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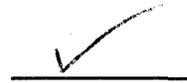
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A BIOGEOGRAPHICAL APPROACH TO PLANT INVASIONS:
ECOLOGY AND EVOLUTION OF AN INVASIVE RUDERAL IN NATIVE AND
INTRODUCED RANGES

by

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M.Sc. University of Florida, 1999

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presented in partial fulfillment of the requirements

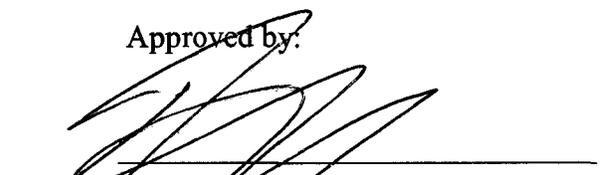
for the degree of

Doctor of Philosophy

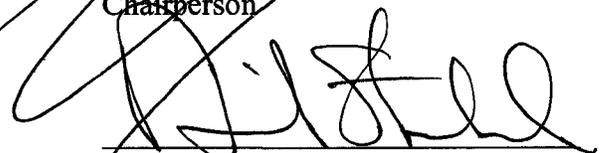
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A Biogeographical Approach to Plant Invasions: Ecology and Evolution of an Invasive Ruderal in Native and Introduced Ranges

Chairperson: Ragan M. Callaway 

Most theory and empirical research on exotic invasions is based on the assumption that problematic exotics are much more abundant in regions where they invade than in regions where they are native. The overwhelming majority of studies on exotics, however, have been conducted solely within the introduced range. I argue and demonstrate that our understanding of invasions is greatly enhanced by comparative studies of exotics in both introduced and native ranges.

The role of disturbance in plant invasions illustrates particularly well the need for studying invasions in a biogeographical context. In field experiments conducted in the native range of *Centaurea solstitialis* and in two regions of its non-native range, I show that disturbance increased *C. solstitialis* abundance and performance far more in the non-native ranges than in the native range. Stronger positive effects of disturbance on *C. solstitialis* abroad than at home indicate that disturbance alone cannot explain the remarkable success of this species in disturbed sites in its non-native regions. The powerful effects of disturbance must act in concert with other factors, allowing *C. solstitialis* to attain community dominance only where it occurs as exotic. A second study further reveals the importance of studying exotics in their native and introduced range. In common garden experiments, I demonstrate a genetically-based shift in the germination strategy of invasive populations of *C. solstitialis*. When introduced to a region with a Mediterranean climate, resembling that in the native range, *C. solstitialis* exhibits similar germination rates as native populations; in contrast, populations introduced to a region with spring and summer rainfall have higher levels of seed dormancy than native populations. Genetic differentiation among these populations, in combination with high genetic variation in non-native populations, a history of multiple introductions from largely overlapping sources, and the outcrossing mating system of *C. solstitialis*, strongly suggest that increased seed dormancy in non-Mediterranean populations is the result of rapid evolution in response to novel selection pressures. I believe this is just the tip of the iceberg; major developments in invasion biology, ecology, and evolution are likely to come from the study of organisms in native and non-native ranges.

-Posible, pero no interesante –repondió Lönnrot-. Usted replicará que la realidad no tiene la menor obligación de ser interesante. Yo le replicaré que la realidad puede prescindir de esa obligación, pero no las hipótesis.

-Possible, but not interesting -Lönnrot answered-. You'll reply that reality hasn't the least obligation to be interesting. And I'll answer you that reality can avoid that obligation, but hypotheses cannot.

From The death and the compass, Fictions, Jorge Luis Borges

ACKNOWLEDGEMENTS

The journey that is about to end started well before five years ago when I arrived at the University of Montana, and, as any other endeavor, is the result of an infinite number of random events, the determinant influence of many extraordinary people, and personal effort. It is unclear for me who to thank for the much needed fortune. I have no doubts, however, regarding the persons I owe gratitude. I need to start with my family, mainly my parents, grandparents and sister, and teachers in my little town, Colonia Barón, in La Pampa, Argentina. They passed on me an early appreciation for the value of education and the importance of pursuing personal goals honestly and through hard work. Diego Villarreal, my mentor as an undergraduate student at the National University of La Pampa, constantly raised the bar and initiated me in ecological research. Diego, with time, became a friend and latter a collaborator; without his commitment in Argentina, the biogeographical scope of this work would not have been possible. I am deeply thankful to Lyn Branch, my Master's adviser at the University of Florida. Much of my success in graduate school is due to the uncountable hours of teaching Lyn gave me in the field and her office. The insightful guidance of Eric Menges, my supervisor at the Plant Lab in Archbold Biological Station, made my first exposure to research in the States an ever lasting experience.

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PREFACE

In contemporary biological invasions, humans assist other organisms to overcome one of the most limiting of ecological factors, dispersal (Eriksson and Ehrlén 1992, Tilman 1997, Seabloom et al. 2003). Once dispersed, introduced individuals (exotics) may face a different set of organizing parameters than in their communities of origin. Understanding these differences may help to explain the unusual success of some species as exotics (Darwin 1859, Elton 1958, Blossey and Nötzold 1995, Callaway and Aschehoug 2000). If so, comparative studies of invasive species where they are native versus where they are exotic are essential. This dissertation is a theoretical analysis and empirical demonstration of the importance of such studies. The dissertation is organized in three chapters. Each chapter was written as a manuscript intended for publication in a scientific journal.

Chapter 1 is an essay review of the literature on exotic plant invasions. This review reveals that most studies have been conducted in only one of the distributional ranges of these organisms, the introduced range. I argue that comparative studies are needed simply to establish the degree to which conspecifics occur at different densities or distributions in their native and introduced range. I review the hypotheses that attempt to explain why exotics are able to attain spectacularly higher density in recipient versus native communities and suggest how more rigorous testing could be achieved. I also touch upon some issues in invasion ecology that do not require an explicit biogeographic perspective, but where new approaches might be beneficial, and highlight how an increased mechanistic understanding of invasions can shed light on how native ecological

systems function. This chapter was published in the *Journal of Ecology* (Hierro et al. 2005).

Chapter 2 investigates the response of an annual plant, *Centaurea solstitialis* (yellow starthistle), to disturbance in its native and non-native range. In this chapter, I challenge the assumption that disturbance *per se* is sufficient to explain the remarkable success of invasive plant species in disturbed conditions in their non-native range. I conclude that disturbance act in concert with other factors, allowing certain species to attain community dominance only where they occur as exotics. This chapter was rejected in *Ecology* and it is now in review in *The American Naturalist*.

The final Chapter explores evolutionary changes in *C. solstitialis* after its introduction into non-native ranges. I show that populations of this species introduced to a region with conditions contrasting those at home exhibit a genetically-based shift in germination strategy; in contrast, no change occurred in populations introduced to a region with conditions similar to those in the native range. I conclude that populations experiencing novel conditions have undergone rapid evolution. This chapter is ready for submission to *Nature*.

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CHAPTER 1

A BIOGEOGRAPHICAL APPROACH TO PLANT INVASIONS: THE IMPORTANCE OF STUDYING EXOTICS IN THEIR INTRODUCED *AND* NATIVE RANGE

Abstract. Most theory and empirical research on exotic invasions is based on the assumption that problematic exotics are much more abundant in the regions where they invade than in the regions where they are native. However, the overwhelming majority of studies on exotic plants have been conducted solely within the introduced range. With few exceptions, ecologists know surprisingly little about the abundance, interaction strengths and ecosystems impacts of even the best-studied exotics in their native range. I argue that taking a biogeographic approach is key to understanding exotic plant invasions. On a descriptive level, unambiguous quantification of distributions and abundances of exotics in native and introduced ranges are crucial. Experiments conducted at a biogeographic scale are also necessary to elucidate the mechanisms that enable highly successful exotics to occur at substantially higher abundance in their introduced versus native communities. I summarize the leading hypotheses for exotic plant success. I assert that tests of these major hypotheses for invasions (the Natural Enemies, Evolution of Invasiveness, Empty Niche and Novel Weapons hypothesis) require comparative biogeographic approaches. In addition to focusing on comparative work in the native and introduced range, I also suggest other approaches that could yield important insight into processes that influence exotic success. Increased understanding of invasions has the potential to provide unique insight into fundamental ecological theory,

including that on individualistic-holistic structure, the role of trophic interactions in population regulation, and the importance of co-evolution in communities.

Keywords: Biological invasions, comparative biogeography, disturbance, EICA, empty niche hypothesis, evolution of invasiveness, exotic plants, natural enemies hypothesis, novel weapons hypothesis, plant demography

INTRODUCTION

Contemporary biological invasions result from man expanding the distributional range of organisms. Species are taken from a native range where their populations are controlled by one set of factors and moved beyond natural dispersal barriers to regions where their abundance may be influenced by a different set of parameters. Although the ecological responses to this breaching of natural barriers to dispersal are fundamentally biogeographical phenomena, until recently, the lion's share of studies of species in the new regions (hereafter exotics) have focused exclusively on their ecology in the communities to which they have been introduced, and ignored the ecology of these species where they are native. While research in recipient communities has certainly enhanced understanding of the detrimental economic (Pimentel *et al.* 2000) and ecological (D'Antonio & Vitousek 1992, Mack *et al.* 2000, Sala *et al.* 2000) effects of exotics and has identified factors that may influence susceptibility of communities to invasion (Crawley 1987, Lonsdale 1999, Davis *et al.* 2000, Mack *et al.* 2000, Sakai *et al.* 2001), progress in understanding the processes that enable exotics to dominate recipient

communities could be greatly accelerated by an increased emphasis on the comparative ecology of plants where they are native and introduced.

Why might such a biogeographic approach to invasion biology be useful? At the descriptive level, comparative studies are needed simply to establish the degree to which conspecifics occur at different densities or distributions in their native and introduced range. Currently, the assumption of greater abundances and overall impacts of species in recipient than in native communities is based almost exclusively on non-quantitative observations. While this assumption appears to be true for a number of species – *Centaurea maculosa* Lam. (spotted knapweed), *Alliaria petiolata* (Bieb.) Cavara & Grande (garlic mustard), *Lonicera japonica* Thunb. (Japanese honeysuckle), and *Bromus tectorum* L. (cheatgrass) come immediately to mind– many exotics occur at only moderate densities in recipient communities and may actually occur at similar densities in communities where they are native. The fraction of exotics that actually occur at significantly higher densities when introduced is not known, mostly because there are few direct comparisons of the density or overall abundance of particular plants in their native and introduced range (but see Woodburn & Sheppard 1996, Edwards *et al.* 1998, Grigulis *et al.* 2001, Paynter *et al.* 2003, Jakobs *et al.* 2004). While there are reports documenting the fact that some species are rare at home and abundant or even superabundant in introduced communities (Lonsdale & Segura 1987, Braithwaite *et al.* 1989, Malecki *et al.* 1993, Eckert *et al.* 1996, Meyer & Florence 1996, Bruce *et al.* 1997, Paynter *et al.* 1998, Memmot *et al.* 2000), these observations remain largely anecdotal.

Beyond documenting differences in abundance of exotics at home and away, a biogeographic perspective is needed to allow rigorous testing of mechanistic hypotheses

that have been advanced to explain exotic plant success. Plants that become superabundant only in the introduced range must be “doing something different” in recipient communities that enables them to attain such dominance. In this chapter, I review the hypotheses that attempt to explain why exotics are able to attain spectacularly higher density in recipient versus native communities and suggest how more rigorous testing could be achieved. I also touch upon some issues in invasion ecology that do not require an explicit biogeographic perspective, but where new approaches might be beneficial, and highlight how an increased mechanistic understanding of invasions can shed light on how native ecological systems function.

PATTERNS IN INVASION BIOLOGY

A common assumption about invasions is that exotic organisms occur at much greater densities and have greater performance in their introduced than native ranges (Crawley 1987, Noble 1989, Blossey & Nötzold 1995). While general observations suggest that this is often true, quantitative data are surprisingly scarce and can be contradictory. We currently do not know what percentage of exotic plants occur at dramatically higher densities in their introduced versus native range; however, considering Williamson’s tens rule (Williamson 1996, Williamson & Fitter 1996), it is probably small. Surely many exotics must occur at similar or even lower densities in recipient communities compared to their native range. For these “weak invaders”, the processes that regulate population numbers in their native and introduced range may be similar. Without empirical estimates, however, it is difficult to generalize about the overall success of exotics or determine how widely various mechanisms for exotic

success might apply. Just as ecologists have long sought to understand what the distribution of interaction strengths might be for members of a community, it would be of great value to determine how the magnitude difference in population size between plants in their native and introduced range is distributed across exotic species.

Based on information published in European and North American floras, Crawley (1987) was one of the first researchers to quantify sizes of organisms in both ranges, showing that exotics often were larger than their native conspecifics. More recently, a similar pattern has been found for marine invertebrates by Grosholz & Ruiz (2003). In a survey of 46 native and 45 introduced populations of *Solidago gigantea* Ait., Jakobs and colleagues (2004) found that total plant biomass was larger among exotic versus native plants. Thébaud & Simberloff (2001), however, found no consistent evidence for increased size among exotics. Height and biomass were also found to be similar in five native and six introduced populations of *Lythrum salicaria* L. (Edwards *et al.* 1998), despite this being the species that inspired the formulation of the evolution of increased competitive ability (EICA) hypothesis (Blossey & Nötzold 1995). Similarly, Paynter *et al.* (2003) reported that *Cytisus scoparius* (L.) Link does not grow faster or taller in recipient communities compared to native communities. *Cytisus scoparius* was first reported to live longer on average in introduced than native communities (Rees & Paynter 1997), but a recent study showed no differences in maximum plant ages between native and exotic populations of this species (Paynter *et al.* 2003). The fecundity of *Chrysanthemoides monilifera* (L.) T. Nord, *Acacia longifolia* (Andr.) Willd. (Weiss & Milton 1984, as cited in Noble 1989), and *C. scoparius* (Rees & Paynter 1997) has been shown to be higher in introduced regions when compared to native ones, but no

differences between regions were found for *Echium plantagineum* L. (Grigulis *et al.* 2001). Populations of *L. salicaria* growing in nutrient-rich habitats were significantly more fecund in the introduced range, but fecundity was similar between ranges for populations growing in nutrient-poor and intermediate habitats (Edwards *et al.* 1998). Recently, Buckley *et al.* (2003) compared seed size between native and exotic populations of *C. scoparius* and *Ulex europaeus* L. They found that *C. scoparius* seeds were significantly heavier in the introduced range compared to the native range, but that there were no differences between ranges in the seed size of *U. europaeus* (Buckley *et al.* 2003). Given the sampling design and impressive array of locations worldwide, Buckley *et al.*'s study is the most comprehensive evaluation for a single species' trait in both ranges, and should serve as a model for future investigations.

Comparisons of the traits of species in their introduced and native range are important, but comparative demographic studies of exotics at home and abroad will ultimately be far more informative for establishing the fundamental patterns of distribution and abundance that are requisite for evaluating hypotheses for invasive success. For exotics that clearly attain higher population sizes in the introduced than native range, understanding the demographic forces that lead to this difference is a necessary first step towards understanding the mechanisms by which some species invade.

To date, only a few studies have taken a comparative biogeographic approach to demography and these have been illuminating. Studies of Scotch broom in Europe and Australia have revealed that *C. scoparius* does not recruit beneath dense stands of conspecifics in the native range (Paynter *et al.* 1998), yet where it is exotic in Australia

seedlings readily establish under monocultural stands of conspecifics (Sheppard *et al.* 2000). Grigulis *et al.* (2001) compared the demography of *E. plantagineum* between native sites in southern Portugal and introduced sites in south-eastern Australia. They found that, although values of many demographic transitions were similar between the native and introduced range, seedling establishment and rates of incorporation of seeds into the seedbank were 2-5 times higher in Australia than Portugal. This result, which would be obscure in the absence of such careful demographic investigation, clearly highlights the importance of establishment limitation in capping the size of populations in the native range (Eriksson & Ehrlén 1992) and suggests where to focus experimental work.

The next step, coupling manipulative experiments of competitors or enemies with demography, is a powerful approach to understanding not only how population processes may differ between ranges but also the mechanisms responsible for population release. For example, the poor success of weed biocontrol, in cases where biocontrol agents establish, often stems from biocontrols attacking weeds at life history stages that are not demographically important (Shea & Kelly 1998, McEvoy & Coombs 1999). Comparative demographic studies of weeds would not only suggest what life history transition most limits population growth but it would also provide clues as to what factors might control population size in the native range.

Observations of exotic plants growing in disturbed areas are common (Elton 1958, Crawley 1987, Mack 1989, Rejmánek 1989, D'Antonio *et al.* 1999). Disturbance-adapted or ruderal species are often short-lived, fast growing and have high fecundity (Grime 1974, 1977, Bazzaz 1979) and, over time, these species are thought to be replaced

by late successional species (Bazzaz 1979, Glenn-Lewin & van der Maarel 1992). However, the post-disturbance response of many exotics seems to differ from natives in that exotics can create stable and long lasting monocultures after disturbance. One way to distinguish between this and the alternative that exotic and native colonizers do not behave differently (Davis *et al.* 2001) is to initiate comparative long-term successional studies in both distributional ranges. Although noticeably rare even in introduced ecosystems (D'Antonio *et al.* 1999, Davis *et al.* 2001), such studies could be accomplished through parallel field experiments where disturbance type and intensity is crossed with seed additions of the focal plant and changes in plant composition are documented through time. Alternatively, establishment of permanent plots in the native and introduced ranges in recently disturbed fields containing a high abundance of the target species would allow documentation of successional trends

HYPOTHESES FOR INVASION SUCCESS

Several hypotheses have been postulated to explain the success of species that are superabundant as exotics (Mack *et al.* 2000, Table 1 – notably hypotheses 1 to 4), but few have received rigorous tests (Shea & Chesson 2002).

The Natural Enemies Hypothesis

One of the oldest and most widely cited hypothesis attributes success to the fact that many exotics, upon introduction, are liberated from their specialist herbivores and pathogens (Darwin 1859, Williams 1954, Elton 1958). Exotics are thought to gain a substantial advantage both because their populations are no longer directly suppressed by

specialist enemies, but also because they obtain a competitive advantage over natives that may disproportionately suffer from native enemy attack. The fundamental assumption is that release from strong suppression by enemies in their native range enables plants to attain higher densities in their introduced range. While native herbivores and pathogens can be quite damaging (Burdon 1987, Crawley 1989, 2002, Burdon & Leather 1990, Bever *et al.* 1997, van der Putten & Peters 1997, Klironomos 2002, Callaway *et al.* 2004), our understanding of the strength and pervasiveness of population-level control of plants by their enemies is surprisingly poor. In fact, many ecologists assert that the relative impact of enemies on *populations* of native plants is “minimal” (Crawley 1989). Even in the context of biological control, detailed demographic data demonstrating strong population-level suppression of exotics are scarce and estimates of how commonly biocontrol agents actually limit the population size of their targets vary widely and are often based on qualitative accounts rather than hard data. Explicit comparisons of the effects of enemies in the native and introduced range are crucial for testing the natural enemies hypothesis.

