Maron J & M. Vila 2007. Exotic Plants in an Altered Enemy Landscape: Effects on Enemy Resistance En: J. Kelley & J. Tilmon (eds.). Specialization, speciation and radiation - The evolutionary biology of herbivorous insects, University of California Press Pp. 280-295

TWENTY

Exotic Plants and Enemy Resistance

JOHN L. MARON AND MONTSERRAT VILÀ

The increasing movement of organisms to new regions by humans is enabling species to breach natural dispersal barriers that normally constrain their geographic distribution. Oddly enough, despite being introduced to areas that may be very different from their home region, some exotics become spectacularly more successful in evolutionarily novel environments than in areas in which they evolved. How some exotics come to dominate these new habitats, despite being often inconspicuous members of their native community, is one of ecology's central mysteries. Unraveling this mystery involves understanding how introduced organisms faced with novel abiotic or biotic conditions make accommodations to their new environments. In this chapter, we consider one dimension of this accommodation process: how exotic plants respond to the altered assemblage of natural enemies they face within their introduced ranges.

Where they are native, plants are attacked by a diverse group of pests, including both specialists and generalists. Together, these enemies can impose diffuse, conflicting, or shifting selection pressures on plants (Hare and Futuyma 1978; Fox 1988; Marquis 1990; Rausher 1992; Pilson 1996; Juenger and Bergelson 1998; but see Maddox and Root 1990). In contrast, exotics face a greatly simplified natural-enemy landscape. Human-mediated transport to new areas instantaneously liberates exotics from their coevolved specialist fauna (Mitchell and Power 2003; Blair and Wolfe 2004; Hinz and Schwarzlaender 2004; Vilà et al. 2005). Indeed, this escape from specialist natural enemies has both been a leading hypothesis for exotic success and a founding principle on which biological control is based (Williams 1954; Maron and Vilà 2001; Keane and Crawley 2002). In addition to escaping from specialists, exotics that lack taxonomic relatives within recipient communities and therefore possess defenses that are chemically unique to the community they invade may also escape from generalists. Host switching by specialists from natives to exotics is also less likely for exotics with no close taxonomic relatives in the recipient community.

Although many exotics escape from consumers, some may actually face greater selection pressure by enemies in their introduced than in their native ranges. The most powerful example of this flip side of enemy escape is weed biological control. When a biocontrol insect is introduced, almost instantaneously, plants that have for decades grown free from specialists can suddenly face devastating attack by these herbivores. Since biocontrol insects are often freed from trophic control themselves, they can build to high numbers and potentially impose greater selection on exotic target plants than they might on their native hosts. Moreover, since some exotics represent a new and underutilized food source for generalists, they may actually accumulate generalist pests in their introduced range (Strong 1974; Auerbach and Simberloff 1988; Jobin et al. 1996; Memmott et al. 2000; Graves and Shapiro 2003; Carroll et al. 2005). This may particularly be the case if exotics have reduced genetic diversity and hence reduced genetic diversity of polymorphic defenses against generalists (Colautti et al. 2004).

Historically, ecologists have emphasized phenotypic plasticity as a primary mechanism by which exotic plants coped with novel abiotic or biotic circumstances in their introduced range (Baker 1974; Wu and Jain 1978; Rice and Mack 1991; Williams et al. 1995). High levels of adaptive plasticity (which might be present in particular species prior to their introduction) have often been often posited as a predictor of invasiveness (Baker 1974; Rejmanek and Richardson 1996; Mal and Lovett-Doust 2005) and important in allowing exotics to cope with a range of heterogeneous environments. Genetic impoverishment from founder effects (Baker 1974; Morgan and Marshall 1978; Barrett and Richardson 1986), the perceived long time span over which it took evolution to operate, and the relatively short invasion history of many exotics have appeared to make evolution an unlikely mechanism that could account for rapid phenotypic adaptation to new conditions. In terms of response to natural enemies, it was assumed that nonnatives that faced reduced selection by enemies should lower levels of defense in a plastic manner, enabling reallocation of resources to growth (Bazzaz et al. 1987). Recently, however, these assumptions have met with reconsideration.

Rapid Evolution of Exotics in Response to Enemy Pressure

Recently, evolution has been considered more seriously within the ecological context of invasions (Huey et al. 2000; Bone and Fares 2001; Lee 2002; Rice and Emory 2003; Stockwell et al. 2003). A growing number of studies show that organisms faced with novel abiotic or biotic conditions can rapidly evolve adaptations to these new conditions (Reznick et al. 1997; Huey et al. 2000; Grant and Grant 2002; Maron et al. 2004a). Indeed, some of the best evidence of rapid evolutionary change has come from exotic plants (Reznick and Ghalambor 2001). Although the greater attention paid to evolutionary processes in invasion biology by ecologists has been fairly recent (Hänfling and Kollman 2002; Lee 2002; Rice and Emory 2003), it is important to note that evolutionary biologists were long ago interested in how exotics adapted to new areas (Baker and Stebbins 1965; Brown and Marshall 1981). Classic studies in the 1960s and 1970s focused on the evolutionary potential of weeds and demonstrated that some exotic populations possessed surprising amounts of genetic variation (Clegg and Allard 1972; Jain and Martins 1979; Brown and Marshall 1981). Other work demonstrated that weeds were capable of undergoing genetically based adaptation to conditions within their introduced ranges (Baker and Stebbens 1965; Baker 1974), as evidenced by the formation of locally adapted races or ecotypes (Hodgson 1964). Only recently, however, have both the ecological and evolutionary aspects of invasions seen a greater coupling (Webber and Schmid 1998; Neuffer and Hurka 1999; Hänfling and Kollman 2002; Maron et al. 2004a; Phillips and Shine 2004; Callaway et al. 2005a, 2005b). This likely reflects a broad trend for greater fusion between ecologists and evolutionary biologists in considering the evolutionary dimension of species interactions.

Here we focus on the specific case of how exotic plants may evolve in response to an altered enemy landscape in the introduced range. We discuss some current hypotheses that make predictions about how enemy defense should evolve in exotic plants and review the empirical tests of these hypotheses. We then summarize results from our own work, where we have compared various aspects of enemy defense in native European and exotic North American genotypes of the short-lived perennial St. John's wort *(Hypericum perforatum).*

Exotics as Substrates for Studying the Evolutionary Response of Plants to Natural Enemies

Since entire assemblages of consumers are often eliminated when plants colonize new regions, species introductions serve as large biogeographical experiments that can allow inferences about how changes in enemy pressure may influence the evolution of plant defense. In native plant-consumer systems, understanding this issue has been challenging. Native plants are usually attacked by tens if not hundreds of herbivores. Surgically removing entire groups of species to examine how they affect the evolution of a particular resistance trait is logistically daunting. Ironically, where this approach has been performed most successfully, it has been on exotic species that have naturalized to their recipient community, rather than on native plants (e.g., North American *Pastinaca sativa* [Berenbaum et al. 1986], North American *Ipomoea purpurea* [Simms and Rausher 1989], North American *Arapidopsis thaliana* [Maurico and Rausher 1997]). Moreover, many native plant–native herbivore systems may be at evolutionary equilibrium, making assessments of directional selection more difficult. However, when plants are introduced to new regions, the identity of consumers, the intensity of their attack, and therefore their overall selective effects often change in predictable ways. For example, exotics are often liberated from their entire suite of specialist enemies in the native range. They may acquire new generalist enemies with different selective effects than those encountered in the native range. Furthermore, for many exotics, since the approximate date of introduction is known, one can conservatively determine the time span over which evolution may have occurred.

By placing native and introduced genotypes in common gardens in both their introduced and native ranges, it is possible to explore how changes in consumer pressure may have influenced exotic plant defense. In common gardens in the native range, one can determine whether exotic plants that are brought home have lost resistance to their native enemies. In the introduced range, by placing biocontrol agents on native and exotic genotypes, one can ask whether exotic plants have lost or gained resistance to specialist herbivores.

Hypotheses and Evidence for Plant Defenses

Recent theories make several predictions about how plant resistance traits should evolve in exotic plants. The "evolution of increased competitive ability" hypothesis predicts that exotic plants that are liberated from specialists should rapidly evolve reduced resistance to this group of consumers (Blossey and Nötzold 1995). This prediction is based on the assumption that plant defenses against specialists are energetically costly, and therefore there is a selective advantage to saving these costs. Although there is certainly some evidence that constitutive defenses might incur allocation costs (Bergelson and Purrington 1996), increasing evidence suggests that costs might be more ecological than energetic (Koricheva 2002). For example plant defense traits can negatively influence plant attractiveness to pollinators (Strauss et al. 1999). Furthermore, allocation costs are expected to be highest for plants growing in low-resource environments. In contrast, successful exotics may be successful because they fill a novel functional role in recipient communities that enables them to tap into "free" or unused resources (Holmes and Rice 1996; Dyer and Rice 1999; Shea and Chesson 2002; Fargione et al. 2003). If this is so, costs of maintaining existing defenses may be minimal.

In addition to losing resistance to specialists, it has also been posited that exotics might rapidly acquire enhanced resistance to generalists (Müller-Schärer et al. 2004; Joshi and Vrieling 2005). For natives, levels of chemical defense are thought to represent a trade-off between two opposing forces (van der Meijden 1996). On one hand, specialists are thought to select for lower levels of qualitative (toxic) defenses because these compounds are often used as host-finding or oviposition cues or even as feeding stimulants by adapted specialists (Rees 1969). Generalists, on the other hand, may select for higher levels of these compounds as greater concentrations provide increased resistance to these consumers (van der Meijden 1996). Thus, if specialists that limit directional selection for increased resistance against generalists are lost in the introduced range, and if exotics accumulate generalists where they are introduced, then selection should favor greater defenses against generalists in recipient communities compared to where they are native (van der Meijden 1996; Müller-Schärer et al. 2004; Joshi and Vrieling 2005).

