Review/synthesis

Invasive plant conundrum: What makes the aliens so successful?

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Abstract

Invasive alien plants have caused extensive economic and ecological damage throughout the world. Not all plant species, however, become invasive outside of their native range. The challenge for land managers and policy makers is to determine what species are most likely to become invasive so that control efforts can be initiated before the alien species becomes widespread. A description of plant characteristics and multiple hypotheses that explain invasibility of some of the world's worst invasive species are provided in this review. Failure to control invasive plants will continue to lead to decreased agricultural production and ecosystem degradation. Control of invasive plants is a daunting task, and will only be accomplished with coordinated efforts of all countries.

Keywords: Biological invasion, Biodiversity, Exotic, Non-native, Pests, Weeds.

Introduction

Invasive alien plant species have caused extensive economic and ecological damage the world over. In the United States alone, invasive plants are estimated to cost about $30 billion annually (Pimentel et al., 2005). Most of this damage, nearly $27 billion, is caused by the reduction in crop yields and the cost for controlling invasive plants in crop fields, while the additional damage is attributed to control of invasive plants in pastures and rangelands. Estimates of the annual costs to the U.S. economy due to all invasive species (including plants, invertebrates, vertebrates, and pathogens) range from $1.1 billion (Office of Technology Assessment, 1993) to $120 billion per year (Pimentel et al., 2005). The large discrepancy between these two estimates is primarily due to a greater number of species used by Pimentel et al. (more than 10 times as many). Invasive aliens, including plants, cost China more than $14 billion annually (Xu et al., 2006). The estimated economic damage from invasive species worldwide totals more than $1.4 trillion, which is about 5% of the global economy (Pimentel et al., 2001).

The ecological damage caused by invasive species has been staggering as well. Once established, invasive species threaten the sustainability of native communities by altering their structure, composition, and functions (Webster et al., 2006). Invasive species are the second leading cause of biodiversity loss worldwide, mainly due to their ability to outcompete and replace native species (Wilcove et al., 1998; Gaertner et al., 2009). Biological invasions have been responsible for at least 3 of the 24 known extinctions of endangered species in the U.S. (Schmitz and Simberloff, 1997) and have contributed to the decline of 42% of the U.S. endangered and threatened species (Wilcove et al., 1998). In other parts of the world, as many as 80% of the endangered species are threatened as a result of invasion by alien species (Pimentel et al., 2005).

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The increasing number of plant species that colonize both agricultural fields and natural areas, potentially threatening productivity, diversity and interactions of native species, have been recognized and become the subject of ecological dialogue and experimentation worldwide in the recent past. For example, in their survey of peer-reviewed literature regarding invasions and alien species, Pyšek et al. (2006) found 329 papers and over 27,000 citations in the period 1981–2003. A search using two key words, "alien species" or "invasion", on Web of Science (ISI Web of Knowledge, Thompson Reuters: http://apps.isiknowledge.com; accessed October 2009) for the same time period revealed 2,005 articles with 62,240 citations. In addition, the same search resulted in 3,038 articles and 22,523 citations for the last five years (2004–2008), reflecting the explosive growth of the field. The majority of the most commonly cited papers are related to plant invasions.

According to the Invasive Species Specialist Group, of the 100 species that have been identified as the worst invasive species in the world, 32 are plants (Lowe et al., 2004; Table 1). Intentionally or unintentionally, introduction of invasive species has been facilitated by humans for millennia (Baker, 1986). Historically, humans have deliberately introduced plants for agricultural production, erosion control, and ornamental purposes. In some cases, multiple introductions have occurred. For example, *Pueraria montana* var. *lobata* (kudzu) is a vine species native to Asia. It was first introduced into the U.S. as an ornamental plant in 1876, but became more widespread when it was encouraged to be used as a forage crop and soil stabilizer by the U.S. Government in the 1930s and 1940s (Forseth and Innis, 2004). Today, its estimated coverage ranges from 1 to 3 million ha in the south-eastern U.S. (Forseth and Innis, 2004), and is considered one of the worst invasive plants in the world (Table 1). Introductions also occur by accidental means such as, ship ballasts, impure agricultural seed, adhesion to humans or animals, or through translocation of machinery and equipment. *Microstegium vimineum* (Trin.) Camus (Japanese stilt grass) is an annual grass that was introduced into the U.S. as a packing material for porcelain in 1919 (Swearingen and Adams, 2008) and is now found throughout the eastern U.S.

The invasive process can be divided into four stages: introduction, establishment, lag period, and expansion (Fig. 1). While many species are introduced into new regions, not all become invasive. Williamson (1993) proposed the 10:10 rule to explain the probability of a species becoming a successful invader, meaning 10% of introduced species become established and 10% of those species established will become invasive. However, other studies suggest that the rate of success is higher (Hayes and Barry, 2008). The ability of an invasive species to become established, i.e. develop a self sustaining population, is dependent on multiple factors, including overcoming environmental conditions that may limit reproduction. After invasive plants become established they may remain in a lag period for some time, which is often attributed to the low initial genetic diversity and the time that it takes for the species to evolve with a new set of environmental constraints (Mack et al., 2000; Sakai et al., 2001). During the expansion stage, invasive plants rapidly expand their range and population size. It is in this stage where most control efforts are made, but this is also the hardest stage to control. Applied ecologists and land managers are often challenged with the task of determining which plant species will become invasive, before they reach