Although researchers have compared levels of pathogen (Mitchell & Power 2003) or herbivore (Memmot *et al.* 2000, Wolfe 2002, Jakobs *et al.* 2004) attack on native and exotic conspecifics or of herbivore damage on exotics and ecologically equivalent natives in recipient communities (Agrawal & Kotanen 2003, Siemann & Rogers 2003c), such studies provide only limited insight into the importance of enemy escape. Differences in consumer pressure between plants in their native and introduced range do not necessarily translate to meaningful differences in plant performance (Siemann & Rogers 2003b). Studies that actually compare the impact of enemies on plant performance in native and

introduced ranges have produced mixed results. Reinhart *et al.* (2003) showed that *Prunus serotina* Ehrh. (black cherry) invasion into Europe is facilitated by soil microbes whereas, in its native range, *P. serotina* is inhibited by soil pathogens. Callaway *et al.* (2004) compared the effects of soil microbes collected from four populations of *C. maculosa* in its native range in western Europe and six populations in the northwestern U.S. where it has invaded. On average, sterilization of European soils caused a 166% increase in the total biomass of *C. maculosa* compared to a 24% increase when North American soils were sterilized. Depending on the population and rhizosphere, sterilization of European soils improved *C. maculosa* growth from as little as 31% to over 900%; whereas the effects of sterilizing North American soils ranged from a 24% decrease in *C. maculosa* growth (suggesting a positive effect of microbes) to a 59% increase. The stronger suppressive effects of European soil biota lend experimental support to earlier demonstrations of much higher fungal and viral infection on plant species in their home ranges than in invaded ranges. In contrast, Beckstead & Parker (2004) showed that the impacts of soil pathogens on dune grass, *Ammophila arenaria* (L.) Link, were of equally strong magnitude in the introduced and native range.

Without knowing whether negative impacts of herbivore or pathogen attack actually limit the abundance of plants in their native range, it is difficult to evaluate the ecological significance of escape from enemies. Studies are needed that both quantify the population-level impact of specialist enemies in the native and introduced range and determine how competitive interactions between natives and exotics may be affected by altered enemy pressure. To date, only DeWalt *et al.* (2004) have taken this approach. They demonstrated that herbivores and fungal pathogens reduce the survival of *Clidemia*

hirta (L.) D. Don in understorey habitats, and thus limit its distribution to open habitats in its native range (Costa Rica), but lack of enemy pressure has apparently allowed forest invasion where it is an exotic (Hawaii).

The Evolution of Invasiveness Hypothesis

Some species may attain dominance in introduced ranges because they experience rapid genetic changes linked to new selection pressures in the novel environment (Carroll & Dingle 1996, Sakai *et al.* 2001, Hänfling & Kollman 2002, Lee 2002, Stockwell *et al.* 2003, Maron *et al.* 2004). Various studies have identified both biotic and abiotic factors as important selective forces in the new environment (see Lee 2002 and Stockwell *et al.* 2003 for reviews). Among biotic agents, rapid evolution can occur not only in response to the presence of a new set of organisms but also to their absence. The Evolution of Increased Competitive Ability (EICA) hypothesis (Blossey & Nötzold 1995) argues that exotics long liberated from their specialist enemies should lose costly traits that confer resistance to their native specialist enemies. Exotics can reallocate resources from the maintenance of resistance to traits, such as size or fecundity that might be under greater selection in the introduced range. Thus, EICA predicts that liberation from natural enemies should result in exotics evolving in ways that enhance their performance in recipient communities. Testing for genetically-based changes in phenotype between exotic and native conspecifics requires growing plants from both ranges together in common gardens and, to date, such tests have produced mixed results. Siemann & Rogers (2003b) showed that in a greenhouse, generalist grasshoppers preferred exotic over native genotypes of *Sapium sebiferum* (L.) Roxb. (Chinese Tallow Tree) seedlings.

Daehler & Strong (1997) showed that specialist planthoppers (*Prokelisia marginata* Van Duzee) were more damaging to exotic *Spartina alterniflora* Loisel. (cordgrass) that had little history of planthopper herbivory compared to either native or exotic genotypes that were used to attack. Siemann & Rogers (2001, 2003c) found that exotic genotypes of *S. sebiferum* were larger and more fecund than native genotypes. Leger & Rice (2003) found that introduced *Eschscholzia californica* Cham. (California poppy) from Chile were larger and more fecund than native Californian conspecifics in common gardens, but only in the absence of competition. On the other hand, Willis *et al.* (2000) grew four species of plants collected from their native European and introduced ranges in a common garden in Britain and found no evidence that exotic plants had evolved increased size. Based on common gardens in Washington, California, Sweden, and Spain, Maron *et al.* (2004) found no evidence that exotic genotypes of *Hypericum perforatum* L. (St. John's Wort) were larger or more fecund than native genotypes although they had lower pathogen resistance and reduced defensive chemistry (Maron *et al.* in press).

Reciprocal common garden studies should be conducted in both the native and introduced range, using plants from multiple populations that are sampled widely across each range. If possible, plants collected as seed from natural populations should be grown in a common environment and the progeny of these individuals should be used in common garden experiments to control for potential maternal effects. In addition, individuals used in common gardens should be genotyped so that invasion history can be inferred and the possibility that any differences are simply due to exotic populations being founded by a small and unrepresentative subset of native genotypes ruled out.

Crossed common garden experiments offer the most complete assessment of evolutionary hypotheses, but they present important ethical and logistic problems. Foremost is the risk of novel genotypes being introduced into new regions. I can not over-emphasize that extreme caution and close follow up is required, with seeds harvested before dispersal and all plants destroyed after research is completed. In addition, to minimize opportunities for gene flow, plants should not be grown in areas immediately adjacent to extant populations of the same species. The logistic difficulties in the implementation of common gardens in different parts of the world are substantial and can only be solved by developing strong international collaborations among scientists. A less powerful alternative is to perform genotypic comparisons in growth chambers where climates from different regions can be simulated. These studies, however, are more limited in reality and replication than field experiments.

So far, tests of the EICA hypothesis have generally compared the phenotypes of natives and exotics that have been grown together in a single greenhouse (Daehler & Strong 1997, Siemann & Rogers 2003b) or in a common garden in the introduced range (Siemann & Rogers 2003c). Environmental conditions in the introduced range might, however, be less favourable to native genotypes and, in a single garden, it is impossible to rule out genotype by environment interactions, leading to greater performance for certain genotypes only in some environments. This point has been well illustrated for work done on St. John's Wort (*Hypericum perforatum*), a plant native to Europe but introduced into North America, Australia, New Zealand and other locales. Based on a limited sample of plants from Europe and North America that were grown in a single common garden in the United Kingdom, Pritchard (1960) reported that exotic genotypes

were more robust than natives. More recently, although Maron *et al.* (2004) obtained a similar result after exotic and native genotypes of St. John's Wort were grown for two years in a common garden in Washington, this pattern disappeared after a further year, and there was no evidence that exotic genotypes were larger or more fecund than natives when grown in California, Sweden and Spain.

The Empty Niche Hypothesis

Although by definition a niche can only exist in the presence of an organism, this hypothesis refers to the possibility that certain exotics may be successful because they have access to resources in the introduced community that no local species utilize (Elton 1958, MacArthur 1970, Levine & D'Antonio 1999, Mack *et al.* 2000, but see Herbold & Moyle 1986). Because species-rich communities are thought to have a more complete use of resources, the lack of empty niches would also explain why they are more resistant to invasion (Elton 1958, MacArthur 1970, Levine & D'Antonio 1999). The related hypothesis of ecological opportunity, stating that extinctions, and in consequence the creation of 'empty' niches, promote the establishment of exotic species, has been proposed to explain successful fish (Christie 1974) and bird (Diamond & Veitch 1981) introductions, as well as the asymmetrical exchange of marine biota following the disappearance of major barriers to biological dispersion (Vermeij 1989, 1991a, b). The theory of fluctuating resource availability, similarly argues that the susceptibility to invasion of a community increases whenever the amount of unused resources in that community is enhanced (Davis *et al.* 2000).

Some exotic plants certainly appear to take advantage of empty niches in the communities they invade. The success of *Centaurea solstitialis* L. in dominating annual grasslands in California, for example, has been proposed to be due to the presence of unused water below 60 cm in the soil profile resulting from a combination of shallow root systems and early senescence of annual grasses (Borman *et al.* 1992, Holmes & Rice 1996, Dyer & Rice 1999). By having an extensive and deep root system, *C. solstitialis* has the potential to exploit this resource (Roché *et al.* 1994). In an experiment assessing the invasibility of several plant functional groups to *C. solstitialis*, Dukes (2001) concluded that by reducing the availability of soil moisture in the summer, functionally diverse communities and monocultures of native *Hemizonia congesta* DC., which like the exotic is a deep-rooted, late-season annual herb, provided more resistance to invasion than communities without summer-active, deep-rooted species. A related study similarly revealed that communities of perennial grasses were less susceptible to invasion than those of annual grasses (Dukes 2002). It is puzzling, however, why deep-rooted natives fail to dominate these grasslands given that they have access to such a rich resource (but see Dyer & Rice 1999).

Although exclusive study of introduced communities can certainly provide some evidence that exotics gain access to “free” or unused resources, parallel studies in both the native and introduced range would offer a far more convincing evaluation of this hypothesis because it would enable one to demonstrate not only that a successful exotic benefits from accessing unused resources in the recipient community, but also that these resources are utilized by other plants in the original community (or in areas of the introduced range where the exotic fails to achieve community dominance). To my

knowledge, no work of this kind has been performed. The presence of an empty niche can be inferred by measuring the availability of resources such as light, water and nutrients in locations suspected to have unused resources and where the niche is thought to be occupied, followed by the determination that those available resources are being used by the target species. Experimentally, plant communities resembling those encountered by an exotic in its native and recipient community can be assembled with the goal of determining how resource availability and use varies between assemblage types. In addition, indirect measurements of resource complementarity, such as relative yield totals (Harper 1977) and proportional deviation of a mixture from its expected productivity (Wardle *et al.* 1997, Loreau 1998) can be used to evaluate whether resource partitioning between the study plant and other members of the assemblage is occurring (e.g., Dukes 2002).

The Novel Weapons Hypothesis

A recent hypothesis emphasizes the importance of allelopathy (*sensu* Muller 1969) in the invasion process and proposes that some exotic plants may succeed because they bring novel ways of interaction to natural plant communities (Callaway & Aschehoug 2000, Bais *et al.* 2003). Specifically, the novel weapons hypothesis argues that exotics exude allelochemicals that are relatively ineffective against well-adapted neighbours in origin communities, but highly inhibitory to naïve plants in recipient communities. Strong tests of this hypothesis must of course involve a comparative biogeographical component. In the first assessment of the novel weapons hypothesis, Callaway & Aschehoug (2000) compared the inhibitory effects of *Centaurea diffusa*

Lam., an invasive Eurasian herb in North America, on three bunchgrass species that co-exist with it in Eurasia to those on three North America bunchgrasses matched with the Eurasian species for genus (or nearly congeneric), morphology and size. *Centaurea diffusa* had much stronger negative effects on North American species unless activated carbon was added to ameliorate the action of allelochemicals, when Eurasian species were more affected. The overall effect of activated carbon on North American species was positive, but it reduced dramatically the biomass of all Eurasian grass species growing with *C. diffusa*. These results suggest that *C. diffusa* produces chemicals that long-term and familiar Eurasian neighbours have adapted to, but its new North American neighbours have not. Biogeographical differences in the resistance or susceptibility of plant communities to *C. diffusa* were further explored by establishing microcosms in which North American and Eurasian plant communities were established in both North American and Eurasian soils (Vivanco *et al.* 2004). The regional source of the plant community was by far the most important factor in resistance to *C. diffusa* – Eurasian communities were much more resistant to invasion.

Similar biogeographic comparisons have been performed with the closely related *C. maculosa*. By integrating ecological, physiological, biochemical signal transduction and genomic approaches, Bais and colleagues (2003) were able to isolate a chemical, (-)-catechin, produced by *C. maculosa* roots that has phytotoxic properties, to determine that the concentration of (-)-catechin is about twice as high in soils occupied by *C. maculosa* in North America than in similar habitats in Europe and to demonstrate that germination and growth of European grasses are more resistant to (-)-catechin than those of North American counterparts.

Using a similar approach to the one employed by Callaway & Aschehoug (2000), Prati & Bossdorf (2004) tested allelopathic effects of *A. petiolata*, an aggressive invader of the understorey of forests in North America, on germination of two congeneric species that co-occur with *Alliaria* in the field - the American *Geum laciniatum* Murray and the European *G. urbanum* L. They also investigated whether the allelopathic potential of *A. petiolata* varied between native European and exotic North American populations of the weed. They found that exotic North American populations of *A. petiolata* significantly reduced the germination of “naïve” North American *G. laciniatum* seeds, but had no effects on “experienced” European *G. urbanum* seeds. Native European *A. petiolata*, on the other hand, significantly reduced seed germination of both North American *G. laciniatum* and European *G. urbanum* in similar proportions. These results partially support the novel weapons hypothesis and suggest that North American *A. petiolata* has lost its detrimental effects on its former European neighbour.

The general picture emerging from research on invasive *Centaurea* species and *A. petiolata* is that chemicals exuding from their roots may disrupt naïve communities in ways that do not occur in their communities of origin. Clearly, it is not possible to explore the novel weapons hypothesis without integrating biogeography into experimental designs. So far, experiments have only been conducted in the greenhouse or *in vitro*, but, as likely allelopathic agents for many invasive species have been identified and are commercially available, it should be relatively simply to apply them in the field at natural concentrations. It may be more difficult, however, to assess the effects of allelochemicals while maintaining appropriate residence times, realistic rates of release or renewability and accounting for the effects of microbial communities.

OTHER RESEARCH NEEDS IN PLANT INVASION BIOLOGY

Several mechanisms have been proposed to explain the variation in community susceptibility to invasion (see Lonsdale 1999, Mack *et al.* 2000, Sakai *et al.* 2001, Table 1 -hypotheses 5 to 7). There are a number of issues here whose further examination can be accomplished by studying exotics only in their introduced range.

The Disturbance Hypothesis

Since exotics that invade disturbed communities are, in general, ruderal species (*sensu* Grime 1974), it is not surprising that they flourish under such conditions. Moreover, according to plant strategy theory, it is expected that exotic *ruderals* will outperform native *competitors* and *stress-tolerants* in early successional stages (Grime 1979, Huston & Smith 1987). What is unclear, though, is why ruderals native to the system are not able to colonize disturbed areas as successfully as exotic ruderals. The disturbance hypothesis argues that differences exist because native ruderals have not experienced the type and intensity of disturbances to which exotics are adapted (Gray 1879, Baker 1974, Mack *et al.* 2000). A puzzling aspect of this proposition, however, is that exotics often thrive even in areas altered by natural disturbances. A longer history with humans and, in consequence, with severe disturbances might have enabled some exotics to gain tenure under a larger suite of disturbed conditions. The disturbance hypothesis is long standing (Gray 1879), but it has received poor examination and further understanding could be obtained by implementing factorial field experiments with treatments mimicking disturbances within local vegetation and adding seeds of both

resident and exotic ruderals. Even better, but perhaps unrealistic for exotic species, would be to simulate disturbances to which both native and exotic ruderals are and are not adapted.

The Species Richness Hypothesis

Elton (1958) first proposed the notion that more diverse communities might be more resistant to invasion than species-poor communities. This idea has been supported by theoretical arguments that lower diversity communities have weaker interspecific interactions and more “empty niches” (MacArthur 1970, 1972, Post & Pimm 1983, Crawley 1987, Drake 1990). Since resource uptake is reduced in species-poor communities (Crawley 1987, Tilman *et al.* 1996, Hooper & Vitousek 1998), the presence of more “free” resource might render species-poor communities more invasible than species-rich communities.

Empirical tests of the effects of species richness on invasibility have produced mixed results (see review by Levine & D’Antonio 1999). Large-scale observational studies have shown a positive correlation between diversity and invasibility, with more diverse communities being more heavily invaded (Kruger *et al.* 1989, Knops *et al.* 1995, Planty-Tabacchi *et al.* 1996, Wiser *et al.* 1998, Lonsdale 1999, Smith & Knapp 1999, Stohlgren *et al.* 1999, Stadler *et al.* 2000, Foster *et al.* 2002). In contrast, experiments using synthetic assemblages that vary in diversity have usually shown the opposite pattern, with more diverse assemblages being less invasible (Knops *et al.* 1999, Naeem *et al.* 2000, Hector *et al.* 2001, Dukes 2002, Stachowicz *et al.* 2002, but see Palmer & Maurer 1997). Part of this discrepancy is clearly scale related (Tilman 1999). Beyond

this, however, large scale observational studies have been correlative, and have not controlled for extrinsic factors such as propagule pressure, disturbance, resource availability and consumers –factors known to co-vary with diversity and that also may influence invasibility (Levine & D’Antonio 1999, Shea & Chesson 2002). Experimental studies, on the other hand, have controlled for these factors essentially by ignoring them, thereby limiting our understanding of how diversity interacts with processes that vary over broader spatial scales.

One factor known to play a key role in influencing invasibility at larger spatial scales is resource availability. Increasing water or nitrogen availability often facilitates invasion (Aerts & Berendse 1988, Bobbink 1991, Hobbs & Mooney 1991, Hobbs & Huenneke 1992, Milchunas & Lauenroth 1995, Maron & Connors 1996, Wedin & Tilman 1996, Davis & Pelsor 2001, Siemann & Rogers 2003a). Foster *et al.* (2002) found that more diverse grassland plots were more heavily invaded and that resource availability explained a greater percentage of the variance in invasibility than did species diversity. Given that resource supply and native diversity appear to have opposite effects on invasion resistance in isolation, a critical issue becomes how these factors interact to influence community invasibility. Does resource supply have primacy over native diversity in influencing invasion resistance? Can any negative diversity-invasibility relationship be fundamentally changed by increasing resource availability? Future studies that examine interactions between different components of native species richness and extrinsic factors such as resource availability or disturbance would yield rich dividends (e.g., Von Holle in press).

The Propagule Pressure Hypothesis

Several authors have pointed out that variations in the level of invasion among recipient communities could simply be due to differences in the number of exotics arriving to the community (Williamson 1996, Lonsdale 1999, Mack *et al.* 2000). Evidence for this assertion comes mainly from studies that relate the number of exotics in a region with isolation from main shipping routes (di Castri 1989, Lonsdale 1999, Mack *et al.* 2000). A growing number of studies also show that seed limitation is common (see reviews by Eriksson & Ehrlén 1992, Turnbull *et al.* 2000), suggesting that propagule pressure can also fundamentally influence the probability of invasion by new species. Yet, while it is clear that adding more seeds to sites can affect establishment success, it is not well understood how the relative importance of propagule pressure compares to that of other processes such as disturbance and resource supply. As such, carefully designed factorial field experiments are needed in which a range of propagule pressures are crossed with different levels of other factors thought to influence invasion. Such experiments would have the added benefit of shedding light on processes that influence the early life-history stages, rather than the adult-adult or seedling-adult interactions that are the focus of many invasion studies.