Evolution in Exotics in Response to Biocontrol

What might be the evolutionary response of exotics to attack by biocontrol agents? As the above arguments suggest, prior to the introduction of biocontrol agents, biocontrol targets may have lost defenses to specialists and therefore be more vulnerable to these agents than they would be at home (Burdon et al. 1981; Müller-Schärer and Steinger 2004). Alternatively, the initial increased vulnerability of some genotypes to biocontrol agents might render populations initially highly variable in their resistance to biocontrol agents (Burdon et al. 1981; Garcia-Rossi et al. 2003). After the introduction of biocontrols, however, one might expect plants to rapidly evolve increased resistance to biocontrol agents. This might occur because selection imposed by biocontrol can be intense. That is, in cases where biocontrol is successful and sustained it is often because biocontrol agents kill plants, just as with chemical control of weeds. It is well known that agricultural weeds have rapidly evolved resistance to a variety of herbicides (Georghiou 1986; Powles and Holtum 1994; Cavan et al. 1998). Native plants in recipient communities may also rapidly evolve resistance to allelopathic chemicals produced by invaders (Callaway et al. 2005a).

Yet, although weeds have great potential to quickly evolve resistance to their biocontrol agents, several factors may hinder this process. For example, if there are negative genetic correlations between resistance and other ecologically important traits, this can retard directional selection toward increased resistance. This was observed by Henter and Via (1995) in their study of pea aphid–parasitoid interactions. They found that despite ample genetic variation for resistance of pea aphids to their common parasitoid, resistance did not increase after several generations of selection. In plant-pathogen systems, disease-resistant genotypes can actually *decrease* in the presence of a pathogen (Parker 1991; Burdon and Thompson 1995), also presumably because of negative genetic correlations. Recent work by Etterson and Shaw (2001) showed that adaptation to climate change by the prairie plant *Chamaecrista fasciculata* was constrained due to among-trait genetic correlations that were antagonistic to the direction of selection.

As well, population limitation produced by biocontrol does not necessarily imply strong selection. Theory predicts that spatial heterogeneity, which provides refuges for plants under attack, can decouple strong population limitation from strong selection (Rohani et al. 1994; Alstad and Andow 1995). Gene flow from populations not under control can erode selection in populations that are under attack. Temporal heterogeneity in selection has been shown to have similar effects. Empirical work has shown that boom-bust dynamics can characterize interactions between biocontrol agents and weeds (McEvoy et al. 1993). In theoretical models, these volatile population dynamics can weaken selective responses by weeds to biocontrol agents (Holt and Hochberg 1997). Holt and Hochberg (1997) argue that heterogeneity in selection may explain why there is limited evidence for the breakdown of evolutionary stability in the case of biological control and yet so many examples of rapid evolution of resistance to chemical control, where control is more geographically uniform. Alternatively, the lack of evidence for evolutionary instability in biological control programs may simply reflect a paucity of adequate research (Kraaijeveld et al. 1998). Since studies are rarely undertaken to understand how the interaction between biocontrol agents and their host plants is played out (Simberloff and Stiling 1996), whether weeds rapidly evolve resistance to biocontrol agents remains a mystery.

Despite the potential for biocontrol targets to rapidly evolve resistance to biocontrol agents, biocontrol theory makes the implicit assumption that interactions between biocontrol agents and target plants are evolutionarily stable (Huffaker et al. 1971). Any evolutionary change on the part of biocontrol targets and controlling agents are assumed to be counterbalancing (i.e., a coevolutionary arms race). What little discussion there has been regarding evolutionary change in target weeds usually concerns how hybridization and introgression among weeds might alter compatibility between hosts and potential control agents (Ehler 1998; but see Pimentel 1986). As Newman et al. (1996) wrote, "because most weed biological control agents are specialists and thought to be adapted to overcome their host's defensive systems, the role of resistance has rarely been considered in weed biological control" (p. 382).

Experimental Evidence for Evolution of Exotic Plant Defense

Enemy resistance has now been compared among native and exotic genotypes for 14 plant species in 18 separate studies (Table 20.1). In these studies, plant resistance to herbivory is defined as either effects of plants on herbivore performance (growth, survival) or the amount of herbivore damage imposed on plants. Eleven studies explored whether exotic genotypes have lost resistance to specialist herbivores; 12 studies compared native and introduced conspecifics for resistance to generalist pests. Of those studies that quantified resistance to generalists, all but the study by Stastny et al. (2005) did so by comparing herbivore performance (larval growth or development time) or herbivore damage to plants in laboratory feeding trials. In contrast, over half of the studies on resistance to specialists occurred in the field, in common gardens. Four of the 12 studies that examined exotic plant resistance to generalists included both common garden and laboratory bioassay studies, while none of the studies on specialists included both laboratory and field tests.

Of the specialist herbivores that have been tested, 7 out of 11 (64%) showed greater performance or higher levels of damage on exotic versus native genotypes. These results, while still limited, suggest that exotics may more commonly lose resistance to specialist herbivores than their native counterparts. In contrast, of the 12 studies on generalists, only 2 (Siemann and Rogers 2003; Maron et al. 2004b) found that exotics had lost resistance to this group of pests. Two studies (Joshi and Vrieling 2005; Leger and Forister 2005) found that exotics actually evolved greater resistance to generalists, as predicted by Müller-Schärer et al. (2004). The majority of studies, however, found no evidence that exotics have altered defense against generalists.

Few studies have examined whether weeds that are biocontrol targets evolve resistance to their agents. The best example of this phenomenon comes from the classic study by Burden et al. (1981). They found that a less-resistant form of skeleton weed *(Chondrilla juncea)* to a rust *(Puccinia chondrillina)* was controlled but replaced through time by two more resistant forms (forms B and C) (Burdon et al. 1981; Cullen and Groves 1981). More recently, Garcia-Rossi et al. (2003) examined differences in herbivore resistance between populations of *Spartina alterniflora* that had never been separated from this species' specialist herbivore, the planthopper *Prokelisia marginata*, and those that had been separated for over 100 years. They found that *Spartina* that had been liberated from its planthopper herbivore was much less resistant and more variable in its resistance than were plants from populations that had always been exposed to *P. marginata*. Garcia-Rossi et al. (2003) predict that biocontrol should rapidly eliminate the less-resistant genotypes, leaving populations of plants with high resistance to *P. marginata*. Finally, the work by Berenbaum and Zangerl is relevant to the issue of whether plants rapidly evolve resistance to specialists once they are introduced. Over the last 125 years, introduced wild parsnip *(Pastinaca sativa)* has evolved increased production of the secondary defensive compound sphondin in response to the introduction (in 1883) of its specialist herbivore, the parsnip webworm, *Depressaria pastinacella* (Berenbaum and Zangerl 1998; Zangerl and Berenbaum 2003).

Response of St. John's Wort to an Altered Enemy Landscape

Background and History

St. John's wort has several attributes that make it an attractive plant to explore how the addition or subtraction of enemies in the introduced range influences the evolution of enemy defense. First, the introduction history of St. John's wort in North America is well documented. *Hypericum perforatum* was first introduced into the eastern United States in 1793 (first reported in Lancaster, Pennsylvania); it was first found in Oregon between 1840 and 1850 and in California by 1900 (Campbell and Delfosse 1984). In the West, plants quickly became established in overgrazed rangelands, spread rapidly, and grew in dense monocultures. Livestock that ate portions of the plant became sick; thus, successful invasion took rangeland out of production. Second, different populations of St. John's wort have experienced divergent histories of herbivore pressure in North America. In western North America, in 1945, Huffaker spearheaded the introduction of a chrysomelid beetle, *Chrysolina quadrigemina* (Coleoptera: Chrysomelidae), to control *H. perforatum* (Huffaker and Holloway 1949; Holloway and Huffaker 1951). This was the first introduction of a biocontrol insect to control an exotic plant in North America. The results were stunning. *Chrysolina quadrigemina* populations established quickly and grew rapidly. Within five years of their introduction, biocontrol beetles had markedly reduced *H. perforatum* populations. The most dramatic effect was in California, where *H. perforatum* was reduced to less than 1% of its former range (McCaffrey et al. 1995; Ritcher 1996).

Although St. John's wort has been present for centuries in central and eastern North America (Sampson and Parker

TABLE 20.1

Outcome of Studies That Have Compared Resistance to Generalist and/or Specialist Herbivores and Pathogens among Native and Introduced Populations

Plant Studied	*Resistance to Generalists*	*Resistance to Specialists*	*Experimental Approach*	*Number of Populations*	*Authors*
Lythrum salicaria	ND	−/ND	FB	1/1	Blossey and Nötzold 1995
		ND	FB	6/6	Willis et al. 1999
Spartina alternaflora		−	FB	5/6[a]	Daehler and Strong 1997
Sapium sebiferum	−		FB	Pooled[b]	Siemann and Rogers 2003
			FB	Pooled[b]	Lankau et al. 2004
Silene latifolia		−	CG-introduced range	20/20	Blair and Wolfe 2004
		−	CG-native range	20/20	Wolfe et al. 2004
Alliaria petiolata	ND	−	FB	8/7	Bossdorf et al. 2004
Hypericum perforatum	−	ND	CG-native range	15/15	Maron et al. 2004b
			CG-introduced range	18/30	
Barbarea vulgaris	ND		CG-native range + FB	3/3	Buschmann et al. 2005
Bunias vulgaris	ND		CG-native range + FB	3/3	Buschmann et al. 2005
Cardaria draba	ND		CG-native range + FB	3/3	Buschmann et al. 2005
Rorippa austriaca	ND		CG-native range + FB	3/3	Buschmann et al. 2005
Senecio jacobaea	+	−	CG-native range	15/16	Joshi and Vrieling 2005
		−	CG-introduced range	4/4	Stastny et al. 2005
Eschscholzia californica	+		FB	4/7	Leger and Forister 2005
Solidago gigantean		−	CG-native range	10/10	Meyer et al. 2005
Ambrosia artemisiifolia	ND	ND[c]	CG-native range CG-introduced range	2/1	Genton et al. 2005

NOTE: −, within a common environment, exotic genotypes have lower resistance than do native conspecifics; +, exotic genotypes have greater resistance than do natives; ND, no difference in resistance; CG, common garden; FB, feeding bioassay; blank cells reflect cases where data were not collected; numbers separated by slash indicate number of native/number of introduced populations sampled.

