Invasive Species in a Changing World

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Chapter 6

Microevolutionary Influences of Global Changes on Plant Invasions

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The succcess of invading species is largely determined by their ability to respond to novel environments in their adopted homes. Flexible responses allow individuals to adjust their growth and reproduction to local conditions, and it is well known that species differ in their capacity for such phenotypic plasticity (Schlichting and Pigliucci 1998). Over longer timescales, however, evolutionary responses are likely to occur through genetic changes in the adaptiveness of populations (Brown and Marshall 1981). An important issue for studies of the spread of invading species is the spatial and temporal scale over which local adaptation can develop. Microevolutionary investigations of plant populations indicate that adaptive responses can occur over short distances and with surprising rapidity (Linhart and Grant 1996). To predict evolutionary responses to environmental change, a knowledge of the amount of genetic variation for physiological and life-history traits of adaptive importance is critical (Geber and Dawson 1993; Mazer and LeBuhn 1999). How this variation is influenced by natural selection will depend on population structure, modes of reproduction, and the specific details of the local physical and biotic environment.

Human-driven global environmental changes in all their complexity provide a new set of ecological and evolutionary challenges for the world's biota. Most consideration of the impact of global change has focused on the problem of species extinctions and the need to preserve biodiversity (Wilson and Peters 1988; Leemans 1996). While there is no doubt that certain aspects of global change, such as habitat loss, are resulting in accelerated species extinctions, less attention has been paid to the ways in which global change might also influence other evolutionary processes such as adaptation and speciation (Lynch and Lande 1993). This neglect may be because of the assumption that the pace of global change is too rapid for organisms to adapt to changing conditions. While it is true that the most obvious influence of climate change involves ecological shifts in the distribution of organisms (Comes and Kadereit 1998), future migrations could be accompanied by the evolution of locally adapted races in species capable of rapid genetic change (Geber and Dawson 1993). This seems especially likely for many invading species because of their high dispersability, prolific regenerative capacities and flexible genetic systems (Baker 1974; Barrett 1992).

While biological invasions constitute part of global environmental change (Vitousek et al. 1996), it is also worth asking how other components of the process of global change are likely to influence the origin and spread of plant invasions. This chapter examines this issue by considering ecological and microevolutionary responses of plant populations to three components of global change: climate change, habitat fragmentation, and impacts resulting from advances in agriculture and biotechnology. These components of global change involve diverse aspects of the physical and biological environments of plant populations. Moreover, successful plant invaders constitute a heterogeneous assortment of species with contrasting taxonomic affinities and life-history traits. This biological complexity makes predictions concerning the evolutionary responses of plants to global change difficult (Geber and Dawson 1993). At the present time we are some way from being able to determine which plant species are likely to become successful invaders and what makes some ecosystems more susceptible to invasion than others (Mooney and Drake 1986; Rejmánek and Richardson 1996; Williamson 1996).

Faced with these uncertainties, broad generalizations concerning evolutionary scenarios become tenuous. For example, in a review of the potential microevolutionary consequences of climate change to plants and animals, Holt (1990) drew attention to the fact that "there is almost no species for which we know enough relevant ecology, physiology, and genetics to predict its evolutionary response to climate change" (p. 311). With this salutory warning firmly in mind, what follows is an attempt to predict some of the potential ecological and evolutionary responses of plant invaders to global changes using evolutionary theory and existing information, scant as it may be, on their ecology and genetics. If nothing else, it is hoped that this review stimulates researchers to consider plant invaders as valuable model systems for investigating genetic and microevolutionary responses to global environmental changes.

Global Changes and Plant Evolution: General Responses

As a prelude to discussing the potential influences of specific components of global change to plant invasions, I begin by briefly reviewing the general evolutionary responses of plants to global environmental change. Two outcomes are most likely—extinction or local adaptation—with the particular response depending on the tempo and nature of change, combined with the biological attributes of individual species. In the first case, progressive extirpation of populations may lead inexorably to species extinction. Species loss can arise through diverse influences, and for some species extinction may be unrelated to the demographic or genetic characteristics of populations (e.g., through environmental catastrophes associated with habitat destruction). Of particular interest to evolutionary biologists are situations where extinction occurs because of the absence of appropriate heritable variation for adaptive traits (Travis and Futuyma 1993). Lack of genetic variation prevents adaptation to new environmental challenges, and the fitness of populations declines to the point where extinction is inevitable. How often populations can evolve rapidly enough to avoid local extirpation in the face of unfavorable environmental change is not well understood, and the importance of adaptive evolution in preventing species extinction is still a controversial topic (Gould 1985). Theoretical models of the evolution of fitness traits attempt to determine the critical rate of environmental change beyond which extinction is inevitable (Lynch and Lande 1993). The models highlight the importance of several key parameters, including the input of mutational variance into a population and its effective size and reproductive system.