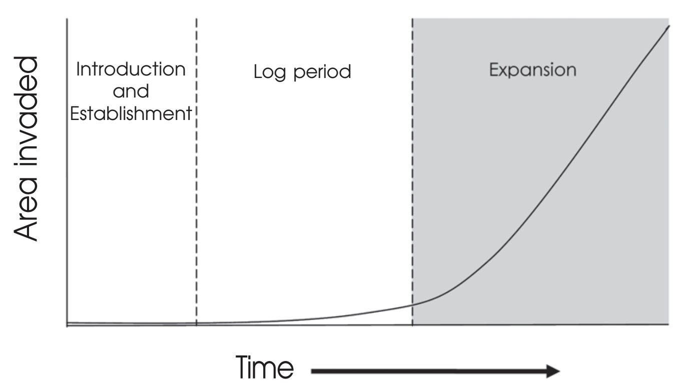

Figure 1. Conceptual diagram depicting the four phases of invasive species development. An alien species must reach the shaded area to be considered invasive; before that period it is generally not considered invasive. Multiple introductions will decrease the time it takes for a species to be considered invasive.

Table 1. Thirty-two of the world's worst invasive species according to the Global Invasive Species Database. Species impact and prominence were used to select species for this list and selections were limited to a single species from each genus (after Lowe et al., 2004).

Scientific name	Common name	Species type	Native range	Invaded range
Acacia mearnsii	black wattle	shrub	Australia	Africa, Asia, Europe, North America
Ardisia elliptica	shoebutton ardisia	tree	Asia	Australia, North America
Arundo donax	giant reed	grass	India	Australia, Africa, Central, North, & South America
Cecropia peltata	pumpwood	tree	Central & South America	Pacific
Chromolaena odorata	Siam weed	herb	Central & South America	Africa, Asia, Pacific
Cinchona pubescens	quinine tree	tree	South America	Pacific
Clidemia hirta	Koster's curse	shrub	Central & South America	Africa, India, Pacific
Euphorbia esula	leafy spurge	herb	Europe	North America
Fallopia japonica	Japanese knotweed	shrub	Asia	Australia, Europe, North America
Hedychium gardnerianum	Kahili ginger	herb	Asia	Africa, Pacific
Hiptage benghalensis	hiptage	shrub	Asia	Australia, Pacific
Imperata cylindrica	cogongrass	grass	Asia	Africa, Australia, Europe, Pacific, North & South America
Lantana camara	lantana	shrub	Central & South America	Australia, Africa, Asia, Europe, Pacific, North America
Leucaena leucocephala	leucaena	tree	Mexico	Australia, Africa, Asia, Pacific, Central, North, & South America
Ligustrum robustum	privet	shrub	Sri Lanka	Pacific
Lythrum salicaria	purple loosestrife	herb	Asia, Europe	Australia, North America
Melaleuca quinquenervia	melaleuca	tree	Australia	Central & North America, Pacific
Miconia calvescens	miconia	tree	Central America	Australia, Pacific
Mikania micrantha	mile-a-minute	vine	Central & South America	Australia, Asia, Pacific
Mimosa pigra	mimosa	shrub	Central & South America	Africa, Asia, Australia, North America
Myrica faya	fire tree	shrub	Europe	Australia, North America
Opuntia stricta	erect pricklypear	shrub	Central, North, & South America	Africa, Australia, Europe
Pinus pinaster	cluster pine	tree	Europe	Africa, Australia, South America
Prosopis glandulosa	mesquite	tree	Central America	Africa, Asia, Australia
Psidium cattleianum	strawberry guava	shrub	South America	Australia, Central America, Pacific
Pueraria montana var. lobata	kudzu	vine	Asia	Europe, North America
Rubus ellipticus	yellow Himalayan raspberry	shrub	Asia	Europe, North America
Schinus terebinthifolius	Brazilian pepper tree	tree	South America	Australia, Central America, Pacific
Spathodea campanulata	African tulip tree	tree	Africa	Australia, Central America, Pacific
Sphagneticola trilobata	wedelia	herb	Central America	Australia, Pacific
Tamarix ramosissima	tamarisk	shrub	Asia	Africa, Australia, North America
Ulex europaeus	gorse	shrub	Europe	Asia, Australia, North & South America, Pacific

the expansion stage. The objective of this review is to explore the ecological traits and environmental milieu that make invasive plants so successful in their introduced range. Characteristics of successful invaders often include: broad ecological requirements and tolerances, sometimes reflected in large geographical ranges (Sax and Brown, 2000; Rejmanek, 1996), *r*-selected life histories (Tominaga, 2003), associations with disturbed or anthropogenic habitats and origins from large continents with diverse biota (Elton, 1958). Characteristics of invaded environments often include: geographical and historical isolation; low diversity of native species (Elton, 1958); high levels of natural disturbance or human activities, and absence of co-adapted enemies, including competitors, predators, herbivores, parasites, and diseases (Davis et al., 2000). The following sections will examine some of these characteristics and associated hypotheses (Table 2) in detail.