[a] Clones rather than populations sampled.

[b] Seeds pooled from collections made across one (Lankau et al. 2004) or two (Siemann and Rogers 2003) provinces in China (native range) and from the Huston metropolitan area (introduced range) in the United States.

[c] Genton et al. (2005) do not report whether the herbivores that attacked plants in the native range were generalists or specialists.

1930; Voss 1985), until recently plants have never been exposed to biocontrol. Only a small number of *C. quadrigemina* were released into eastern Ontario in 1969. These insects have since spread in Ontario and to Minnesota, but populations remain at low density and their impacts on St. John's wort populations appear minimal (Harris and Maw 1984; Fields et al. 1988; Hoebeke 1993; Julien and Griffiths 1998).

Control of St. John's wort in portions of the West was successful because beetles killed their host plants. Larvae feeding on the new leaves and stems that are produced in winter and spring have the greatest impact on plant survival. Although adult beetles can completely defoliate plants and destroy flowers and seeds, it is usually larval feeding that kills plants (Holloway et al. 1957).

Interestingly, plants growing in the shade gained a refuge from biocontrol, because the beetles performed more poorly in the shade. Biocontrol in other regions in the West (as well as Australia and other countries) has not always been as universally successful as in California. Poor control is due to several factors, including reduced efficacy of *C. quadrigemina* in colder climates, the presence of more extensive shaded habitat, and summer rain, which allows plants with a less extensive root system to survive. Summer rain also appears important because it enables *H. perforatum* to recover from defoliation (Huffaker 1957; Harris and Maw 1984; Williams 1984).

Additional biocontrol agents have been introduced subsequent to the initial establishment of *C. quadrigemina*. These have included a buprestid root-boring beetle, *Agrilus hyperici*, a gall-forming midge, *Zeuxidiplosis giardi*, and a second chrysomelid beetle, *Chrysolina hyperici*. In Canada, the aphid *Aphis chloris* has also been introduced. These agents add to biocontrol effectiveness in areas where performance by *C. quadrigemina* has been poor (i.e., cool, wet areas). However, since *C. quadrigemina* has been the most common and also the most effective biocontrol agent throughout most of the West, we focus on whether plants have evolved resistance to this herbivore in particular.

Another attribute of St. John's wort that makes it an attractive plant to study the evolution of defense is that the secondary chemistry is reasonably well understood. Individuals produce several toxic defensive compounds (i.e., qualitative defenses), chief of which are hypericin and pseudohypericin. These polycyclic naphthodianthrones (Trifunovic et al. 1998) are produced by glands located along the outer edge of leaves. These powerful photo-oxidants are light activated and cause cell damage. Like many allelochemicals, these compounds appear to have different effects on adapted and nonadapted enemies (Feeny 1992). Hypericins have been shown to be effective at deterring generalist insect herbivores (Arnason et al. 1983, 1992; Fields et al. 1990; Mitch 1994; Sirvent et al. 2003), they can be toxic to large grazing mammals (Giese 1980), and they have potent antimicrobial properties that provide defense against generalist pathogens (Arnason et al. 1983). While generalist insect herbivores avoid consuming portions of leaves containing glands that sequester hypericin (Guillet 1997), specialists use hypericin as a host-finding cue (Rees 1969). Guillet et al. (2000) found that a specialist noctuid (Lepidoptera) caterpillar had higher rates of ingestion when fed plant tissue high in hypericin compared to when fed tissue low in hypericin.

Experimental Approach

We have compared levels of genetically based enemy resistance between introduced and native genotypes of St. John's wort by growing plants in common gardens. Common garden studies enable one to control for environmental effects on phenotypes and examine the degree to which phenotypic variation may be genetically based (assuming no substantial maternal effects are present). By placing the progeny of plants from native European populations and exotic western and central North American populations into common gardens in North America (Washington and California) we have examined (1) if plants from central North America that have not been exposed to biocontrol for the last century have lost resistance to the specialist biocontrol beetle, *C. quadrigemina,* and (2) whether plants from western North America that have been exposed to this agent since the mid- to late 1940s have rapidly evolved resistance to *C. quadrigemina*. By growing exotic and native genotypes in common gardens in Europe (Spain), we explored (1) whether exotics have lost resistance to generalist soil pathogens from the native range, and (2) whether exotics have altered resistance to a native specialist aphid *(A. chloris)* that has been introduced into North America and Australia as a biocontrol agent. In addition, by examining the defensive chemistry of plants in multiple common gardens, we quantified levels of constitutive defenses in plants across gardens, asking whether exotic and native genotypes consistently differ in their levels of qualitative defenses against generalists.

COMMON GARDEN EXPERIMENTS IN THE INTRODUCED RANGE

We collected seed capsules of *H. perforatum* from 18 populations across Europe, 18 populations from western North America, and 14 populations across central North America (seed collection methods are outlined by Maron et al. [2004a]). We established common gardens in Snohomish, Washington, in May 2000 and in Pope Valley, California, in March 2001. The Washington garden contained plants from all 50 populations, whereas (due to space and logistical considerations) the California garden contained plants from only 36 populations. In each garden we created 10 (Washington) or 9 (California) experimental blocks, with each block containing six plots. Plants in half of these plots were exposed to herbivory by *C. quadrigemina*; and plants in the remaining plots were protected from herbivory. Control plants were kept free of larval beetles by spraying individuals once in spring with an insecticide (Isotox). Any adult beetles found on control plants were regularly removed by hand throughout summer.

Within each treatment type, plots within a block contained plants from one of the three regions. One individual from each population within a region was represented in each plot. Different blocks contained unique individuals collected from different maternal plants in each source population. Plants from the same region that were in "exposed" or "protected" herbivory treatments within the same block were maternal sibs and likely clones since St. John's wort produces over 90% of its seeds apomicticly (Arnholdt-Schmitt 2000; Mayo and Langridge 2003). Plant, plot, and block spacings are given elsewhere (Maron et al. 2004a).

We quantified variation in resistance to *C. quadrigemina* in two ways. First, we counted the number of beetles that accumulated on plants in the year after introduction. Since beetles were free to move between plants in common gardens, the cumulative number of beetles that accumulated on particular genotypes in control plots across a season provided one metric of resistance (Maddox and Root 1987). We censused beetles on plants in Washington in 2001 and 2002. In 2002, the beetle population crashed and beetle numbers were extremely low. Second, we determined the effects of biocontrol beetles on plant fecundity by comparing seed production of plants exposed and protected from herbivory. We estimated plant fecundity by harvesting, drying, and weighing seed capsules at the end of summer and then converting capsule weight to capsule number based on regressions of relationships between these two variables.

COMMON GARDEN EXPERIMENTS IN THE NATIVE RANGE

In an additional common garden, in an old field at the Universitat Autònoma de Barcelona campus field station in Bellaterra, Spain, we determined whether North American and European genotypes differed in their resistance to several native enemies that naturally colonized plants. We assessed resistance to three generalist soil pathogens: *Colletotrichum* sp. (Coelomycetes), *Alternaria* sp. (Hyphomycetes), and *Fusarium oxysporum* (Hyphomycetes). These generalist soil fungal pathogens are dispersed by water (Andrés et al. 1989) and cause necrosis (or anthracnose, in the case of *Colletotricum*). We also assessed resistance to the specialist aphid *A. chloris*. In this garden we quantified resistance to these pests in two ways. For soil pathogens, on control plants we compared how the number of plants attacked by pathogens differed among European and North American populations. We also compared the survival of plants from both regions that were either exposed or protected from pathogen attack. For aphids, on control plants we determined how the number of aphid colonies per plant differed among plants from Europe and North America.

In 2002, we planted seedlings from 30 source populations into this garden, 15 each from Europe and North America. Due to space limitations we omitted central North American populations. Plots contained different individuals from each western North American or European source population. Half of the plots were sprayed with fungicide to suppress native fungal pathogens; plants in the remaining plots were exposed to natural levels of pathogen attack (see Maron [2004b] for a full description of the plot layout). In midsummer of 2002 and 2003, when aphid numbers were at their peak, we censused the number of aphids on plants by counting the number of aphid clumps per plant. This metric is a good estimator of aphid load per plant. During their first summer in Spain, experimental plants remained pathogen free. However, this changed in 2003, and starting in January of this year, we censused plants every two weeks, noting pathogen infection.

DEFENSIVE CHEMISTRY

To determine how defensive chemistry differed between native and introduced genotypes, we sampled leaf tissue of plants that we grew in Washington, and in a second common garden in Spain (at the Mas Badia Experimental Field Station near Girona, Spain (latitude 42° 19′). Sampling and methods for chemical analyses are detailed elsewhere (Maron et al. 2004b).

Results

RESISTANCE TO SPECIALIST BIOCONTROL AGENTS

We found no consistent evidence that St. John's wort from introduced populations had either lost or gained resistance to the specialist biocontrol agent, *C. quadrigemina*. In the common garden in California, in the year following their introduction into the garden, there were no significant differences in the number of adult beetles on plants from the native versus introduced region (Fig. 20.1A) (repeated measures nested ANOVA, $P = 0.44$). Instead, larger plants had more beetles (plant volume and beetle numbers log transformed; $R^2 = 0.25$, $P < 0.0001$). Although beetle addition significantly reduced seed capsule production (Fig. 20.1B) (ANOVA, $P < 0.0001$), there was no difference in the negative effects of beetle herbivory among plants from the three regions (i.e., no significant region by treatment interaction, ANOVA, $P = 0.15$).

In Washington in 2001, again one year after beetles had been introduced to the common garden, we found significantly more beetles on western North American genotypes than on European or central North American plants (Fig. 20.1A) (repeated measures nested ANOVA, $P < 0.03$). However, since in 2001 plants from western North America were larger than plants from the other two regions (Maron et al. 2004a) it is likely that, as in California, larger plants attracted more beetles. In both common gardens, plants from different populations also differed significantly in the number of beetles found on them (repeated measures nested ANOVA, $P < 0.008$ and $P < 0.003$ for California and Washington, respectively).