IMPLICATIONS FOR UNDERSTANDING THE NATURE OF NATIVE SYSTEMS

Beyond simply understanding why exotics succeed in recipient communities, the study of exotic species could shed new light on several fundamental issues in basic ecology. Species introductions are grand scale ‘experiments’ where the abiotic and biotic background and co-evolutionary history of interacting species are manipulated, providing

an opportunity to tease apart how such factors might influence population abundance of particular species. If appropriately designed biogeographic experiments consistently find evidence for release from natural enemies as the driver for successful invasions, then top down effects in natural communities would appear to have been substantially underestimated. If studies of invaders in their origin and invaded communities show that empty niches are crucial for invasion, then the composition and function of natural communities must be remarkably limited by regional species pools, local adaptation must be overrated and the diversity-invasion resistance hypothesis would gain mechanistic credibility. Finally, contrasting allelopathic interactions among plants from different biogeographical regions have profound implications for plant community theory. Plant communities are widely thought to be “individualistic”, composed primarily of species that have similar adaptations to a particular physical environment. This traditional view downplays any persistent and powerful role of co-evolution in shaping the structure of interactions, and does not account for facilitation between species. However, if some exotic plants succeed because they bring novel mechanisms of interaction to natural plant communities, then natural plant communities may be more tightly knit than generally thought. Continuing with this line of thought, novel weapons suggest that interactions among plant species may drive natural selection in communities and imply that natural biological communities may evolve in some way as functionally organized units.

Whilst a greater emphasis on biogeographic comparisons will yield invaluable information on invasion processes, perhaps the potential for supporting or challenging general ecological paradigms is even more important. As for fundamental questions about community theory raised by invasions themselves, the few experiments conducted

with explicit biogeographical treatments have raised questions about general community theory, provided insight into the nature of trophic interactions in ecosystems, elucidated the role of soil microbes in population regulation and suggested that co-evolutionary processes may be important for the organization of natural communities. This may be only the beginning.

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Table 1. Major hypotheses for the success of exotic plants in recipient communities.

Hypotheses 1 to 4 require an explicit comparison between native and introduced ranges to be critically evaluated. Hypotheses 5 to 7 can be assessed by studying exotics only in their introduced range.

Hypothesis Name	Definition	References
1. Natural Enemies	Exotics are released from natural enemies that control their population growth	Darwin 1859, Williams 1954, Elton 1958
2. Evolution of Invasiveness	Exotics experience rapid genetic changes linked to new selection pressures in the novel environment	Blossey & Nötzold 1995, Lee 2002, Stockwell <i>et al.</i> 2003
3. Empty Niche	Exotics utilize resources unused by the locals	Elton 1958, MacArthur 1970
4. Novel Weapons	Exotics bring novel ways of biochemical interaction to recipient communities	Callaway & Aschehoug 2000, Bais <i>et al.</i> 2003
5. Disturbance	Exotics are adapted to disturbances' type and intensity that are novel to natives	Gray 1879, Baker 1974
6. Species Richness	Species-rich communities are more resistant to invasion than species-poor communities	Elton 1958, MacArthur 1970, 1972
7. Propagule Pressure	Variations in levels of invasion among recipient communities are due to differences in the number of exotics arriving to the community	di Castri 1989, Williamson 1996, Lonsdale 1999

CHAPTER 2

DISTURBANCE FACILITATES INVASION, BUT EFFECTS ARE STRONGER ABROAD THAN AT HOME

Abstract. Disturbance is one of the most important factors promoting exotic invasion. However, if disturbance *per se* is sufficient to explain exotic success, then “invasion” abroad should not differ from “colonization” at home. Comparisons of the effect of disturbance on organisms in their native and invaded ranges are crucial to elucidate whether this is the case; however, such comparisons have not been conducted. I investigated the effect of disturbance on the success of the Eurasian native, *Centaurea solstitialis*, in two invaded regions, California and Argentina, and one native region, Turkey, by conducting field experiments consisting of simulating different disturbances and adding locally collected *C. solstitialis* seeds. I also tested differences among *C. solstitialis* genotypes in these three regions and the effects of local soil microbes on *C. solstitialis* performance in greenhouse experiments. Disturbance increased *C. solstitialis* abundance and performance far more in non-native ranges than in the native range, but *C. solstitialis* biomass and fecundity were similar among populations from all regions grown under common conditions. Eurasian soil microbes had stronger suppressive effects on *C. solstitialis* biomass than Californian and Argentinean soil biota, suggesting that escape from soil pathogens may contribute to the disproportionately powerful effect of disturbance in invaded regions.

Key words: Biological invasions; *Centaurea solstitialis*; community invasibility; disturbance; invasive plants; ruderals.

INTRODUCTION

In contemporary biological invasions, humans assist other organisms to overcome one of the most limiting of ecological factors, dispersal (Eriksson and Ehrlén 1992, Tilman 1997, Seabloom et al. 2003). Once dispersed; however, introduced individuals (exotics) may face different limitations to their abundance and distribution than in their communities of origin. Understanding these differences may help to explain the unusual success of some species as exotics (Darwin 1859, Elton 1958, Blossey and Nötzold 1995, Callaway and Aschehoug 2000). If so, comparative ecological studies of invasive species where they are native versus where they are exotic are essential. Also, analyzing the relative importance of factors influencing invasive organisms over large geographical scales may yield unique insight into ecological and evolutionary theory (Callaway et al. 2005, Hierro et al. 2005, Sax et al. 2005). Most research on invasion biology, however, has been conducted only in non-native ranges, and has not incorporated the biotic and abiotic conditions that affect exotics at home (see Hierro et al. 2005).

Disturbance commonly enhances the abundance and distribution of exotic plants (Gray 1879, Elton 1958, D'Antonio et al. 1999). The positive role of disturbance in some plant invasions appears to help many newcomers to establish nearly monospecific stands (e.g., Maddox and Mayfield 1985, Whisenant 1990). However, research on the role of disturbance in invasions has followed the trend of research in invasion biology in general. There are many observational (see D'Antonio et al. 1999 for a comprehensive review)

and experimental studies (e.g., Hobbs and Atkins 1988, Burke and Grime 1996, Leishman and Thomson 2005) linking disturbance to exotic success in regions of introduction, but we know very little about how disturbance affects exotics in their native range. Specifically, we do not know if disturbance triggers the same spectacular response in the abundance of invaders where they are natives as where they are exotics.

Given the ruderal life history of many exotic plants, it is not surprising that they flourish in disturbed habitats (Baker 1974, Grime 1974). Proposed general mechanisms by which disturbance promotes invasions include reduction of competitive pressure from other plants, stimulation of germination, and alteration of resource levels (D'Antonio et al. 1999), all of which favor the ruderal strategy. If the success of exotics in disturbed places is due to their ruderal nature and these mechanisms are sufficient to explain why exotics thrive under such conditions, then exotics should respond similarly to disturbance where they are native. In other words, we do not know if invasion abroad is different from colonization at home (see Thompson et al. 1995, Davis et al. 2001, Grime 2001). Invasion may not differ from colonization, or alternatively disturbance may operate in association with other proposed mechanisms for exotic plant success (i.e., enemy release, empty niches, evolutionary change, novel weapons), and cause species to attain community dominance only where they occur as exotics.

The effect of disturbance on invasion is not limited to the direct responses of exotic species. The success of an invader can also be influenced by the response of resident native species to disturbance, which can depend on the familiarity of a community with a particular disturbance regime (D'Antonio et al. 1999). Indeed, as early

as 1879, Gray speculated that exotics dominate in disturbed areas because they are adapted to disturbances that are novel to the locals.

I used an explicitly biogeographic approach to investigate the response of an annual plant, *Centaurea solstitialis* L., Asteraceae (yellow starthistle), to disturbance in its native and non-native range. I pursued this objective by conducting the same disturbance and seed addition experiments in one region of origin, southern Turkey, and two regions in the introduced range of *C. solstitialis* that vary considerably in climate and the dominant plant functional group, California and central Argentina. Because there are many kinds of disturbance, I included three disturbance types in our experimental protocol, soil turnover to represent plowing, fire, and clipping to represent haying or vertebrate herbivory. I also conducted greenhouse experiments to see if biogeographic results could be explained by regional genotypic differences and/or by the effects of local soil microbes.

In its native range *C. solstitialis* is largely confined to disturbed sites and is considered a typical ruderal species (Davis 1975, Uygur et al. 2004). In both California and central Argentina, *C. solstitialis* is one of the most abundant invasive exotic species (Pitcairn et al. 1998, J.L. Hierro and D. Villarreal, unpublished data), and although its occurrence is also often associated with disturbed areas (Maddox et al. 1985, J.L. Hierro and D. Villarreal, unpublished data), the role of disturbance in its invasion success has received surprisingly little attention (Gerlach and Rice 2003). Here I focus on four fundamental questions: 1) does the response of *C. solstitialis* to disturbance vary between its native and introduced ranges?, 2) is this response consistent for two climatically and ecologically contrasting regions where *C. solstitialis* has been introduced?, 3) do *C.*

solstitialis populations exhibit genetically-based differences in size and fecundity among studied regions?, and 4) does the effect of soil biota on *C. solstitialis* growth vary among these regions?

METHODS AND MATERIALS

Biology and invasion history of the study plant

Centaurea solstitialis is often considered to be native to southern Europe; however, Prodan (1930, as cited in Maddox 1981, Maddox et al. 1985) argued that southern Europe was actually invaded by *C. solstitialis* from eastern Eurasia, which is considered by Prodan as the primary distributional range of the plant. The genus *Centaurea* exhibits its greatest diversity in eastern Eurasia (Wagenitz 1955, as cited in Maddox et al. 1985, Davis 1975), providing support to this view. Therefore, I used Turkey as the native region.

Centaurea solstitialis plants germinate in autumn, form a rosette during winter, bolt and send up stalks with floral buds in the spring, flower in mid-late summer, and die by the end of the same season or in early autumn (Sheley and Larson 1994). Less important germination events can also occur in the spring and even well into the growing season (Maddox 1981, Hergoz and Randall 1992, H. Troiani, National University of La Pampa, personal communication). In late summer, flowers mature and produce two types of achenes (hereafter referred as seeds). Ray flowers produce dark seeds without a pappus, while disk flowers set light colored seeds with a pappus. Flower heads produce about four times more pappus than non-pappus seeds (Benefield et al. 2001, Gerlach and Rice 2003). Seed production in invaded sites in California has been estimated to vary

from 500 to 27,200 seeds/m² (Pitcairn et al. 2002), transient seedbank densities range from about 3,400 to 10,100 seeds/m² (DiTomaso et al. 1999), and persistent soil seed densities vary between 1,800 and 7,400 seeds/m² (Joley et al. 2003, as reported by Uygur et al. 2004). Uygur and colleagues (2004) reported transient soil seed densities in Turkey of 360 to 14,000 seeds/m² and persistent seedbank densities of 440 to 1,470 seeds/m². In central Argentina, transient seedbank densities of *C. solstitialis* range from 0 to 21,590 seeds/m² in fields where mature plants occur, and persistent seedbank densities between 0 and 18,600 seeds/m² (C. Lortie and J.L. Hierro, unpublished data).

In studies of plant remains in adobe bricks from buildings of the Spanish (1769 to 1824) and Mexican (after 1824) periods in California, records of *C. solstitialis* occur only after 1824 (Hendry 1931, Hendry and Bellue 1936). The first specimen was collected in 1869 at Oakland, California (Maddox 1981). The introduction history of *C. solstitialis* in California (Gerlach 1997) and Argentina (Hijano and Basigalup 1995) is based on records of imported alfalfa seeds. These records indicate that *C. solstitialis* populations in these regions are derived from multiple introductions over decades and a broad suite of similar source populations (California: Chile (Spanish origin), France, Italy, Spain, and Argentina; Argentina: Chile (Spanish origin), France, Italy, and Syria). Probable introduction dates are ~1850 for California (Gerlach 1997) and ~1870 for central Argentina (Hijano and Basigalup 1995).

Six exotic insect species have been introduced for biological control of *C. solstitialis* in the western United States, four of which are now abundant in California (Pitcairn et al. 2002). Insects attack plants at the flowering stage and their larvae consume developing seeds. No insects have succeeded in controlling *C. solstitialis*

(DiTomaso and Gerlach 2000, Pitcairn et al. 2002). No control agent has been introduced into Argentina (G. Logarzo, South American Biological Control Laboratory USDA-ARS, personal communication), and the presence of native natural enemies is unknown.

Study sites

Field experiments were conducted in the Sierra Foothill Research & Extension Center (SFREC) in northern California (N 39° 16', W 121° 18', 346 m elevation), Estancia La Mercedes in La Pampa province, Argentina (S 36° 40', W 64° 38', 269 m elevation), and Boyunduruk Batti in Turkey (N 36° 51', E 30° 25', 1100 m elevation). Table 1 displays information on climate, soil, and vegetation at the experimental sites in the three regions. A 5% HCl test indicated that soils at all sites are non-calcareous. Vegetation at the California site was dominated by Eurasian annual grasses and herbs (Table 1), such as *Bromus diandrus*, *B. hordeaceus*, *Hordeum murinum*, *Lolium multiflorum* and *Trifolium hirtum*. In sharp contrast, the site in central Argentina was dominated by native perennial bunchgrasses, including *Piptochaetium napostense*, *Poa ligularis*, *Stipa clarazii*, *S. tenuissima*, accompanied by subordinate annual and perennial herbs such as *Gnaphalium gaudichaudianum* and *Baccharis sp.* (Table 1). In Turkey, the site was grassland dominated by one native perennial species, *H. bulbosum*, and less important annual and perennial species, including *Avena barbata*, *B. squarrosus*, *Trifolium sp.*, and *Cichorium intybus* (Table 1). Sites in California and central Argentina have been historically grazed but have never been plowed. The site in Turkey has also been grazed,

and used for wheat and barley production without the addition of fertilizers. Cropping ceased four years prior to our study.

Disturbance and seed addition experiments

Experiment I. – In January 2002 in central Argentina, August 2002 in California, and July 2003 in Turkey, I selected a natural grassland representative of each region without *C. solstitialis* but, based upon the abundance of the weed nearby, apparently ideal for *C. solstitialis* if dispersed there. Selected sites were isolated by at least five km from other populations of this plant and main roads to minimize potential influences of the seedbank. Study sites in all regions were fenced to prevent damage from domestic animals. Logistic constraints related to carrying out field experiments at such global scale and concerns about spreading a noxious weed into uninvaded grasslands limited my ability to replicate sites within each region. In March 2002 in Argentina, October 2002 in California, and September 2003 in Turkey, I marked 60 1 m x 1 m experimental plots, each plot separated by 0.50 m. Vegetation in the space between plots was mowed at the beginning of the experiment and periodically throughout the study. I assigned one of each of the following four treatments to 15 randomly selected plots at each site: (1) soil turnover, (2) fire, (3) clipping, and (4) no disturbance. Soil turnover was performed with a shovel to a depth of 0.30 m, mixing vegetation and litter. For the fire treatment, a fire was started in a corner of the plot and allowed to burn inside a metal frame 1 m x 1 m wide x 0.30 m tall. For the clipping treatment, vegetation was clipped once to a height of 1 cm and removed from plots. In the 15 undisturbed plots, I recorded percent cover of plant species, bare ground, and litter to estimate initial conditions at each study site

(Table 1). Once treatments were established, and before the arrival of autumn rains in California and Turkey, I added 200 locally collected pappus seeds of *C. solstitialis* to the 0.50 m x 0.50 m in the center of each experimental plot, which allowed for a buffer zone. I only used seeds that looked healthy and to be filled with an embryo (see Gerlach and Rice 2003 for the protocol I followed). To keep seeds from being moved out of the plots, I placed 0.50 m x 0.50 m wide x 0.15 m tall wood frames around the seeded center of plots. Frames were removed shortly after the first rains, which occurred two, 16, and 26 days after adding seeds in Argentina, California, and Turkey, respectively. At the end of each season, I counted the number of *C. solstitialis* individuals present in the 180 experimental plots, with the exception of the late fall census in 2002 in California. *Centaurea solstitialis* densities were calculated per square meter. At the peak of flowering, during the summer following the addition of seeds (January 2003, August 2003, and August 2004 in Argentina, California, and Turkey, respectively), I determined levels of invasion/colonization in all plots as proportion of plant establishment (number of plants present in plots in the summer divided by the number of seeds added to plots in the fall), height, and number of flower heads of *C. solstitialis*. To estimate plant fecundity, I counted the number of inflorescences of five randomly selected individuals in each experimental plot and took the mean of these plants as the number of flower heads per plant in each plot. When the number of plants was less than five, I counted inflorescences of all individuals present in the plot and averaged them to obtain the number of inflorescences per plant. In addition, I estimated the percent cover of plant species, bare ground, and litter in all experimental plots.

Experiment II. – In an effort to determine whether disturbance in invaded regions had consistent effects on *C. solstitialis*, I conducted the disturbance and seed addition experiment for a second time in the two non-native regions. I was unable to repeat this experiment in the native range due to logistical difficulties. In California and Argentina, the second experiment was started in autumn 2003. The experiment was conducted within the fenced enclosure used in the first experiment, but in new plots located five m away from the first year's plots. I used the same general location in the two different years to minimize the spread of the weed in uninvaded grasslands. The experimental protocol was identical to that in *Experiment I*. Initial conditions recorded in the 15 undisturbed plots are shown in Table 2. In Argentina, the experiment was initiated in March 2003 and in California in October 2003, before autumn rains. The first rains occurred two and seven days after the addition of *C. solstitialis* seeds in Argentina and California, respectively. As in *Experiment I*, I recorded the number of *C. solstitialis* plants throughout the growing season, assessed the proportion of seeds that established plants, measured size and fecundity of *C. solstitialis*, and estimated percent cover of plant species, bare ground, and litter in experimental plots in the summer following the addition of seeds in each region (January 2004 in Argentina and August 2004 in California).

Common garden experiment

Because we used local seed sources in our field experiments, I assessed the potential for differences in genotype among *C. solstitialis* populations in California, Argentina, and the native range to explain our biogeographic comparisons by conducting

a common garden experiment in a greenhouse in The University of Montana campus. I used seeds from six *C. solstitialis* populations in California, six populations in central Argentina, five populations in Turkey, and five populations in Georgia, near Turkey and also within the native range of this plant (see Table 3 for locations). Seeds were collected in January 2002 in Argentina, August 2002 in California, and August 2004 in Turkey and Georgia. For each population, I planted five seeds in each of five 2500 cm³ plastic pots. Seedlings in pots were then thinned to one individual and watered periodically to field capacity throughout the experiment. Pots were filled with a mixture of 2 parts sand to 1 part soil. Soil was collected from a grassland site located near Missoula, Montana, USA. The sand was 20/30 grit, corresponding to mean diameters of 0.85 mm and 0.60 mm, respectively. At senescence (~ eight months of growth), I counted the number of flower heads produced by each individual, harvested plants, dried them at 60 °C until constant weight, and determined total biomass.