Resource uptake and use efficiency

The ability to effectively capture resources, a typical *r*-selected plant trait, is critical to the success of invasive plants. Generally, species-rich communities are thought to utilize all available resources, making it difficult for invasive species to become established in such communities compared to less diverse communities (Diversity-Invasibility hypothesis; Elton, 1958). If a community does not utilize all available resources (water, nutrients, and light) there is an 'empty niche' that leaves it susceptible to invasion (Elton, 1958; MacArthur, 1970). For example, in the western U.S., *Centaurea solstitialis* L. (yellow star-thistle) is an invasive species that

Table 2. Proposed hypotheses to explain the invasiveness of some of the worst invasive alien species.

Hypothesis	Proposed by	Examples	Citation
Diversity-Invasibility Hypothesis	Elton, 1958	*Crepis tectorum*, U.S.A.	Naeem et al., 2000
		Centaurea solstitialis, U.S.A.	Dukes, 2001
		Imperata cylindrica, U.S.A.	Collins et al., 2007
Empty Niche Hypothesis	Elton, 1958; MacArthur, 1970	*Spartina* spp. Pacific	Daehler and Strong, 1996
		Centaurea solstitialis, U.S.A.	Dukes, 2002
		Rosa rubiginosa, Argentina	Aguirre et al., 2009
Enemy Release Hypothesis	Elton, 1958; Keane and Crawley, 2002	*Silene latifolia*, U.S.A.	Wolfe, 2002
		Solanum mauritianum, S. Africa	Olcker and Hulley, 1991
		Clidemia hirta, Pacific	DeWalt et al., 2004
Evolution of Increased Competitive Ability Hypothesis	Blossey and Nötzold, 1995	*Lythrum salicaria*, U.S.A.	Blossey and Nötzold, 1995
		Tricadica sebifera, U.S.A.	Siemann and Rogers, 2001
		Solidago gigantean, Europe	Jakobs et al., 2004
Propagule Pressure Hypothesis	Williamson, 1996	*Alliaria petiolata*	Anderson, 1996
		Lythrum salicaria, U.S.A	Mullin, 1998
Invasional Meltdown Hypothesis	Simberloff and Von Holle, 1999	*Festuca arundinacea*, U.S.A.	Belote and Jones, 2009
		Pinaceae spp. , Argentina	Nunez et al. 2008
		Carpobrotus spp. , France	Bourgeois et al. 2005
Fluctuating Resource Hypothesis	Davis et al., 2000	*Lythrum salicaria,* U.S.A.	Mullin, 1998
		Lantana camara, Australia	Duggin and Gentle, 1998
		Imperata cylindrica, U.S.A.	Jose and Tripathi, 2008
Novel Weapons Hypothesis	Callaway and Aschehoug, 2000	*Lantana camara*, India	Sharma et al., 2005
		Typha angustifolia , U.S.A.	Jarchow and Cook, 2009
		Centaurea maculosa, U.S.A.	Thorpe et al., 2009
Rhizochemical Dominance Hypothesis	Daneshgar and Jose, 2008	*Imperata cylindrica*, U.S.A.	Collins et al., 2008
		Mikania micrantha, China	Chen et al., 2009

displaces native vegetation by utilizing water resources below the rooting zone of native species (Holmes and Rice, 1996). However, when the species was grown in a microcosm experiment with *Hemizonia congesta* DC. (hayfield tarweed), growth was reduced compared to when it was grown with other native plants (Dukes, 2002). The authors hypothesized that this was because *H. congesta* and *C. solstitialis* have similar morphology and growth habits which led to a competition for similar resources. *Centaurea solstitialis* became invasive when it was grown with native plants that did not fully utilize all resources, leaving an empty niche for this species to become established.

Similar to the Empty Niche hypothesis, the Fluctuating Resource hypothesis states that as resources become available within a given area, that area will become more susceptible to invasion (Davis et al., 2000). According to the authors, excessive nutrients become available primarily in two ways. The first is when native plants decrease uptake because of decreased populations following a disturbance or predatory outbreak. The second occurs when more nutrients become available from external or internal sources, such as increased precipitation or accelerated mineralization. Because invasive plants are often successful in capturing excessive nutrients better than native species, this leaves the community vulnerable to invasion. Using *Lantana camara* L. (lantana) as an example, Duggin and Gentle (1998) illustrated this concept in a series of experiments conducted in New South Wales, Australia. Native to Central and South America, *L. camara* is an invasive shrub that has been introduced in over 60 countries throughout the world. It can grow in a variety of soil types and habitats, but generally does not occur in undisturbed forests (Sharma et al., 2005). Duggin and Gentle (1998) tested the impacts of fertilization, biomass removal and fire on *L. camara* germination, survival, and growth. These authors reported that while fertilization alone had little effect on plant development, fertilization combined with biomass removal or burning significantly increased *L. camara* germination, survival, and growth. This increase in invasion success was correlated with increased light, water, and nutrient availability and would explain why the species performs better in disturbed areas. Similar results have been observed for *Imperata cylindrica* (L.) Beauv. (cogongrass), an invasive C_4 perennial grass species native to Asia. The species will often exist only in sparse patches in undisturbed forests (MacDonald, 2004), but becomes dominant following fire (Jose and Tripathi, 2008).