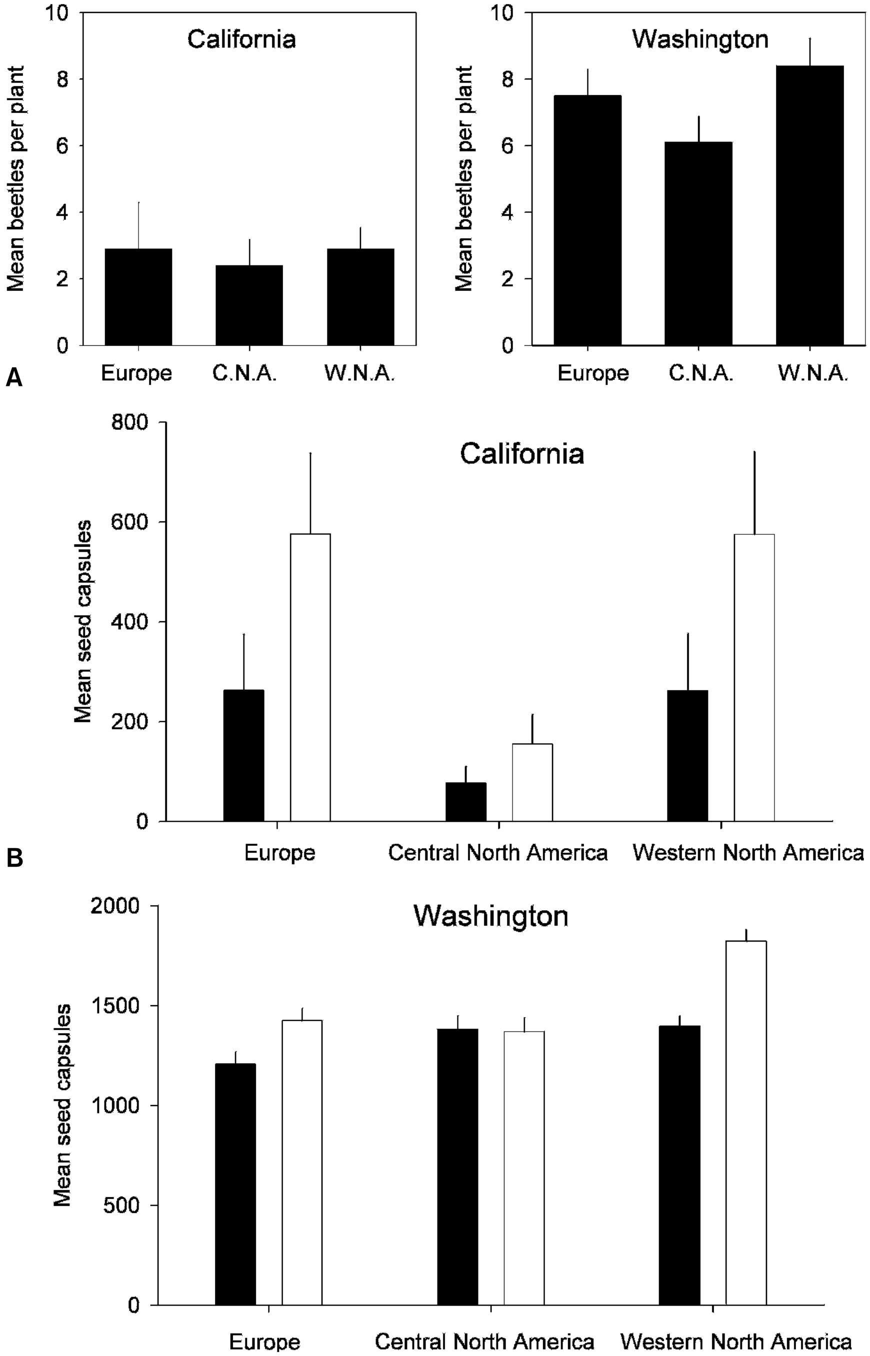

FIGURE 20.1. A. Mean (+SEM) number of biocontrol beetles (*Chrysolina quadrigemina*) found on plants from different regions (C.N.A., Central North America; W.N.A., Western North America) in common gardens in California in 2002 (*upper left*) and in Washington in 2001 (*upper right*). Values are from the census in which beetles were at their seasonal peak. B. Mean effect of beetle (*Chrysolina quadrigemina*) herbivory on seed capsule production in California and Washington. Black bars, plants exposed to bioncontrol beetles; clear bars, plants protected from herbivory. Regional means are the average of population means in each region.

In Washington, herbivory by beetles reduced seed capsule production; overall, control plants produced significantly more seed capsules than those exposed to biocontrol (Fig. 20.1B) (ANOVA, $P < 0.0001$). The impact of beetle herbivory on per capita seed production varied by region of plant origin (significant treatment by region interaction; ANOVA, $P < 0.004$); the magnitude reduction in seed capsule production scaled positively with beetle numbers (ANOVA, $P < 0.002$). Since plants from Europe and central North America supported fewer beetles than did plants from western North America, beetles had less impact on their per capita seed production than for genotypes from western North America. Herbivory on plants from European and central North American populations reduced their seed production by an average of 15% and 0.8%, respectively. In contrast, herbivory resulted in a 23% drop in the per capita seed production of plants from western North American populations. After statistically controlling for differences among plants in beetle numbers, western North American plants still suffered significantly greater reductions in seed production than did plants from the other two regions (ANCOVA, $P < 0.009$).

In 2002, the beetle population across the Washington garden was much reduced compared to 2001. On average, there were 1.7 (± SEM 0.26), 1.4 (± SEM 0.19), and 0.92

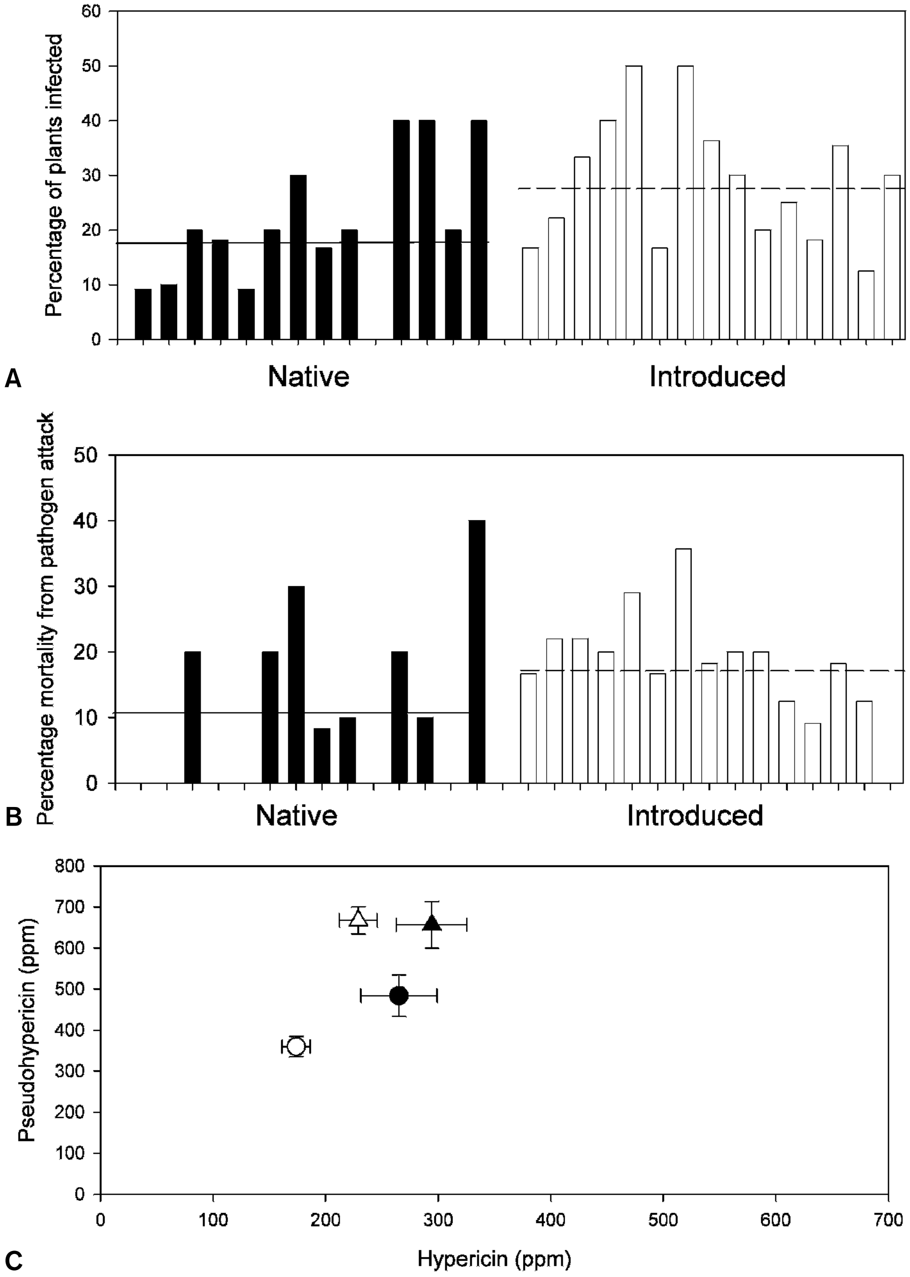

FIGURE 20.2. In common garden in Spain, percentage of individuals within native European (closed bars) and introduced North American (open bars) populations that were infected by pathogens (A) or died after infection (B). Horizontal lines are the mean of population means from European or North American populations. Lines that differ in style (i.e., solid versus dashed lines) indicate statistically significant differences between regions. (C) Relationship between mean of population means (±SEM) hypericin and mean of population means (±SEM) pseudohypericin among St. John's wort grown in Washington (circles) and Spain (triangles) common gardens. Open symbols, nonnative populations; closed symbols, native populations.