Soil biota experiment

I also examined whether soil microbes in native and introduced regions had differential effects on *C. solstitialis* growth. I collected soils from two sites in California (N 37° 45', W 119° 51' and N 37° 47', W 121° 11'), three sites in Argentina (S 36° 58', W 64°16'; S 36° 42', W 64° 36', and S 36° 26', W 64° 17'), and five sites in Eurasia (three in Turkey, N 37° 00', E 30° 30'; N 36° 57', E 30° 29', and N 36° 56', E 30° 26', and two in Georgia, N 41° 44', E 44° 44' and N 42° 42', E 42° 03'). After collection, soils were immediately subjected to slow air-drying to mimic drying conditions that would occur during natural drought. One-half of the soils were then treated by triple

autoclaving on three successive days to kill soil microbes. Pure sterile and non-sterile soils were used to grow *C. solstitialis* plants from seeds collected from a single population in Turkey (N 36° 53', E 30° 22', 1290 m elevation) in two to ten 250 ml pots per site–soil treatment combination. Plants were grown for 53 days while being fertilized once every two weeks with 10 ml of 0.34 g/L solution of Miracle Grow Professional (15N-2P-20K) fertilizer and watered to field capacity every 2–3 days. Fertilization was intended to neutralize potential differences in nutrient flushes among sites caused by the sterilization of soil. At the end of the experiment, plants were harvested, dried at 60 °C, and weighed for total biomass.

Plant density in naturally occurring populations

I measured plant density in naturally occurring populations of *C. solstitialis* in three disturbed sites in summer 2003 and 2004 in each of the three regions to evaluate whether levels of invasion and colonization in experimental plots matched general *C. solstitialis* abundances in the regions where I worked and to compensate for the lack of replicated experiments within a region. At each site, plant density was determined in five 1 m x 1 m plots. Sites in all three regions have a long history of natural and prescribed fire and domestic grazing. In Turkey, two of the sites had been used for agricultural purposes in the past. In all cases, sites were located within the general region where disturbance and seed addition experiments were conducted (California: (1) N 39° 14', W 121° 19', 92 m elevation, (2) N 39° 15', W 121° 19', 170 m elevation, and (3) N 39° 15', W 121° 20', 137 m elevation; central Argentina: (1) S 36° 26', W 64° 17', 194 m elevation, (2) S 36° 40', W 64° 38', 244 m elevation, and (3) S 36° 42', W 64° 36', 240

m elevation; Turkey: (1) N 36° 54', E 30° 29', 430 m elevation, (2) N 36° 54', E 30° 28', 635 m elevation, and (3) N 36° 53', E 30° 26', 997 m elevation). Sites 1 and 2 in Turkey were destroyed by vandals and flooding in the winter of 2004; thus, density in summer 2004 was measured only at site 3.

Precipitation during the study

Total rainfall in the 2002-03 season in California (785 mm) and 2002 in central Argentina (748 mm) was slightly above the annual mean for both regions (749 and 686 mm, respectively). In contrast, 2003-04 was drier than average in California (658 mm), but more importantly 99% of the rainfall occurred between October and March, resulting in considerable drought during the late spring and summer. Similarly, rainfall in 2003 in Argentina was only 378 mm, the fifth driest year since 1911. Precipitation in the 2002-03 season in Turkey (550 mm) was close to the mean value (527 mm), but in 2003-04 precipitation was almost twice the average (926 mm).

Statistical analyses

I compared *C. solstitialis* densities among regions at the end of each season for individual treatments with one-way ANOVA and Tukey post-hoc comparisons. Due to the lack of data in the late fall 2002 census in California; differences between Argentina and Turkey for this sampling date were evaluated with t-tests. Likewise, I compared *C. solstitialis* densities between regions at the end of each season for individual treatments in *Experiment II* with t-tests. When needed, data were transformed to meet ANOVA assumptions of normality and homoscedasticity. When transformations did not correct

violation of ANOVA's assumptions, I compared the three regions with Kruskal-Wallis tests and post-hoc comparisons were conducted with Tukey tests performed on the ranks (Zar 2003). For cases in which comparisons were conducted between two regions, non-parametric tests were conducted with Mann-Whitney.

Data for *C. solstitialis* proportional establishment, patch height, and number of inflorescences per plant in the summers following seed additions were analyzed using a randomized complete block design, where regions were treated as blocks. In this design, both region and disturbance treatments were considered fixed factors. Pairwise comparisons between disturbance treatments within a single region and those between regions for a single disturbance treatment were performed using Tukey's method. I transformed data as needed to improve normality and homogeneity of variances. Percent cover of *C. solstitialis* versus that of all other plant species combined present in plots in the summer following seed additions were analyzed using paired-sample t tests.

Data from the common garden experiment were analyzed with two-way ANOVA with region of origin as fixed factor and population nested within region. *Centaurea solstitialis* biomass in the soil biota experiment was analyzed with three-way ANOVA, where soil origin and soil treatment were treated as fixed factors and site was nested within soil origin. I transformed data with the square root function to meet ANOVA assumptions and improve the distribution of residuals.

Finally, I assessed differences in plant density of naturally occurring populations of *C. solstitialis* among all three regions using nested ANOVA, where site was nested within region, with post-hoc comparisons again performed using Tukey tests. Computations were conducted with SPSS 10.0 (SPSS 2000) and JMP 5.1.1 (SAS 2004).

RESULTS

Disturbance and seed addition experiment I

As expected, disturbance enhanced the abundance and performance of *C. solstitialis* plants in all three regions, but the effects of disturbance were far greater in the non-native ranges than in the native range (Figs. 1 and 2; proportional establishment, $F_{\text{region } 2,168}=90.84, p<0.001, F_{\text{disturbance treatment } 3,168}=73.33, p<0.001, F_{\text{region} \times \text{treatment } 6,168}=19.20, p<0.001$; patch height, $F_{\text{region } 2,136}=79.04, p<0.001, F_{\text{disturbance treatment } 3,136}=28.57, p<0.001, F_{\text{region} \times \text{treatment } 6,136}=6.34, p<0.001$; fecundity, $F_{\text{region } 2,136}=43.19, p<0.001, F_{\text{disturbance treatment } 3,136}=38.52, p<0.001, F_{\text{region} \times \text{treatment } 6,136}=5.84, p<0.001$). Soil turnover and fire in California and soil turnover in Argentina were the treatments where the weed experienced its greatest success (Figs. 1 to 3).

Soil turnover. – In plots with soil disturbance, the density of *C. solstitialis* was consistently more than one order of magnitude higher in the non-native sites than in the native site (late fall, $t_{28}=15.07, p<0.001$; late winter, $F_{42}=211.15, p<0.001$; late spring, $F_{42}=174.57, p<0.001$; summer, $F_{42}=134.80, p<0.001$; Fig. 1). Interestingly, *C. solstitialis* density continued to increase through the spring months in both invaded regions, indicating extended germination, but this did not occur in Turkey, where plant density remained almost unchanged during the experimental period.

The proportion of *C. solstitialis* seeds that established plants in the summer in the soil-disturbance treatment was 25 and 20 times greater in California and Argentina than in Turkey, respectively (Fig. 2-A). Additionally, in non-native regions *C. solstitialis* establishment was about 29 times (California) and five times (Argentina) greater in plots

with soil disturbance than in non-disturbed controls, but establishment was not statistically different between these treatments in Turkey.

Centaurea solstitialis plants were more than twice as tall in Argentina than in Turkey, and 40% taller in California than in Turkey (Fig. 2-B). Plants were also nearly 50% taller in Argentina than in California. In non-native regions, *C. solstitialis* plants growing in soil-disturbance plots were taller than those in non-disturbed plots. In contrast, *C. solstitialis* height was similar in disturbed and non-disturbed treatments in Turkey.

Centaurea solstitialis fecundity was nearly 90% and 60% greater in Argentina and California than in Turkey, respectively, but differences were not significant (Fig. 2-C). In Argentina, *C. solstitialis* fecundity was nearly five times higher in soil disturbance than in the control. In Turkey, plants were also much more fecund in soil-disturbance than in no disturbance plots. In California, however, there was no significant difference in the number of flowers per *C. solstitialis* individual between the soil disturbance treatment and the control.

By the summer of 2003, *C. solstitialis* had formed virtual monocultures in the soil-disturbance treatment in California and Argentina (cover of *C. solstitialis* vs. cover of all other plant species combined, California, $t_{14}=-12.50$, $p<0.001$; Argentina, $t_{14}=-35.70$, $p<0.001$; Fig. 3). In sharp contrast, the proportional cover of *C. solstitialis* in this treatment in its native range was less than half that in the non-native ranges, and it did not differ from the cover of all other plant species combined ($t_{14}=0.33$, $p=0.75$).

Fire. – In the fire treatment, *C. solstitialis* density was initially higher in Turkey than in Argentina (late fall, $t_{28}=-5.01$, $p<0.001$, late winter, $\chi^2_2=13.10$, $p=0.001$), but

because of a continuous decrease in density from late fall to summer in the native range and no major changes in Argentina, density did not differ between these regions in late spring and summer (Fig. 1). California and Turkey, on the other hand, had nearly identical *C. solstitialis* densities in late winter, but density was much higher in California than in Turkey by late spring ($F_{2,42}=27.54$, $p<0.001$) and summer ($F_{2,42}=35.76$, $p<0.001$). As in the soil disturbance treatment, I observed a second wave of germination in the spring in the non-native regions, but this was much stronger in California than in Argentina. *Centaurea solstitialis* density in this treatment was consistently higher in California than in Argentina throughout the experiment.

The proportional establishment of *C. solstitialis* in burned plots was more than four times higher in California than in Turkey, but differences between Argentina and Turkey were not significant (Fig. 2-A). In California, the establishment of the weed in burned plots was 27 times greater than in plots without disturbance; in Argentina, fire had no effect relative to the control, and in Turkey, the proportional establishment of *C. solstitialis* was also much higher in burned plots than in the controls.

The height of mature *C. solstitialis* in the fire treatment abroad was twice that in the same treatment at home (Fig. 2-B). Relative to the controls, plants in California and Argentina were nearly 70% and 45% taller in burned plots, respectively. In contrast, *C. solstitialis* plants in Turkey were no taller in plots with fire than in plots without this disturbance.

In burned plots, the number of flower heads of *C. solstitialis* was approximately 15 and 9 times higher in California and Argentina than in the native range, respectively (Fig. 2-C). In non-native regions, fire promoted four and three times greater flower

production in California and Argentina, respectively, but at home in Turkey there were no differences in flower production in burned versus control plots.

California was the only region where fire promoted the establishment of near monocultures of *C. solstitialis* ($t_{14}=-9.20$, $p<0.001$, Fig. 3). In Argentina, differences between the cover of *C. solstitialis* and the cover of other species were not significant ($t_{14}=-1.04$, $p=0.32$). More importantly, in Turkey the pattern in the fire treatment was reversed in comparison to California, and the cover of other species there was significantly higher than the cover of *C. solstitialis* ($t_{14}=9.41$, $p<0.001$).

Clipping. – In clipped plots, Argentina tended to have higher *C. solstitialis* densities in late fall than Turkey ($t_{28}=1.75$, $p=0.09$), and during the rest of the year densities were roughly three times higher in Argentina (late winter, $\chi^2_2=13.33$, $p=0.001$; late spring, $\chi^2_2=11.40$, $p=0.003$; summer, $\chi^2_2=14.74$, $p=0.001$, Fig. 1). In contrast, clipped plots in California had higher plant densities than in Turkey only in late winter.

Clipping promoted *C. solstitialis* establishment much more in Argentina than in Turkey, but California and Turkey did not show significant differences (Fig. 2-A). Plant establishment was also higher in Argentina than in California in this treatment. California was the only region where the establishment of *C. solstitialis* in clipped plots was significantly higher than in the controls.

Centaurea solstitialis height was significantly greater in Argentina than in its native range, but height was similar in California and Turkey (Fig. 2-B). No region showed significant differences in plant size between the clipping and control treatment.

Centaurea solstitialis in the clipping treatment did not show statistical differences in the number of flowers produced among all three regions (Fig. 2-C). Similarly,

clipping did not promote significantly higher flower production than in controls in any region.

The percent cover of other species in this type of disturbance was higher than that of *C. solstitialis* in all three regions, but differences between these plant groups were significant only in California and Turkey (California, $t_{14}=4.68$, $p<0.001$; Argentina, $t_{14}=1.11$, $p=0.29$; Turkey, $t_{14}=17.57$, $p<0.001$; Fig. 3).

No disturbance. – Similar to the clipped plots, *C. solstitialis* densities in control plots only tended to be higher in Argentina than the native region at the beginning of the growing season (late fall, $t_{28}=1.86$, $p=0.07$), but *C. solstitialis* densities were significantly higher in Argentina than in Turkey by late winter ($\chi^2_2=19.39$, $p<0.001$), late spring ($\chi^2_2=18.77$, $p<0.001$) and summer ($\chi^2_2=25.52$, $p<0.001$; Fig. 1). Control plots in California had higher *C. solstitialis* densities than in Turkey in late winter and late spring, but there was no difference between these regions by the end of the growing season (Fig. 1).

Proportional establishment of *C. solstitialis* in undisturbed plots was much higher in Argentina than in the native range, but this did not differ between California and Turkey (Fig. 2-A). Establishment of *C. solstitialis* in the control was also significantly higher in Argentina than in California. There were no significant differences in *C. solstitialis* height in the control plots among regions (Fig. 2-B). The production of flowers, in turn, was higher in Argentina than Turkey, but it did not differ significantly between California and Turkey (Fig. 2-C). The cover of other plants was significantly higher than cover of *C. solstitialis* in the controls in all three regions ($t_{14}=24.06$, $p<0.001$;

$t_{14}=4.88$, $p<0.001$; $t_{14}=77.67$, $p<0.001$ for California; Argentina, and Turkey, respectively; Fig. 3).

Disturbance and seed addition experiment II

The important positive effect of disturbance on the abundance and performance of *C. solstitialis* in California and Argentina was confirmed by the repetition of the disturbance and seed addition experiment (Figs. 4 and 5; proportional establishment, $F_{\text{region } 1,112}=29.52$, $p<0.001$; $F_{\text{disturbance treatment } 3,112}=124.01$, $p<0.001$; $F_{\text{region} \times \text{treatment } 3,112}=61.42$, $p<0.001$; patch height, $F_{\text{region } 1,83}=82.75$, $p<0.001$; $F_{\text{disturbance treatment } 3,83}=20.19$, $p<0.001$; $F_{\text{region} \times \text{treatment } 3,83}=0.91$, $p=0.44$; fecundity, $F_{\text{region } 1,83}=250.29$, $p<0.001$; $F_{\text{disturbance treatment } 1,83}=716.54$, $p<0.001$; $F_{\text{region} \times \text{treatment } 3,83}=0.50$, $p=0.69$). Virtually all metrics of invasion, however, were lower in the summer of 2004 relative to that of 2003 in both regions (Figs. 4 and 5). In the dry conditions of the 2003-04 growing season, fire in California and soil turnover in Argentina were the treatments with the strongest positive effects on *C. solstitialis*. These treatments were the only ones in the summer of 2004 in which the cover of *C. solstitialis* was higher than the cover of all other plant species combined (California-fire, $t_{14}=-4.19$, $p=0.001$, *C. solstitialis* cover = $35\% \pm 3.25$, mean \pm SE; Argentina-soil turnover, $t_{14}=-5.76$, $p<0.001$, *C. solstitialis* cover = $62\% \pm 4.60$). In clipping and no disturbance treatments, on the other hand, the cover of other species was, as in the previous summer, higher than that of *C. solstitialis* (California-clipping, $t_{14}=59.13$, $p<0.001$, cover = $2\% \pm 0.62$; California-no disturbance, $t_{14}=27.70$, $p<0.001$, cover = $0.40\% \pm 0.21$; Argentina-clipping, $t_{14}=8.69$, $p<0.001$, cover = $9\% \pm 3.13$; Argentina-no disturbance, $t_{14}=5.73$, $p<0.001$, cover = $10\% \pm 5.02$).

In spite of general similarities, there were a number of important differences between *Experiment I* and *II*. First, in the soil turnover treatment, proportional establishment of *C. solstitialis* was greater in Argentina than in California (Fig. 5-A). Second, in clipped plots, the density of *C. solstitialis* was higher in California than Argentina throughout the year with the exception of late spring (Fig. 4). Third, in clipped and control plots, no significant variation was detected in *C. solstitialis* establishment between non-native regions (Fig. 5-A). Fourth, differences in *C. solstitialis* size between non-native regions in the summer of 2004 were more pronounced than in the summer of 2003, and *C. solstitialis* was consistently taller in Argentina than California, except in undisturbed plots (Fig. 5-B). Fifth, drought conditions affected the flower production of *C. solstitialis* more severely in California than in Argentina, and *C. solstitialis* individuals were much more fecund in Argentina than California across treatments (Fig. 5-C). Finally, the percent cover of the combination of all other species was higher than the cover of *C. solstitialis* in soil turnover in California ($t_{14}=32.87$, $p<0.001$, *C. solstitialis* cover = $5\% \pm 0.58$), which was a complete reversal in the relative importance of these two plant groups when compared to that of the previous summer, and in the fire treatment in Argentina ($t_{14}=6.54$, $p<0.001$, *C. solstitialis* cover = $21\% \pm 3.55$).

Common garden experiment

Total *C. solstitialis* biomass and inflorescence number did not differ ($F_{2,19}=1.26$, $p=0.31$ and $F_{2,19}=2.91$, $p=0.08$, respectively) among populations from California (biomass, 1.23 ± 0.07 g; flower heads, 7.67 ± 0.53) central Argentina (biomass, $1.28 \pm$

0.09 g; flower heads, 8.07 ± 0.40) and Eurasia (biomass, 1.04 ± 0.07 g; flower heads, 6.32 ± 0.29).

Soil biota experiment

Sterilization of native Eurasian soils caused a significant 75% increase in the total biomass of *C. solstitialis*. In contrast, sterilization caused a non-significant 40% increase in the biomass of *C. solstitialis* in California soils and a 20% decrease in Argentinean soils ($F_{\text{soil origin } 2,7}=0.74$, $p=0.51$; $F_{\text{sterilization treatment } 1,107}=2.12$, $p=0.15$; $F_{\text{origin} \times \text{treatment } 2,107}=6.76$, $p=0.002$; Fig. 6).

Plant density in naturally occurring populations

The density of *C. solstitialis* in naturally occurring populations in summer 2003 was around four to five times higher in the invaded regions than in the native region ($F_{2,6}=9.90$, $p=0.01$; California vs Turkey, $p=0.002$; Argentina vs Turkey, $p<0.001$; Fig. 7). No differences were detected between Argentina and California ($p=0.25$).

After the dry spring of 2004 in California and the exceptionally dry year of 2003 in Argentina, *C. solstitialis* densities were similar between these regions and between them and Turkey after its very wet year ($F_{2,4}=1.10$, $p=0.42$; Fig. 7). Importantly, densities in the summer following the very wet year in Turkey (2003-04) were still three-four times less than those following a normal rainfall year in California (2002-03) and Argentina (2002).

DISCUSSION

Disturbance and exotics in native versus non-native ranges

Perhaps the most accepted truism in invasion biology is that disturbance promotes exotic invasion (Gray 1879, Elton 1958, D'Antonio et al. 1999). My results support this perspective, but I found that disturbance has far stronger effects in the non-native ranges of *C. solstitialis* than in its native range (Figs. 1 and 2). This finding questions the assumption that disturbance *per se* is sufficient to explain the remarkable success of invasive plant species (and specifically *C. solstitialis*) in disturbed conditions in their non-native ranges. The powerful effects of disturbance must act in concert with other factors, allowing certain species to attain community dominance only where they occur as exotics (Fig. 3). Of the factors investigated here, escape from soil pathogens seems to have an important contribution (Fig. 6). The experimental field evidence matches our descriptive measures on *C. solstitialis* density (Fig. 7) and general field observations in disturbed areas in California, Argentina, and Turkey. In many disturbed areas in California and Argentina I have observed near monocultures of *C. solstitialis*, but I have never seen monocultures in Turkey or in the Georgian Caucasus, also within the native range of *C. solstitialis*. However, because my experiments were not conducted at many sites within each region, my results must be interpreted with caution until they are confirmed or rejected by spatially replicated experiments within regions.