Rapid growth and reproduction

Invasive plants often form dense monocultures with high productivity, sometimes at rates much higher than what they are capable in their native range (Hierro et al., 2005). In addition to higher rates of productivity, some invasive plants produce larger individuals in invaded populations. The Evolution of Increased Competitive Ability (EICA) hypothesis (Blossey and Nötzold, 1995) states that reduced herbivory in the introduced range causes an evolutionary shift in resource allocation from herbivore defense to growth. As a result, according to EICA, introduced genotypes are expected to grow more vigorously than conspecific native genotypes. The authors hypothesized that in the absence of specialized enemies, invasive plant genotypes allocate more resources to biomass production and reduce resources to defense mechanisms, thereby increasing the abundance of high biomass producing individuals. This hypothesis has been supported by several recent studies. In a common garden experiment in the southern U.S., Siemann and Rogers (2001) used *Triadica sebifera* (L.) Small (Chinese tallow tree) to test the EICA hypothesis. *Triadica sebifera* is a fast-growing tree species that is native to Asia, but has been introduced to the U.S. (Bruce et al., 1997). Results from the 14-year-old experiment indicated that *T. sebifera* trees had greater biomass and fewer leaf defense chemicals in invasive genotypes compared to native genotypes (Siemann and Rogers, 2001). Jakobs et al. (2004) compared the populations of *Solidago gigantea* Aiton (giant goldenrod), a rhizomatous perennial herb, in its native range, North America, to its invaded range, Europe. The authors reported that average population size, density and total plant biomass were greater in the invaded range. Evolution, however, is not the only way in which plants increase resource allocation in favour of defence. Cheplick (2005) reported an increase in resource allocation in favour of growth in *M. vimineum*, which was due to phenotypic plasticity rather than genetic evolution.

Many invasive plants are ruderal (*r*-strategists) species, such as *Lythrum salicaria* L. (purple loosestrife), *I. cylindrica*, and *Schinus terebinthifolius* Raddi (Brazilian pepper) that can quickly occupy large extent of area in a short period of time (Ewel, 1979; Mullin, 1998; Jose et al., 2002). The ability to spread rapidly and grow quickly helps to ensure that invasive species dominate the disturbed areas. However, not all invasive species require disturbance to become productive. *Pueraria montana* is capable of occupying undisturbed areas by allocating resources to growth instead of structure. The species can grow up to 20 cm in a single day, easily overtopping any tree species, produces up to 1900 g of biomass annually, and has a leaf area index of up to 7.8 (Forseth and Innis, 2004).

The ability to produce an abundance of long-lasting viable seeds also increases species invasiveness (Propagule Pressure hypothesis, Williamson, 1996). *Lythrum salicaria* is a wetland perennial herb that is native to Eurasia, but has invaded most of North America. In its native range the species occupies less than 5% of vegetative cover, but in invaded areas it can form dense, monospecific stands (Mullin, 1998). Although any wetland is susceptible to *L. salicaria* invasion, disturbed areas with bare soil are most vulnerable (Mullin, 1998). Once established, the species produces abundant quantities of seed, with each stem producing over 100,000 seeds, 60% of which remains viable for up to 20 years (Mullin, 1998). The high amount of viable seed makes long-term control efforts difficult, and this characteristic is not unique to *L. salicaria*. *Acacia mearnsii* De Wild. (black wattle), *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard), and *M. vimineum* are three examples of other plant species that are difficult to control because of high seed production and viability (Anderson et al., 1996; Gibson et al., 2002; de Neergaard et al., 2005).

Modifying their environment

Invasive plants can increase their competitive ability by modifying the invaded environment. One of the ways this is done is through the production of allelochemicals by invasive plants that inhibit the growth of native plants; also referred to as the Novel Weapons hypothesis (Callaway and Aschehoug, 2000; Bias et al., 2003). For example, field observations indicate seedling recruitment to be minimal underneath *L. camara*, which has been attributed to allelochemicals produced by the species (Sharma et al., 2005). Maiti et al. (2008) used extracts from *L. camara* leaves to suppress *Mimosa pudica* L. (sleeping grass) seed germination and growth in a laboratory experiment that support these field observations. Not all aspects of allelochemical production, however, are negative. Kong et al. (2006) suggested allelochemicals produced by *L. camara* could be used to improve the control of invasive plants in aquatic ecosystems.

In addition to the production of allelochemicals that inhibit native plant growth, some invasive plants can also lower soil pH and alter nutrient cycling within the native community (Callaway and Aschehoug, 2000; Drenovsky et al., 2007). Decreased pH can lower nutrient availability and lead to decreased native plant growth, particularly on nutrient poor sites. Collins and Jose (2008) reported that *I. cylindrica* decreased soil pH in recently invaded areas in the southeastern U.S. *Pinus* forests. Although *Mikania micrantha* H.B.K. (mile-a-minute vine), a fast growing perennial vine native to Central and South America, decreased soil pH in a subtropical forest in China, Chen et al. (2009) reported increased NH_4^+ and net soil nitrification. Allelochemicals released by *M. micrantha* actually increased soil fertility, which probably enabled the species to become invasive. It is obvious that allelochemicals produced by invasive plants exert both direct and indirect influence on native species. Daneshgar and Jose (2008) proposed a new hypothesis, the Rhizochemical Dominance hypothesis that integrates several of these mechanisms in explaining the success of invasive plants. This hypothesis attributes invasive success to allelopathy (novel weapons) and alteration of soil chemical properties by the rhizosphere exudates of the invader, which in turn favours its own growth while inhibiting the growth of competing vegetation. These chemical alterations may include changes in soil pH, and nutrient levels and availability.