Changing environmental conditions commonly result in migration and hence shifts in the geographical distribution and abundance of plant species. Migration in response to past climate change is well documented and depends, in part, on dispersal biology and the availability of migration routes (Comes and Kadereit 1998; Taberlet et al. 1998). Species on islands and isolated habitat fragments, or those with poor dispersal powers, are most vulnerable to extinction if environmental conditions deteriorate. Migration can set the stage for local adaptation in response to divergent selection pressures as long as appropriate genetic variation is present within colonizing populations. Evidence that this has occurred during the Pleistocene, in response to past climate change, comes from numerous studies that have documented evolutionary differentiation in adaptive traits among populations that now occupy glaciated regions (e.g., Mooney and Billings 1961; Cwynar and MacDonald 1987). Recent phylogeographic studies using molecular markers provide opportunities to determine the migrational histories and genealogical relationships of plant invasions associated with past and future climate change (Soltis et al. 1997; Comes and Kadereit 1998; Schaal et al. 1998; Taberlet et al. 1998). A major challenge will be to try to use this phylogeographic information to devise methods that enable determination of the tempo of adaptive change in traits during the invasion process.

What plant traits are likely to be favored by natural selection during global change? This is a difficult question to address because of the diverse environmental influences that characterize each of its components. Nevertheless, if we accept that future ecosystems are likely to experience increased disturbance and greater habitat fragmentation, then it seems likely that opportunistic species with short life cycles, well-developed dispersal powers, and high reproductive output will be favored over longer-lived, more slowly growing species (Bazzaz 1996; Grime 1997). The former suite of traits are characteristic of life-history syndromes variously described as weedy (Baker 1965), *r*-selected (MacArthur and Wilson 1967), ruderal (Grime 1979), or invasive (Barrett 1992). The rapid life cycles of species with these syndromes and their well-developed phenotypic plasticity may provide greater responsiveness to rapidly changing environments. Thus disruptive land-use practices seem likely to favor opportunistic species of early successional habitats with traits that predispose them to become invaders. Under global change, invasiveness may become more prevalent as a plant strategy even in communities that have up to now been relatively immune from biological invasions (e.g., tropical forests, Groom and Schumaker 1993; arctic vegetation, Callaghan et al. 1997). Interestingly, it has been suggested that species with these traits were also favored following past climate change based on palaeobotanical evidence (DiMichele et al. 1987). Invasions are not only a part of global environmental change, but an increase in the abundance of plant invaders in regional floras seems likely to be promoted further by global change.

What information do we need to predict plant responses to global environmental changes? Ecologists are currently spending considerable effort in trying to predict how vegetation will respond to climate change (Walker and Steffen 1996). Part of this research has involved the screening of plant traits and the classification of species into a smaller number of functional groups (Grime 1997; Lavorel et al. 1997; Westoby 1998). This information is being used in models that attempt to predict how changes in temperature and CO_2 will influence the productivity and composition of vegetation. No comparable research program has been developed by plant evolutionary biologists to predict how global change might influence population genetics and plant fitness. While considerable information is available for hundreds of plant species concerning the amounts and organization of variation at allozyme loci, and their association with life history and ecology (Hamrick and Godt 1997), it is still unclear to what extent this class of genetic variation is a reliable predictor of heritable variation in adaptive traits. The best way of finding out whether populations are capable of responding to a specific environmental change is to first identify which traits are of adaptive importance in the new selection regime and then determine how much quantitative genetic variation is available for selection (Mitchell-Olds and Rutledge 1986; Mitchell-Olds and Bergelson 1990; Mazer and LeBuhn 1999). This is a relatively straightforward exercise, but it is time consuming and has only been attempted for a relatively small number of wild plant populations. Invading species are abundant and possess many attributes that make them ideal candidates for this type of study. Unfortunately, little work has been conducted on their genetics and almost none within a global change framework (but see Curtis et al. 1994; Bazzaz et al. 1995).

Climate Change

There is incontrovertible evidence that climate acts as a powerful selective agent on plant traits. The convergent evolution of morphological and physiological traits in phylogenetically diverse families occupying similar climatic regimes provides one source of evidence (Box 1981; Nobel 1991). In addition, the formation within species of climatic ecotypes or races associated with latitude and altitude also demonstrates that adaptive responses can occur at a microevolutionary level (Clausen et al. 1947; Briggs and Walters 1997). Future global climate change is likely to involve three main aspects of the physical environment that are biologically relevant to plant populations: (1) increasing temperatures and accompanying changes in precipitation and evapotransporation, (2) changes in seasonality, and (3) increases in CO_2. There is insufficient information to predict at a local level how these changes will influence vegetation, but it seems reasonable to assume that plant populations will respond through plastic responses over short timescales (e.g., acclimation of physiology to temperature) and over longer time spans through adaptive changes driven by natural selection.