Recent studies have demonstrated the importance of belowground pathogens in exotic plant invasions (Klironomos 2002, Callaway et al. 2004). My findings of stronger suppressive effects of Eurasian soil biota on *C. solstitialis* growth indicate that this plant may have escaped soil pathogens at home (Fig. 6). Furthermore, larger *C. solstitialis* plants in non-sterilized than sterilized Argentinean soils suggest a positive effect of soil

microbes on the invader's performance in this region (see Reinhart and Callaway 2004). Escape from soil pathogens at home and/or positive effects of soil microbes abroad are mechanisms that could explain the greater performance and abundance of *C. solstitialis* abroad. As in other studies, however, my work examined the effects of soil microbes on individual plant performance; I do not know whether they can affect population dynamics and generate the contrasting numerical abundances between native and non-native regions I document here. Moreover, in an experiment investigating feedback interactions between *C. solstitialis* and the microbial community that develops around its roots, I did not find biogeographical differences in feedback loops as it has been demonstrated for another exotic *Centaurea* (Callaway et al. 2004).

Plants grown from seeds collected from many populations in the three study regions were not different in size or fecundity. Although there was a tendency for plants in introduced ranges to be more fecund than plants in the native range, this tendency is unlikely to generate the overall 240% and 150% increase in *C. solstitialis* flower production in California and Argentina, respectively, relative to the native range measured in my field experiment. Therefore, there was no evidence that the highly contrasting responses of *C. solstitialis* to disturbance at home versus abroad were due to genetic differences between native and introduced populations (see Lee 2002, Maron et al. 2004, Bossdorf et al. 2005).

Several other mechanisms not investigated here may possibly interact with disturbance to drive greater success in invaded regions, including the release in non-native regions from aboveground specialist herbivores and pathogens that control plant population growth in native locales (see Elton 1958, DeWalt et al. 2004). The fact,

however, that my experiment assessed invasion/colonization levels after the addition of the same number of seeds in each region and throughout a single annual cycle rules out the possibility that capitula seed predators, the most commonly selected insects for biological control, are responsible for invasion success. If the absence of natural enemies is the co-mechanism, then enemies that attack seeds in the soil, seedlings, or rosettes must be involved. However, higher seedling densities in fire and clipped treatments in the late fall in Turkey than in central Argentina (late fall census is not available for California, Fig. 1) suggest that seed and seedling mortality was not greater at home than abroad. Marked declines during the rosette stage (winter months, Fig. 1) in these treatments in Turkey, on the other hand, may have been due to the effect of consumers, but I saw no evidence of aboveground herbivory in the field. Similarly, I did not observe signs of seed, seedling, or rosette consumption or obvious aboveground infections in the soil-disturbance treatment in Turkey, where recruitment was exceedingly low and almost undistinguishable from plots without disturbance throughout the duration of the experiment (Fig. 1). Additionally, it is unclear why enemies would have stronger negative effects on plants in the soil disturbance treatment than in any other disturbance treatment at home. The decline in plant density observed in our experiments in Turkey corresponds with general declines observed during the rosette and flowering stage reported by Uygur and colleagues (2004) in other regions of Turkey. However, they did not know the causes of the decline either. If the natural enemies hypothesis applies at all to the invasion success of *C. solstitialis*, an important implication of my work is that enemies must have their effects very early in plant development.

Variation in the response of resident vegetation to disturbance is another factor that could have caused the far greater success of *C. solstitialis* in invaded ranges than in its native range. Perhaps other members of the plant communities in Turkey, in particular those of the ruderal community, are able to colonize disturbed areas more rapidly than members of the ruderal community in the introduced regions, creating higher competitive conditions in native than in invaded communities. In fact, in the late fall sampling in Turkey (Fig. 1), it was difficult to identify *C. solstitialis* seedlings due to the presence of a dense cover of other members of the Asteraceae family that looked similar to juvenile individuals of our target species in a number of disturbed plots. Additionally, the cover of other plant species in Turkey was significantly higher than the cover of *C. solstitialis* in all treatments in the summer with the exception of soil disturbance where percent cover of these two groups was similar (Fig. 3). In contrast, *C. solstitialis* formed near monocultures in soil-disturbance plots in both recipient communities and in burned plots in California (Fig. 3). In combination, these results support to some extent the idea that differences in the resilience of the plant community could have affected the response of *C. solstitialis* to disturbance in each of the studied regions.

A similar hypothesis was proposed by Asa Gray over 120 years ago. Gray (1879) thought that exotic plants may thrive in disturbed areas because they are adapted to disturbances that are novel to the locals. Since “the locals” in California are represented almost exclusively by exotics from Eurasia, in my study this hypothesis might apply better to central Argentina where grasslands are dominated by native bunchgrasses (Table 1). Moreover, a recent study showed that present dominance of exotic annual grasses themselves in California grasslands may be due to disturbance (Corbin and D’Antonio

2004). Although the simulation of a novel disturbance such as plowing in Argentina promoted *C. solstitialis* abundance and performance more than any other treatment when compared to Turkey and other treatments in Argentina (Figs. 2 and 3), the success of this weed was greater in this non-native region than at home in virtually every disturbance type, including natural disturbance such as fire (Fig. 2-B and 2-C). Perhaps, a longer history with humans and, in consequence, with severe disturbance enables this plant to gain tenure over natives under a large suite of disturbance types. However, proportional establishment and fecundity were higher in Argentina than Turkey even in the absence of disturbance (Fig. 2), reinforcing the idea that other factors in addition to disturbance promote greater success in non-native relative to origin ranges.

The observation that *C. solstitialis* can form dense and almost monospecific stands in recipient regions has prompted some researchers to propose that allelopathy could be behind its invasion success (e.g., Maddox et al. 1985), and there is good evidence that allelopathy may play a role in plant invasions (Hierro and Callaway 2003) including invasion by other *Centaurea* species (Callaway and Aschehoug 2000, Bais et al. 2003, Vivanco et al. 2004). However, recent experiments coordinated in three different laboratories have not found convincing evidence that *C. solstitialis* is allelopathic (R.M. Callaway, S. Strauss, J.M. Vivanco, J. Yoder, unpublished data), suggesting that the novel weapons hypothesis (Callaway and Aschehoug 2000, Callaway and Ridenour 2004) is unlikely to explain the disproportional success of this species in non-native ranges.

The results from the disturbance and seed addition experiment are consistent with measurements of density obtained in natural *C. solstitialis* populations in disturbed sites

in the three regions (Fig. 7). My measurements in Turkey appear to be quite conservative for *C. solstitialis* abundance in general as a different study describes densities about one order of magnitude lower at all measured sites in this country (Uygur et al. 2004). Therefore, it is highly unlikely that I simply chose places to work in Turkey where *C. solstitialis* performs poorly. Densities of *C. solstitialis* in California in the summer of 2003, on the other hand, were comparable to those at three other sites studied over seven years (Pitcairn et al. 2002), indicating that densities I recorded in 2004 are exceptionally low for this region, and were due to the dry spring season of that year. Adequate or high precipitation in the spring appears to greatly increase the abundance of *C. solstitialis* in California (J. DiTomaso, UC Davis, personal communication). There are no previous measurements of density in Argentina for comparison to my densities; however, the extreme drought conditions during the year previous to our 2004 measurements suggest that the 2003 densities are more representative.

Disturbance and community invasibility

Limited establishment in plots without disturbance in California (Figs. 1 to 5) highlights the important role of disturbance for *C. solstitialis* invasion. Surprisingly, such a dependency on disturbance to invade California grasslands has largely been overlooked in the literature. However, in a comparison of life history traits among three *Centaurea* species, Gerlach and Rice (2003) related the invasiveness of *C. solstitialis* to its ability to respond readily to open and disturbed patches with reduced competition from annual grasses. The importance of disturbance, especially soil turnover, for *C. solstitialis* to attain community dominance is also clear in central Argentina (Figs. 1 to 5).

In contrast to the strong context-specificity of invasions found by others (e.g., D'Antonio 1993, Lambrinos 2002), and despite substantial variation in rainfall patterns and dominant plant functional groups between California and Argentina, I found that disturbance to plant communities in both regions prompted invasion and domination by *C. solstitialis* in a very similar manner. The far better response of *C. solstitialis* to disturbance abroad than at home, however, indicates that disturbance is only part of the answer for why this species is such a dominant invader.

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Table 1. Characteristics of experimental sites in California, Argentina, and Turkey.¹

Characteristics	Sites		
	California	Central Argentina	Turkey
Mean annual precipitation	749 mm, October to May, Mediterranean	686 mm	527 mm, October to June, Mediterranean
Mean annual temperature	17°C Maximum = 24°C Minimum = 10°C	15°C Maximum = 22°C Minimum = 8°C	14°C Maximum = 22°C Minimum = 6°C
Soil texture (%)	50 sand, 12 clay, 38 silt	70 sand, 2 clay, 28 silt	58 sand, 20 clay, 22 silt
Soil total N and C (%)	0.38 N, 4.56 C	0.16 N, 1.62 C	0.20 N, 2.34 C
Soil pH	5.85	7.68	7.29
Soil depth (m)	> 1.00	> 1.00	0.60
Bare ground (%)	3	1.5	16
Litter (%)	45	14	7
Annual grasses (%)	50	< 1	11
Annual herbs (%)	2	12	2
Perennial grasses (%)	0	64	53
Perennial herbs (%)	0	8	11

¹ Data on soil particle size distribution and chemistry are means of five soil samples collected from the top 10 cm. Soil depths are also means of five measures. Percent cover of bare ground, litter, and plants are means of 15 1 m x 1 m plots obtained in fall 2002 in California and Argentina, and fall 2003 in Turkey.

Table 2. Initial conditions of the disturbance and seed addition experiment II in California and Argentina.

Characteristics	Sites	
	California	Central Argentina
Bare ground (%)	0	11
Litter (%)	0	28
Annual grasses (%)	66	2
Annual herbs (%)	34	18
Perennial grasses (%)	0	36
Perennial herbs (%)	0	5

Table 3. Location and elevation of *Centaurea solstitialis* populations from which seeds were collected to conduct the common garden experiment.

Region of origin	Location name	Latitude and longitude	Elevation (m)
California	1. Princeton	39° 24' N 122° 01' W	19
California	2. SFREC	39° 14' N 121° 19' W	92
California	3. Putah Creek	38° 31' N 121° 46' W	9
California	4. Nute Road	38° 48' N 121° 11' W	118
California	5. Jepson Prairie	38° 17' N 121° 49' W	8
California	6. Payne Ranch	39° 01' N 122° 21' W	349
Central Argentina	16. Ruta 154-km 17	37° 45' S 64° 01' W	165
Central Argentina	17. Ruta 14-km 200	36° 41' S 65° 30' W	340
Central Argentina	18. R35-30 km R14	36° 58' S 64° 17' W	175
Central Argentina	19. Ruta 14-km 160	36° 42' S 65° 3' W	304
Central Argentina	20. La Primavera	36° 26' S 64° 17' W	194
Central Argentina	21. La Baya Vieja-8	36° 40' S 64° 36' W	240
Turkey	35. Saklikent	36° 53' N 30° 22' E	1290
Turkey	36. Sermet	37° 45' N 30° 33' E	1052
Turkey	37. Egirdir	37° 57' N 30° 47' E	1034
Turkey	38. Burdur	37° 52' N 30° 25' E	908
Turkey	39. Urunlu	37° 03' N 31° 35' E	763
Georgia	41. Gori	41° 00' N 44° 08' E	667
Georgia	42. Igoeti	41° 59' N 44° 23' E	707

Georgia	43. Saguramo	41° 53' N 44° 44' E	504
Georgia	44. Kumisi	41° 36' N 44° 47' E	544
Georgia	45. Bolnisi	41° 26' N 44° 37' E	478

FIGURE LEGENDS

Figure 1. Annual patterns of *C. solstitialis* density for each treatment in its introduced (California and central Argentina) and native (Turkey) range in the disturbance and seed addition experiment I. Data are means \pm 1 SE. Data from late fall census in California are not available. Different letters indicate significant differences ($p < 0.05$) between regions at each sampling date as determined by t-tests and Tukey tests.

Figure 2. Proportional establishment (A), size (B), and fecundity (C) of *C. solstitialis* in its introduced (California and central Argentina) and native (Turkey) range at the end of the disturbance and seed addition experiment I. Data are means + 1 SE. Bars with different uppercase letters indicate significant differences ($p < 0.05$) between regions for a single disturbance treatment and those with different lowercase letters indicate significant differences between disturbance treatments within a single region according to Tukey tests.

Figure 3. Cover of *C. solstitialis* in experimental plots in native (Turkey) and introduced (California and central Argentina) ranges at the end of the disturbance and seed addition experiment I. Data are means + 1 SE. Asterisks above bars show significant differences ($p < 0.05$) between the cover of *C. solstitialis* and that of all other plant species combined as indicated by paired-sample t tests. Higher cover of *C. solstitialis* than cover of all other species is indicated by a plus sign in parentheses; a minus sign indicates the inverse relationship between these groups.

Figure 4. Annual patterns of *C. solstitialis* density for each treatment in two regions of its introduced range (California and central Argentina) in the disturbance and seed addition experiment II. Data are means \pm 1 SE. Different letters indicate significant differences ($p < 0.05$) between regions at each sampling date as determined by t-tests and Mann-Whitney.

Figure 5. Proportional establishment (A), size (B), and fecundity (C) of *C. solstitialis* in two regions of its introduced range (California and central Argentina) at the end of the disturbance and seed addition experiment II. Data are means + 1 SE. Bars with different uppercase letters indicate significant differences ($p < 0.05$) between regions for a single disturbance treatment and those with different lowercase letters indicate significant differences between disturbance treatments within a single region according to Tukey tests.

Figure 6. Total biomass of *C. solstitialis* grown in sterilized and non-sterilized soils collected from two introduced regions (California and central Argentina) and the native range (Eurasia). Data are means + 1 SE. Bars with different letters show significant differences ($p < 0.05$) between sterilization treatments for each region as indicated by Tukey tests.

Figure 7. Density of *C. solstitialis* in naturally occurring populations in summer in introduced (California and central Argentina) and native (Turkey) ranges. Data are means + 1 SE. Bars with different letters show significant differences ($p < 0.05$) among

regions for each year as indicated by Tukey tests.