Modifications to the invaded environment can also occur aboveground. This is frequently accomplished by invasive plants through the alteration of the native community fire regime (Brooks et al., 2004). In many cases, fire can promote invasive species and invasive species can promote fire, resulting in a positive feedback cycle that decreases native species abundance as invasive species become more dominant (Brooks et al., 2004). *Tamarix ramosissima* Ledeb. (tamarisk) is an invasive perennial shrub native to Eurasia. Litter produced from *T. ramossisima* burns readily and increases fire frequency in riparian ecosystems, resulting in increased dominance of *T. ramossisima* (Busch and Smith, 1993). Invasive species can also decrease fire frequency in native communities. Stevens and Beckage (2009) observed a lower density of *S. terebinthifolius* in areas that were burned frequently in *Pinus*-savanna ecosystems in the southern U.S. In areas that were fire suppressed, *S. terebinthifolius* became more abundant and inhibited fires within the community resulting in further dominance of the invasive species. It is also possible for invasive species to affect ecosystem processes in such a way to facilitate invasion by other alien invasive species (Invasional Meltdown hypothesis, Simberloff and Von Holle, 1999). Among the examples to support this hypothesis are invasive plants that modify the environment, e.g. increased nitrogen fixation or alteration of the fire regime, which then facilitates invasion by other invasive plant species and by invasive animals that encourage the spread of invasive plant species through seed dispersal and selective browsing of native plants.

Genetic variability and evolutionary genetics

The ability of a potentially invasive plant to adapt to the invaded environment is critical to its success as an invasive species (Lee, 2002; Ren and Zhang, 2009). Some invasive plants have the phenotypic plasticity to tolerate a broad range of environmental conditions, which increases the potential number of sites they can invade (Richards et al., 2006). Annapurna and Singh (2003) illustrated this concept with *Parthenium hysterophorus* L. (congress grass), an invasive plant in India. The authors reported significant phenotypic plasticity in response to a gradient of soil conditions. If a species does not exhibit phenotypic plasticity to environmental conditions and only a few individuals of a species are introduced, a population bottleneck can occur. This can result in the lower genetic diversity of the invasive plant compared to the same plant in its native range (Sakai et al., 2001). During this time the invasive plant population may undergo a lag period until genetic diversity increases by evolution, additional introductions occur, or hybridization occurs with a native species (Sakai et al., 2001). However, while hybridization may increase the genetic diversity of an invasive species, it may result in decreased abundance of the native species, which is particularly damaging to native species with small populations (Levin et al. 1996). For example, *Cercocarpus traskaie* Eastw., a rare shrub species located only off an island in southern California, is hybridizing with the invasive plant *C. betuloides* Torrey & A. Gray (birch-leaf mountain mahogany) and is threatened with assimilation.

Plants may also be able to persist as invasive despite control efforts that attempt to eliminate them. Herbicides are a common management tool used to control invasive species throughout the world. However, nearly 200 invasive plants (332 biotypes) are considered resistant to herbicides and resistance has increased dramatically over the past 30 years with the increase in herbicide use (Heap, 2009; Fig. 2). Nine invasive plants are resistant to glyphosate, which limits the effectiveness of glyphosate-resistant crops. Crop mimicry is another way in which invasive plants are able to persist despite control efforts. *Echinochloa crus-galli* (L.) P. Beauv. (barnyard grass) is a C_4 wetland grass that is native to Eurasia. When grown with *Oryza sativa* L. (rice), it is difficult to identify and remove *E. crus-galli* during manual weedings because of the close resemblance with the crop (Barrett, 1983).

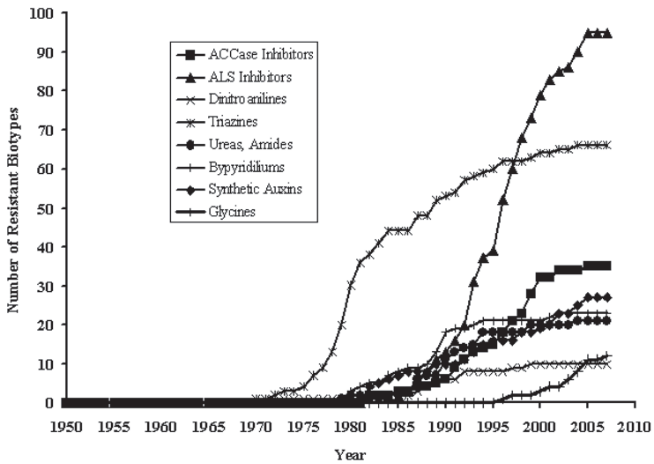

Figure 2. Change in the number of herbicide resistant invasive plants (332 biotypes) from 1950 to 2007. The biotypes are grouped by herbicide mode of action. The increase in herbicide resistant invasive plants has been dramatic over the past thirty years and correlates with the increase in herbicide use throughout the world (Heap 2009). Source: Ian Heap, http://WeedScience.com.

