

Invasive species and climate change: an agronomic perspective

Lewis H. Ziska · Dana M. Blumenthal ·
G. Brett Runion · E. Raymond Hunt Jr ·
Hilda Diaz-Soltero

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Abstract In the current review we wish to draw attention to an additional aspect of invasive species and climate change, that of agricultural productivity and food security. We recognize that at present, such a review remains, in part, speculative, and more illustrative than definitive. However, recent events on the global stage, particularly in regard to the number of food riots that occurred during 2008, even at a time of record harvests, have prompted additional interest in those factors, including invasive species, which could, through climatic uncertainty, alter food production. To that end, as agricultural scientists, we wish to begin an initial evaluation of key questions related to food production and climate change including: how vulnerable is agriculture to invasive species?; are current pest management strategies sufficient to control invasive outbreaks in the future?; what are the knowledge gaps?; can we provide initial recommendations for scientists, land managers and policy makers in regard to available resources? Our overall goals are to begin a synthesis of potential impacts on productivity, to identify seminal research areas that can be addressed in

L. H. Ziska (✉)
Crop Systems and Global Change Laboratory, USDA-ARS, Beltsville, MD 20705, USA
e-mail: l.ziska@ars.usda.gov

D. M. Blumenthal
Rangeland Resource Research Unit, USDA Agricultural Research Service,
Cheyenne, WY 82001, USA

G. B. Runion
National Soil Dynamics Laboratory, USDA Agricultural Research Service,
411 South Donahue Drive, Auburn, AL 36832, USA

E. R. Hunt Jr
Hydrology and Remote Sensing Laboratory, USDA Agricultural Research Service,
Beltsville, MD 20705, USA

H. Diaz-Soltero
USDA, Senior Invasive Species Coordinator, 1201 Eye St. NW, Washington, DC 20005, USA

future research, and to provide the scientific basis to allow agronomists and land managers to formulate mitigation and adaptation options regarding invasive species and climate change as a means to maintain food security.

1 Introduction

In order to supply sufficient food to feed a world population approaching 7 billion, agronomists and plant scientists have developed high-yielding strains of a small subset of the world's plant and animal species that can produce supra-natural yields when grown in monocultures. They have accomplished this feat by a historically unprecedented global movement of plant and animal DNA across borders and the adoption and proliferation of this DNA on every continent (save Antarctica). For example, in North America less than 10% of agricultural species are derived from native plants.

The widespread introduction and distribution of economically desired plants and animals has also helped to transform what had been biogeographically distinct flora and fauna into what has been described as an indistinct, homogenous “soup” (Mooney and Hobbs 2000). Although the vast majority of such species do no harm, and, in fact, are necessary to maintain high agricultural productivity, a small percentage of them can spread rapidly beyond their introduced areas and become invasive species.

What is meant by the term, “invasive”? Invasive refers to any organism that is outside of its native geographic range that may or has become injurious to animal or human health, the economy and/or natural environment. There are, unfortunately, a number of terms that are used interchangeable with “invasive” including, “noxious”, “alien”, “non-indigenous” and “exotic” (Ziska and George 2004). However, the 1999 Executive Order #13112 defines for federal agencies the terms “invasive” species and “alien” species as follows. “Alien” species means, with respect to a particular ecosystem, any species, including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem. This term would also include non-indigenous, or exotic species. In contrast, “invasive or noxious species” means an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human or animal health.” (National Invasive Species Council 2006).

While nomenclature is often misapplied, the damage done by invasive species is universally acknowledged. Among invasive insects, pathogens and weeds, crop losses have been assessed at \$58 billion dollars with an additional \$4 billion in management costs as of 2000 (Table 1; Pimental et al. 2000). Overall, a quarter of the United States (U.S.) agricultural gross national product is lost each year to invasive species. If climate change can (or is) altering the biological success of invasive species with additional effects on agricultural productivity, then characterizing those effects is of paramount importance to food security.

The scope of the problem of invasive species biology, the basis for their colonization and spread, our ability to predict which species may become invasive, and the appropriate management strategies are the focus of an increasing number of scientific and policy studies (Enserik 1999; Levine et al. 2003; Kolar and Lodge 2001; Evans 2003, inter alia). These studies indicate that the principal impetus for species

Table 1 Average annual invasive species crop losses and related control costs (taken from Pimental et al. 2000)

Pest	Percent invasive (%)	Percent loss (%)	Crop loss (\$ billion)	Control cost
Insects	40	13	14	500 million
Plant Pathogens	65	12	21	599 million
Weeds	73	12	23	3,000 million
Total		37	58	4,000 million

introductions is, and will continue to be, the exponential growth in international trade and travel. However, not all introductions of foreign material result in an invasive pest. Whether the introduction of a new species results in its becoming invasive or not depends, in part, on the biological and physical characteristics of the habitat where it is initially introduced. Those habitat characteristics are greatly influenced by climate (Scherm and Coakley 2003).

Climate, in turn, is being altered by human activity (IPCC 2007). How will anthropogenic climatic change alter the biological success of invasive species? These aspects are beginning to be addressed in a number of seminal papers (e.g. Dukes 2000; Moore 2004; Vila et al. 2007). However, to date, the focus has been on environmental damage of unmanaged systems (e.g. Mooney and Hobbs 2000) and not agriculture per se. For example, in the most recent national assessment of climate change impacts on the United States (Karl et al. 2009), invasive species are not considered in the chapter on agriculture. Yet, at present, it is acknowledged that invasive species can, and do, limit agricultural productivity (e.g. Table 1). Even for assessments that link the issue of climate change to food security (e.g. Battisti and Naylor 2009; Lobell and Field 2007; Lobell et al. 2008) the role of invasive species is not considered. Given the number of food riots which occurred in 2008, and the recognition that food scarcity may be associated with extreme climatic events, it seems imperative to us that we begin to examine how human-induced climatic variables may alter the damage related to the introduction and spread of invasive species in agriculture.

As such, the current review is our attempt to address those aspects of anthropogenic climate change that are likely to impact three categories of invasive species pests of critical significance to agriculture: plant pathogens, insects, and weeds. It can be argued that such climatic forcings are also likely to change endemic pest species as well. However, we would emphasize that endemic pests are much more likely to have antagonists and natural enemies in their naturalized habitat (Torchin et al. 2003). In contrast, invasive pests in new geographical ranges tend to be limited more by climate than by biotic interactions (Scherm and Coakley 2003).

In the current review, our specific goals are to examine the probable and potential links between (1) climate change and invasive species establishment, dominance and spread; and (2) climate change and potential changes in the prevention, control, and eradication of such species. By doing so, we hope to begin a synthesis and assessment of potential threats in regard to agricultural productivity and food security, and to devise a suitable strategy to mitigate or avoid these effects. We hope that such a strategy will: (1) emphasize areas of scientific uncertainty that require greater attention and experimentation; and (2) devise preliminary recommendations to adapt agricultural practices so as to reduce the negative impact of invasive species. We recognize that given the scarcity of available data any review is likely to be

tentative. However, we feel that sufficient published data are now available to derive a preliminary set of key scientific and policy recommendations that assess the potential vulnerability of U.S. agriculture to the risks posed by anthropogenic climate change and invasive species.

2 Human induced climate change: a brief review

Increasing human populations necessitate increasing resources, particularly energy and food. As the global demand for these necessities intensifies, fossil fuel burning and deforestation by humans will continue to be sources of atmospheric carbon dioxide. Since 1958, atmospheric carbon dioxide has increased by ~24% to a current level of 385 parts per million (ppm; IPCC 2007). Recent data indicate that atmospheric levels of carbon dioxide have risen 35 percent faster since 2000 than scientists had predicted (Canadell et al. 2007), due, in part, to the planet's decreased ability to re-absorb emitted carbon. Current projections indicate a CO₂ concentration ([CO₂]) between 600 and 1000 ppm by the year 2100 (IPCC 2007).