Figure 1

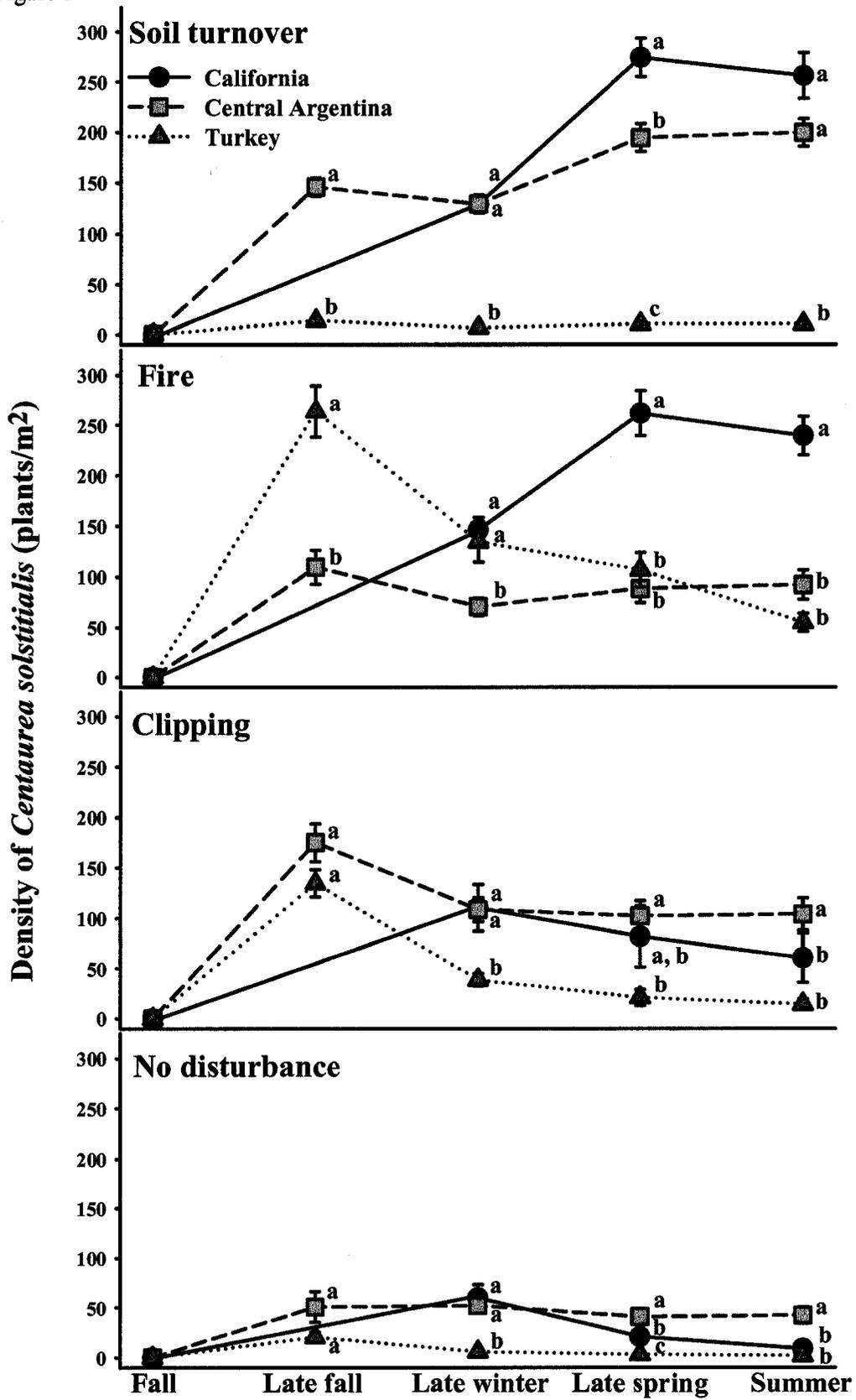


Figure 2

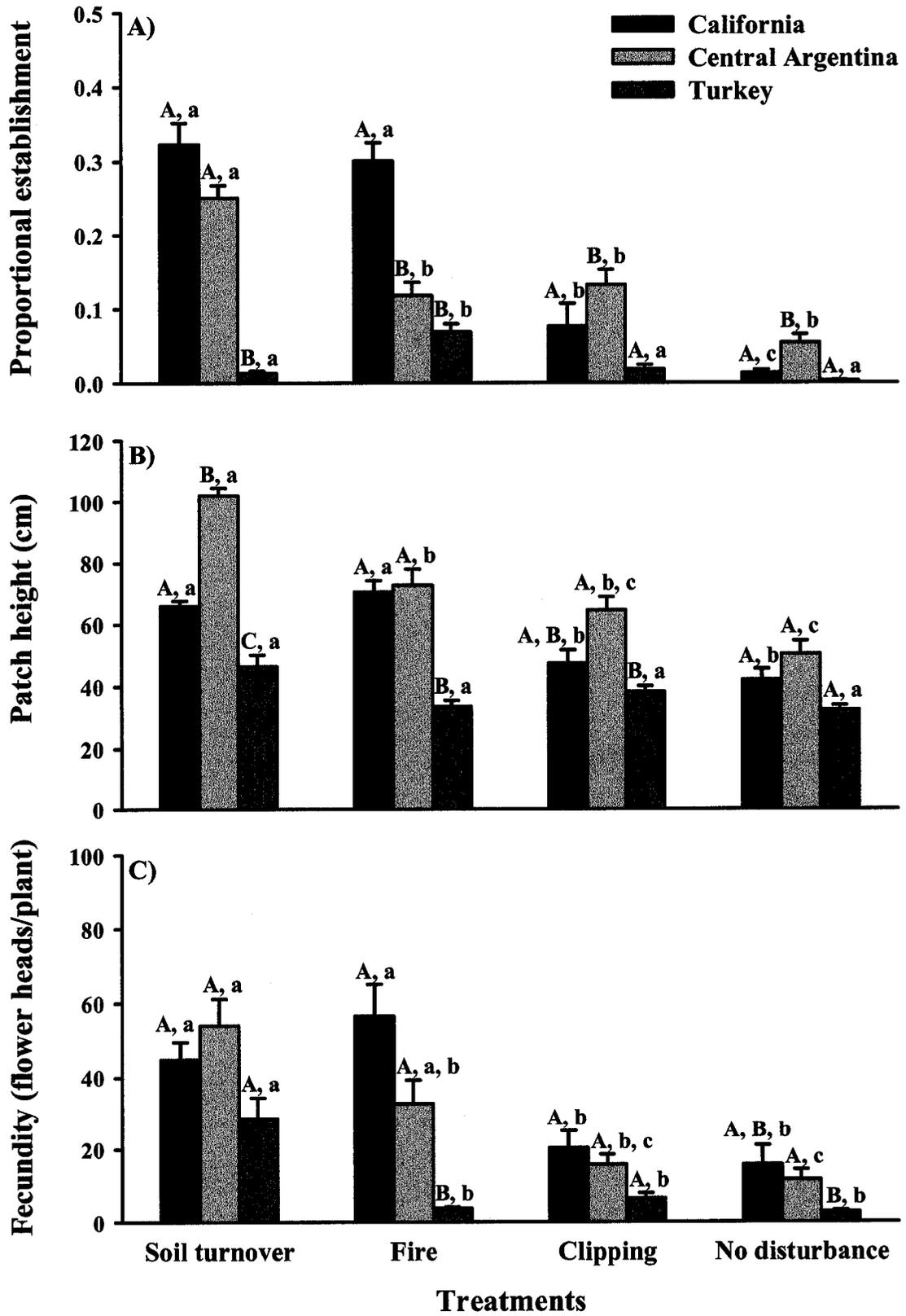


Figure 3

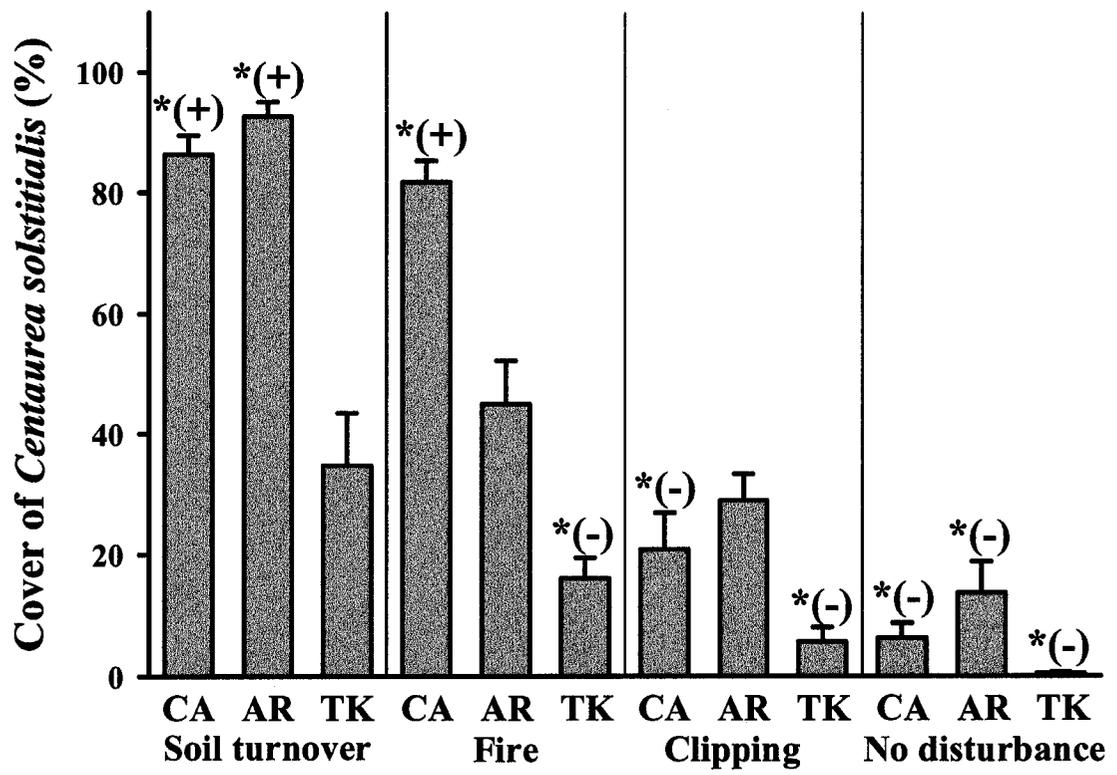


Figure 4

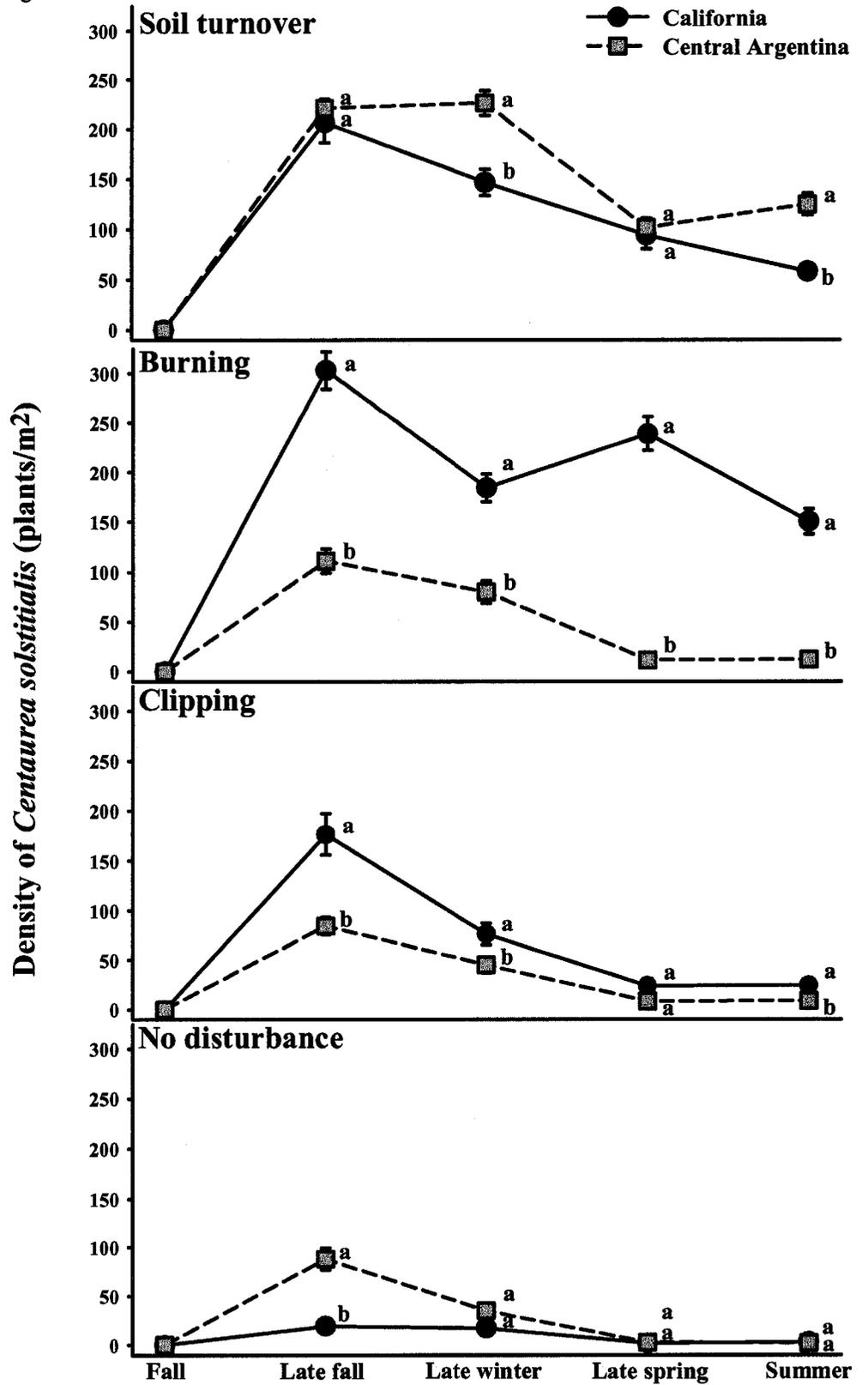


Figure 5

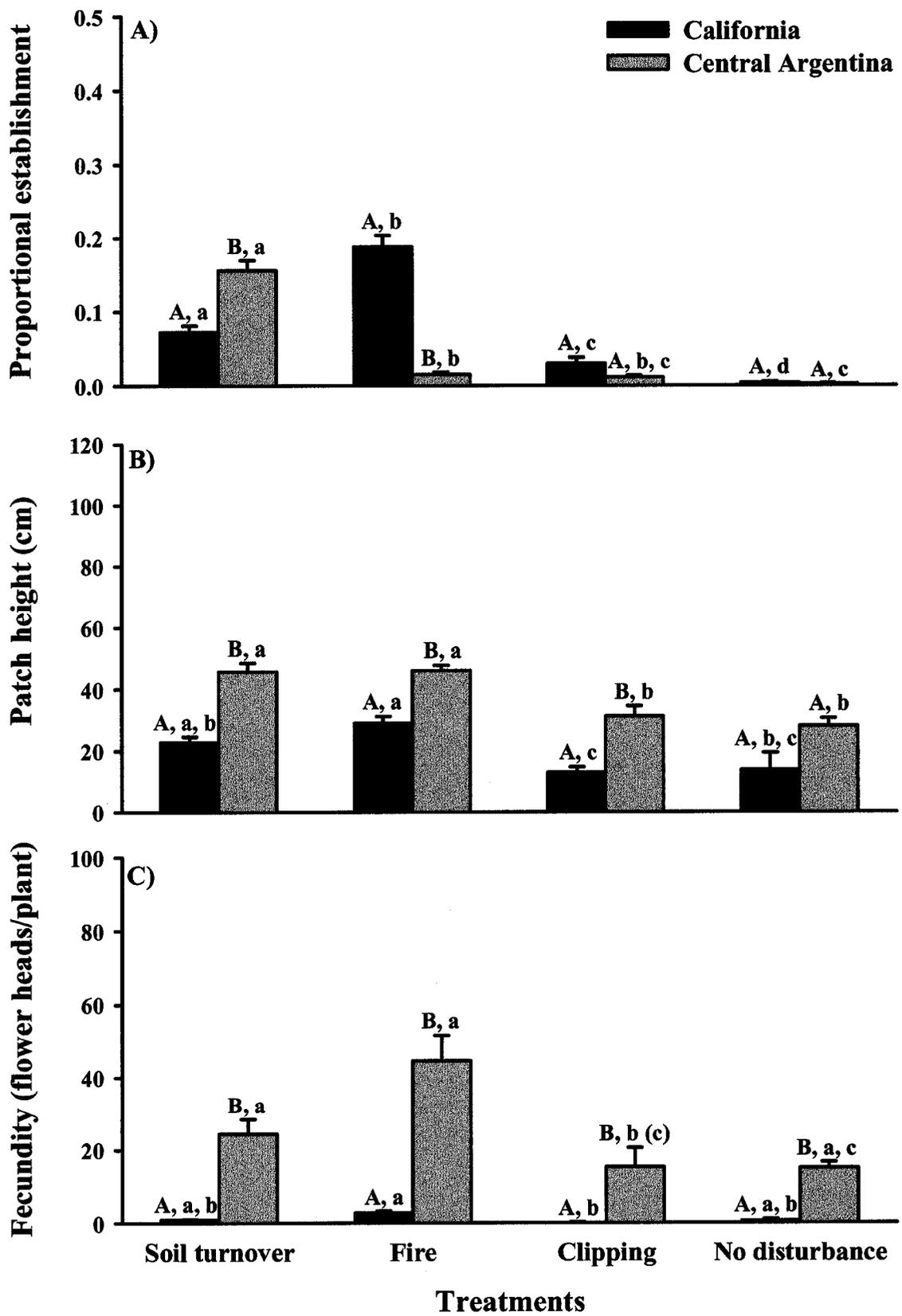


Figure 6

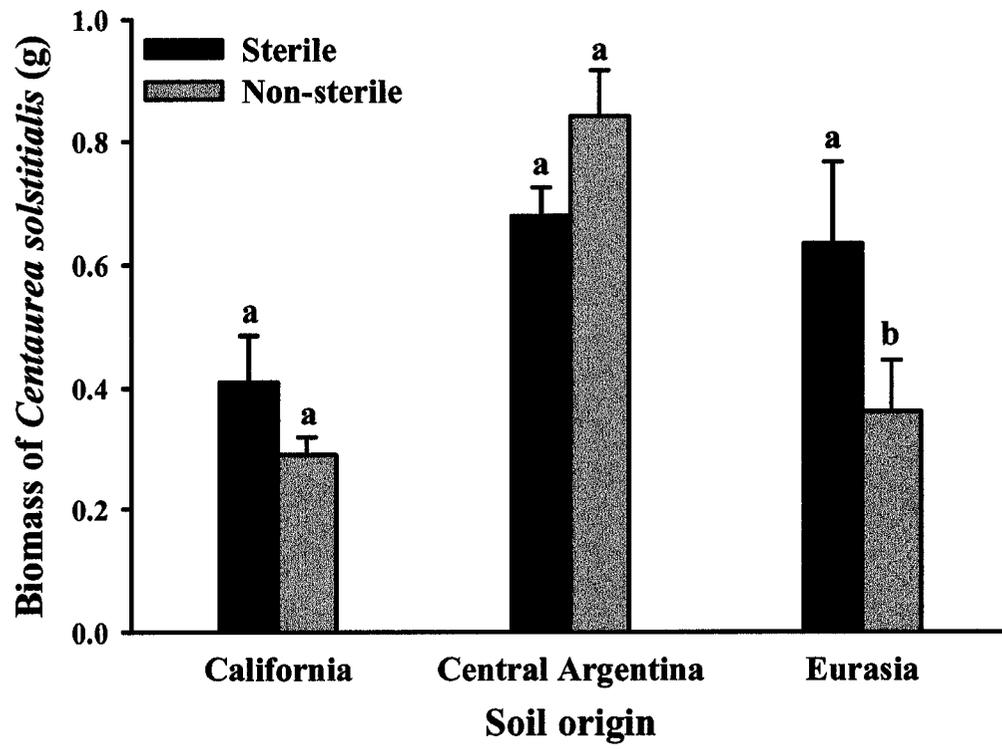
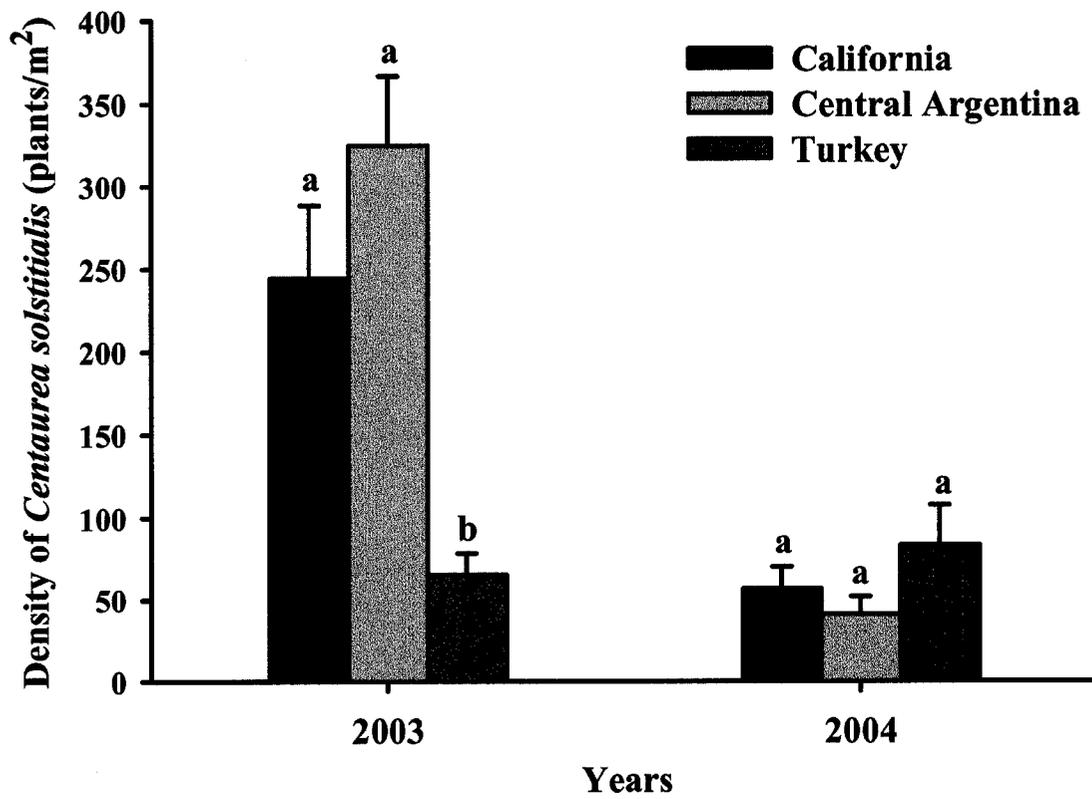


Figure 7



CHAPTER 3

RAPID EVOLUTION BY INVASIVE PLANTS: THE IMPORTANCE OF NOVEL CONDITIONS

Abstract. Plants transported by humans to regions where they are not native (exotics) commonly face novel selective forces and possess, through a history of multiple introductions and perhaps hybridization among previously distant populations, high genetic variation upon which selection can act (Ellstrand & Schierenbeck 2000, Bossdorf et al. 2005, Novak & Mack 2005). Therefore, exotic plants are highly likely to experience rapid evolution by means of natural selection. Here I show that the ruderal Eurasian native *Centaurea solstitialis* L. (Asteraceae) appears to have undergone rapid evolution in germination life history in central Argentina, where climate and plant communities differ substantially from conditions at home, but no evidence of evolution in California, where climate and plant communities are similar to those in the native range. Additionally, the two seed morphs produced by this plant differed in germination pattern only in genotypes from Argentina. Until now, research on the evolution of exotic plants has focused on genetically based changes in size and fecundity between native and introduced populations presumably driven by escaping specialist enemies (Blossey & Nötzold 1995, Maron et al. 2004, Bossdorf et al. 2005). My results broaden the suite of life history traits subject to selection and the selective forces operating on them during invasion. My work also provides an explanation for why climate matching between native and introduced ranges is not needed for exotic plants to succeed.