Reproductive and Genetic Consequences

What impacts are these changes in climate likely to have on the reproduction and genetics of plant invaders? Although a truly global perspective is hard to assess, some educated guesses can be made for particular geographical regions. The distribution of many species is currently limited by climatic conditions, and it is likely that increased temperatures and a longer growing season will favor their spread to more northern latitudes, especially in North America and Europe (Woodward 1987). An increase in the length of the growing season could have important influences on the reproductive capacity of populations. In many annual species, seed production is highly plastic and is strongly correlated with plant size (Harper 1977). A longer growing season would result in increased biomass and higher seed output. Such an effect might also arise from other elements of global change, such as elevated CO_2 levels, especially in C_3 plants, and through increased inputs of atmospheric nitrogen (Bazzaz 1996). Moreover, in higher latitudes, seed maturation in plant populations is often curtailed by low temperatures or frost so that any amelioration of climate could act to boost fertility. Any of these influences would have the effect of increasing the reproductive output of populations with potentially important genetic consequences because of the well-established theoretical relationship between population size and genetic diversity (Barrett and Kohn 1991; Ellstrand and Elam 1993). While population growth rates are obviously influenced by a variety of biotic and abiotic factors, it seems likely that elevated fertility, associated with a longer growing season, would result in increased population sizes, particularly for species at the margins of their range.

Firbank et al. (1995) examined the effects of a range of temperature and CO_2 levels on biomass and seed production in the annual grass *Vulpia ciliata*. They found that while CO_2 had little effect on these traits, at higher temperatures plants grew more quickly and achieved their highest biomass and seed production. They suggested that under global change this species has the potential for more rapid population growth and a northward range shift in the United Kingdom, as long as the open habitats that it normally occupies do not become dominated by species that are more competitive, or have higher rates of population increase. The influence of increased temperatures due to global warming on the northward spread of invading plant species in the Northern Hemisphere has been considered by Beerling (1993), who also points out that ecological interactions need to be carefully considered when predicting rates of spread based on dispersal and climatic variables (and see Huntley 1991).

A longer growing season and larger population sizes could be important for the reproductive biology of invading species that are animal-pollinated. Increased pollinator activity encouraged by warmer temperatures and a longer summer would have the effect of increasing fruit and seed set (Grime 1997). Plants occurring in small, isolated populations, typical of the early stages of colonization, are more likely to suffer pollen limitation than are those occurring in large populations. Indeed, the problem of reduced fertility, under low-density conditions, is thought to be a major factor responsible for the selection of mechanisms promoting self-fertilization in flowering plants (Lloyd 1980). Evidence that population size influences the probability of seed set comes from a study by Ågren (1996) of the insect-pollinated invader purple loosestrife (*Lythrum salicaria*, Lythraceae). In this species, plants were more likely to experience pollen limitation, owing to low pollinator service, if they occurred in small versus large populations. Increased fertility of *L. salicaria* populations is of particular significance for the spread of the species in North America since seed viability is exceptionally high and sexual reproduction is the principal means of population growth (Thompson et al. 1987).

Many plant species, including those with high invasive powers, have mixed mating systems with the frequency of cross-and self-fertilization depending on levels of pollinator activity. Increases in population size and plant density could have the effect of altering mating patterns toward increased outcrossing because pollinators prefer larger, more rewarding populations. Several studies have demonstrated that the demographic characteristics of populations, including their size and density, influence selfing rates in this manner (Barrett and Eckert 1990; Karron et al. 1995). Such effects are important because the mating system is a primary determinant of the amounts and organization of genetic variability within and among plant populations (Brown 1979). Outcrossing species maintain higher levels of polymorphism and allelic variability and are more heterozygous than species with higher selfing rates (Hamrick and Godt 1989). Alterations in mating pattern owing to climate-induced demographic changes to populations could therefore have important genetic and evolutionary consequences for plant invaders. However, predicting these consequences for particular species and locations will be difficult since, as discussed in the following sections, other components of global change, such as habitat fragmentation may have more dramatic influences on the demography and genetics of populations, nullifying effects that may arise from climatic warming alone.

Sexuality in Clonal Populations

Another potential influence of climate change on plant invasions concerns the increased seasonality and more pronounced wet and dry cycles that are predicted to occur in certain regions. One particular class of invaders—aquatic weeds—may be especially influenced by these changes. Many aquatic weeds reproduce primarily by clonal propagation in their introduced ranges, and hence populations are often genetically depauperate and composed of one or at most a few genotypes (Barrett et al. 1993). Restricted sexual reproduction can arise because of a variety of ecological and/or genetic factors. In some species, such as the free-floating aquatic water hyacinth (*Eichhornia crassipes*, Pontederiaceae), sexual recruitment is largely prevented because of an absence of suitable ecological conditions for seedling establishment in introduced habitats (Barrett 1980). Populations frequently inhabit canals, drainage ditches, and reservoirs with steep sides and little exposed shoreline. Wet, exposed mud is a prerequisite for germination and seedling establishment so that populations are largely asexual despite the widespread formation of seed. In its native range in lowland South America, *E. crassipes* reproduces sexually, owing to the striking seasonal fluctuations in water level that characterize the aquatic habitats it occupies in Amazonia and the Pantanal. Climate-change-induced fluctuations in water level in the introduced range would have the effect of mimicking the changes that are a predictable feature of the species' natural environments. This would encourage bursts of sexual activity and lead to an increased amount of genetic diversity in populations. More frequent sexuality in aquatic invaders could have important implications for attempts at biological control since there is evidence that species that reproduce primarily by clonal means are considerably easier to control than are those in which sexual reproduction predominates (Burdon and Marshall 1981; Barrett 1989). Genetic diversity reduces the impact of predators, parasites, and diseases on host populations, especially in combination with frequency-dependent selection (Hamilton 1980).