The documented increases in atmospheric [CO₂] will change the biology of invasive agricultural diseases, insects and weeds in two elementary ways. The first change is associated with climate stability, or the abiotic changes in the physical environment. For example, the recent increases in atmospheric [CO₂] have been accompanied by documented anthropogenic increases in other radiation trapping gases, including methane (CH₄; 0.9% increase per year), nitrous oxide (N₂O) (0.25% per year), and chlorofluorocarbons (CFCs; 4% per year). Recent evaluations by the Intergovernmental Panel on Climate Change (IPCC 2007) based, in part, on an assessment by the U.S. National Academy of Sciences, indicate that the rise of [CO₂] and associated "greenhouse" gases could lead to a 3 to 12°C increase in global surface temperatures, with subsequent consequences on weather patterns, particularly precipitation frequency and amounts as well as the occurrence of extreme weather events (IPCC 2007). The second likely consequence is associated with the [CO₂] "fertilization" effect on plant biology. The colonization of plants on land occurred at a time when atmospheric [CO₂] appears to have been four or five times the present concentration (Bowes 1996). The recent and projected increases in atmospheric carbon dioxide represent a rapid global increase in an essential abiotic resource, exceeding anything plants have experienced for many millions of years (Pearson and Palmer 2000; Crowley and Berner 2001). Numerous reviews and meta-analyses (e.g. Ainsworth et al. 2002), indicate that recent and projected increases in anthropogenic [CO₂] are likely to stimulate photosynthesis, growth and reproduction for a wide range of plant species. Such changes in plant biology, in addition to directly impacting invasive weed species, will likely have an indirect effect on invasive insect and pathogen relationships with their plant hosts.

Climate change is not the only global change that is occurring. One can argue that widespread regional changes in land use, nitrogen deposition, and tropospheric ozone are also factors of consequence with respect to invasive agricultural species. However, for purposes of the current review, we wish to focus on *global* climatic factors, specifically rising [CO₂], increasing surface temperature, and the likely instability of weather/precipitation patterns.

3 Invasive pathogens

Pathogens are considered among the most important invasive species for plants and livestock. Between 1940 and 1970, fewer than five non-indigenous plant pathogen species invaded the U.S. per decade (National Research Council 2002). By the early 1990s, an estimated 239 species of non-indigenous plant pathogens had become established in the U.S., including a number of pathogens that are highly damaging to agriculture (Table 2). The increase in the number of exotic pathogens reflects a rising invasion pressure correlated with the increasing volume of global trade, as pathogens arrive on infested or infected plant materials. As global change intensifies, there are a number of potential environmental drivers that are likely to exacerbate the spread and establishment of invasive plant pathogens associated with agriculture, including the following:

Severe weather Asian soybean rust (rust), *Phakopsora pachyrhizi*, has the potential to inflict major damage to U.S. soybean production. Soybean yield reductions and production cost increases have been attributed to rust in Africa, Asia, Australia, and South America. *Rust* can infect over 95 species of plants, including soybeans, peas and beans. Soybean rust was detected in 15 U.S. states in 2006, but severe rust epidemics did not occur. By the end of 2006, the presence of rust had been confirmed in 42 counties in North Carolina, 28 counties in Arkansas, 27 in Alabama, 26 in Louisiana, 24 in Florida, 21 in South Carolina, 19 in Tennessee, 18 each in Kentucky and Virginia, 17 in Georgia, nine in Mississippi, eight in Illinois, seven in Texas, six in Indiana, and five in Missouri (Fig. 1). It is thought that fungal spores of *P. pachyrhizi* arrived from South America, carried by Hurricane Ivan in 2004 (Del Ponte et al. 2006). Warming sea temperatures have been projected with climate change, and while it is unclear if the number of storms will increase, potential increases in storm severity are expected (Webster et al. 2005). Greater winds associated with such storms could be an additional factor in the spread of soybean rust and other invasive pathogenic spores to agricultural areas.

Table 2 Examples of non-indigenous plant pathogens of agriculture introduced to, or first detected in, the United States since 1990 (updated from Scherm and Coakley 2003)

Pathogen	Disease	State or region	Reference
<i>Claviceps africana</i>	Sorghum ergot	Southern/central states	<i>Plant Disease</i> 82:356 (1998)
<i>Phakopsora pachyrhizi</i>	Soybean rust	Southern states	<i>Plant Disease</i> 89:774 (2005)
<i>Tilletia indica</i>	Karnal bunt	Southwestern states	<i>Plant Disease</i> 81:1370 (1997)
<i>Cucurbit aphid-borne yellow virus</i>	Cucurbit yellows	California	<i>Plant Disease</i> 77:1169 (1993)
<i>Oidium</i> sp.	Powdery mildew of tomato	California	<i>Plant Disease</i> 80:1303 (1996)
<i>Potato mop-top virus</i>	Triperte pomovirus	Maine	<i>Plant Disease</i> 87:872 (2003)
<i>Phytophthora porri</i>	Cabbage rot	Wisconsin	<i>Plant Disease</i> 78:1123 (1994)
<i>Plum pox virus</i>	Sharka	New York, Pennsylvania	<i>Plant Disease</i> 84:202 (2000)
<i>Xanthomonas axonopodis</i> Pv. Citri	Citrus canker	Florida	<i>Plant Disease</i> 85:340 (2001)

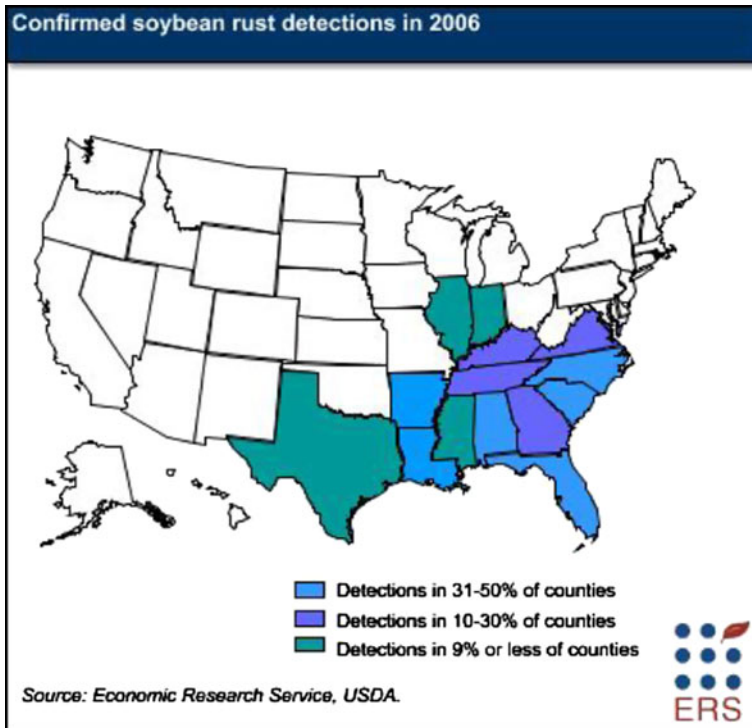
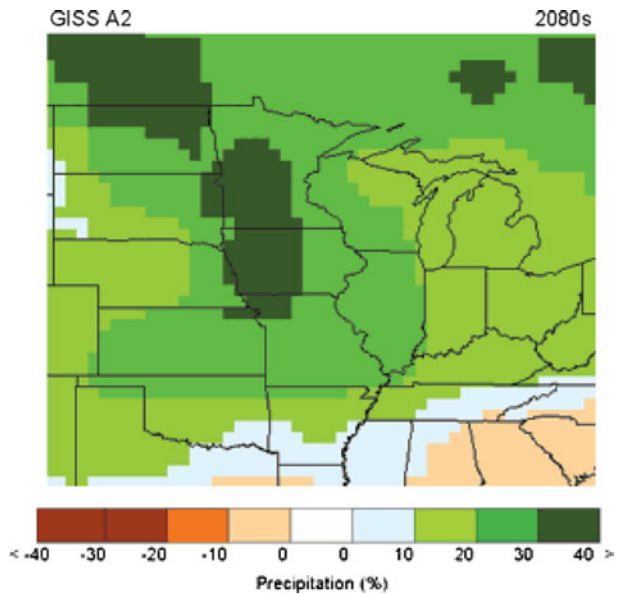