(± SEM 0.16) beetles per plant for plants from Europe, central North America, and western North America, respectively. In contrast to results from 2001, the number of adult beetles on plants from the three regions was not significantly different (ANOVA, $P = 0.16$).

In Spain, resistance to the specialist native aphid, *A. chloris*, also was not different between plants from Europe and North America. There was no significant difference in the number of aphid colonies that naturally colonized plants from Europe and North America (nested ANOVA, $P = 0.44$).

RESISTANCE TO GENERALIST PATHOGENS

In contrast to these varied results on resistance against specialists, we found strong support for St. John's wort from exotic populations having reduced resistance to generalist consumers. Introduced genotypes of St. John's wort from western North America that were grown in Europe had lower resistance to generalist soil pathogens than did native St. John's wort. Levels of pathogen attack (Fig. 20.2A), and mortality due to this attack (Fig. 20.2B) were both higher among plants from western North American populations compared to native European populations.

DEFENSIVE CHEMISTRY

In common gardens in North America and Europe, exotic North American genotypes produced significantly less hypericin compared to European genotypes (Fig. 20.2C). There was no difference in mean hypericin values between western and central North American genotypes (post hoc comparison, $P = 0.19$), despite their different presumed histories of herbivore pressure. Exotic genotypes in Washington (the only garden where it was measured) also produced, on average, 19% less hypericide than did European genotypes, a significant difference (Maron et al. 2004b). We found no significant differences in levels of pseudohypericin between native and exotic genotypes across gardens in Washington and Spain.

Explanation of Results from Work on St. John's Wort

Our results from work on St. John's wort provide an intriguing counterpoint to the studies we reviewed. We found that exotic St. John's wort populations (1) have reduced resistance to generalists (pathogens), (2) lower chemical defenses (which are likely most effective against generalists) compared to plants from native populations, but (3) no loss or gain in resistance to specialist insects. In contrast, among the studies we reviewed, there was more support for a loss of resistance in exotics to specialist enemies, and there was generally no difference among native and introduced plants in resistance to generalist enemies (Table 20.1).

Why might our results differ from those of other studies? One possibility is that we studied generalist pathogens, whereas other studies have investigated resistance to generalist herbivores. We think it more likely, however, that the answer may lie in how selection operates on St. John's wort defense in the native range. We speculate that generalist pathogens may be a potent source of selection on native St. John's wort. In natural populations in Spain, we have witnessed the wholesale die-off of dense St. John's wort populations from pathogen attack. Moreover, in a survey of 43 different populations across Western Europe, an average of 18% of the plants sampled showed evidence of attack by pathogens. Nearly one-third of sampled populations had at least one plant that was dead, apparently from pathogen assault (Vilà et al. 2005). While many specialist insects also attack *H. perforatum* in Europe (Wilson 1943), many of these species possess behavioral or biochemical adaptations to overcome the photoactivated defenses of *Hypericum* (Rees 1969; Arnason et al. 1992; Guillet et al. 2000). Thus, toxic defenses against generalist pathogens may be favored in Europe (sensu van der Meijden 1996). In North America, St. John's wort clearly escapes from its specialist herbivores (except where plants have been exposed to biocontrol). But because of its rather novel chemistry (we know of no abundant and widespread native *Hypericum* species that grow in identical habitats as *H. perforatum*) it may also escape from generalist herbivores. In fact, in the introduced range only 4% of the plants have signs of herbivore damage compared to 23% in the native European range (Vilà et al. 2005). As well, in our common gardens in North America, plants attracted few generalist herbivores. Given both the limited level of attack in North America by generalist enemies at large, and the fact that costs of pathogen resistance are often much higher than those of herbivore resistance (Bergelson and Purrington 1996), selection in North America may favor an overall decline in defense investment to generalist pathogens as opposed to specialist insects.

But why has St. John's wort from western North America not rapidly evolved resistance to specialist biocontrol agents? With regard to the biocontrol beetle *C. quadrigemina*, it may be that in western North America, although local populations are suppressed by this beetle, disturbed areas where populations have undergone local suppression may be recolonized by propagules from nearby areas where plants have escaped control. Since St. John's wort gains a refuge from beetle herbivory in the shade (Holloway 1957), plants escaping control in the shade could provide propagules that recolonize sunny areas. This process could decouple population regulation from an evolutionary response to strong selection (Holt and Hochberg 1997). It would be interesting to test whether there are differences in resistance between genotypes from western North America that have long grown in the shade with those that have grown in the sun. Alternatively, it may be that (by chance) populations we sampled have not faced a long history of repeated biocontrol. To our knowledge, western North America plants used in our common garden in Spain have never been exposed to the biocontrol agent *A. chloris*, so this might explain why we found no evidence that plants from western North America had greater resistance to this specialist.

Of course, the reasoning outlined above is speculative. What it suggests, however, is that a key to interpreting work in this area is an increased understanding of the relative magnitude of selective effects of generalists versus specialists in native and introduced populations. Future studies would benefit from a tighter coupling of observational data from souce populations (levels and identity of enemy attack) and common gardens (genetically based differences in defense between exotics and natives in progeny from source populations).

Among-Population Variation in Enemy Resistance

An important ancillary benefit of the growing interest in comparative studies of resistance among exotic and native genotypes is the focus on population-level comparisons. In contrast, research on the evolution of defense in native systems has almost exclusively examined the causes and consequences of variation in resistance within single populations, since individuals are the unit upon which selection acts. As such, our understanding of sources of variation in resistance across larger spatial scales is limited. Even for populations in close proximity we are mostly ignorant about what drives among-population variation in resistance.

A robust result shared among many of the studies we reviewed is that there are substantial levels of among-population variation in resistance, even among introduced populations. In our work, we found 3.6-fold differences in levels of hypericin among introduced populations, and 4.2-fold differences among native populations for plants grown in our Washington common garden. We have found similarly high levels of genetically based variation in other traits (seed production, plant size) among native and introduced populations as well (Maron et al. 2004a). For natives, if genetically based levels of resistance reflect past selective effects of consumers (Berenbaum et al. 1986; Marquis 1992), then these data strongly suggest that enemy pressure and selection on resistance traits vary dramatically, even among populations from within a small portion of the distribution of a species. This in turn provides interesting support for coevolutionary "hotspots" and "coldspots" (sensu Thompson 1999a, 1999b), which for chemical defense has been best documented in poisonous snake-newt interactions (Brodie and Brodie 1999; Geffeney et al. 2002). A future challenge for those interested in native plant–consumer dynamics will be to understand what the sources and consequences of this variation are for plant fitness, abundance, and dynamics. For those interested in the evolutionary trajectory of exotics, it suggests that the view of plants universally going from being well defended where they are native to poorly defended where they are introduced is overly simplistic.

Are Differences in Exotic and Native Phenotypes the Product of Evolution?

Throughout this chapter, we have implied that differences in resistance between exotics and natives in common environments suggest evidence for rapid evolutionary effects. It is important to stress, however, that this need not be the case. Several crucial pieces of evidence are needed before concluding that differences in phenotypes between natives and exotics are driven by evolution. First, one must rule out founder effects. If exotic populations are, by chance, founded by individuals with low resistance, differences between natives and exotics have nothing to do with evolution. Genetic data can be used to shed light on invasion history. For example, for St. John's wort we analyzed variation in neutral amplified fragment length polymorphism (AFLP) makers among introduced and native genotypes. These data showed substantial neutral genetic variation and suggested that St. John's wort has been introduced multiple times, from multiple source populations, into North America (Maron et al. 2004a).

Second, one should rule out maternal effects. Maternal effects occur when differences in maternal environment influence how seeds are provisioned, which then affects trait values of juvenile or adult plants. Thus, if the maternal environment is universally different between native and introduced populations, this could potentially produce a consistent difference in phenotype between natives and exotics, even when they are grown in a constant environment. One indirect approach to examine whether maternal effects might be important is to compare seed weight between native and introduced populations. We have done this for St. John's wort and found no significant differences in seed weights between populations from Europe, western North America, or central North America (J.L.M., unpublished data). Of course a more direct and powerful approach involves growing plants for two or more generations in a common environment, collecting seeds from these plants, and using them as the source of material for common garden experiments.

Third, since an assumption behind comparative studies of exotic and natives is that enemy defense can evolve in the introduced range, ideally one should measure the heritability of putative defensive traits to ensure that this assumption is correct. Where heritability of resistance traits has been assessed for native plants, it is usually the case that heritabilities are greater than zero, implying they can evolve (Maddox and Root 1987; McCrea and Abrahamson 1987; Fritz and Price 1988; Kennedy and Barbour 1992). Fourth, a sufficient number of populations should be examined so that levels of resistance across a reasonable portion of the native and introduced range can be determined (Bossdorf et al. 2005). Of the 19 comparisons made between exotic and native genotypes from the papers we reviewed, only an average of 8 populations were tested from the native range and 9 were tested from the native range. Since these tests assume that sampled populations represent the situation across an entire range, future studies should sample a greater number of populations. In our experience, adding populations often increases the among-region variance. Thus, somewhat counterintuitively, sampling only a few populations may actually increase the probability of finding differences between regions.

Two aspects of how exotics respond to altered enemy pressure in the introduced range have thus far received relatively scant attention. The first concerns tolerance. It is not clear how selection on tolerance might operate in the introduced range. The answer to this will of course depend on whether tolerance has significant costs (Agrawal et al. 1999), how tolerance and resistance trade off with each other, if at all (Strauss and Agrawal 1999), and the prevalence of generalist herbivores that graze on exotics in the introduced range (Müller-Schärer et al. 2004). Only two studies have explicitly compared tolerance between exotic and native genotypes, and neither of these studies found significant differences in tolerance (van Kleunen and Schmid 2003; Bossdorf et al. 2004). In our work on St. John's wort, we have similarly found no evidence for differences in tolerance to simulated herbivory between native and exotic plants (R.B. and J.L.M., unpublished data). The second issue concerns whether induced defenses differ between native and exotic genotypes. We know of no explicit comparison that has been made in levels of induced defenses between native and exotic conspecifics.

