant's natural enemies.

Using their compilation of estimated rates of evolution in plants, Bone and Farres (2001) explored specific trends with regard to differences among traits, life-history correlates and responses to environmental conditions. Physiological traits (e.g. resistance to heavy metals, herbicide or herbivores) were found to evolve faster than morphological trends (e.g. leaf length, biomass, achene volume). Annual plants may be expected to adjust more quickly in absolute time because of their short generation time, while long-lived plants may experience stronger selection pressure per generation (assuming constant selection pressure) and therefore evolve more quickly when generation time is standardized. Indeed, no overall difference in rates of evolution was found between annuals and perennials, when similar traits were compared.

Table 7.3 lists a selection of studies that addressed experimentally genetic changes in plants introduced into a novel habitat. Table 7.3a summarizes studies with *Lythrum salicaria* which compared plant performance and herbivore defence traits of plant populations from native (Europe) and introduced (USA, Australia) habitats. Although increased performance and reduced defence, as predicted by the EICA hypothesis, have been found repeatedly in introduced plants, as compared with their native conspecifics, the results here remain equivocal, as do those for the proposed cause of change (Table 7.3a). These *L. salicaria* studies, which probably constitute the best currently available dataset on this issue, indicate dependency of the findings on the test conditions and the herbivore species involved (Willis *et al.*, 2000; Thébaud and Simberloff, 2001). Future studies should involve reciprocal transplants (Gandon and Van Zandt, 1998), experimental reduction of potential maternal effects, the explicit testing of tolerance as an alternative to defence by resistance (Strauss and Agrawal, 1999; Willis *et al.*, 1999; DeJong and van der Meijden, 2000; Rogers and Siemann, 2002), and the control/monitoring of local antagonists colonizing the test plants.

Selected studies on other plant species are compiled in Table 7.3b. Thus, an increasing number of studies document evolutionary changes in a variety of plant traits during the invasion process. Possible outcomes for plant performance that might be expected when specialized herbivores are introduced as biological control agents are listed in Table 7.4, based on both theoretical predictions and empirical evidence (e.g. Crawley, 1983, 1997). The hypothesis of a change from a prevalent annual or biennial, monocarpic habit in the native temperate European habitat to a biennial or perennial, polycarpic habit associated with the invasion process into North American temperate regions, and the expected

Table 7.3. Genetic changes observed in introduced plant populations.

(a) Studies with *Lythrum salicaria*.

Type of experiment (pot/garden/field, type of transplant	Studied traits of plants and herbivores	Change in studied trait in novel habitat	Proposed cause of change	References
Pot experiment in the open field, transplant (1 site)	Biomass Height Leaf-feeder performance Root-feeder performance	Increased Increased No effect Increased	PIE	1
Garden plot, transplant (1 site)	Shoot biomass Colonization by leaf-feeder	Increased Preferred	PIE	2
Pot/garden plot, reciprocal transplant (2 sites)	Plant performance variates	Slightly increased or no effect	Multiple introduction SOR	3
Greenhouse, transplant (1 site)	Performance of specialist Performance of generalist Leaf phenolic content (defence)	No effect No effect Decreased	Little evidence in support of PIE	4

(b) Selected studies involving other plant species (see text for details)

Plant spp., type of experiment	Studied traits of plants and herbivores	Change in studied trait in novel habitat	Proposed cause of change	References
Four biennials, garden plot, transplant	Plant performance variates	No effect	No genetic response (plasticity)	5
Spartina alterniflora, greenhouse, transplant	Herbivore resistance	Decreased	SGI (+ PIE/drift)	6
	Aggregation by planthoppers	Increased		
Solidago spp., garden plot and field study, transplant	Flowering time	Earlier in the north	PIE	7
	Size at flowering	Reduced		
Capsella bursa pastoris, garden plot, transplant	Flowering time	Early in desert, late in coastal and snowy forest sites	SOR	8
Sapium sebiferum, garden plot, transplant	Plant size	Increased	PIE	9
	Probability of seed production	Increased		
	Foliar C/N ratio	Increased		
	Tannin concentrations	Reduced (defence)		
Senecio jacobaea, greenhouse/garden plot, reciprocal transplant	Plant size, reproductive	Increased	SOR and/or PIE	10
	Biomass, secondary plant compounds	Increased		
	Herbivore resistance	Reduced		
Centaurea maculosa,	Life cycle	Perennial and polycarpic, flowering in the first year	SOR and PIE	11
Tripleurospermum perforatum,				12
Verbascum thapus,				13
Senecio jacobaea				10, 14

SGI, single genotype introductions, an extreme founder effect; SOR, sorting-out, differential establishment of genotypes; PIE, post-invasion evolution that includes mutation and recombination.