Fig. 1 States reporting confirmed detections of Asian soybean rust (*Phakopsora pachyrhizi*) in the continental United States As Of 2006. (Economic Research Service, ERS)

Water Stem, black or cereal rusts are an increasing concern for wheat growers globally. These diseases are caused by the fungus *Puccinia graminis* and infestation by this pathogen can result in significant loss of wheat yield. An epidemic of stem rust associated with a new wheat strain (UG 99) is currently spreading across Africa, Asia and the Middle East, provoking extensive concern. Losses are often severe (50% to 70%) over a large area and individual fields can be totally destroyed. Damage is greatest when the disease becomes severe before the grain is completely formed. In areas favorable for disease development, susceptible cultivars cannot be grown. The grain is shriveled due to the damage to the conducting tissue, resulting in fewer nutrients being transported to the grain. With respect to climate it is important to note that in addition to wind, urediniospores and aeciospores (such as stem rust) germinate when in contact with free water (Wanyera et al. 2006). Consequently, rain is necessary for effective deposition of spores in regional spore transport. A number of climatic models project increased precipitation and an increased frequency of extreme precipitation events in a number of areas where wheat is grown (Fig. 2) (Rosenzweig et al. 2002). Such increases in precipitation and a wetter environment are likely to contribute to the success of stem rust establishment since many fungi require free water not only for deposition but also for spore germination. Conversely, droughts could result in less pathogen spread, but would present their own problems with respect to crop yield.

Fig. 2 Projected changes in precipitation for the Midwestern United States based on Goddard Institute for Space Studies, projected “middle of the road” increases in anthropogenic greenhouse gases. The map shows the upper Midwest, around the great lakes region of the United States



Temperature Grey leaf spot (*Cercospora zea-maydis*) was first documented in the U.S. in 1924 (Ward et al. 1999). It remained virtually obscure until the early 1970s (Leonard 1974), then expanded rapidly in the corn belt from eastern Colorado to Wisconsin and Minnesota from 1988 through 1995. In addition to North America, *C. zea-maydis* has also expanded rapidly in other locations. It is now considered a pandemic disease of corn in Africa (Ward et al. 1999). Yield losses in infected fields can vary substantially (e.g. Table 1, Ward et al. 1999) but are usually considered significant (Ward et al. 1997).

Temperature, in addition to moisture, is a key factor in the growth and sporulation of a number of pathogens, including *C. zea-maydis*. While adaptation of no-till and increased corn residual matter probably helped to increase the spread of *C. zea-maydis*, lesion expansion increases exponentially with temperature up to 27°C at high humidity in controlled studies (Paul and Munkvold 2005). At present, average Spring temperatures in the Midwest are approximately 17°C, and even a small increase in surface temperatures could have a large impact on the colonization and sporulation rates of *C. zea-maydis* (Paul and Munkvold 2005). The most recent IPCC report (IPCC 2007) projects a 1.1 to 6.4°C increase in global surface temperature by the end of the current century with the average rate of warming over each inhabited continent likely to be at least twice as large as that experienced during the twentieth century. In addition to any direct effect of increasing temperature, seasonal temperatures are also projected to rise disproportionately faster during the winter (IPCC 2007). Winter is a significant factor in pathogen mortality, with more than 99% of pathogen populations experiencing mortality (Burdon and Elmqvist 1996). Rising winter temperature may remove this thermal limitation for pathogen morbidity with a subsequent increase in the range and distribution of *C. zea-maydis* and other plant pathogens.

Carbon dioxide The current and projected increases in atmospheric [CO₂] will not affect pathogens directly. However, plant hosts per se are likely to respond directly to rising carbon dioxide; thus, a number of host–pathogen interactions are possible. For example, kudzu (*Pueraria montana* var. *lobata*) is a leguminous vine established on 3 million hectares in North America, principally in the southeastern U. S. It can serve as an alternative host for Asian soybean rust (see above). Kudzu has been shown to be directly stimulated by rising atmospheric levels of [CO₂] (Sasek and Strain 1988). CO₂ induced increases in the kudzu canopy could potentially trap more spores of Asian soybean rust, with a greater dissemination and distribution of the pathogen.

There are a number of recognized [CO₂] induced changes that could, potentially, alter host–pathogen interactions in ways difficult to predict. At the leaf level, CO₂ induced reductions in stomatal aperture could reduce infection of stomatal inhibiting pathogens such as *Xanthomonas* (Rudolph 1993). The *Xanthomonas* genus is associated with a number of invasive pathogens (e.g., *X. axonopodis* pv. *citri*). Similarly, CO₂-induced changes in leaf surface characteristics such as epicuticular waxes or leaf thickness could reduce disease incidence by pathogens that infect via direct penetration (Hibberd et al. 1996). Conversely, CO₂-induced changes in stomatal aperture could increase leaf water content with a subsequent promotion of foliar fungi (Thompson and Drake 1994), while CO₂ stimulation of photosynthesis could increase leaf carbohydrate and promote growth and sporulation once infection occurs (Hibberd et al. 1996). Increased fungal fecundity (spores produced per lesion area) have been reported to occur at elevated [CO₂] for *Colletotrichum gloeosporioides* (Chakraborty et al. 2000). At the whole plant level, stimulation of plant biomass by increasing [CO₂] would increase the mass of host tissue for infection (e.g. kudzu and Asian soybean rust). Conversely, larger plants could tolerate more severe levels of infection without yield loss. In addition, it is possible that elevated CO₂ could increase the production of secondary defensive compounds which could aid in reducing pathogenesis (Runion et al. 1999). At the plant community level, CO₂ induced increases in plant density and height could increase humidity within the crop canopy, promoting growth and sporulation of most leaf infecting fungi (Scherm and Coakley 2003).

4 Invasive insects

Invasive insects are among the most recognized vectors of agricultural damage on a panoptic scale. For example, introduction of the boll weevil (*Anthonomus grandis*) from Mexico at the beginning of the twentieth century resulted in billions of dollars of damage and the almost complete eradication of the cotton crop in the U.S. The red imported fire ant (*Solenopsis invicta*) arrived at the port of Mobile, Alabama from sub-Amazonian South America in the 1930–40s and expanded through the Southeastern U.S. The physiology and behavior of the ant has allowed it to survive both drought and flood conditions; it has effectively expanded its range to include more than 300 million acres in 13 states and Puerto Rico since its introduction (Jeter et al. 2002). As with pathogens, almost all invasive insect introductions are likely to be through trade. However, their establishment, spread and biological success are likely to be altered by climatic change in a number of exceptional ways.