Finally, common garden studies should ideally be conducted in multiple locations (sensu Clausen et al. 1940). As Rice and Mack (1991) have stated, "although the potential for ecotypic variation and evolutionary change can be studied within a common garden or glasshouse environment, its demonstration requires a reciprocal transplant experiment in the field" (p. 98). Our previous results serve to highlight this fact. When we compared seed capsule production of native and exotic genotypes of St. John's wort, results from one or even two gardens were not necessarily mirrored across all gardens (Maron et al. 2004a). For example, there were strong differences in fecundity between western North American and European plants in common gardens in Washington and Sweden but not in California and Spain. Similarly, we found that exotic St. John's wort populations produced significantly less of the secondary compound, pseudohypericin, in our common garden in Spain. However, this was not the case in Washington (Maron et al. 2004a). Had we established only one common garden, we would have come to erroneous conclusions regarding trait differences between native and exotic genotypes.

Conclusions

While a growing body of work shows that exotic plants often have genetically based differences in herbivore defense compared to their native conspecifics, ascribing these differences to rapid evolution will require more detailed study than has occurred to date. In particular, future studies will need to sample a greater number of populations across the native and introduced range and couple common garden results with data from which the invasion history of particular species can be inferred. As well, a greater congruence of methodology will aid in the synthesis of results. To date, studies have used different approaches to measuring resistance. Some studies have estimated resistance by measuring herbivore performance on plants, while others have examined the fitness effects of the consumers on plants in the field—a more direct estimate of resistance. Finally, many studies have assayed resistance by measuring levels of chemical defense. Future studies would be bolstered by making a more direct link between levels of particular secondary chemicals that are assayed and effects on consumers (sensu Berenbaum and Zangerl 1998).

More generally, future interpretation of comparative biogeographic studies of plant defense will be strengthened by resolution of several issues. The first involves understanding the selective impacts of specialists versus generalists in native populations. Current theories regarding how plant defense should evolve in exotic plants predict different outcomes for defenses against specialists versus generalists (Blossey and Nötzold 1995; van der Meijden 1996; Müller-Schärer et al. 2004; Joshi and Vrieling 2005). These are predicated on the notion that exotics escape from specialists, whereas this may or may not be the case for generalists. But for exotics to truly escape from specialists, the selective impacts of these enemies must be relatively strong across the native range. At the very least, specialists must impose stronger selective effects than generalists where plants are native. If this is not the case, exotics may have little to escape from. The second issue, related to the first, concerns how one classifies consumers that attack plants in their native range. Consumers do not always neatly fit into a tidy specialist-generalist dichotomy. Although some specialists are highly restricted in their host use, others are likely more polyphagous than is appreciated (Novotny et al. 2002). By the same token, although particular species of generalists may feed on many taxonomically diverse species, some individuals may "specialize" on particular host plants. Thus, making accurate predictions about how enemy defense may evolve in exotic plants will require more detailed natural history data on the selective pressures imposed by consumers across native populations that are sampled. Finally, there is the question of what plant traits confer resistance to particular types of consumers. The most frequently used organizing hypothesis is that toxic "qualitative" defenses deter generalists and that less-toxic, digestibility-reducing "quantitative" defenses deter specialists (Feeny 1976; Rhoades and Cates 1976). Thus, escape from specialists is thought to result in the loss of quantitative defenses but not qualitative defenses (Müller-Schärer et al. 2004). Many resistance traits, however, may not be so easily assigned to one of these two discrete groups (Stamp 2003). Surely toxic qualitative defenses provide some measure of defense against specialists, just as less-toxic quantitative defenses must provide some resistance to generalists. Similarly, rather than assigning consumers into the discrete groups of generalist or specialist, greater natural history information is needed on the particular consumers that plants escape from when introduced, their feeding proclivities, and the traits that confer resistance to them. In the future, a more nuanced approach to defense and enemy specialization will be required to make better sense of biogeographic comparisons among plant populations.

Finally, we close this chapter by making a plea that was first made by Harper in 1977. Biocontrol represents an excellent opportunity to infer how particular specialist herbivores may influence the evolution of resistance in plants that have been naïve to specialist herbivory for decades. New biocontrol introductions are increasing, and it would be extremely valuable, and easy, to save seeds from a variety of populations of exotics prior to when they become targets for biocontrol so that future researchers could directly compare phenotypes of ancient versus contemporary genotypes to directly determine whether biocontrol is a potent selective force on exotics.

Acknowledgments

We greatly thank D. Ewing and P. Matas for greenhouse assistance in Washington and Spain, respectively. R. Bommarco, B. Clifton, S. Elmendorf, D. Grosenbacher, J. Jones, T. Hirsch, T. Huettner, J. Pijoan, and M. Wolven helped establish and maintain the Washington common garden and K. Parker graciously allowed us to establish research plots on her land. I. Gimeno and L. Marco helped to establish and maintain the Spanish common gardens. We thank A. Angert, D. Ayers, J. Combs, U. Gamper, S. Gardner, D. Greiling, F. Grevstad, J. Hess, R. Keller, P. Kittelson, E. Knapp, E. Ogheri, P. Pysek, A. Sears, R. Sobhian, A. Stanley, J. Taft, E. Weber, A. Weis, and A. Wolf for helping with seed collection. John Aranson collaborated with work on plant chemistry; students and staff at the University of Ottawa who assisted with the phytochemcial analysis included Andrew Knox, Alex Turcotte, Andrew Burt, and John Livesey. This work was supported by grants to J.L.M. from NSF grants DEB-0296175 and OPP-0296208 and from a fellowship from the Catalunya PIV. The Institut de Ciència i Technologia Ambientals, Universitat Autònoma de Barcelona kindly provided working space. M.V. was supported by MCYT grant REN2000-0361 GLO.

References Cited

Agrawal, A. A., S. Y. Strauss, and M. J. Stout. 1999. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. Evolution 53: 1093–1104.

Alstad, D. N., and D. A. Andow. 1995. Managing the evolution of insect resistance to transgenic plants. Science 268: 1894–1896.

Andrés de, M. F., F. García-Arenal, M. M. López, and P. Megarejo. 1998. Patógenos de plantas descritas en España. Editorial de Ministerio de Agricultura, Pesca y Alimentacíon, Madrid.

Arnason, J. T., G. H. N. Towers, B. J. R. Philogene, and J. D. H. Lambert. 1983. The role of natural photosensitizers in plant resistance to insects, pp. 139–151. In A. Hedin (ed.), Plant resistance to insects. ACS Symposium Series 208. American Chemical Society, Washington, DC.

Arnason, J. T., Philogene, B. J. R., and G. H. N. Towers. 1992. Phototoxins in plant-insect interactions, pp. 317–341. In G. A. Rosenthal and M. R. Berenbaum (eds.), Herbivores: their interactions with secondary plant metabolites. Academic Press, New York.

Arnholdt-Schmitt, B. 2000. RAPD analysis: a method to investigate aspects of the reproductive biology of *Hypericum perforatum* L. Theor. Appl. Genet. 100: 906–911.

Auerbach, M., and D. Simberloff. 1988. Rapid leaf-miner colonization of introduced trees and shifts in sources of herbivore mortality. Oikos 52: 41–50.

Baker, H. G. 1974. The evolution of weeds. Annu. Rev. Ecol. Syst. 5: 1–24.

Baker, H. G., and G. L. Stebbins (eds.). 1965. The genetics of colonizing species. Academic Press, New York.

Barrett, S. C. H., and B. J. Richardson. 1986. Genetic attributes of invading species, pp. 21–33. In R. H. Groves and J. J Burdon (eds.), Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Bazzaz, F. A., N. Chiariello, P. D. Coley, and L. Pitelka. 1987. The allocation of resources to reproduction and defense. Bioscience 37: 58–67.

Berenbaum, M. R., and A. R. Zangerl. 1998. Chemical phenotype matching between plant and its insect herbivore. Proc. Natl. Acad. Sci. USA 95: 13743–13748.

Berenbaum, M. R., A. R. Zangerl, and J. K. Nitao. 1986. Constraints on chemical coevolution: wild parsnips and the parsnip webworm. Evolution 40: 1215–1228.

Bergelson, J., and C. B. Purrington. 1996. Surveying patterns in the cost of resistance in plants. Am. Nat. 148: 536–558.

Blair, A. C., and L. M. Wolfe. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. Ecology 85: 3035–3042.

Blossey, B., and R. Nötzold. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J. Ecol. 83: 887–889.

Bone, E., and A. Farres. 2001. Trends and rates of microevolution in plants. Genetica 112–113: 165–182.

Bossdorf, O., S. Schröder, D. Prati, and H. Auge. 2004. Palatability and tolerance to simulated herbivory in native and introduced populations of *Alliaria petiolata* (Brassicaceae). Am. J. Bot. 91: 856–862.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144: 1–11.

Brodie, E. D. III, and E. D. Brodie Jr. 1999. Predator-prey arms races. BioScience 49: 557–568.

Brown, A. H. D., and D. R. Marshall. 1981. Evolutionary changes accompanying colonization in plants, pp. 73–98. In G. G. E. Scudder and J. L. Reveal (eds.). Evolution today. Proceedings of the Second International Congress of Systematics and Evolutionary Biology. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, PA.

Burdon, J. J., and J. N. Thompson. 1995. Changed patterns of resistance in a population of *Linum marginale* attacked by the rust pathogen *Melampsora lini*. J. Ecol. 83: 199–206.

Burdon, J. J., Groves, R. H., and J. M. Cullen. 1981. The impact of biological control on the distribution and abundance of *Chondrilla juncea* in south-eastern Australia. J. Appl. Ecol. 18: 957–966.

Buschmann, H. P. J. Edwards, and H. Dietz. 2005. Variation in growth pattern and response to slug damage among native and invasive provenances of four perennial Brassicaceae species. J. Ecol. 93: 322–334.

Callaway, R. M., W. M. Ridenour, T. Laboski, T. Weir, and J. M. Vivanco. 2005a. Natural selection for resistance to the allelopathic effects of invasive plants. J. Ecol. 93: 567–583.