Reduced enemies of invasive plants

Nearly every plant species has a set of enemies that reduce their populations, whether it is a fungus that causes plant tissue necrosis, or a herbivore that removes the plant entirely. The enemies can either be specialists, attacking only a single species, or generalists, attacking multiple species. Within their native range, invasive plants are subject to specialized enemies that have evolved with the plant and limit plant population growth. Outside of the native range, invasive plants are often not suppressed by these specialized enemies and are only preyed upon by generalist enemies. Invasive plants are believed to gain an advantage over native species in the invaded range because of the apparent lack of specialized enemies. The increased performance of invasive plants because of the absence of specialized enemies is referred to as the Enemy Release hypothesis (Elton, 1958; Keane and Crawley, 2002).

Several examples of Enemy Release hypothesis exist for multiple species. Wolfe (2002) tested this hypothesis on *Silene latifolia* Poir. (white campion), a small (< 1 m tall) short lived perennial plant, using populations from native European and invaded U.S. range. The author recorded damage by phloem feeding insects, floral herbivory, fungal disease, and fruit and seed predation, and observed greater damage on European plants for each group. In addition, Wolfe observed damage caused by specialist enemies on European plants, but little of specialist enemy damage on invasive U.S. populations. Mitchell and Power (2003) sampled viruses and fungi (rust, smut, and powdery mildew) on 473 plants that were invasive to the U.S., but native to Europe. They found that invasive plants had 84% fewer fungi and 24% fewer viruses compared to the same plants in their native range.

While lack of specialized enemies contributes to increased invasiveness, resistance to generalist enemies can increase invasiveness as well. For example, in the eastern U.S., *M. vimineum* is an invasive, shade-tolerant, annual, C_4 grass species native to Asia that frequently outcompetes native species, reducing tree growth and biodiversity (Gibson et al., 2002). This problem is exacerbated with the presence of *Odocoileus virginianus* Zimm. (white-tailed deer). *Odocoileus virginianus*, a generalist herbivore whose populations have risen exponentially over the past century, are known to browse over 100 plant species native to the eastern U.S. (Rooney, 2001). While large populations of *O. virginianus* regularly decrease native herbaceous and woody species understory vegetation, they are reluctant to browse upon *M. vimineum*. Webster et al. (2008) reported that preferential foraging by *O. virginianus* reduced native vegetation cover and density, resulting in increased abundance of *M. vimineum* because of reduced competition for light in their study conducted at Great Smoky Mountains National Park in the U.S. Furthermore, chronic browsing by *O. virginianus* inhibited the ability of native species to recover from *M. vimineum* invasion during times of drought, when the species was susceptible to becoming overtopped. This resulted in a successional state that resisted transition which, in turn, contributed to dominance by *M. vimineum* (Webster et al., 2008).

Combating invasive species: An idealistic dream?

As the review has shown, invasive plants use multiple strategies to gain dominance in their introduced habitats which has made it nearly impossible to control them. Ecologists, conservation biologists, farmers, land managers, and policy makers alike have begun to recognize invasive species as 'bioterrorists' that threaten the biosecurity of many countries. Deficiencies in policy and political will, research and management funding, persistent gaps in scientific knowledge and lack of public awareness have all been identified as causes of current global invasive species dilemma. If effective management strategies involving coordinated proactive and reactive programmes are not immediately institutionalized, invasive plants will dramatically and permanently alter the structure and function of agricultural and forest lands.

In spite of the increasing damage and threats from invasive species, only a handful of countries have come up with effective infrastructures to deal with the problem. In many parts of the world, invasive species are still being used for food and fiber production and for reforestation and restoration. Invasive species represent not only a biological dilemma, but a complex societal dilemma, with need for a more comprehensive awareness, management strategies, coordinated programs, and effective laws if we are to avoid bequeathing future generations with devastated agricultural fields and degraded ecosystems (Miller and Schelhas, 2008). Since invasive species do not recognize the political boundaries set by humans, it is important to work within a collaborative environment to design adaptive management strategies to control them. It is perhaps overly idealistic to think that people can collaborate across institutional boundaries and local to global scales to carry out the complex tasks of prevention, early detection, and eradication of invasive species (Miller and Schellas, 2008), but such a strategy is the only true weapon in our arsenal at this point.

References

Anderson, R.C., Dhillion, S.S., and Kelley, T.M. 1996. Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in central Illinois. Restor. Ecol., 4: 181–191.

Annapurna, C. and Singh, J.S. 2003. Phenotypic plasticity and plant invasiveness: case study of congress grass. Curr. Sci., 85: 197–201.

Aguirre, G.U. Ciuffo, G.M., and Ciuffo, L.E.C. 2009. Genetic differentiation of Rosa rubiginosa L. in two different Argentinean ecoregions. Plant Syst. Evol., 281: 183–192.

Baker, H.G. 1986. Patterns of plant invasion in North America. In: Mooney, H.A. and Drake, J.A. (eds.). *Ecology of biological invasions of North American and Hawaii*, Wiley, New York, NY., USA, pp. 44–57.

Bias, H.P., Vepachedu, R., Gilroy, S., Callaway, R.M., and Vivanco, J.M. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. Science, 301: 1377–1380.

Barrett, S.C.H. 1983. Crop mimicry in weeds. Econ. Bot., 37: 255–282.

Belote, R.T. and Jones, R.H. 2009. Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms. Biol. Invasions, 11: 1045–1052.

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

Bourgeois, K., Suehs, C.M., Vidal, E., Medail, F. 2005. Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. Ecoscience, 12: 248–256.