Severe weather The soybean aphid (*Aphis glycines*) was first reported in Minnesota in 2001 and by 2003 had spread to 21 states and three Canadian provinces. Damage to soybean is still being assessed, but recent data suggest that, depending on the level of infestation, yield losses up to 50% can occur (Beckendorf et al. 2008). Like many other insects, wind is a significant factor in distribution and colonization of the soybean aphid. Consequently, climate change projected increases in storm severity could augment the number of species and distance traveled by invasive insects. For example, the longest weather associated migration of an insect is that which occurred in 1988 when desert locusts from Africa were found in Caribbean islands and the east coast of South America (Rosenberg and Burt 1999). The locusts were transported on a sub-tropical low pressure wave and the resulting hurricane for a distance of 4,500 km. Thus, it is conceivable that invasive insects from Africa, South America and the Caribbean could be blown into the U.S. via hurricanes and become established. This may be the way that the Cactus moth (*Cactoblastis cactorum*) entered southern Florida from the Caribbean Islands a decade ago. This invasive insect has expanded its range dramatically along the southeastern and gulf coasts of the U.S. and is of very significant concern to our trade partners in Mexico who have a significant cactus agro-business. The situation with this pest is of such magnitude that both USDA Agricultural Research Service (ARS) and USDA-Animal and Plant Health Inspection Service (APHIS) are engaged in widespread monitoring of its potential range and are deeply concerned about the impact of east–west hurricanes in rapidly dispersing this species towards Mexico.

Water Swede midge (*Contarinia nasturtii*) is a Eurasian pest of crucifers, especially those grown in clay soil. The Swede midge is an exotic cecidomyiid fly, one of a diverse family that has over 1,200 species native to North America. In 2001, Canadian researchers discovered that this invasive was causing damage to 85% of the broccoli crop in Ontario. It was detected in Niagara County, NY in September 2004. As of 2007, the invasive had been reported in 21 counties in New York. Cornell University scientists estimate that New York could lose a major portion of their \$87 million broccoli crop in addition to the state's \$6 million yield in other cruciferous crops if the swede midge is not properly managed. A recent study on the distribution and abundance of this invasive in the western portion (Prairie ecotone) of North America indicated that above average precipitation would be one factor in its spread (Olfert et al. 2006). Precipitation may also play an important role in the spread of red imported fire ants (*S. invicta*), an invasive insect which can damage citrus and livestock (Jeter et al. 2002). At present, its westward expansion is limited by moisture, but changes in frequency and distribution of precipitation associated with climate change could facilitate their spread. In general, precipitation extremes such as droughts and floods are associated with climatic change but also with changes in insect behavior. For example, flooding may be a factor in negatively impact soil-dwelling insects (Watt and Leather 1986), while drought could increase plant carbohydrate concentration making host plants more attractive to insects.

Temperature The European corn borer (*Ostrinia nubilalis*; ECB) was first discovered in New England in the early twentieth century. This invasive insect has spread into Canada and westward to the Rocky Mountains (Capinera 2002). It can attack corn and any herbaceous plant with a stem large enough for the larvae to enter,

hence it can be a significant factor in yield loss for a range of agricultural crops. Temperature is a major regulator of corn borer development. Accumulated temperature units (degree-days, base 50) can be used to predict the seasonal occurrence of the subsequent life stages for ECB. Similarly, Africanized bees moving northward through South and Central America can readily capture both feral and managed European honey bee colonies with subsequent impacts on fruit production. As with ECB, temperature can play a major role in the northward migration of this invasive species (Fig. 3).

Given that temperature is among the central regulating factors controlling the development and fecundity of invasive insects, climate warming is likely to increase their geographical distribution (both in latitude and altitude) and/or enhance their capacity for over-wintering. While long-term records are rare, aphid flight activity has been continuously recorded in the United Kingdom (U.K.) since 1964. These data indicate accelerated flight phenology by 3–6 days, corresponding to an increase of 0.4°C in mean temperature from 1964 (Fleming and Tatchell 1995). Similar analyses across a number of aphid species project an advance in the timing of their spring migration by 2 weeks for every 1°C increase in winter temperature (Harrington 2002). The range expansion of invasive insects will also depend on the temperature sensitivity of the host plant(s), and is likely to be species specific. Still, if

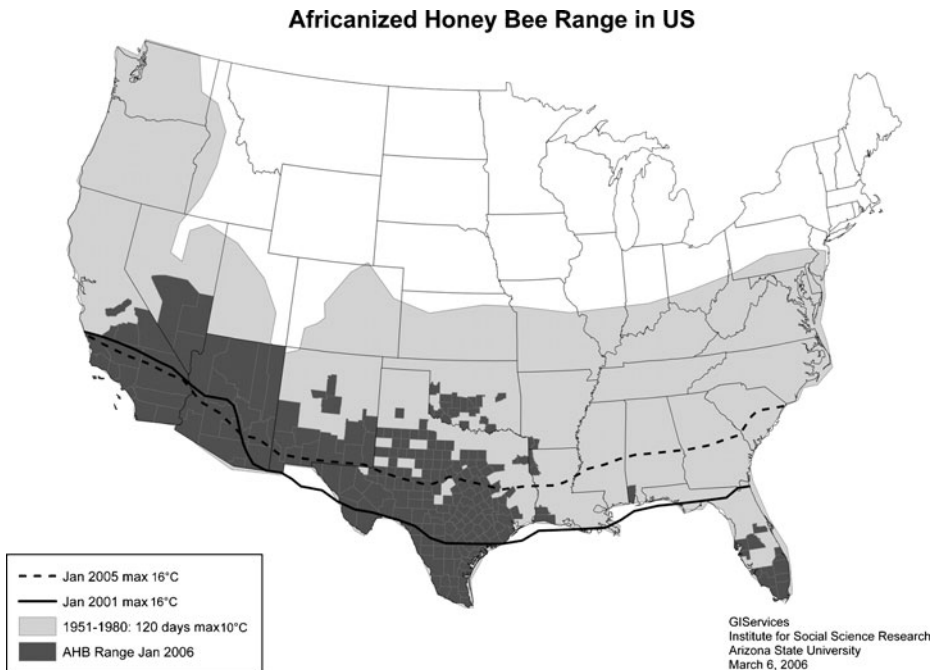


Fig. 3 Current and projected range of Africanized honey bees as a function of air temperature. The *black area* is where the Africanized honeybee is currently. The *grey area* is the area that could support the bee if temperatures increase ca. 4°C (120 days where the maximum temperature is above 10°C). The *filled line* is the limit where the maximum temperature was 16°C maximum in January 2001 and the *dashed line* shows the area where the maximum January temperature was 16°C in 2005

temperature expands the range of invasive insects, this could bring them into contact with other potential crop hosts present at distant locations. This has been suggested by Cannon (1998) who examined the spread of invasive insects in northwestern Europe and the implications for insect invasions in the U.K. While not specific to invasive insects per se, it is worth noting that insect herbivory has increased sharply during previous geological warming periods (Curran et al. 2008).

Carbon dioxide As with pathogens, it is more likely that invasive insect biology will be impacted by the direct physiological effects of $[\text{CO}_2]$ on host plant metabolism. Atmospheric $[\text{CO}_2]$ induced changes in plant metabolism at the leaf level are likely to include increased C:N ratios, altered concentrations of defensive (allelopathic) compounds, changes in carbohydrate and fiber content, and increased water content. At the whole plant level, changes in allometry and phenology can influence time to flowering, flower number and pollen production (Ziska and Bunce 2006). At the level of community, plant competition may be altered with a resultant change in species number or species diversity (Ziska and Goins 2006). Overall, these changes could alter invasive insect–host interactions by either altering the insects feeding behavior or by altering plant defenses.