INTRODUCTION

In his seminal work on seed bank dynamics, Cohen (1966) predicted that the optimal fraction of germinating seeds in annual plants depends on the probability of successful reproduction. If this probability is high, the optimal yearly germination fraction is also high. Conversely, if the probability of reproductive success is low, the optimal strategy is low proportional germination and the development of a seed bank. Most research has supported Cohen's predictions (Ross & Harper 1972, Harper 1977, Venable & Brown 1988, Baskin & Baskin 1998). Because there are important consequences for fitness, germination strategy is likely under strong selection (Cohen 1966, Harper 1977, Brown & Venable 1986). Here I show a substantial genetically-based shift in the germination strategy of a species in an invaded region that is different in climate and plant communities from the region of origin, and evidence for a minor maternally based change in an invaded region similar in climate and plant communities to the region of origin.

Centaurea solstitialis is an annual plant of Eurasian origin that has been introduced around the world as a contaminant of alfalfa seeds (Maddox et al. 1985). As in the native range, the climate in most introduced regions is Mediterranean (Maddox et al. 1985) with summer drought and winter rain. However, highly successful invasion of *C. solstitialis* has also occurred in central Argentina, where the rainfall pattern is the opposite of Mediterranean; rainfall occurs primarily in summer. In its native range, *C. solstitialis* is largely confined to disturbed sites and is a typical ruderal species (Uygur et al. 2004). Previous work comparing the invasion success of *C. solstitialis* in two introduced

regions, California and central Argentina, shows that despite contrasting rainfall patterns and different plant community types (annual versus perennial grasses, respectively) between these regions, *C. solstitialis* dominate plant communities under disturbed conditions in both regions (Hierro et al. *in review*).

The introduction history of *C. solstitialis* in California (Gerlach 1997) and Argentina (Hijano & Basigalup 1995) is based on records of imported alfalfa seeds. These records indicate that *C. solstitialis* populations in these regions are derived from multiple introductions over decades and a broad suite of similar source populations (California: Chile (Spanish origin), France, Italy, Spain, and Argentina; Argentina: Chile (Spanish origin), France, Italy, and Syria). Probable introduction dates are ~1850 for California (Gerlach 1997) and ~1870 for central Argentina (Hijano & Basigalup 1995). The likelihood of high genetic variation in Californian and Argentinean introduced populations of *C. solstitialis* is further increased by the predominantly self-incompatible mating system of this plant (Sun & Ritland 1998). That is, outcrossing species partition most of their genetic diversity within rather than among populations, so that even a few immigrants can carry much of the species' genetic variation (Novak & Mack 2005). In fact, molecular techniques revealed that populations of *C. solstitialis* in western United States have high genetic variation and were founded by a large number of genotypes (Sun 1997). Multiple introductions from largely overlapping source populations into regions with contrasting biotic and abiotic conditions provide the context in which I investigated rapid evolutionary changes in *C. solstitialis*.

METHODS AND MATERIALS

Seed biology of the study plant

Seed heteromorphism (*sensu* Venable 1985) is relatively common in the Asteraceae (Harper 1977, Venable 1985). As in other members of this family, floret and achene (seed) development occurs centripetally in *C. solstitialis* (Maddox et al. 1996). The outermost florets of the receptacle are sterile, subsequent florets develop into dark seeds without a pappus, and florets in the center of the receptacle produce light to brown seeds with a pappus. Reported ratios of pappus to non-pappus seeds are 5.6 to 1 (Maddox 1981) and 5.7 to 1 (Benefield et al. 2001). Seed morphs in *C. solstitialis* differ in dispersal time; while pappus seeds are dispersed in summer, non-pappus seeds are retained in the capitula and disperse in winter.

Until now, information on germination of *C. solstitialis* comes exclusively from populations in western United States, particularly California. Joley and colleagues (1992, 1997, 2003) found that seeds stored under warm (~21°C) and dry conditions for a minimum of two months germinated in larger proportions and at higher temperatures than freshly collected seeds, and proposed that seeds are conditionally dormant when freshly ripe. Presumably, after-ripening may prevent premature germination from occasional late summer or early autumn rains in California (Joley et al. 1997). Additionally, because of after-ripening, seeds are highly germinable before the beginning of the autumn rains; thus, germination of *C. solstitialis* and climate are well synchronized in California (Joley et al. 1997, 2003). Such synchronization is also apparent in the delayed dispersal of non-pappus seeds because most of these seeds are released after the first seasonal rains, a period during which water availability peaks in this region (Joley et al. 1997). Notably,

the opposite scenario of poor coordination between *C. solstitialis* germination and seasonal rainfall occurs in central Argentina (see below).

Light is required for *C. solstitialis* seeds to attain maximum germination (Joley et al. 1997, 2003). Base temperature for germination has been determined to be 2°C (Roché et al. 1997), optimal constant temperatures for germination of both fresh and stored seeds were established at 10°C, 15°C, and 20°C (Joley et al. 1997), and maximum germination under alternating temperatures was measured at 15/5°C and 20/10°C for fresh seeds collected in July and 15/5°C, 20/10°C, 25/15°C, and 30/20°C for fresh seeds collected in August and seeds collected in July and stored for two months (Joley et al. 1997). Thus, my experiments were conducted under optimal germination conditions (see Methods).

Joley and others (1992, 1997) found no differences in germination percentages between pappus and non-pappus seeds under light and the temperatures previously mentioned. In another experiment, however, conducted under a daily photoperiod of 8 h light:16 h dark and intermittent light at 20°C, germination of pappus and non-pappus seeds was similar in the daily photoperiod treatment, but higher for pappus seeds in the intermittent light treatment (Joley et al. 1997). Pappus seeds also exhibited higher germination than non-pappus seeds under darkness over a broad temperature range (Joley et al. 1997). Also, in a study evaluating the response of pappus and non-pappus seeds to red light (i.e., activation of the phytochrome), which was applied at different times during imbibition, pappus seeds had higher germination percentages than non-pappus seeds for most light periods (Joley et al. 2003).

Germination experiment 1

In my first experiment, I used only pappus seeds to compare germination rates of Californian and Argentinean populations in a common garden in a growth chamber. Conditions in the growth chamber were set at 16°C, the mean of the average temperature for California in October (17°C) and average temperature for central Argentina in April (15°C), months at which *C. solstitialis* commonly germinates in these regions, and a light:dark cycle of 12:12 hours. Photosynthetically active radiation (PAR) reaching seeds was 287 $\mu\text{mol m}^{-2} \text{s}^{-1}$, as measured with a LI-250 light meter.

Seeds were collected from six naturally occurring populations of *C. solstitialis* in January 2002 in Argentina and August 2002 in California (populations 1 to 6 and 16 to 21 in Table 1). Collections were made from at least 30 individuals per population and seeds from individual plants were pooled for each population. Seeds were stored in paper bags at room temperature until I initiated the experiment in May 2004. Joley and colleagues (1992) reported 99.4% germination for seeds stored in the laboratory at 21°C for six years. In this and all other experiments, I only used seeds that looked healthy and filled with an embryo. Seeds were germinated in nine-cm petri dishes containing 3.0 g of sterilized cotton, a filter paper placed on the cotton, and 50 ml of distilled water. After 16 days, I added an extra 10 ml of distilled water to each capsule to keep seeds wet. I used 90 seeds per population, and these were divided among three petri dishes (30 seeds each). Petri dishes were placed randomly inside the growth chamber and they were rotated regularly throughout the duration of the experiment. Seeds were considered germinated after the emergence of the radicle and were removed from the capsules immediately after germination. Germination was assessed daily for a week and then at larger time intervals

for a total of 38 days (see x-axis in Fig. 1A). I used two metrics of germination, cumulative percent germination at the end of the experiment and germination speed calculated as $(\sum n_t)/(n_f * t)$, where n_t is the cumulative proportion germinating at each sampling time, n_f is the cumulative proportion germinating at the end of the experiment, and t is the number of sampling times (Noe & Zedler 2000). Ungerminated seeds were assessed for viability using the tetrazolium test (Cottrell 1947). In all experiments, plant material was autoclaved after finishing activities. Data were analyzed with two-way ANOVA with seed origin as fixed factor and population nested within seed origin. Germination and viability data were transformed with the arcsine and logarithmic function, respectively, to meet ANOVA assumptions and improve the distribution of residuals.

Field common gardens

I conducted a reciprocal common garden experiment in California and Argentina in which I buried pappus and non-pappus seeds of *C. solstitialis* placed into mesh bags. Seeds were collected as in *Germination experiment 1* in August 2003 in California and February 2004 in Argentina from one population in each region and were then buried in three different locations in each region (California: 1) 39° 14' N, 121° 19' W, 92 m elevation; 2) 39° 15' N, 121° 19' W, 170 m, and 3) 39° 15' N, 121° 20' W, 137 m; central Argentina: 1) 36° 40' S, 64° 38' W, 244 m elevation; 2) 36° 40' S 64° 36' W, 240 m, and 3) 36° 26' S 64° 17' W, 194 m elevation). I used only one population per region to minimize risks of introducing new genotypes in the event that seeds escape from bags. Selected populations (populations 2 and 20 in Table 1) displayed typical germination

strategies for each region in *Germination experiment 1*. Twenty seeds from each origin-type combination (California-pappus, California-non-pappus, Argentina-pappus, Argentina-non-pappus) were placed into ten individual 5 cm x 5 cm mesh bags. Four bags, each containing a particular combination of seed origin and type, were then side-sealed to form 10 four-bags groups about 10 cm x 10 cm in size. Each of the 10 groups was randomly buried at five cm depth with a separation of five cm between groups. I buried bags in April 2004 in Argentina and October 2004 in California, before the first autumn rains. After six months, I removed bags and determined percent germination based on the number of empty split seed coats. Seeds buried in Argentina were accidentally destroyed before testing viability; consequently, the tetrazolium test was applied only on ungerminated seeds buried in California. Legend in Fig. 1B describes analyses of germination data. Viability data were analyzed with a three-way ANOVA with seed origin and seed type as fixed factors and site as random factor. I log and arcsine transformed germination and viability data, respectively, to meet ANOVA assumptions and improve the distribution of residuals.

Germination experiment 2

I conducted a second common garden experiment in the growth chamber with a larger number of populations collected in a different summer to compare germination rates of the populations from California and Argentina to germination of populations from the native range, specifically Turkey and Georgia, the proposed center of origin of *C. solstitialis* (Maddox et al. 1985). Conditions in the growth chamber were as described for *Germination experiment 1*. In California, seeds were collected from 14 populations

(populations 2 to 15 in Table 1) in August 2004. Seeds in Argentina were also collected from 14 populations (populations 20 to 33 in Table 1) in January 2005. In the native range, seeds were collected from six populations in Turkey and five populations in Georgia (Table 1) also in August 2004. The 11 populations from the native range were considered together in the data analysis. Because it is impossible to simultaneously collect seeds in northern and southern hemispheres, for this experiment collections were practiced earlier in California than Argentina, the reverse timing relative to *Germination experiment 1*, to evaluate whether differences in collection times between these regions could have affected germination patterns in my first experiment. In all populations, seeds were collected from 30 individuals and sibling seeds were kept in separated envelopes. Seeds were stored in paper bags at room temperature until I initiated the germination experiment in April 2005. Seeds were germinated in nine-cm petri dishes containing three filter papers Whatman #3 and 10 ml of distilled water, and they were watered as needed throughout the experiment. I used 90 pappus and 90 non-pappus seeds per population, each seed type distributed in three petri dishes (30 seeds per petri dish). Each seed in petri dishes came from a different individual. Germination was assessed daily for a week and then at larger time intervals for a total of 30 days (see x-axis in Fig. 2). Metrics of germination and test of viability were as in *Germination experiment 1*. Germination and viability data were analyzed with three-way ANOVA, where seed origin and type were included as fixed factors and population was nested within origin. Post-hoc comparisons were performed with Tukey tests. I applied arcsine transformation to both germination metrics and viability data to meet ANOVA assumptions and improve the distribution of residuals.

Maternal effects

I used seeds from the same six populations in California and central Argentina employed in *Germination experiment 1*, seeds from Turkey populations 34 to 38 in Table 1, and the five populations from Georgia used in *Germination experiment 2* to test for maternal effects. Plants from all populations were grown under common conditions in a greenhouse. For each population, I planted five seeds in each of five 2500 cm³ plastic pots. Seedlings in pots were then thinned to one individual and watered when needed throughout the experiment. Pots were filled with a mixture of 2 sand:1 soil proportion. Soil was collected from a grassland site located near Missoula, Montana. The sand was 20/30 grit, corresponding to mean diameters of 0.85 mm and 0.60 mm, respectively. Once plants flowered, I cross-pollinated all flower heads produced by the five individuals within a population with a brush every 1-2 days until flowers senesced. Populations were separated by at least 1.5 m and flower heads were bagged to avoid pollination among populations. At senescence (~ eight months of growth), plants were harvested and pappus and non-pappus seeds were collected. Two months after collection, I used these seeds to conduct a third germination experiment under the same conditions as in *Germination experiment 2*. Because of limitations in the number of seeds obtained from plants grown in the greenhouse, I used a minimum of 10 and a maximum of 30 pappus and non-pappus seeds per population. For this reason seeds from populations were germinated in one to three petri dishes, each containing 10 seeds. Two populations from Turkey (34 and 38 in Table 1) did not produce non-pappus seeds; thus, final sample size for this type of seeds from the native range was eight populations (three from Turkey and

five from Georgia). Germination assessment and viability test were as in *Germination experiment 2*. Germination and viability data were analyzed with three-way ANOVA, where seed origin and type were included as fixed factors and population was nested within seed origin. Post-hoc comparisons were performed with Tukey. I applied the arcsine transformation to germination and viability percentages to meet ANOVA assumptions and improve the distribution of residuals.

RESULTS

Germination experiment 1

Percent germination at the end of the experiment was 141% higher in seeds from California than in those from Argentina, and Californian seeds germinated 22% faster than Argentinean seeds (Fig. 1A). Viability of ungerminated seeds was similar between California and Argentina (99.7% and 97.9%, respectively; $F_{\text{seed origin } 1,10}=0.76$, $p=0.40$), demonstrating that differences in germination between populations from these introduced regions were due to higher dormancy in seeds from Argentina.

Field common gardens

In general, the results from this field experiment were consistent with the results from the growth chamber. After six months, percent germination was 118% higher for seeds from California than Argentina (Fig. 1B). Importantly, genotypes from California and Argentina showed the same patterns of germination in the field in California *and* Argentina; there was no interaction between region of experimentation and seed origin ($F_{1,228}=0.84$, $p=0.36$). Unexpectedly, however, percent germination was higher for both

seed genotypes in Argentina than California, despite much higher rainfall in California than Argentina during the time seeds were in the ground; 669 mm vs. 212 mm, respectively. The causes of this result are unclear. For ungerminated seeds, viability of the seeds from Argentina was slightly higher than that of Californians (pappus, 95% and 89%; non-pappus, 97% and 91%, respectively; $F_{\text{seed origin } 1,2}=15.81$, $p=0.06$; $F_{\text{seed type } 1,2}=3.22$, $p=0.22$; $F_{\text{site } 2,2}=2.28$, $p=0.33$; for all interactions, $p>0.33$), again demonstrating that differences in germination were due to differences in dormancy.

Germination experiment 2

Seeds from California and Eurasia germinated in larger proportions and faster than seeds from Argentina (Fig. 2). Non-pappus Californian seeds had greater cumulative germination than both non-pappus and pappus Eurasian seeds, and pappus Californian seeds had greater cumulative germination than pappus Eurasian seeds. The rate of germination was similar among all seed types from California and Eurasia. Unique among all three seed origins, seed morphs in Argentinean genotypes differed in germination (Fig. 2). No genotype showed differences in viability between pappus and non-pappus ungerminated seeds. Consequently, and because both pappus and non-pappus seeds came from the same mothers, eliminating the possibility of maternal effects (Rossiter 1996), differences in germination between Argentinean seed morphs seem to be genetically determined. While Californian and Argentinean seeds that did not germinate exhibited similar viability (pappus, 90% and 95%; non-pappus, 93% and 95%, respectively), Argentinean seeds were significantly more viable than Eurasian seeds (74% and 57% for pappus and non-pappus seeds, respectively; $F_{\text{seed origin } 2,36}=26.21$,

$p < 0.0001$; $F_{\text{seed type } 1,158} = 1.76$, $p = 0.19$; $F_{\text{origin} \times \text{seed type } 2,158} = 2.50$, $p = 0.09$;); thus, reduced germination in seeds from Argentina was again due to higher dormancy in genotypes from this region than genotypes from either California or Eurasia. Non-pappus Californian seeds were significantly more viable than both non-pappus and pappus Eurasian seeds, and pappus Californian seeds were more viable than non-pappus Eurasian seeds; therefore, higher germination in Californian than Eurasian genotypes was due to an overall lower viability in the Eurasians.

Maternal effects

Biomass and fecundity of *C. solstitialis* plants grown under the same conditions in the greenhouse were similar ($F_{2,19} = 1.26$, $p = 0.31$ and $F_{2,19} = 2.91$, $p = 0.08$, respectively) among populations from all regions. Again, I found significantly reduced germination percentage and rate in seeds from Argentina than in seeds from California and Eurasia (Fig. 3). Unlike the results in the second growth chamber experiment, however, Eurasian seeds germinated in non-significant larger proportions than the Californians. For Argentinean genotypes, germination percentage and rate were again higher for pappus than non-pappus seeds, but differences were not statistically significant, probably because sample size here was smaller than in the second germination experiment. Viability of ungerminated seeds was similar among all origin-seed type combinations (pappus-California, 93%; -Argentina, 94%; -Eurasia, 97%; non-pappus-California, 94%; -Argentina, 93%; -Eurasia, 92%; $F_{\text{seed origin } 2,14} = 0.004$, $p = 0.99$; $F_{\text{seed type } 1,47} = 0.33$, $p = 0.57$; $F_{\text{origin} \times \text{seed type } 2,47} = 0.36$, $p = 0.70$). This experiment demonstrates that greater dormancy in Argentinean populations has a genetic basis. Greater germination in Californian than

Eurasian genotypes in the second growth chamber experiment, on the other hand, seems to have been due, at least partially, to maternal effects.

DISCUSSION

Genetic differentiation for seed dormancy among populations has been shown for a number of species (Baskin & Baskin 1998), including exotics (Naylor 1983, Wu et al. 1987, Meyer & Allen 1999). My results are unique in that I compared native and introduced populations, and detected a genetically based change from populations in the region of origin only in introduced populations experiencing novel conditions. Molecular studies are needed to conclusively eliminate the possibility of founder effects, but our findings strongly suggest that *C. solstitialis* has evolved higher seed dormancy in central Argentina in response to novel selection pressures experienced in this region. This conclusion is drawn from: 1) the history of multiple introductions and outcrossing mating system of *C. solstitialis*, which like in California may provide high genetic variation to populations in Argentina and thus minimize the chances for the occurrence of stochastic processes such as genetic drift, 2) the largely common Mediterranean origins of both Californian and Argentinean populations, which reduces the likelihood that seeds in Argentina came from particular founder native populations pre-adapted to environmental conditions in this region, and 3) the sharply contrasting climate and biotic conditions between Argentina and Eurasia.