1, Blossey and Nötzold (1995); 2, Blossey and Kamil (1996); 3, Willis and Blossey (1999); 4, Willis *et al.* (1999); 5. Willis *et al.* (2000); 6, Daehler and Strong (1997); 7, Weber and Schmid (1998); 8, Neuffer and Hurka (1999); 9, Siemann and Rogers (2001); 10, J. Joshi, Zürich, Switzerland, 2002, personal communication; 11, Müller (1989a); 12, H. Hinz, Delémont, Switzerland, 2002, personal communication; 13, Juvik and Juvik (1992); 14, P. McEvoy, Corvallis, Oregon, 2002, personal communication.

Table 7.4. Expected consequence of observed genetic changes in introduced plant populations, and expected consequence for herbivore impact on individual plants.

Observed changes in	Expected herbivore impact on individual plants
Herbivore preference and and performance	Corrected for plant size, increased preference and performance (due to relaxed resistance) may result in increased impact
Plant biomass	Corrected for herbivore level, increased biomass may lead to reduced impact, but larger plants may attract more herbivores, equalizing this effect
Flowering phenology	Earlier and shorter flowering period may reduce overlap with specialized seed-feeding insects
Plant life cycle	Prevalence of a perennial and polycarpic life cycle may have evolved in the absence of root-feeders, but plants may then be more vulnerable to subsequent biological control agents
Relative growth rate and specific leaf area	Thinner and less-rough leaves may facilitate feeding by chewing and sucking insects

the invasion process into North American temperate regions, and the expected differential impact of root-herbivores appear to be especially worthwhile for explicit testing. In their native range, both between- and within-population variation in life cycle has been observed for a number of plant species, with partial evidence of a genetic basis (e.g. see the references in Table 7.3b). As an example, *Centaurea maculosa* (‘*maculosa*’ in North America is generally a misnomer for *Centaurea stoebe* ssp. *micranthos*; cf. Ochsmann, 2001) introduced into British Columbia (Canada) and Montana (USA) are nearly exclusively short-lived, perennial tetraploids (native to eastern Europe), while the most abundant and widely distributed *C. maculosa* in western Europe (= *C. stoebe* ssp. *stoebe*; Ochsmann, 2001) is a diploid biennial (Müller, 1989a,b). These diploid populations are also the main source of subsequent introductions of specialized root-feeders (Müller, 1989b; Müller *et al.*, 1989). As shown by a coarse population model derived from data from a common environment experiment, the potential for high seed production early in life, together with the perennial life cycle, may have favoured the spread of the tetraploid plants in North America (Müller, 1989a). Root-feeding herbivores are known preferentially to attack and kill larger plants (e.g. Müller, 1983, 1989b; Wesselingh *et al.*, 1993, 1997), and we might therefore speculate that a predominantly perennial, polycarpic life cycle might have been able to evolve (most likely through sorting-out or hybridization processes) and spread only in environments free of (specialized) root-herbivores, such as after transcontinental introductions. A similar conclusion can be derived from a modelling study by Klinkhamer *et al.* (1997), which found the optimal life-history solution to be semelparity (monocarpic life cycle) or mast years, if herbivores attracted by flowering plants mainly reduce plant survival. Interestingly, we would then expect an increased effect of root-feeding biological control agents on these introduced genotypes as compared with the conspecifics from their native range.

Once the impact on individual plants is known, the more crucial question of how this will translate into population-level interactions remains, as the success of biological weed control is measured in terms of reductions in population density and range of weed infestations (Crawley, 1989a). If plant recruitment is not seed limited, then insects that reduce seed production will have no impact on plant population dynamics. On the other hand, herbivore functional and numerical responses are seldom linear and will vary between species and environments (Crawley, 1997). Thus, owing to the many unknown aspects in this scaling-up process, generalizations on the impact of expected changes in plant traits during the invasion process on biological control success will remain problematic. Only detailed case-by-case studies, based on thorough experimental investigations, will allow us to make realistic predictions.

A pragmatic alternative approach is to look at plant attributes related to successes and failures in weed biocontrol projects. Plant attributes associated with good control were found to be a biennial life cycle (as opposed to annual), no seed bank, low power of regrowth, limited seed dispersal and genetic uniformity (see below) (Crawley, 1989b, 1997), which partly confirms our predictions.

Outlook

Recent developments in evolutionary theory, quantitative genetics and molecular tools offer a new integral approach to investigating genetic factors that affect invasion success and its consequences for classical biological control measures. Recently published reviews on genetics and invasion (Lee, 2002), resistance costs to herbivory (Strauss *et al.*, 2002) and the evolution of host specificity (van Klinken and Edwards, 2002), to list only a few, document the increasing scientific interest in combining ecological and evolutionary aspects related to biological invasions and weed biocontrol. It is being increasingly recognized that biological control offers an ideal opportunity to merge disciplines such as population dynamics with population genetics. The topic of this book is therefore well in line with these recent developments.