Leaf sucking insects could be affected by qualitative leaf changes associated with rising $[\text{CO}_2]$. Mites number among the worst invasive species (e.g. rust mite, *Aceria anthocoptes*, gall mite, *Aceria malherbae*). For mites, increased epidermal or leaf thickness could reduce infestations (Joutei et al. 2000) as could CO_2 -induced increases in non structural carbohydrates (Heagle et al. 2002). Phloem feeders such as invasive aphids (e.g., the mealy plum aphid, *Hyalopterus pruni*, the Russian wheat aphid, *Diuraphis noxia*) could also be less responsive to CO_2 induced changes in leaf quality. However, increases in population density have been observed for invasive aphids, such as the green peach aphid (*Myzus persicae*) on plants grown at elevated $[\text{CO}_2]$ (Bezemer et al. 1998). Increases in nymph production have been observed for the invasive foxglove aphid (*Aulacorthum solani*) on bean (*Vicia faba*; Awmack et al. 1997). The basis for the increase performance of these invasive aphids on elevated $[\text{CO}_2]$ grown plants is uncertain. At the whole plant and community level, increased leaf damage could be compensated by increased leaf production at higher $[\text{CO}_2]$, but it is unclear if this would also stimulate additional insect feeding. The impact of increased $[\text{CO}_2]$ on induced changes in secondary defensive compounds, particularly an increase in C:N ratio, have not been adequately resolved (Ziska and Runion 2007). Recent data have suggested that future levels of carbon dioxide could inhibit plant defenses in soybean when attacked by an invasive insect, Japanese beetle (*Popillia japonica*; Zavala et al. 2008). While such insects are not a significant problem on soybean production per se, they may limit yields when present with other leaf-eating pests.

5 Invasive weeds

Among invasive pests, weeds lead to the greatest direct economic losses and the greatest control costs in crop production (Table 1). Moreover, such estimates do not consider other peripheral damage (e.g. property) related to changes in fire frequency and fire intensity induced by the spread of flammable invasive species such

as cheatgrass (*Bromus tectorum*; Smith et al. 1987); they do not consider reductions in rangeland productivity associated with the spread of such invasive weeds as Canada thistle (*Cirsium arvense*) or spotted knapweed (*Centaurea maculosa*); nor do they consider changes in water rights, water quantity or quality associated with the spread of aquatic invasives such as water hyacinth (*Eichhornia crassipes*). Given the geographical extent of invasive weeds and their impact, what aspects of climate change are likely to alter their distribution, establishment and damage?

Severe weather Wind is a widely recognized means for seed dispersal in weed species, including the invasive weeds yellow salsify (*Tragopon dubuis*), spotted knapweed (*Centaurea biebersteinii*), leafy spurge (*Euphorbia esula*), orange hawkweed (*Hieracium aurantiacum*), Canada thistle (*Cirsium arvense*), perennial sowthistle (*Sonchus arvensis*), and musk thistle (*Carduus nutans*) inter alia. Any increase in severe weather; particularly wind, is likely to aid seed dispersal of these and other invasive weeds. In addition, rising [CO₂] levels may also help in wind dispersal indirectly by either increasing the height of the plant or by increasing plant size. The latter would increase the number of seeds for whole plants or plant parts that distribute seed by wind (e.g. diffuse knapweed). Given the ability of some invasive weeds to produce seed (e.g. spotted knapweed can produce up to 25,000 seeds per plant) increases in weather extremes could have a significant effect on the rate and range of invasive weed dispersal.

Water Although moisture is a recognized factor in weed seed establishment and final plant size, little is known about interactions between altered precipitation and invasion. Recent experimental results from the USDA-ARS laboratory in Ft. Collins (Blumenthal et al. 2008) suggest that increases in snowfall or changes in snowfall variability may exacerbate the invasion of forbs in mixed-grass prairie ecosystems. Changes in prairie vegetation have implications for range management, particularly forage availability.

At the whole plant level, changes in precipitation and water availability are likely to effect invasive weeds of agricultural importance in a number of ways. Rangeland invasive weeds that impact grazing, from cheatgrass (*Bromus tectorum*) to yellow star thistle (*Centaurea solstitialis*), depend on moisture for seed germination. More moisture is associated with over-wintering and increased seed production for both species (Patterson 1995a). However, both species are also drought adapted, cheatgrass being able to complete its life-cycle quickly on available moisture, whereas star thistle can develop a deeper root system than many native plants. Timing of precipitation may also be critical. For example, greater Spring-time moisture associated with El Nino events may expand cheatgrass habitat (Bradley and Mustard 2005). Overall, changes in the timing and amount of precipitation are likely to alter a number of biological aspects of invasive weeds including germination, plant size, seed production, and the distribution of water borne seeds. At the community level it is probable that precipitation extremes will favor competition between invasive weeds and crops with subsequent negative effects on crop productivity (Patterson 1995b).

Temperature Along with precipitation, temperature is a primary abiotic variable that affects invasive weed biology. The probable impact of rising temperatures favoring the expansion of invasive weeds into higher latitudes is of particular concern.

Many of the worst invasives for warm season crops in the Southern U.S. originated in tropical or warm temperature areas; consequently, northward expansion of these invasives may accelerate with warming (Patterson 1993). For example, itchgrass (*Rottboellia cochinchinensis*), an invasive weed associated with significant yield reductions in sugarcane for Louisiana (Lencse and Griffin 1991), is also highly competitive in corn, cotton, soybean, grain sorghum, and rice systems (e.g. Lejeune et al. 1994). The response of this species to a 3°C increase in average temperature stimulated biomass and leaf area by 88% and 68% respectively (Patterson et al. 1979), suggesting projected increases in maximum growth for the Middle Atlantic States (Patterson et al. 1999). Northward migration of other invasive weeds, such as cogongrass (*Imperata cylindrica*) and witchweed (*Striga asiatica*), is also anticipated (Patterson 1995a). Conversely, additional warming could also restrict the southern range of other invasive weeds such as wild proso millet (*Panicum miliaceum*) or Canada thistle (Ziska and Runion 2007).

One of the most interesting forecasts regarding global warming and an invasive weed was made almost two decades ago in regard to Northward migration of kudzu (*Pueraria lobata*), an ubiquitous invasive of the Southeastern U.S. Tom Sasek and Boyd Strain at Duke University observed that the latitudinal distribution at that time was limited to regions South of the Mason–Dixon line by low winter temperatures of -15°C (Fig. 7 in Sasek and Strain 1990). A more recent evaluation of current distribution suggests that kudzu has moved northward. There are now Midwestern populations (Fig. 4a) and the migration appears to be associated with an increase in minimum winter temperatures (Fig. 4b). How much of this latitudinal migration is solely attributable to increasing winter temperatures is unclear, but the Northward spread of kudzu is consistent with the Sasek and Strain hypothesis.

At the community level, if temperature changes the range of both agronomic crops and invasive weeds it would have significant implications for weed/crop competition and productivity. For example, estimated crop losses due to weeds without the use of herbicides are substantially larger in the South than in the North in both corn (22 vs. 35%) and soybeans (22 vs. 64%; Bridges 1992). This may be associated with the southern presence of perennial invasive weeds (e.g. itchgrass) which are currently limited in northern states by low winter temperatures (Bunce and Ziska 2000). Crop-invasive competition could also be impacted with differential responses to rising temperatures and floral reproduction or differences in soil temperature and emergence rates (Ziska and Runion 2007).

Overall, the projected warming may be exceeding maximum rates of plant migration observed in post-glacial time periods (Malcolm et al. 2002), resulting in preferential selection for the most mobile plant species. A number of characteristics associated with long-distance dispersal are commonly found among invasive plants (Rejmanek 1996) suggesting that they will be among the fastest to migrate with increasing temperatures (Dukes and Mooney 2000).