Brooks, M.L., D'Antonio C.M., Richardson D.M., Grace J.B., Keeley J.E., DiTomaso J.M., Hobbs R.J., Pellant M., and Pyke D. 2004. Effects of invasive alien plants on fire regimes. BioScience, 54: 677–688.

Bruce, K.A., Cameron, G.N., Harcombe, P.A., and Jubinsky, G. 1997. Introduction, impact on native habitats, and management of a woody invader, the Chinese Tallow Tree, *Sapium sebiferum* (L.) Roxb. Nat. Area. J., 17: 255–260.

Busch, D.E. and Smith, S.D. 1993. Effects of fire on water and salinity relations of riparian woody taxa. Oecologia, 94: 186–194.

Callaway, R.M. and Aschehoug, E.T. 2000. Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. Science, 290: 521–523.

Chen, B.M., Peng, S.L., and Ni, G.Y. 2009. Effects of the invasive plant *Mikania micrantha* HBK on soil nitrogen availability through allelopathy in South China. Biol. Invasions, 11: 1291–1299.

Cheplick, G.P. 2005. Biomass partitioning and reproductive allocation in the invasive, cleistogamous grass *Microstegium vimineum*: influence of the light environment. J. Torrey Bot. Soc., 132: 214–224.

Collins, A.R., Jose, S., Daneshgar, P., and Ramsey, C. 2007. Elton's hypothesis revisited: an experimental test using cogongrass. Biol. Invasions, 9: 433–443.

Collins, A.R. and Jose, S. 2008. Cogongrass invasion alters soil chemical properties of natural and planted forestlands. In: Kohli, R.K., Jose, S., Singh, H.P., and Batish, D.R. (eds). *Invasive Plants and Forest Ecosystems*, CRC Press, Boca Raton, FL., USA, pp. 295–323.

Daehler, C.C. and Strong, D.R. 1996. Status, prediction and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biol. Conserv., 78: 51–58.

Daneshgar, P. and Jose S. 2008. Mechanisms of plant invasion: a review. In: Kohli, R.K., Jose, S., Singh, H.P., and Batish, D.R. (eds). *Invasive Plants and Forest Ecosystems*, CRC Press, Boca Raton, FL., USA, pp. 11–28.

Davis, M.A., Grime, J.P., and Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invisibility. J. Ecol., 88: 528–534.

de Neergaard, A., Saarnak, C., Hill, T., Khanyile, M., Berzosa, A.M., and Birch-Thomsen, T. 2005. Australian wattle species in the Drakensberg region of South Africa – An invasive alien or a natural resource? Agr. Syst., 85: 216–233.

DeWalt, S.J., Denslow, J.S., and Ickles, K. 2004. Natural-enemies release facilitates habitat expansion of invasive tropical shrub *Clidemia hirta.* Ecology, 85: 471–483.

Drenovsky, R.E. and Batten K.M. 2007. Invasion by *Aegilops triuncialis* (Barb Goatgrass) slows carbon and nutrient cycling in a serpentine grassland. Biol. Invasions, 9: 107–116.

Duggin, J.A. and Gentle, C.B. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforest-open forest ecotones in north-eastern NSW, Australia. Forest Ecol. Manag., 109: 279–292.

Dukes, J.S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia, 126: 563–568.

Dukes, J.S. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. Ecol. Appl., 12: 602–617.

Elton, C.S. 1958. *The ecology of invasion by animals and plants*. T Metheun and Co., London.

Ewel, J.J. 1979. Ecology of *Schinus*. In: Workman, R. (ed.). *Schinus - Technical Proceedings of Techniques for Control of Schinus in South Florida: A Workshop for Natural Area Managers*. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, FL., USA, pp. 7–21.

Forseth, Jr. I.N. and Innis, A.F. 2004. Kudzu (*Pueraria montana*): History, physiology, and ecology combine to make a major ecosystem threat. Crit. Re. Plant Sci., 23: 401–413.

Gaertner, M., Den Breeyen, A., Hui, C., and Richardson, D.M. 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog. Phys. Geog., 33: 319–338.

Gibson, D.J, Spyeareas, G., and Benedict, J. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. J. Torrey Bot. Soc., 129: 207–219.

Hayes, K.R. and Barry, S.C. 2008. Are there any consistent predictors of invasion success? Biol. Invasions, 10: 483–506.

Heap, I.M. 2005. International Survey of Herbicide Resistant Weeds. http://www.weedscience.org. (accessed September 2009).

Hierro, J.L., Maron, J.L., and Callaway, R.M. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J. Ecol., 93: 5–15.

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

Jakobs, G., Weber, E., and Edwards, P.J. 2004. Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. Divers. Distrib., 10: 11–19.

Jarchow, M.E. and Cook, B.J. 2009. Allelopathy as a mechanism for the invasion of *Typha angustifolia*. Plant Ecol., 204: 113–124.

Jose, S., Cox, J., Miller, D.L., Shilling, D.G., and Merritt, S. 2002. Alien plant invasions: The story of cogongrass in southeastern Florida. J. Forest., 100: 41–44.

Jose, S. and Tripathi, N. 2008. Role of natural and anthropogenic disturbance in exotic invasions: Predicting *Imperata cylindrica* invasion of southeastern forests using ecological niche modeling. 93rd ESA Annual Meeting. August 2-8. Milwaukee, WI.