Many plant species reproduce exclusively by clonal propagation at the limits of their range. For example, the common reed (*Phragmites australis*) in northern Europe often flowers so late that its ability to produce viable seeds before winter dieback is limited (McKee and Richards 1996). Low temperatures can inhibit any one of several stages in the sexual cycle, including flowering, gamete development, pollen-tube growth, ovule fertilization, and seed maturation. In addition, unfavorable environmental conditions at range limits can result in a lack of pollinators in animal-pollinated species, or prevent seed germination and seedling establishment. With an ameliorating climate in northern latitudes, it seems likely that some species that were formerly exclusively clonal may experience more suitable environmental conditions for sexual reproduction. An intriguing issue is whether these populations can take advantage of changed climatic conditions by reproducing sexually after many generations of clonal propagation. This may not be straightforward because there is some evidence that clonal populations may lose the facility for sexual reproduction because of the accumulation of sterility mutations causing sexual dysfunction (Klekowski 1988, 1997). For example, fruit and seed set are very low in populations of the self-compatible, clonal aquatic swamp loosestrife (*Decodon verticillatus*, Lythraceae) at the northern periphery of its range in North America. Populations are often composed of one or a few clones and hence are nearly genetically uniform (Dorken and Eckert

1999). Interestingly, the low fertility of clones is maintained under favorable environmental conditions in the glasshouse and with supplemental hand pollination. This suggests that genetic factors must play a major role in sexual dysfunction, and this has been confirmed in a population of *D. verticillatus* from Ontario by controlled crosses. Recessive mutations impairing pollen-tube growth were found to be the major cause of low fertility (Eckert et al. 1999). It would be of interest to determine the prevalence of sterility mutations in other clonal plants, particularly those at the margins of their ranges where sexual reproduction is rarely observed. Lack of sex severely limits adaptive responses to environmental change and also constrains dispersal potential and opportunities for climate-induced migration.

Land-Use Change and Habitat Fragmentation

While climate change will undoubtedly have ecological and evolutionary consequences for plant biodiversity, the effects of habitat destruction through agriculture, forestry, industrial development, and human settlement are more potent and immediate forces of global environmental change. These activities, which are a direct consequence of expanding human populations, lead to alterations of natural landscapes and the replacement of mature, species-rich ecosystems by early successional states. As discussed earlier, vegetation of this type is largely composed of opportunistic, short-lived species with well-developed dispersal powers. Disruptive land-use practices and the spread of open, disturbed environments will therefore change the average life span of vegetation in many locations, favoring species that exhibit rapid population turnover.

Ecology and Genetics of Metapopulations

What are the likely demographic and genetic consequences of these changing land-use patterns for plant populations with different life histories? Invasive species are likely to be favored by the spread of open, disturbed environments. In contrast, for species adapted to later successional vegetation, the loss and fragmentation of habitats will result in reductions in effective population size and a progressive loss of fitness (Barrett and Kohn 1991; Ellstrand and Elam 1993). This is because small populations are more vulnerable to genetic erosion owing to increased opportunities for the stochastic loss of diversity (Bijlsma et al. 1994). In addition, mating among relatives, a characteristic of small populations, reduces the viability and fertility of offspring due to inbreeding depression (Charlesworth and Charlesworth 1987). Since habitat fragmentation increases the isolation of populations, a critical issue for the long-term persistence of populations is the extent to which gene flow acts to restore the diversity that is continually eroded through genetic drift. Efforts to investigate this problem require studies at the metapopulation level since it is at the landscape scale that the degree of connectedness among populations can best be appreciated (Sork et al. 1999).

Recent studies of two plant invaders illustrate the importance of considering landscape-level processes when evaluating the genetic consequences of habitat fragmentation. *Eichhornia paniculata* (Pontederiaceae) is a neotropical, tristylous, annual aquatic of ephemeral ponds, drainage ditches, and rice fields. Barrett and Husband (1997) investigated the influence of spatial isolation on the genetic diversity of populations among regions in northeastern Brazil. The regions chosen varied in the density of populations distributed across the landscape because of differences in the availability of suitable aquatic habitats. Populations occurring in areas with few other populations were significantly less variable at both allozyme and mating-system loci than those from regions with high population densities. This pattern reflects the relative importance of gene flow and genetic drift in determining the amount of genetic variation within populations. Genetic drift has been shown to reduce diversity in many *E. paniculata* populations because of their small effective size (Husband and Barrett 1992).