Carbon dioxide The recent and projected increase in atmospheric carbon dioxide will directly affect invasive weed biology. Projected increases in atmospheric $[\text{CO}_2]$ have been shown to significantly stimulate growth and development in hundreds of plant species (see Kimball 1983; Kimball et al. 1993; Poorter 1993). Given that plant photosynthesis and growth are stimulated by rising $[\text{CO}_2]$, what is the likely response of invasive weeds of agricultural significance?

An increasing number of studies have begun to quantify the response of individual invasive species to future, projected increases in atmospheric carbon dioxide concentration (Huxman et al. 1999; Dukes 2002; Ziska and George 2004; Rogers et al. 2008). For example, Canada thistle, showed a relatively strong growth response, increasing by ~70% with elevated CO₂ (Table 3). This is potentially worrisome given that Canada thistle is ranked as the number one invasive agronomic weed in North America (Skinner et al. 2000). Although most research has examined the responses of plant to future [CO₂] levels, it is important to emphasize that present [CO₂] already represents a significant increase over pre-industrial levels. Even though a limited amount of data is available, the average response of invasive weeds to [CO₂] changes during the twentieth century is striking, increasing by ~90%, an increase significantly higher than for native species (see Table 3 in Ziska and George 2004).

Examining the impact of recent or projected increases in [CO₂] on individual invasive weeds provides a sense of the potential increases in their growth and reproduction. However, it is the aggregate response of invasive weeds within a plant community that should provide the best estimate of whether rising [CO₂] is altering the success of these species. Unfortunately, actual field data are rare, with only a handful of studies that have addressed this question. For native communities, Dukes (2002) reported a 70% increase in yellow star thistle biomass relative to a 30% increase in native plant biomass with a doubling of [CO₂]. Similar preferential growth of other invasives with elevated [CO₂] in plant communities has been reported for Japanese honeysuckle (*Lonicera japonica*; Belote et al. 2003), English laurel (*Prunus laurocerasus*; Hattenschwiler and Korner 2003), and red brome (*Bromus madritensis*; Smith et al. 2000).

Although these data have implications for agriculture, particularly for range management, they do not address the impact of invasive agronomic weeds that are wild relatives of crop species grown in the U.S. These weeds (e.g. shattercane,

Fig. 4 a. Shift in northernmost detection of kudzu (*Pueraria lobata*) from 1971 to 2006. The 1971 line is from Clyde Reed, “Common Weeds of the United States” a USDA-ARS publication. Estimates of kudzu distribution in 2006 for Nebraska, Missouri, Illinois, Indiana, Ohio and Pennsylvania were evaluated using three separate sources: (a) National Resource Conservation Service NRCS), database of invasive U.S. Species (plants.usda.gov/java/profile?symbol=PUMO) (b) the National Agricultural Pest Information Service (NAPIS) in cooperative agreement between the Animal Plant Health Information Service (APHIS) and Purdue University as part of their Cooperative Agricultural Pest Survey (CAPS) program (ceris.purdue.edu/napis/pests/weeds/imap/kudzu.html), and (c) the Department of Natural Resources (DNR) for the states of Pennsylvania, Ohio, Indiana, Illinois, and Missouri, including the publication of “The Green Plague Moves North” by the Illinois DNR. At least one county was chosen as the northernmost county within a state reporting a new kudzu population in order to determine the northernmost range. Counties within a given state were only included if the presence of kudzu was verifiable from at least two of these sources. Southeastern Nebraska and Western Pennsylvania were considered the end points of the Midwestern populations. Specific counties sampled were: Otoe Co (NE), Reynolds, Phelps and Howard Co (MO), Fayette, Shelby, Macon and Woodford Co (IL), Vanderburgh, Martin, Owen and Johnson Co. (IN), Belmont, Athens, Scioto Co. (OH), Allegheny CO. (PA). **b.** Average temperature (+95% confidence interval) for the coldest recorded day of year for 16 counties along northern limit for kudzu (*Pueraria lobata*; Fig. 4a) in the Midwestern United States, (1972–2006). Meteorological data for a given county was evaluated with respect to long-term multi-year data availability, and proximity to urban heat islands. County meteorological data were evaluated from a larger database contained within the National Climatic Data Center (NCDC) in Asheville, NC (hurricane.ncdc.noaa.gov) from 1972 through 2006. An average temperature of -15°C has been suggested as the lower temperature limit for overwintering in kudzu (Sasek and Strain 1990)

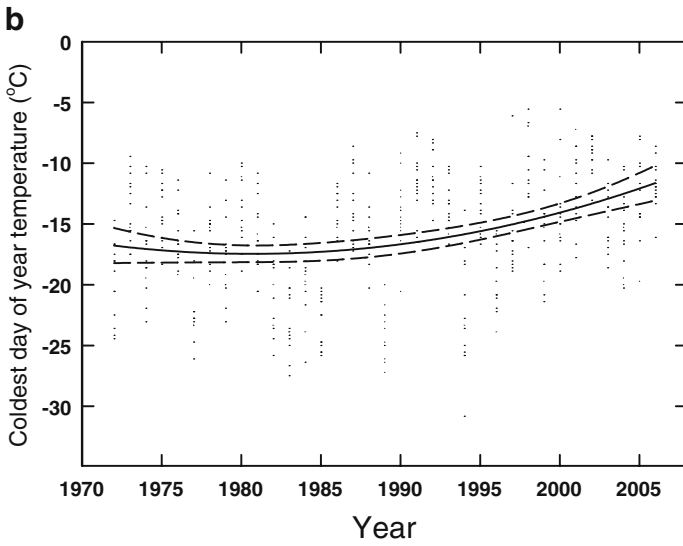


Table 3 Overview of potential response of selected noxious, invasive weeds to either recent or projected changes in the concentration of atmospheric carbon dioxide [CO₂]

Species	Common name	Recent	Projected	Reference
<i>Albutilon theophrasti</i>	Velvetleaf	1.3–1.58	0.88–2.29	Bazzaz et al. (1989), Bunce (2001), Dippery et al. (1995), Morose and Bazzaz (1994)
<i>Avena fatua</i>	Wild oat	NA	1.84	Freeden and Field (1995)
<i>Brassica kaber</i>	Wild mustard	NA	1.27–1.30	Wayne et al. (1999)
<i>Bromus madritensis</i>	Red brome	NA	1.09–1.51	Huxman et al. (1999), Smith et al. (2000)
<i>Bromus tectorum</i>	Cheatgrass	NA	1.39–1.93	Poorter (1993), Smith et al. (1987)
<i>Centaurea maculosa</i>	Spotted knapweed	2.15	1.46	Ziska (2003a)
<i>Centaurea solstitialis</i>	Yellow star thistle	1.87	1.15–1.68	Dukes (2002), Poorter et al. (1996), Ziska (2003a)
<i>Cirsium arvense</i>	Canada thistle	1.58–2.84	1.69–1.70	Ziska (2002, 2003a, b)
<i>Convolvulus arvensis</i>	Field bindweed	1.85	1.36	Ziska (2003a)
<i>Datura stromonium</i>	Jimsonweed	NA	1.76	Garbutt and Bazzaz (1984)
<i>Elytrigia repens</i>	Quackgrass	NA	1.12–1.68	Tremmel and Patterson (1993), Ziska and Teasdale (2000)
<i>Euphorbia esula</i>	Leafy spurge	1.95	1.43	Ziska (2003a)
<i>Hydrilla verticillata</i>	Waterthyme	NA	1.04–1.46	Chen et al. (1994)
<i>Lonicera japonica</i>	Japanese honeysuckle	NA	2.34–3.60	Belote et al. (2003), Sasek and Strain (1991)
<i>Prosopis glandulosa</i>	Honey mesquite	1.53	1.11–1.37	Polley et al. (1994, 1996, 2002)
<i>Pueraria montana</i>	Kudzu	NA	1.20–2.15	Sasek and Strain (1988)
<i>Sonchus arvensis</i>	Perennial sowthistle	2.09	1.66	Ziska (2003a)