Callaway, R. M., J. L. Hierro, and A. S. Thorpe. 2005b. Evolutionary trajectories in plant and soil microbial communities: *Centauria* invasions and the geographic mosaic of coevolution, pp 341–363. In D. F. Sax, S. D. Gaines, and J. J. Stachowicz (eds.) Exotic species, bane to conservation and boon to understanding: ecology, evolution and biogeography. Sinauer, Sunderland, MA.

Campbell, M. H., and E. S. Delfosse. 1984. The biology of Australian weeds. 13. *Hypericum perforatum*. J. Aust. Inst. Ag. Sci. 50: 63–73.

Carroll, S. P., J. E. Loye, H. Dingle, M. Mathieson, T. R. Famula, and M. P. Zaluck. 2005. And the beak shall inherit: evolution in response to invasion. Ecol. Lett. 8: 944–951.

Cavan, G., Biss, P., and S. R. Moss. 1998. Herbicide resistance and gene flow in wild oats *(Avena fatua* and *Avena sterilis* ssp. *ludoviciana)*. Ann. Appl. Biol. 133: 207–217.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. The effects of varied environments on North American plants. Carn. Inst. Wash. pub. no. 520. Carnegie Institute of Washington, Washington, DC.

Clegg, M. T., and R. W. Allard. 1972. Pattern of genetic differentiation in the slender wild oat species *Avena barbata*. Proc. Natl. Acad. Sci. USA 69: 1820–1824.

Coluatti, R., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecol. Lett. 7: 721–733.

Cullen, J.M., and R.H. Groves. 1981. The population biology of *Chondrilla juncea* L. in Australia. Proc. Ecol. Soc. Aust. 10: 121–134.

Daehler, C.C., and D. R. Strong. 1997. Reduced herbivore resistance in introduced smooth cordgrass *(Spartina alterniflora)* after a century of herbivore-free growth. Oecologia 110: 99–108.

Dyer, A.R., and K.J. Rice. 1999. Effect of competition on resource availability and growth of a California bunchgrass. Ecology 80: 2697–2710.

Ehler, L.E. 1998. Invasion biology and biological control. Biol. Control 13: 127–133.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Metheun, London.

Etterson, J.R., and R.G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. Science 294: 151–154.

Fargione, J., C.S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proc. Nat. Acad. Sci. USA 100: 8916–8920.

Feeny, P. 1976. Plant apparency and chemical defense, pp. 1–40. In J. W. Wallace and R.L. Mansell (eds.), Recent advances in phytochemistry, vol. 10. Plenum Press, New York.

Feeny, P. 1992. The evolution of chemical ecology: contributions from the study of herbivorous insects, pp. 1–44. In G.A. Rosenthal and M.R. Berenbaum (eds.), Herbivores, their interactions with secondary plant metabolites, 2nd ed., vol. 2. Academic Press, San Diego.

Fields, P.G., J.T. Arnason, and B.J.R. Philogene. 1988. Distribution of *Chrysolina* spp. (Coleoptera: Crysomelidae) in eastern Ontario, 18 years after their initial release. Can. Enotomol. 120: 937–938.

Fields, P.G., J.T. Arnason, and B.J.R. Philogene. 1990. Behavioural and physical adaptations of three insects that feed on the phototoxic plant *Hypericum perforatum*. Can. J. Bot. 68: 339–346.

Fox, L.R. 1988. Diffuse coevolution within complex communities. Ecology 69: 906–907.

Fritz, R.S., and P.W. Price. 1988. Genetic variation among plants and insect community structure: willows and sawflies. Ecology 69: 845–856.

Garcia-Rossi, D., N. Rank, and D.R. Strong. 2003. Potential for self-defeating biological control? Variation in herbivore vulnerability among invasive *Spartina* genotypes. Ecol. Appl. 13: 1640–1649.

Geffeney, S., E.D. Brodie Jr., and P.C. Ruben. 2002. Mechanisms of adaptation in a predator-prey arms race: TTX-resistant sodium channels. Science 297: 1336–1339.

Genton, B.J., P.M. Kotanen, P.O. Cheptou, C. Adolphe, and J.A. Shykoff. 2005. Enemy release but no evolutionary loss of defence in a plant invasion: an inter-continental reciprocal transplant experiment. Oecologia 146: 404–414.

Georghiou, G. P. 1986. The magnitude of the resistance problem, pp. 14–43. In Pesticide resistance: strategies and tactics for management. National Academy Press, Washington, DC.

Giese, A.C. 1980. Hypericism, pp. 229–255. In K.C. Smith (ed.), Photochemical and photobiological reviews. Plenum Press, New York.

Grant, P.R., and B.R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296: 707–711.

Graves, S.D., and A.M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biol. Conserv. 110: 413–433.

Guillet, G. 1997. Ecophysical importance of phototoxins in plant-insect relationships. Ph.D. dissertation, University of Ottawa, Ottawa, Canada.

Guillet, G., C. Podesfinski, C. Regnault Roger, J. T. Arnason, and B. J. R. Philogene. 2000. Biochemical and behavioral adaptations of generalist and specialist herbivorous insects feeding on *Hypericum perforatum* (St. John's wort). Environ. Entomol. 29: 135–139.

Hänfling, B., and J. Kollman. 2002. An evolutionary perspective on invasions. Trends Ecol. Evol. 17: 545–546.

Hare, J.D., and D.J. Futuyma. 1978. Different effects on variation in *Xanthium strumarium* L. (Compositae) on two insect seed predators. Oecologia 37: 109–12.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Harris, P., and M. Maw. 1984. *Hypericum perforatum* L., St. John's wort (Hypericaceae), pp. 171–177. In J.S. Kelleher and M.A. Hulme (eds.), Biological control programmes against insects and weeds in Canada 1969–1980. Commonwealth Agricultural Bureaux, Slough, UK.

Henter, H.J., and S. Via. 1995. The potential for coevolution in a host-parasitoid system. I. Genetic variation within an aphid population in susceptibility to a parasitic wasp. Evolution 49: 427–438.

Hinz, H.L., and M. Schwarzlaender. 2004. Comparing invasive plants from their native and exotic range: what can we learn from biological control? Weed Technol. 18: 1533–1541.

Hodgson, J.M. 1964. Variations in ecotypes of Canada thistle. Weeds 12: 167–171.

Hoebeke, E.R. 1993. Establishment of *Uropora quadrifasciata* (Diptera: Tephritidae) and *Chrysolina quadrigemina* (Coleoptera: Chrysomelidae) in portions of the eastern United States. Entomol. News 104: 143–152.

Holloway, J.K. 1957. Weed control by insect. Sci. Am. 197: 56–62.

Holloway, J.K., and C.B. Huffaker. 1951. The role of *Chrysolina gemellata* in the biological control of Klamath weed. J. Econ. Entomol. 44: 244–247.

Holmes, T.H., and K.J. Rice. 1996. Patterns and growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Ann. Bot. 78: 233–243.

Holt, R.D., and M.E. Hochberg. 1997. When is biological control evolutionarily stable (or is it)? Ecology 78: 1673–1683.

Huey, R.B., G.W. Gilchrist, M.L. Carlson, D. Berrigan, and L. Serra. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science 287: 308–309.

Huffaker, C. B. 1957. Fundamentals of biological control of weeds. Hilgardia 27: 101–157.

Huffaker, C.B., and J.K. Holloway. 1949. Changes in range plant populations structure associated with feeding of imported enemies of Klamath weed (*Hypericum perforatum* L.). Ecology 30: 167–175.

Huffaker, C. B., P. S. Messenger, and P. DeBach. 1971. The natural enemy component in natural control and the theory of biological control, pp. 16–67. In C. B. Huffaker (ed.), Biological Control. Plenum Press, New York.

Jain, S.K., and P.S. Martins. 1979. Ecological genetics of the colonizing ability of rose clover (*Trifolium hirtum* All.). Am. J. Bot. 66: 361–366.

Jobin, A., U. Schaffner, and W. Nentwig. 1996. The structure of the phytophagous insect fauna on the introduced weed *Solidago altissima* in Switzerland. Entomol. Exp. Appl. 79: 33–42.

Johshi, J., and K. Vrieling. 2005. The enemy release and EICA revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecol. Lett. 8: 704–714.

Juenger, T., and J. Bergelson. 1998. Pairwise versus diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. Evolution 52: 1583–1592.

Julien, M.H., and M.W. Griffiths (eds.). 1998. Biological control of weeds. CABI Publishing, New York.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17: 164–170.

Kennedy, G. G., and J. D. Barbour. 1992. Resistance variation in natural and managed systems, pp. 13–41. In R. S. Fritz and E. L. Simms (eds.), Plant resistance to herbivores and pathogens. University of Chicago Press, Chicago.

Koricheva, J. 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. Ecology 93: 176–190.

Kraaijeveld, A. R., J. J. M. van Alphen, and H. C. J. Godfray. 1998. The coevolution of host resistance and parasitoid virulence. Parasitology 116: S29–S45.

Lankau, R. A., W. E. Rogers, and E. Siemann. 2004. Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecol. Entomol. 29: 66–75.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends Ecol. Evol. 17: 386–391.

Leger, E. A., and M. L. Forister. 2005. Increased resistance to generalist herbivores in invasive populations of California poppy *(Eschscholzia californica)*. Divers. Distrib. 11: 311–317.

Maddox, G. D., and R. B. Root. 1987. Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*: genetic variation and heritability. Oecologia 72: 8–14.

Maddox, G. D., and R. B. Root. 1990. Structure of the encounter between goldenrod *(Solidago altissima)* and its diverse insect fauna. Ecology 71: 2115–2124.

Mal, T. K., and J. Lovett-Doust. 2005. Phenotypic plasticity in vegetative and reproductive traits in the invasive weed, *Lythrum salicaria* (Laythraceae), in response to soil moisture. Am. J. Bot. 92: 819–825.

Maron, J. L., and M. Vilà. 2001. Do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95: 363–373.