Lythrum salicaria is one of the most aggressive invaders of wetland environments in North America. Comparisons between native (southwestern France) and introduced (Ontario, Canada) populations of this species have also provided evidence for the relative importance of gene flow and genetic drift in the maintenance of the species' tristylous mating system (Eckert and Barrett 1992; Eckert et al. 1996). French populations surveyed were predominantly tristylous, whereas those in Ontario were often missing mating types. This pattern was associated with differences in ecology and metapopulation structure between the two regions. French populations of *L. salicaria* occur primarily in roadside ditches associated with the agricultural landscapes of the region. The distribution of populations results in a high level of connectivity, providing opportunities for gene flow among populations. Metapopulation models indicate that levels of gene flow on the order of $m \geq 0.05$ can account for the maintenance of tristyly even in small populations (Eckert et al. 1996). In contrast, introduced Ontario populations are more isolated from one another, and opportunities for missing morphs to establish in nontristylous populations through gene flow are restricted. Assessing the degree of connectivity of invading plant populations will be important for determining how susceptible populations are to genetic erosion and fitness loss.

What lessons can be drawn from these two studies in predicting the likely genetic impacts of land-use change on invading species? It is important to appreciate that the spatial distribution and dynamics of populations across the landscape are relevant not only for understanding the nature of the invasion process and modeling its likely outcome (e.g., Higgins et al. 1996; Shigesada and Kawasaki 1997), but also for revealing that these aspects of population structure have important genetic and evolutionary consequences. Rates of gene flow and extinction and recolonization cycles have been shown to play a critical role in governing the partitioning of genetic variation within and among populations as well as the maintenance of variation by the entire metapopulation (McCauley 1993; Harrison and Hastings 1996). Over the past decade, metapopulation theory has advanced much more rapidly than our attempts to collect relevant empirical data. This is especially the case for plants where relatively few species have been investigated from a metapopulation perspective (Husband and Barrett 1996). Invading species could provide useful model systems for investigating these problems because of their rapid population turnover and prolific colonizing powers.

Mating Systems and Reproductive Assurance

Colonizing populations of *Eichhornia paniculata* and *Lythrum salicaria* are prone to loss of mating types through genetic drift, and this can interfere with normal reproductive function. This raises the question of what mating systems are favored in invading species, and how often plants in disturbed environments are unable to reproduce sexually because of an absence of pollinators or mates. If, as discussed earlier, we assume that future land-use change will result in an expansion of open, disturbed habitats, then species capable of founding new populations from single propagules, and then persisting during initial periods of low population density, seem likely to be favored. These requirements favor species that are self-compatible and capable of autonomous self-pollination. Indeed, selfing has been consistently identified as a common mating strategy in colonizing species (Brown and Burdon 1987). Of course, long-term persistence through clonal regeneration is also possible in colonists, but alone this will not provide for the generation of genetic diversity and would thus impede future opportunities for local adaptation.

Not all successful invading species that rely on sexual reproduction are selfers, indicating that some outcrossers can overcome the constraints imposed by colony foundation and low-density conditions during the invasion of patchy habitats. Pannel and Barrett (1998) recently addressed this issue theoretically by examining the benefits of reproductive assurance in selfers versus outcrossers in the context of a metapopulation. In their model they determined the seed productivity that would be required by an obligate outcrosser, in comparison with a selfer, for its maintenance in a metapopulation with varying immigration and colony extinction rates, and contrasting life-history attributes. They found that the strength of selection favoring reproductive assurance was strongest when colony extinction rates in a metapopulation increased and the number of immigrants to a site and the proportion of sites occupied decreased. Selection for reproductive assurance was diminished in perennial plants and for those with a seed bank since populations with these attributes have more than one opportunity to reproduce. The models indicate that selfing will be most advantageous when a species is uncommon across the landscape, and will decrease in importance as local population densities increase.

This work suggests that an optimal mating system for a sexual invader in a fragmented landscape should include the ability to modify selfing rates according to local ecological and demographic conditions. When populations are small, or at low density, plants should self to maximize fertility, thus increasing population growth rates. However, when populations are large and pollinators and/or mates are not limiting, outcrossing and its attendant genetic benefits will be more beneficial. Clearly, sexual systems such as rigid self-incompatibility or dioecy will not generally provide this type of mating flexibility (although see Becerra and Lloyd 1992). This is more likely to be achieved in self-compatible plants, especially those that display prepotency of outcross over self-pollen. In these species the mating system is responsive to the size and composition of pollen loads received by stigmas, with outcross pollen favored in competitive situations, but self-pollen capable of fertilizing ovules when populations are small or pollen vectors are limiting (Cruzan and Barrett 1996).