Recent changes refer to the increase in [CO₂] from 250–300 ppm (sub-ambient) to 360–400 ppm (current ambient concentration); projected changes refer to the increase in [CO₂] from 360–400 ppm to 600–800 ppm, a value expected to occur before the end of the current century. Values given are the ratio of plant biomass produced at the two [CO₂] comparisons (i.e. a value of 1 indicates no response to increasing CO₂ while a value of 2 indicates a doubling in biomass)

NA not available

wild rice) are considered among the most troublesome because they are genetically similar to the crop, and many of the farming practices (planting date, fertilizer requirement, etc.) benefit the growth and reproduction of both the domestic crop and its wild relative. To date, we could find only one comparative study on cultivated and wild rice lines, indicating that wild lines may be more responsive to [CO₂] than cultivated lines (Ziska and McClung 2008).

Overall, the available data, while limited, suggest an important role of recent and projected atmospheric [CO₂] increases as a potential factor in the differential selection of invasive weeds. The greater response of invasive weeds to rising [CO₂] is consistent with the resource management hypothesis of Blumenthal (2005, 2006) and recent comparisons of invasive species and their indigenous congeners (Song et al. 2009): i.e., that fast growing weedy species that benefit more from human-induced changes such as CO₂ enrichment will also benefit most from escaping their natural enemies. If so, this suggests that rising CO₂ could favor invasive species relative to functionally similar native species. This has obvious implications for CO₂-induced changes in the establishment and spread of invasive weeds, with increasing competition and production losses in rangelands and crops.

6 Summary

We have presented, whenever possible, data on how global abiotic parameters associated with climatic change are likely to affect the biology of invasive pathogens, insects and weeds and the subsequent consequences with respect to crop production. However, we recognize that, at best, these descriptions are limited to a given level of biological organization (e.g., leaf), usually for a specific host–crop interaction and are not always applicable to a community or region. In our view, there is a clear need to scale-up these preliminary results as a means to determine the vulnerability of U.S. agriculture to invasive species in an uncertain climate. One impetus for doing so is to prevent the unexpected. For example, the role of temperature and climate change in the spread of invasive insects (e.g. pine bark beetle) and subsequent destruction of forests while not foreseen, is now widely acknowledged, (e.g. Kurz et al. 2008); yet, a similar analysis of the vulnerability of agricultural productivity in North America to rising temperature and invasive insects has not, to our knowledge, been conducted. Overall, while we recognize that a number of significant impacts associated with temperature, extreme weather events and carbon dioxide are likely, the interaction between these abiotic parameters, invasive biology and agricultural productivity remains, in our view, inadequately characterized.

7 Invasive species management: preparing for the future

At present there are a number of means by which invasive species are tracked, monitored and their impact mitigated or minimized. Here we discuss how the current management strategies could be transformed to meet the challenge of an uncertain climate.

Detection/Prediction Early detection and rapid response (EDRR) remains a cornerstone of the USDA's Animal Plant Health Inspection Service (APHIS), Natural Resources Conservation Service (NRCS) and US Forest Service (USFS) efforts to detect and respond to invasive species. This approach is applied at the entry level in over 330 U.S. airports and harbors to prevent the introduction of invasive species, and to address the eradication of recognized nascent invasive populations. The approach is also used in the management of invasive species in 192 million acres of national forests and grasslands. NRCS technical assistance staff provides guidance and expertise on invasive species management to private landowners, including farmers and ranchers. Much of the early detection for agriculture occurs at the state or county level with extension programs and/or staff in the state departments of agriculture (DA) or natural resources (DNR) who are responsible for identifying and reporting the appearance of invasive species. For example, the first detection of Asian soybean rust was by the Louisiana Department of Agriculture and Forestry in 2004. The USDA's Natural Resource Conservation Service (NRCS) maintains the PLANTS database (www.plants.usda.gov) which is a primary resource for helping private and public landowners in detecting invasive weeds.

A number of models are used to categorize potential invasive threats; (for a partial listing of available models go to <http://invasivespecies.nbio.gov/models.html>).

These models fall along three broad categories: (a) Comparison of the climatic and geographical ranges in native and introduced species to determine their potential as invasives (e.g. CLIMEX, Sutherst et al. 1999); (b) Evaluation of common traits by taxa among organisms known to be invasive; and, (c) A “risk-assessment” approach that evaluates intrinsic and extrinsic factors related to invasive success (e.g. Rejmanek 2000).

Remote sensing offers an additional tool to detect the occurrence of invasive species (e.g. Parker-Williams and Hunt 2004; Lawrence et al. 2005), particularly invasive plants. At present there are no general principles that can be used to determine a baseline presence of invasive species among co-occurring native vegetation at different amounts of plant cover. In addition, a number of invasive weeds may not be detectable with satellite or airborne remote sensing. Even the most obvious invasive weeds may not be evident at the initial stages of invasion, when only a few individuals are present. Therefore, additional study is needed at a landscape scale to develop predictive temporal geospatial models of invasive species occurrence, particularly for agricultural areas of consequence (e.g. Midwest). At present, the U.S. Geological Survey and ARS are leading research in this area (e.g. Graham et al. 2008; Anderson et al. 2004a, b).

Biological control Empirically, biological control of invasive species is likely to be affected by increasing atmospheric $[\text{CO}_2]$ and climatic uncertainty with respect to temperature and/or precipitation (Norris 1982; Froud-Williams 1996). It has been suggested (Gutierrez 2000) that climate, particularly temperature, would have differential effects on predator–prey relationships for insect pests, but it is unclear if this would apply to invasive insects where endemic predators may be absent. It seems likely that climatic variability, in addition to rising $[\text{CO}_2]$, would alter the efficacy of the biocontrol agent by altering the development, morphology and reproduction of the target pest. Direct $[\text{CO}_2]$ effects could also result in qualitative changes in the host plant (e.g. changes in C:N ratio) with subsequent effects on biocontrol efficacy. Overall, synchrony between the development and reproduction of potential biocontrol agents and invasive species is unlikely to be maintained with a greater incidence of climatic extremes. At present we could find no experimental data regarding the impact of a climatic change variable (e.g. CO_2 , warmer temperatures) on the efficacy of a biocontrol agent in agriculture. Such studies should be a principle focus of future research on biological control.

Physical control A primary method of weed control used in agriculture around the world is the physical removal of invasive weeds by humans, animals or mechanical means. The impact of climatic change and rising $[\text{CO}_2]$ on physical removal of invasive agricultural weeds has not been determined experimentally to our knowledge. It has been suggested that rising CO_2 levels could result in further below-ground carbon sequestration, particularly in root or rhizome growth of perennial weeds, with subsequent effects on increasing asexual reproduction (e.g. Rogers et al. 1994). Data for invasive weeds confirm this, indicating a significant increase in root to shoot ratio for four of five invasive species for recent increases in atmospheric carbon dioxide (Fig. 5). If greater below-ground growth for these invasives results in greater asexual reproduction, this will have a negative effect on physical weed control (e.g. plowing) since this type of control would increase weed spread.