Maron, J. L., M. Vilà, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004a. Rapid evolution of an invasive plant. Ecol. Monogr. 74: 261–280.

Maron, J. L., M. Vilà, and J. Arnason. 2004b. Loss of enemy resistance among introduced populations of St. John's wort, *Hypericum perforatum*. Ecology 85: 3243–3253.

Marquis, R. J. 1990. Genotypic variation in leaf damage in *Piper arieianum* (Piperaceae) by a multispecies assemblage of herbivores. Evolution 44: 104–120.

Marquis, R. J. 1992. The selective impacts of herbivores, pp. 301–325. In R. S. Fritz and E. L. Simms (eds.), Plant resistance to herbivores and pathogens. University of Chicago Press, Chicago.

Maurico, R., and M. D. Rausher. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. Evolution 51: 1435–1444.

Mayo, G. M., and P. Langridge. 2003. Modes of reproduction in Australian populations of *Hypericum perforatum* L. (St. John's wort) revealed by DNA fingerprinting and cytological methods. Genome 46: 573–579.

McCaffrey, J. P., C. L. Campbell, and L. A. Andres. 1995. Biological control in the western United States: accomplishments and benefits of regional research, pp. 281–285. In J. R. Nechols, L. A. Andres, J. W. Beardsley, R. D. Goeden, and C. G. Jackson (eds.), Univ. Calif. Div. Agric. Nat. Res. pub. 3361 . Davis, CA.

McCrea, K. D., and W. G. Abrahamson. 1987. Variation in herbivore infestation: historical vs. genetic factors. Ecology 68: 822–827.

McEvoy, P. B., N. T. Rudd, C. S. Cox, and M. Huso. 1993. Disturbance, competition and herbivory effects on ragwort *Senecio jacobaea* populations. Ecol. Monogr. 63: 55–75.

Memmott, J., S. V. Fowler, Q. Paynter, A. W. Sheppard, and P. Syrett. 2000. The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. Acta Oecol. 21: 213–222.

Meyer, G. R., R. Clare, and E. Weber. 2005. An experimental test of the evolution of increased competitive ability hypothesis in goldenrod, *Solidego gigantean*. Oecologia 144: 299–307.

Mitchell, C. G., and A. G. Power. 2003. Release of invasive plants from fungal and viral pathogens. Nature 421: 625–627.

Mitich, L. W. 1994. Intriguing world of weeds: Common St. Johns wort. Weed Technol. 8: 658–661.

Morgan, G. F., and D. R. Marshall. 1978. Allozyme uniformity within and variation between races of the colonizing species *Xanthium strumarium* L. (Noogoora burr). Aust. J. Biol. Sci. 31: 284–292.

Müller-Schärer, H., and T. Steinger. 2004. Predicting evolutionary change in invasive, exotic plants and its consequences for plant-herbivore interactions, pp. 137–162. In , L. E. Ehler, R. Sforza, and T. Mateille (eds.), Genetics, evolution and biological control. CABI Publishing, Wallingford, UK.

Müller-Schärer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants: implications for biological control. Trends Ecol. Evol. 19: 417–422.

Neuffer, B., and H. Hurka. 1999. Colonization history and introduction dynamics of *Capsella bursa-pastoris* (Brassicaceae) in North America: isozymes and quantitative traits. Mol. Ecol. 8: 1667–1681.

Newman, R. l., D. Thompson, and D. Richman. 1998. Conservation strategies for the biological control of weeds, pp. 371–396. In P. Barbosa (ed.), Conservation biological control. Academic Press, New York.

Novotny, V., Y. Basset, S. E. Miller, G. D. Weiblen, B. Bremer, L. Cizek, and P. Drozd. 2002. Low host specificity of herbivorous insects in a tropical forest. Nature 416: 841–844.

Parker, M. A. 1991. Nonadaptive evolution of disease resistance in an annual legume. Evolution 54: 1209–1217.

Phillips, B. L., and R. Shine. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proc. Natl. Acad. Sci. USA 101: 17150–17155.

Pilson, D. 1996. Two herbivores and constraints on selection for resistance in *Brassica rapa*. Evolution 50: 1492–1500.

Pimentel, D. 1986. Population dynamics and the importance of evolution in successful biological control, pp. 3–18. In , J. M. Franz (ed.), Biological plant and health protections. Springer-Verlag, New York.

Powles, S. B., and J. A. M. Holtum. 1994. Herbicide resistance in plants. Lewis Publishers, Boca Raton, FL.

Rausher, M. 1992. Natural selection and the evolution of plant-insect interactions, pp. 20–88. In B. D. Roitberg and M. B. Isman (eds.), Insect chemical ecology: an evolutionary approach. Chapman and Hall, New York.

Rees, C. J. C. 1969. Chemoreceptor specificity associated with choice of feeding site by the beetle, *Chrysolina brunsvicensis* on its food-plant, *Hypericum hirsutum*. Entomol. Exp. Appl. 12: 565–583.

Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? Ecology 77: 1655–1661.

Reznick, D. N., and C. K. Ghalambor. 2001. The population biology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112–113: 183–198.

Reznick, D. N, F. H. Shaw, R. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies *(Poecilia reticulata)*. Science 275: 1934–1937.

Rhoades, D. F., and R. G. Cates. 1976. Towards a general theory of plant antiherbivore chemistry, pp. 168–213. In J. W. Wallace and R. L. Mansell (eds.), Recent advances in phytochemistry, vol. 10. Plenum Press, New York.

Rice, K. J., and N. C. Emory. 2003. Managing microevolution: restoration in the face of global change. Front. Ecol. 1: 469–478.

Rice K. J., and R. N. Mack. 1991. Ecological genetics of *Bromus tectorum*. III. The demography of reciprocally sown populations. Oecologia 88: 91–101.

Ritcher, P. O. 1996. Biological Control of Insects and Weeds in Oregon. Ag. Ex. Sta. Oregon State Univ. Tech. Bull. 90: 1–39.

Rohani, P., H. C. J. Godfray, and M. P. Hassell. 1994. Aggregation and the dynamics of host-parasitoid systems: a discrete generation model with within-generation redistribution. Am. Nat. 144: 491–509.

Sampson, A. W., and K. W. Parker. 1930. St. Johns-wort on rangelands of California. Calif. Agric. Exp. Sta. Bull. 503.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends Ecol. Evol. 17: 170–176.

Siemann, E., and W. E. Rogers. 2003. Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84: 1489–1505.

Simberloff, D., and P. Stiling. 1996. How risky is biological control? Ecology 77: 1964–1974.

Simms, E. L., and M. D. Rausher. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea* II. Natural selection by insects and costs of resistance. Evolution 43: 573–585.

Sirvent, T. M., S. B. Krasnoff, and D. M. Gibson. 2003. Induction of hypericins and hyperforins in *Hypericum perforatum* in response to damage by herbivores. J. Chem. Ecol. 29: 2667–2681.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. Q. Rev. Biol. 78: 23–55.

Stastny, M., U. Schaffner, and E. Elle. 2005. Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? J. Ecol. 93: 27–37.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends Ecol. Evol. 18: 94–101.

Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. Trends Ecol. Evol. 14: 179–185.

Strauss, S. Y., D. H. Siemens, M. B. Decher, and T. Mitchell-Olds. 1999. Ecological costs of plant resistance in the currency of pollination. Evolution 53: 1105–1113.

Strong, D. R. 1974. Rapid asymptotic species accumulation in phytophagous insect communities: the pests of Cacao. Science 185: 164–1066.

Thompson, J. N. 1999a. The raw material for coevolution. Oikos 84: 5–16.

Thompson, J. N. 1999b. Specific hypotheses on the geographic mosaic of coevolution. Am. Nat. 153: S1–S14.

Trifunovic, S., V. Vajs, S. Macura, N. Juranic, Z. Djarmati, R. Jankov, and S. Milosavljevic. 1998. Oxidation products of hyperforin from *Hypericum perforatum*. Phytochemistry 49: 1305–1310.

van der Meijden, E. 1996. Plant defense, an evolutionary dilemma: contrasting effects of (specialist and generalist) herbivores and natural enemies. Entomol. Exp. Appl. 80: 307–310.

van Kleunen, M., and B. Schmid. 2003. No evidence for an evolutionary increased competitive ability (EICA) in the invasive plant, *Solidago canadensis*. Ecology 84: 2816–2823.

Vilà, M., J. L. Maron, and L. Marco. 2005. Evidence for the enemy release hypothesis in *Hypericum perforatum* L. Oecologia 142: 474–479.

Voss, E. G. 1985. Michigan flora, part II: Dicots (Saururaceae-Cornaceae). Cranbrook Institute of Science, Cranbrook, MI.

Weber, E., and B. Schmid. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced into Europe. Am. J. Bot. 85: 1110–1121.

Williams, D. G., R. N. Mack, and R. A. Black. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology 76: 1569–1580.

Williams, J. R. 1954. The biological control of weeds, pp. 95–98. In Report of the Sixth Commonwealth Entomological Congress, London.

Williams, K. S. 1984. Climatic influences on weeds and their herbivores: biological control of St. John's wort in British Columbia, pp. 127–132. In E. S. Delfosse (ed.), Proceedings of the VI international symposium for the biological control of weeds. Agriculture Canada, Ottawa, ON.

Willis, A. J., M. B. Thomas, and J. H. Lawton. 1999. Is the increased vigour of invasive weeds explained by a trade-off between growth and herbivore resistance? Oecologia 120: 275–283.

Wilson, F. 1943. The entomological control of St. John's wort (*Hypericum perforatum* L.). Council Sci. Ind. Res. Austr. Bull. 169: 1–88.

Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. Ecol. Lett. 7: 813–820.

Wu, K. K., and S. K. Jain. 1978. Genetic and plastic responses in geographic differentiation of *Bromus rubens* populations. Can. J. Bot. 56: 873–879.

Zangerl, A. R., and M. R. Berenbaum. 2003. Phenotype matching in wild parsnip and parsnip webworms: causes and consequences. Evolution 57: 806–815.