How often is plant reproductive success pollen limited, especially in invading species? Comparisons of fruit and seed set in naturally pollinated flowers versus those that have received supplemental hand pollination can be used to assess the incidence of pollen limitation in plant populations. A survey of 258 species of flowering plants by Burd (1994) indicated that 62 percent were pollen limited at some times or locations. Few of the species included in this survey could be legitimately classified as successful invaders, presumably because most investigators interested in pollen limitation assumed that this group would be unlikely to suffer from low fertility due to insufficient pollination. This may not be a safe assumption, especially in animal-pollinated invaders encountering novel environments. As discussed earlier, pollen limitation occurs in small populations of *Lythrum salicaria* (Ågren 1996), even in its native range, and has also been documented in *Eichhornia crassipes* at the margin of its adventive range in California (Barrett 1980). At present our ability to predict which species are likely to suffer from pollen limitation is hampered by a lack of information on the ecological mechanisms responsible. A recent attempt to investigate the correlates of pollen limitation using the techniques of comparative biology identified several life-history traits that decreased the likelihood of pollen limitation, the most obvious of which were self-compatibility and the facility for autonomous self-pollination (Larson and Barrett 2000). Experimental studies that compare the fertility of open- versus hand-pollinated flowers of outcrossing invaders under diverse environmental and demographic conditions, including those expected to occur under various global change scenarios, would be valuable in assessing the role that pollen limitation may have on the invasion process.

Agriculture and Biotechnology

One of the major causes of global land-use change is the clearance of self-sustaining wild vegetation and its replacement by cultivated lands used for agriculture, horticulture, and forestry. Cultivated lands are those regularly used to grow domesticated plants, ranging from agroforestry to permanent multi-cropping systems, to fodder species grown for animal grazing. The world total of cultivated lands is estimated to have increased since 1700 by 466 percent with a total of 12×10^6 km^2 of land brought into cultivation during this period (Richards 1990). While in some areas the pace of conversion has slowed or even stopped (e.g., Europe), at a global level cultivated lands are increasing to keep pace with the needs of an expanding human population.

The fundamental biological characteristic that unites cultivated lands and distinguishes them from almost all natural ecosystems is their dramatic reduction in ecological and genetic diversity. Cultivated lands appear as vast areas of environmental homogeneity with a high level of spatial and temporal predictability associated with land-use and management practices. One of the major goals of modern crop husbandry is to minimize the heterogeneity of the physical and biotic components of the environment in an effort to produce a uniform set of growing conditions. Through modern plant breeding and biotechnology, monocultures of genetically uniform crops contribute to the biological impoverishment of arable land. The application of pesticides, fungicides, and herbicides further reduces biological complexity in order to maximize the yields of cultivated plants.

Evolution of Agricultural Weeds

Invading plants have been associated with agriculture since its very beginnings. Agricultural weeds originated from pioneers of the early stages of secondary succession and possessed life-history traits that enabled them to rapidly colonize arable fields (Bunting 1960). Unlike natural migrations resulting from past climate change, or invasions of waste and derelict land, plants that colonize agricultural ecosystems confront a distinct set of challenges, the most serious of which is the grower's determination to eradicate them through increasingly sophisticated weed control technologies. Is there evidence that invaders have responded to these challenges by evolving strategies that promote their own fitness? In common with several other anthropogenically driven environmental changes (e.g., pollution and heavy metal contamination, see Bradshaw and McNeilly 1991), the selection intensities imposed by agricultural practices are often considerably stronger than those evident in natural ecosystems. Indeed, some of the best examples of natural selection involve environmental pressures imposed by such human-related activities (Endler 1986; Gould 1991). Not surprisingly then, there is good evidence that some weed species have evolved races specifically adapted to agriculture (Barrett 1988). In some cases the degree of specialization is so fine-tuned that the invaders are incapable of surviving outside of the crop environment despite their abundance within fields. The existence of these satellite weeds of crops should warn us against any generalizations concerning the "ideal attributes" of invading species (Baker 1965). Instead of exhibiting broad ecological tolerance to a wide range of environments, a typical feature of many invaders, agricultural weed races usually possess several croplike traits, which gives them poor survival in most other environments.

Perhaps the most remarkable example of this phenomenon involves the evolution of crop mimicry among annual barnyard grasses (*Echinochloa* spp.). A handful of *Echinochloa* species are commonly found in and around cultivated rice fields in most regions of the world. However, in several Asian countries (e.g., China and Japan), hand-weeding has been practiced over a long period, and this has led to the evolution of rice mimicry (Barrett 1983, 1987). Barnyard grasses that are most different in appearance to the crop are preferentially removed from fields. Over time this favors a syndrome of traits that makes plants difficult to distinguish from cultivated rice because of convergent morphology and phenology. For example, *Echinochloa phyllopogon* (= *E. oryzicola*) is so similar in appearance to rice that it usually goes unnoticed during most of the growing season and seeds are harvested along with the rice because both plants reach maturity at the same time.

Today, because of the distribution of rice seed contaminated with barnyard grasses, the mimics occur in many regions of the world where cultivated rice is grown. In most of these areas, hand-weeding is no longer practiced, and the fate of the mimics depends on their ability to tolerate improved agronomic practices, including weed control by herbicides. Recent evidence suggests that at least in some regions, these invaders have the necessary genetic variation to enable evolutionary responses to these new challenges. In California, where *E. phyllopogon* was introduced from Japan at the beginning of rice cultivation in 1915 (Barrett and Seaman 1980), the species has recently developed resistance to Londax, the major herbicide controlling barnyard grasses in rice (D. Bayer, personal communication). This example is not an isolated case, and there are

now growing concerns that increased worldwide herbicide use is resulting in the spread of a new class of agricultural invaders: herbicide-resistant weeds.