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

Kong, C. H., Wang, P., Zhang, C.X., Zhang, M.X., and Hu, F. 2006. Herbicidal potential of allelochemicals from

Lantana camara against *Eichhornia crassipes* and the alga *Microcystis aeruginosa.* Weed Res., 46: 290-295.

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

Levin, D.A., Francisco-Ortega J., Jansen, R.K. 1996. Hybridization and the extinction of rare plant species. Conserv. Biol., 10: 10–16.

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. 2004. *100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database*. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12p.

MacArthur, R.H. 1970. Species packing and competitive equilibruium for many species. Theor. Popul. Biol., 1: 1–11.

MacDonald, G.E. 2004. Cogongrass (*Imperata cylindrica*) – Biology, ecology and management. Crc. Cr. Rev. Plant Sci., 23: 367–380.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H. Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecol. Appl., 10: 689–710.

Maiti, P.P., Bhakat, R.K., Bhattacharjee, A. 2008. Allelopathic effects of *Lantana camara* on physiobiochemical parameters of *Mimosa pudica* seeds. Allelopathy J., 22: 59–67.

Miller, J.H. and Schelhas, J.W. 2008. Adaptive collaborative restoration: a key concept for invasive plant management. In: Kohli, R.K., Jose, S., Singh, H.P., and Batish, D.R. (eds). *Invasive Plants and Forest Ecosystems*, CRC Press, Boca Raton, FL., USA, pp. 251–265.

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

Mullin, B.H. 1998. The biology and management of purple loosestrife (*Lythrum salicaria*). Weed. Technol., 12: 397–401.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., and Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos, 91: 97–108.

Nunez, M.A., Relva M.A., Simberloff, D. 2008. Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina. Austral Ecol., 33: 317–323.

Office of Technology Assessment, United States Congress. 1993. Harmful nonindigenous species in the United States. Washington, D.C. 391p.

Olcker, T. and Hulley, P.E. 1991. Impoverished insect herbivore faunas on the exotic bugweed *Solanum mauritianum* Scop relative to indigenous *Solanum* specis in Natal Kwazulu and the Transkei. J. Entomol. Soc. S. Afr., 54: 39–50.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., and Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agr. Ecosyst. Environ., 84: 1–20.

Pimentel, D. Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ., 52: 273–288.

Pyšek, P., Richardson, D.M., and Jarosik, V. 2006. Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. Preslia, 78: 437–468.

Rejmanek, M. 1996. A theory of seed plant invasiveness: The first sketch. Biol. Conserv., 78: 171–181.

Ren, M.X. and Zhang, Q.G. 2009. The relative generality of plant invasion mechanisms and predicting future invasive plants. Weed Res., 49: 449–460.

Richards, C.L, Bossdorf, O., Muth, N.Z., Gurevitch, J., and Pigliucci, M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol. Lett., 9: 981–993.

Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry, 74: 201–208.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst., 32: 305–332.

Sax, D.F. and Brown, J.H. 2000. The paradox of invasion. Global Ecol. Biogeogr., 9: 363–371.

Schmitz, D.C. and Simberloff, D. 1997. Biological invasions: A growing threat. Issues Sci. Technol., 13: 33–40.

Sharma, G.P., Raghubanshi, A.S., and Singh, J.S. 2005. Lantana invasion: An overview. Weed Biol. Manag., 5: 157–165.

Sharma G.P. and Raghubanshi A.S. 2009. Plant invasions along roads: a case study from central highlands, India. Environ. Monit. Assess., 157: 191–198.

Siemann, E, and Rogers, W.E. 2001. Genetic differences in growth of an invasive tree species. Ecol. Lett., 4: 514–518.

Simberloff, D. and Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions, 1: 21–32.

Stevens, J.T. and Beckage, B. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*) New Phytol., 184: 365–375.

Swearingen, J.M. and Adams, S. 2008 Japanese stilt grass: *Microstegium vimineum* (Trin.) Camus. National Park Service, Plant Conservation Alliance, Alien Plant Working Group. http://www.nps.gov/plants/alien (accessed September 2009).

Thorpe, A.S., Thelen, G.C., Diaconu, A., and Callaway, R.M. 2009. Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. J. Ecol., 97: 641–645.

Tominaga, T. 2003. Growth of seedlings and plants from rhizome pieces of cogongrass (*Imperata cylindrica* (L.) Beauv.). Weed Biol. Manage., 3: 193–195.

Webster, C.R., Jenkins, M.A., Jose, S. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. J. Forest., 104: 366–374.

Webster, C.R., Rock, J.H., Froese, R.E., and Jenkins, M.A. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10-year results. Oecologia, 157: 497–508.

Wilcove, D.S., Rothstein, D., Dubow, J., Philips, A., and Losos, E. 1998. Quantifying threats to imperiled species in the United States. BioScience, 48: 607–615.

Williamson, M. 1993. Invaders, weeds, and the risk from genetically manipulated organisms. Experientia, 49: 219–244.

Williamson, M. 1996. Biological invasions. Chapman & Hall, London, New York ,Tokyo.

Wolfe, L.M. 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am. Nat., 160: 705–711.

Xu, H.G., Ding, H., Li, M.Y., Qiang, S., Guo, J.Y., Han, Z.M., Huang, Z.G., Sun, H.Y., He, S.P., Wu, H.R., and Wan, F.H. 2006. The distribution and economic losses of alien species invasion to China. Biol. Invasions, 8: 1495–1500.