Why then would rapid germination of a large number of seeds be favored in the native range and California, but selected against in Argentina? Strong selection for rapid germination and site pre-emption is likely to occur in a Mediterranean system like

California, where dominant Eurasian winter annuals germinate soon after the first autumn rains (Chiariello 1989). Similarly in the native range, strong selection for rapid germination can be exerted by the Mediterranean rainfall pattern and a ruderal community likely to exhibit high resilience to intense disturbance as a result of an evolutionary history with humans (Gray 1879). In contrast, a risk-spreading strategy to avoid unfavourable growing conditions (Venable & Brown 1988) is likely to be much more advantageous in central Argentina. There, seedlings emerging in the fall (the typical season for germination of *C. solstitialis*) face a dry winter (Fig. 4); under such conditions, seeds that do not germinate with autumn rains can germinate later and take advantage of reliable rains that start in spring and last until the middle of fall. Indeed, second germination pulses of *C. solstitialis* have been recorded in the spring in Argentina (Hierro et al., *in review*). Notably, Argentinean non-pappus seeds, which are retained in the capitula and commonly disperse in winter, displayed the highest levels of dormancy in my experiments (Figs. 1B, 2 and 3). Like dormancy, seed heteromorphism is widely considered a risk-spreading strategy in annual plants (Venable 1985). Unique among all three studied genotypes, pappus and non-pappus seeds from Argentina diverged in germination, emphasizing the adaptive value of a risk-spreading strategy for *C. solstitialis* in this region.

Selection pressure for rapid germination can, in addition, be relaxed in a system dominated by native perennial grasses and where native ruderals are not adapted to human disturbance. Rapid germination in such a system is unnecessary, and could even expose early germinants to fatal levels of competition from perennial natives. Keeping a higher proportion of seeds dormant and waiting for disturbance to create favourable

patches is probably a better strategy in Argentina. The largely Eurasian origin and annual life cycle of current California flora suggest that rapid evolution in Argentinean populations may have resulted not only from experiencing a novel climate but also novel neighbours (Callaway et al. 2005, Thompson 2005).

We do not propose that evolved higher seed dormancy is the mechanism by which *C. solstitialis* dominates plant communities in central Argentina, but we believe that this germination strategy may be crucial for establishment and persistence in this region. Furthermore, such rapid evolutionary adjustment provides an explanation for why so many exotic species are successful in regions with climates different from those in the regions where they originated.

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Table 1. Location and elevation of *Centaurea solstitialis* populations used in this study.

Region of origin	Location name	Latitude and longitude	Elevation (m)
California	1. Princeton	39° 24' N 122° 01' W	19
California	2. SFREC	39° 14' N 121° 19' W	92
California	3. Putah Creek	38° 31' N 121° 46' W	9
California	4. Nute Road	38° 48' N 121° 11' W	118
California	5. Jepson Prairie	38° 17' N 121° 49' W	8
California	6. Payne Ranch	39° 01' N 122° 21' W	349
California	7. Grass Valley	39° 12' N 121° 06' W	210
California	8. Yuba City	38° 60' N 121° 40' W	1
California	9. Chico	39° 50' N 121° 54' W	68
California	10. Hwy 5-22	41° 60' N 122° 37' W	967
California	11. Hwy 5-23	41° 32' N 122° 29' W	816
California	12. Hwy 5-24	40° 60' N 122° 25' W	695
California	13. Hwy 5-25	40° 25' N 122° 17' W	193
California	14. Hwy 5-26	39° 54' N 122° 12' W	98
California	15. Hwy 5-27	39° 19' N 122° 12' W	27
Central Argentina	16. Ruta 154-km 17	37° 45' S 64° 01' W	165
Central Argentina	17. Ruta 14-km 200	36° 41' S 65° 30' W	340
Central Argentina	18. R35-30 km R14	36° 58' S 64° 17' W	175
Central Argentina	19. Ruta 14-km 160	36° 42' S 65° 3' W	304
Central Argentina	20. La Primavera	36° 26' S 64° 17' W	194
Central Argentina	21. La Baya Vieja-8	36° 40' S 64° 36' W	240

Central Argentina	22. Point 289	36° 31' S 64° 54' W	211
Central Argentina	23. Point 290	36° 50' S 64° 16' W	205
Central Argentina	24. Point 291	37° 16' S 64° 17' W	192
Central Argentina	25. Point 292	37° 39' S 64° 08' W	220
Central Argentina	26. Point 293	37° 54' S 63° 41' W	176
Central Argentina	27. Point 294	38° 11' S 64° 04' W	67
Central Argentina	28. Point 295	36° 12' S 64° 37' W	227
Central Argentina	29. Point 296	36° 15' S 65° 9' W	287
Central Argentina	30. Point 297	36° 18' S 65° 40' W	342
Central Argentina	31. Point 298	36° 42' S 65° 09' W	333
Central Argentina	32. Point 299	36° 41' S 65° 42' W	333
Central Argentina	33. Ruta 5 y 10	36° 30' S 63° 56' W	160
Turkey	34. Saklikent	36° 53' N 30° 22' E	1290
Turkey	35. Sermet	37° 45' N 30° 33' E	1052
Turkey	36. Egirdir	37° 57' N 30° 47' E	1034
Turkey	37. Burdur	37° 52' N 30° 25' E	908
Turkey	38. Urunlu	37° 03' N 31° 35' E	763
Turkey	39. Sutaular	37° 41' N 30° 51' E	932
Georgia	40. Gori	41° 00' N 44° 08' E	667
Georgia	41. Igoeti	41° 59' N 44° 23' E	707
Georgia	42. Saguramo	41° 53' N 44° 44' E	504
Georgia	43. Kumisi	41° 36' N 44° 47' E	544
Georgia	44. Bolnisi	41° 26' N 44° 37' E	478

FIGURE LEGENDS

Figure 1. A) Germination rates of pappus seeds of *C. solstitialis* from non-native populations in California and central Argentina under common conditions in a growth chamber. Symbols are means of six populations \pm 1 SE. Cumulative germination at the end of the experiment, $F_{\text{seed origin } 1,10}=19.38$, $p=0.001$; speed of germination, $F_{\text{seed origin } 1,10}=7.71$, $p=0.02$. B) Percent germination of pappus and non-pappus seeds of *C. solstitialis* from non-native populations in California and central Argentina in a reciprocal common garden experiment conducted in these two regions. Bars are means of three sites \pm 1 SE. Four-way ANOVA (region of experimentation, seed origin, and seed type as fixed factors and site nested within region of experimentation): $F_{\text{region } 1,4}=13.03$, $p=0.02$; $F_{\text{seed origin } 1,228}=15.48$, $p<0.001$; $F_{\text{seed type } 1,228}=11.02$, $p<0.01$; $F_{\text{region} \times \text{seed type } 1,228}=3.94$, $p=0.05$; all other interactions $p>0.13$. Different letters on bars indicate significant differences between treatments ($p<0.05$) as determined by Tukey.

Figure 2. Germination rates of pappus and non-pappus seeds of *C. solstitialis* from non-native populations (California and central Argentina) and native populations (Eurasia) under common conditions in a growth chamber. Symbols are means \pm 1 SE of 14 populations in each of the introduced regions and 11 populations in the native range. Cumulative germination at the end of the experiment, $F_{\text{seed origin } 2,36}=63.75$, $p<0.0001$; $F_{\text{seed type } 1,192}=8.92$, $p<0.01$; $F_{\text{seed origin} \times \text{seed type } 2,192}=19.76$, $p<0.0001$; speed of germination, $F_{\text{seed origin } 2,36}=77.75$, $p<0.0001$; $F_{\text{seed type } 1,192}=5.62$, $p=0.02$; $F_{\text{seed origin} \times \text{seed type } 2,192}=9.97$, $p<0.0001$. Different letters indicate significant differences between treatments ($p<0.05$)

for cumulative germination on day 30 (lowercase) and speed of germination (uppercase) as determined by Tukey.

Figure 3. Germination rates under common growth chamber conditions of seeds obtained from *C. solstitialis* plants from California, central Argentina, and Eurasia grown under common greenhouse conditions (i.e., evaluation of maternal effects). Symbols are as in Fig. 2 and they represent means \pm 1 SE of six populations in each of the introduced regions, 10 populations for pappus seeds in the native range, and eight populations for non-pappus seeds also in this range. Cumulative germination at the end of the experiment, $F_{\text{seed origin } 2,19}=29.84$, $p<0.0001$; $F_{\text{seed type } 1,62}=2.21$, $p=0.14$; $F_{\text{origin} \times \text{seed type } 2,62}=1.49$, $p=0.23$; speed of germination, $F_{\text{seed origin } 2,19}=13.28$, $p<0.0001$; $F_{\text{seed type } 1,62}=0.69$, $p=0.41$; $F_{\text{origin} \times \text{seed type } 2,62}=0.09$, $p=0.91$. Different letters indicate significant differences between treatments ($p<0.05$) for cumulative germination on day 30 and speed of germination as determined by Tukey.

Figure 4. Climatic diagrams for Davis (California) and Santa Rosa (central Argentina) along with the annual cycle of *C. solstitialis*. Climatic data are for the period 1961-1990 for Davis and 1941-1990 for Santa Rosa. Ticks separating *C. solstitialis* phenological stages are dashed to indicate overlap between stages (e.g., although most germination and emergence occur in the fall, these events can also occur in the spring).

Figure 1

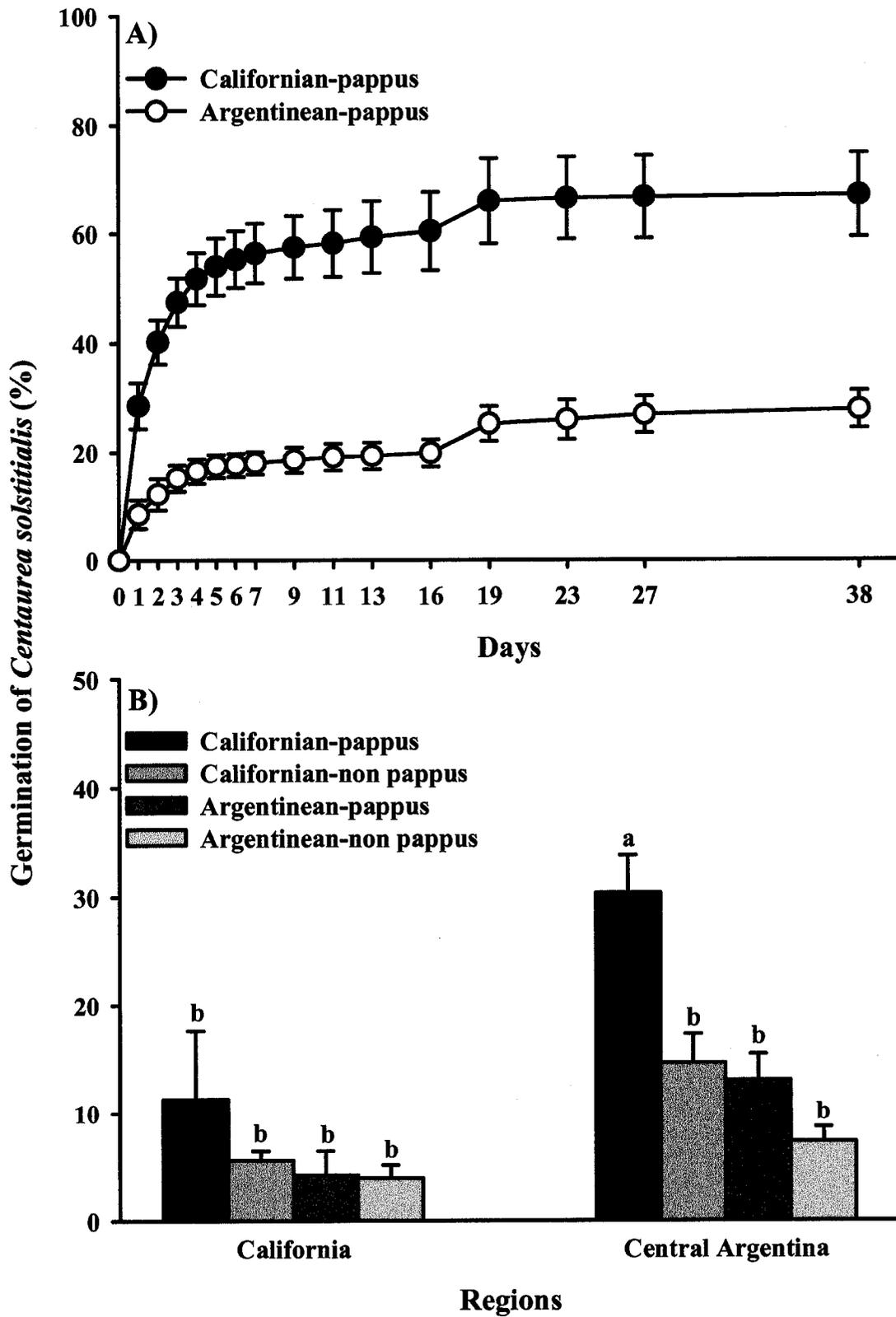


Figure 2

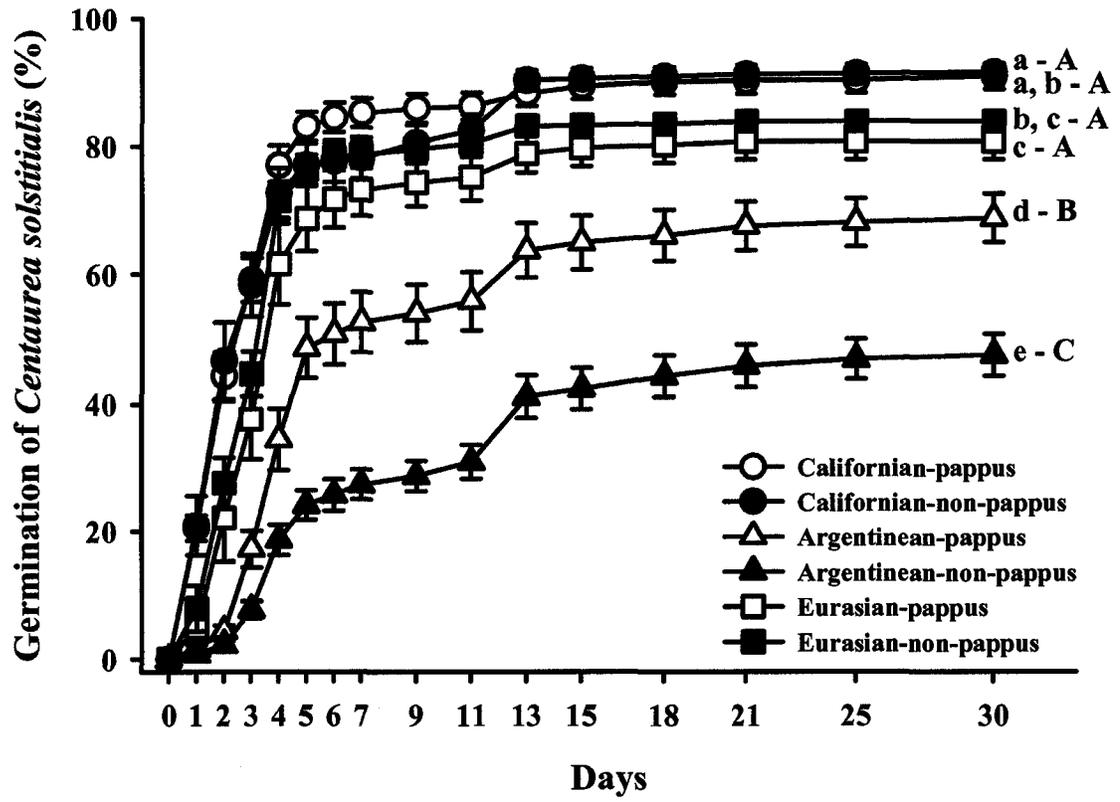


Figure 3

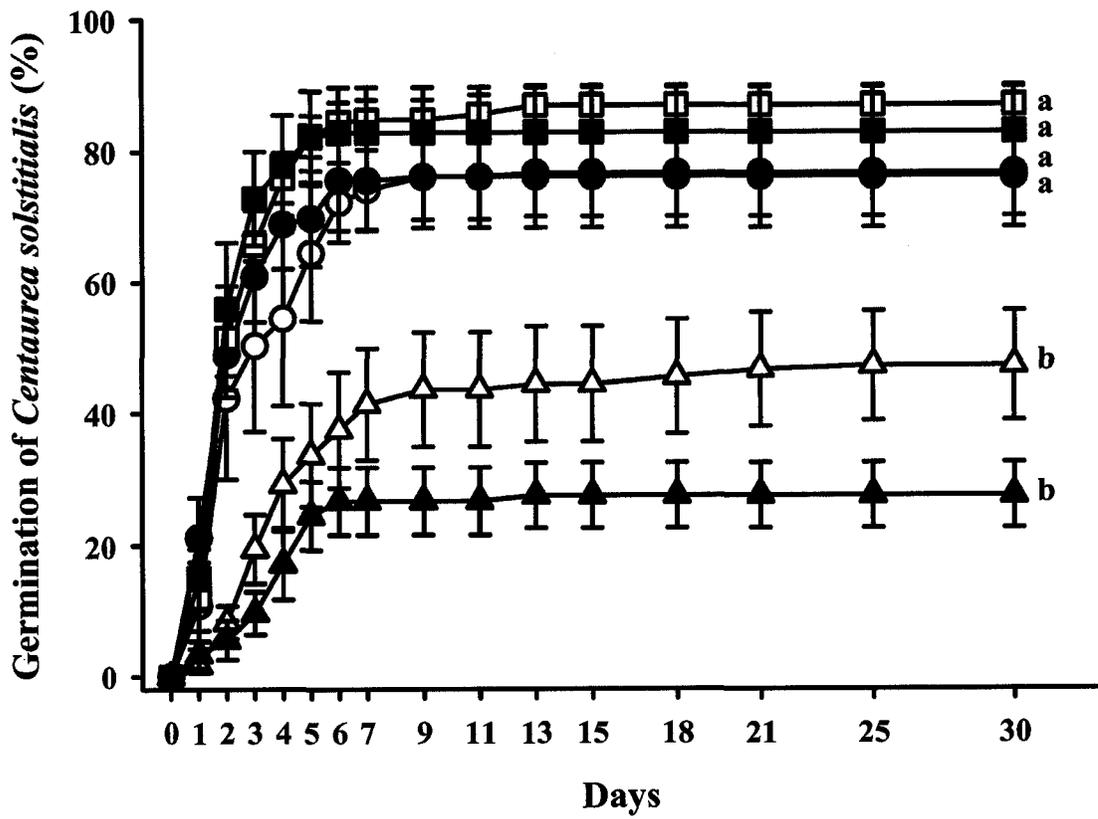


Figure 4