We are well aware that the scope of our study, i.e. predicting consequences of evolutionary change in invasive plants for plant–herbivore interactions, will involve unravelling innumerable processes, from changes in gene frequencies to plant fitness, population dynamics and community interactions, a clearly unrealistic objective. We hope, however, to have pointed to further interesting studies that address important processes at the various levels of integration. Six such emerging topics are briefly outlined below. In particular, studies in the context of classical biological weed control programmes offer a great opportunity for testing hypotheses that might result in findings contributing to the advance of both theory and practical application, in both biological control and invasion ecology.

Emerging research topics

1. Reciprocal transplant experiments could be used in combination with a phenotypic or genotypic selection analysis (Lande and Arnold, 1983; Mauricio and Mojonnier, 1997; Joshi *et al.*, 2001) to examine the direction and strength of selection in the native and the novel habitat. This would not only allow one to contrast current selection pressures acting on plant traits with evolved changes in these traits, but also to assess the adaptive value of trait variation in different environments.

2. Little is still known on evolutionary trajectories of defence traits when selection pressures are relaxed in the novel environment. It seems especially worthwhile to explore this trade-off for plants differing in their history of selection by herbivores, under different competitive environments, and in the presence and absence of native generalist herbivores. The introduction of biological control agents is expected to reverse the selection pressure on defence traits (see above). Where and when biological control agents were introduced are often well documented, allowing exploration of the pace of evolutionary change in reversed direction. Results of such studies would allow an extension of the EICA hypothesis by including selection history (in both the native and the introduced area) and the effects of generalist herbivores present in the invaded habitat.

3. Tolerance as a defence mechanism needs further attention. Mainly due to the fact that tolerance does not directly affect preference and performance of the antagonists and, thus, does not impose selection on the antagonists, plant–herbivore relationships and population dynamics might be expected to remain more stable (and biological control more sustainable) when tolerance is involved than when resistance is involved (Fineblum and Rausher, 1995; Strauss and Agrawal, 1999; Roy and Kirchner, 2000; Tiffin and Inouye, 2000).

It was even recently suggested that evolution of tolerance could promote an apparently mutualistic relationship between herbivores and their host plant. Selection from herbivores, resulting in increased branching, could have served to increase overall plant fitness even in the absence of herbivory (Järemo *et al.*, 1999; Strauss and Agrawal, 1999). This, in turn, could give these plants a competitive advantage over plants that have evolved under reduced levels of herbivory. If these plant traits are maintained in the new habitat through competitive interactions with native plant species, biocontrol success could be hampered. These hypotheses warrant rigorous testing.

4. Changes in the prevalent life cycle between the native and invaded habitat, and their effects on antagonists, could be studied in reciprocal transplant experiments under open-field conditions. A long-term study to follow the population dynamics of both the insect and the plant populations would be especially rewarding, with the plants grown in mono- and mixed populations of native and introduced genotypes, and herbivores being excluded or allowed to interfere.

5. The observed increased susceptibility in hybrids towards their natural enemies remains intriguing (Fritz *et al.*, 1999). The environmental dependency of hybrid resistance relative to the resistance levels of the parental taxa, especially, might deserve more careful studies. Assuming different defence chemicals to be involved in the parents, we might speculate joint occurrence in the hybrid, but at concentrations too low to influence insect performance negatively, resulting in increased susceptibility.

6. Increased synergism between biological control projects and basic research should be easy to achieve. As an example, host-specificity screening tests generally involve individuals of the weed species to be controlled in both the introduced (target) and the native (host) area. Careful examination of plant responses, as well as preference and performance of the candidate specialist herbivores, would allow the study of trade-offs between plant defence and fitness for native and introduced plant genotypes. Further, collection and storage of seed material from the target populations prior to release, together with a carefully elaborated release design, would allow the genetic composition of the plants during the invasion process to be followed in the presence and absence of specialist antagonists. Similarly, potential genetic changes in the control agents during their population increase and spread could be followed by comparing population samples in the release area at regular time intervals.

Acknowledgements

We thank Dieter Ebert, Jasmin Joshi, Peter McEvoy, Urs Schaffner, Klaas Vrieling, René Sforza and two anonymous referees for helpful comments. H.M.S. appreciated the hospitality of D. Matthies and the University of Marburg, Germany while writing parts of this review. This review was partly supported by the Swiss National Science Foundation through grant numbers 31–65356.01, to H.M.S., and 31–67044.01, to T.S., and through the National Centre of Competence in Research (NCCR) ‘Plant Survival’.

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