Spread of Herbicide-Resistant Weeds

Beginning with the introduction of 2,4-D in 1946, agrochemical companies have developed a wide spectrum of selective herbicides aimed at reducing weed populations in cultivated lands. The use of herbicides simplifies weed management in most cropping systems so that growers no longer need to use tillage, burning, cover crops, fallow and crop rotation as strategies for reducing weed infestations. However, the reliance on a single means of control has drawbacks, especially if the efficacy of the method is threatened by the evolution of herbicide resistance in weed populations (Le Baron and Gressel 1982; Caseley et al. 1991). Resistance refers to the ability of some individuals to survive a herbicide treatment that under normal conditions would effectively control the weed population. The ability to survive is heritable, and selection of resistant genotypes can eventually result in control failure. Typically, resistant individuals occur at very low frequencies in weed populations usually ranging from 1 in 100,000 to 1 in 100 million. However, because of the high survival value of resistance genes in the face of repeated herbicide sprays, and the prodigious reproductive capacities of many weeds, the spread of individuals able to tolerate herbicides can be remarkably rapid.

Despite early predictions that herbicide resistance was unlikely to become widespread in weed populations (Harper 1956; Gressel and Segel 1978), a 1997 international survey recorded 188 cases of herbicide-resistant weeds in forty-two countries (Heap 1997). A total of 126 weed species are now known to have evolved resistance to one or more herbicides with, the vast majority of cases occurring in developed countries where herbicides are the primary method of weed control. Following the first report of triazine-resistant common groundsel (*Senecio vulgaris*) in 1968 (Ryan 1970), most early cases of herbicide resistance involved this class of herbicides. By 1983 triazine-resistant weeds accounted for 67 percent of the documented reports of herbicide resistance. Today, however, this figure has dropped to 15 percent because of the introduction of many new herbicides with differing modes of action. Of these, resistance to acetolactase synthase inhibitors, bipyridyliums, phenylureas, and ACCase (acetylcoenzyme A carboxylase) inhibitors is most commonly reported. In contrast, few weeds have evolved resistance to chloracteamides, diphenylethers, and glyphosphate, despite their widespread use. It is clear that the likelihood of weeds evolving resistance to herbicides varies with species and the mode of action of the herbicide.

Particularly alarming has been the development of cross-resistance and multiple resistance in weed populations. In the former, a weed genotype is resistant to two or more herbicides due to a single resistance mechanism whereas the latter refers to situations where plants possess two or more distinct resistance mechanisms. These forms of resistance have developed when growers switch herbicides because the initial herbicide becomes ineffective. Weeds that have multiple resistance to a broad spectrum of herbicides are the most difficult to control and are therefore of greatest concern to growers. Several grass species (e.g., *Lolium rigidum* in Australia, *Alopecurus myosuroides* in Europe, and *Avena fatua* in North America, reviewed by Heap, 1997) fall into this category; and of these, *L. rigidum* (annual ryegrass) is fast developing a reputation in Australia as a "superweed" because of its resistance to a wide variety of different herbicides.

Biotechnology and Weed Invasions

Will future developments in genetic engineering and biotechnology thwart the spread of herbicide-resistant weeds? Unfortunately, this does not seem likely. One of the major commercial applications of biotechnology to crop production has been the development of herbicide-resistant crops (Gasser and Fraley 1989; Caseley et al. 1991; Lal and Lal 1993). Those already on the market include soybeans resistant to glyphosphate and sulfonylurea herbicides and corn resistant to imazethapyr. It seems likely that in the future biotechnology companies will place heavy emphasis on the development and marketing of many additional herbicide-resistant varieties. Rather than reducing herbicide use, these developments are likely to lead to a stronger dependency and prolonged use of herbicides, thus increasing the probability of developing more resistance in weed populations. Future management strategies that include ways to reduce herbicide use through a combination of lower application rates, diverse cropping systems, and rotation offer the best long-term solutions for developing farming systems that are not reliant on crops that have been genetically transformed to tolerate herbicide applications.

The final issue concerning the relationships between agriculture, biotechnological change, and plant invasions involves the potential threats to the environment posed by genetically engineered (transgenic) organisms. A considerable literature has developed in recent years on this topic (e.g., Colwell et al. 1985; Tiedje et al. 1989; Mooney and Bernardi 1990; Raybould and Gray 1993; Russo and Cove 1995; Snow and Palma 1997), but from the perspective of plant invasions the problem largely boils down to two main questions: Will transgenic crops themselves become invasive? Could the transfer of genes from transgenic crops to their wild relatives through natural hybridization result in the origin of more aggressive weedy types? There is a diversity of opinions concerning these two scenarios. Most scientists agree that transgenic

crops are rather unlikely to become successful invaders since the majority of genetic changes brought about by human domestication have resulted in traits with low survival value outside the crop environment (e.g., loss of seed dispersal, lack of dormancy, high palatability, and poorly developed chemical defences against pest and diseases). However, the occurrence of weedy hybrids containing genetic constructs from transgenic crops that confer increased invasibility is certainly possible, since many crops co-occur in fields with interfertile relatives and hybridization between crops and weeds is commonplace (Ellstrand and Hoffman 1990). Recently, genes for herbicide resistance engineered into outcrossing oilseed rape (*Brassica rapus*) were found to persist for several generations in hybrids between the transgenic rape and wild radish (*Raphanus raphanistrum*) under field conditions (Chèvre et al. 1997). Even in predominantly selfing plants, rare outcrossing events can result in genetic exchange between plants. For example, Bergelson et al. (1998) found that transgenic plants of the weed *Arabidopsis thaliana* resistant to the herbicide chlorsulphuron were twenty times more likely to donate pollen to wild-type plants than were other lines of the species containing the same mutant alleles. Introduction of transgenes for herbicide, disease, or pest resistance into weedy relatives of crops could increase their fitness in the crop environment and further exacerbate existing weed problems. Assessing the fitness effects and potential for invasiveness of such transgenes in weed species has rarely been attempted (but see Bergelson 1994; Purrington and Bergelson 1995).

The most obvious strategy to prevent the ecological risks associated with biotechnology involves a ban on the future development of transgenic crops. While this is unlikely to occur, especially in North America, recent developments in Europe involving protests and social action against biotechnology companies and widespread consumer distrust of products arising from genetic engineering, should give the more optimistic advocates of biotechnology cause for thought. In the meantime simple measures such as the growing of transgenic crops in areas where wild relatives are rare or absent should mitigate problems of genetic exchange between crops and weeds and reduce the likelihood of the accidental origin of novel plant invaders through genetic engineering.

Final Remarks

Global changes involve diverse environmental influences, many of which are likely to act as important selective pressures on plant populations. Predicting the particular microevolutionary responses to these changes is a difficult task without knowledge of the amounts and patterns of genetic variation for adaptive traits and the nature of selection acting on these traits. Whether various global change scenarios might lead to genetic alterations that promote increased plant invasiveness is at present unclear. Based on a review of several invaders (animals and micro-organisms), Williamson (1996) claimed that "the critical difference between success and failure [of an invader] will often come from differences at around 10 genes or fewer" (p. 154). Unfortunately, no work has been conducted on the genetic basis of invasiveness in plants, so it would be premature to speculate how many genes may be responsible in most cases. There is still considerable debate on the genetics of adaptation, and especially on whether genetic changes at a small number of loci are sufficient to promote significant changes in ecology (Orr and Coyne 1992).

Quantitative trait loci (QTL) mapping studies of adaptive characters that determine fitness offer the best hope for understanding the genetic architecture of plant invasiveness (see Mitchell-Olds 1995). However, in the future, even if we do determine the number of loci governing traits associated with colonizing ability, this information will be of little value without knowledge of the ecological context in which a particular invasion occurs. Genotypes may behave in a benign manner in some environments, whereas in other ecological settings they can be transformed into aggressive invaders. If we are interested in understanding the biological basis of invasions, the ecological and genetic dimensions of the problem should not be separated.

One of the most remarkable aspects of biological invasions is how unpredictable they are. Because of this, we should not be surprised if totally unexpected plant invaders appear, aided by new environmental conditions arising from global change. One potential mechanism by which this seems likely to occur is through hybridization, the mixing of genetically distinct gene pools. This may be especially important under global change scenarios of increased landscape disruption and the spread of disturbed habitats. These conditions have long been recognized as fertile ground for fostering genetic exchange between species (Anderson 1948). Several well-known cases of plant invasions promoted by interspecific hybridization resulting in new taxa are already known (Raybould et al. 1991; Soltis et al. 1995; Abbott 1992), and we should expect additional examples in the future, given the weak reproductive isolating mechanisms that are typical in many plant taxa.

A more insidious and less appreciated mechanism promoting invasiveness is the potential mixing of genetically differentiated population systems within outcrossing species in their alien ranges. The spectacular spread of the hypervariable Patterson's curse, *Echium plantagineum* (Boraginaceae) in Australia (Brown and Burdon 1983) and *Lythrum salicaria* in North America (Thompson et al. 1987), seems likely to have been promoted by crosses between genotypes introduced from different parts of Europe. Out of such a diverse "hybrid soup" inevitably comes genetic combinations with novel phenotypes. While the majority are usually maladapted, some will eventually display high fitness and superior colonizing ability. Further selection aided by abundant genetic variation will refine these phenotypes to local conditions. The expansion and mixing of plant distributions, aided by the globalization of world trade and the burgeoning horticultural industry, seem likely to provide more opportunities for the future genesis of new plant invasions.

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