Chemical control Rapid increase in chemical applications of pesticides during the 1950s and 60s brought with it the recognition that climate, particularly changes in temperature, wind speed, soil moisture and humidity, can influence the efficacy of chemical management (reviewed in Muzik 1976). For example, increasing temperatures and greater metabolic activity could increase herbicide effectiveness, while drought and a subsequent decline in growth rate could have the opposite effect. In general, pesticides are more effective when applied to plants that are rapidly growing and metabolizing under stress-free conditions.

At present almost no information is known regarding potential interactions between CO₂/climate change and the chemical management of invasive insects or pathogens. There are initial studies indicating a potential decline in chemical efficacy with rising [CO₂] and/or temperature for some weeds (Ziska and Goins 2006; Archambault 2007). For example, there are data for two invasive agricultural weeds, Canada thistle and quackgrass (*Elytrigia repens*), demonstrating that elevated levels of carbon dioxide can reduce herbicide efficacy (Ziska and Teasdale 2000; Ziska et al. 2004). The basis for the reduction in efficacy is unclear. In theory, rising [CO₂] could reduce foliar absorption of pesticides by reducing leaf stomatal aperture or leaf number or by altering leaf or cuticular thickness. In addition, [CO₂]-induced changes in transpiration could limit uptake of soil-applied pesticides. For weed control, the timing of pesticide application could be affected if elevated [CO₂] decreases the time that the weed spends in the seedling stage (i.e. the time of greatest chemical susceptibility). For Canada thistle, increasing [CO₂] appears to have induced greater below-ground growth of roots, diluting the active ingredient of the herbicide and making chemical control less effective (see Fig. 1 in Ziska et al. 2004). While incomplete, these data indicate an essential research need in determining methods by which chemical efficacy could be improved as CO₂ increases and the climate changes.

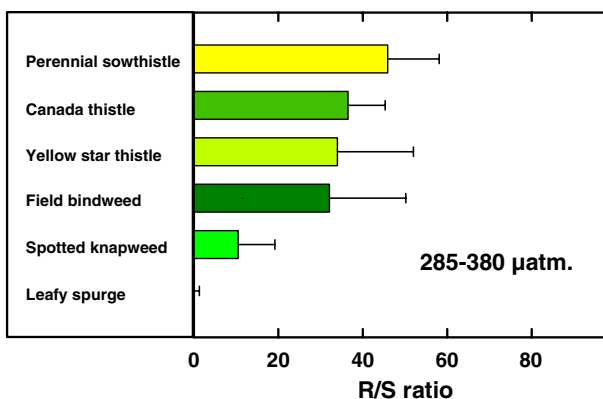


Fig. 5 Documented changes in the ratio of root to shoot biomass for six invasive agricultural weed species for the increase in atmospheric carbon dioxide concentration that occurred during the twentieth century. The six species are: Perennial sowthistle (*Sonchus arvensis* L.), Canada thistle *Cirsium arvense* (L.) Scop., Yellow star thistle (*Centaurea solstitialis* L.), field bindweed (*Convolvulus arvensis* L.), spotted knapweed (*Centaurea maculosa* Lam.) and leafy spurge (*Euphorbia esula* L.). Significant increases were observed for all species except leafy spurge. Data from Ziska (2003a, b)

8 Scientific uncertainties

Biological Most of the experimental data regarding global change on agricultural invaders have reported the impact of a single environmental factor even though a number of abiotic factors are likely to change concurrently. Changes in carbon dioxide, temperature and precipitation act at different spatial and temporal scales, and they complicate our general understanding of invasive species with respect to their biology and potential impact on crop production. For example, the invasive weed kudzu is known to respond strongly to rising carbon dioxide (Forseth and Innis 2004) and is likely to move Northward with warming temperatures (Sasek and Strain 1990). Kudzu is an alternate host for Asian soybean rust, an invasive pathogen. Consequently, the understanding of multiple climatic interactions on kudzu migration and fecundity will further our understanding of additional threats poised by Asian soybean rust. A number of studies are beginning to address potential interactions among climate variables with respect to invasive pests (e.g. Mitchell et al. 2003; Salinari et al. 2006) but specific studies related to climate interactions of agricultural invasives remain scarce particularly at the field level. Understanding such interactions is crucial to understand the biology and epidemiology of agricultural invasives as well as their potential ability to inflict crop losses.

Although genetic adaptation is an integral aspect of all living organisms, the potential evolutionary consequences of global change, particularly among invasive genera, have received little attention. There are a number of examples in the evolutionary literature that have documented biotic or abiotic induced changes in genetic adaptation (e.g. Lande and Shannon 1996; Travis and Futyuma 1993). This would suggest that anthropogenic climate change could also act as a driver for evolutionary adaptation. Insect-related studies documenting climate change induced adaptation are available for *Drosophila subobscura* (Rodriguez-Trelles and Rodriguez 1998). Chakraborty et al. (2000) has suggested similar changes for pathogens (e.g. *C. gloeosporioides*, Chakraborty and Data 2002). A single study has documented rapid genetic changes in field mustard (*Brassica nigra*) with drought (Franks et al. 2007). However, our understanding of anthropogenic, climate-driven evolutionary change, particularly gene flow and hybridization (Brasier et al. 1999) in agricultural invasives is almost non-existent. The exposure of invasive species to rapidly changing biotic and abiotic environments, with subsequent evolutionary opportunities, is likely to enhance the fecundity, range and probable impacts of such invasives (Scherm and Coakley 2003). This is of particular concern given the short generation time of many pests and their capacity for rapid evolutionary response to environmental extremes (e.g. Franks et al. 2007).

It is also important to recognize a similar response within agroecosystems themselves to anthropogenic climate change. Understanding such responses is essential to assess the likely vulnerability of these systems to new invaders and a critical step in devising suitable strategies to negate or lessen subsequent impacts. For example, if rising CO₂ is a factor in the stimulation of invasive weeds, can it also be used by breeders to improve existing agricultural cultivars to become more competitive against potential invasives? Could development of such cultivars lessen any climate-induced changes in productivity related to invasive plants? A recent study by Ziska and McClung (2008) suggests that red rice, an invasive weed of cultivated rice in the U.S., may also serve as a unique source of genes to increase the adaptability of

rice cultivars to climatic change. Efforts to select for crop lines tolerant to projected invasive pests that are likely to proliferate with climate change represents another means to reduce crop vulnerability. Such efforts could reduce the negative impact of invasive agricultural pests. However, at present almost nothing is known regarding potential opportunities to increase the adaptive capacity of agricultural species to such biotic threats in the context of a changing climate.

Forecasting The old adage is “Forewarned is forearmed”. Such an axiom certainly applies to invasive species in agriculture. Yet, long-term field observations to obtain real time-series data on movement and numbers of invasives are rare. Such monitoring could provide insight into changing populations and behavioral patterns in relation to communities and climates (Lawton 2000). Recently, the long-term ecological research (LTER) sites, originally designed to monitor ecosystems of interest to conservation, have also included preliminary data on community composition, invasive species, and global warming (Roy et al. 2004). The inclusion of additional information on climate and invasives for LTER sites is one means to increase baseline biodiversity information without incurring large costs. In addition to using existing data networks, the strategic placement of other monitoring sites would be invaluable. For example, transportation corridors may serve as means for rapid dispersment of invasive species (e.g. Gelbard and Belnap 2003; Tyser and Worley 1992). The placement of invasive monitoring stations along key transportation corridors, particularly near large ports, could be an efficacious strategy to identify new and rapidly spreading invasive threats. Temporal, geographical, and biological information regarding the demographics of a given invasive is an obvious factor in devising suitable containment or eradication strategies for that species. For example, the date of introduction is usually known for a given invasive, but monitoring data on the temporal range and rate of spread of that invasive species within a given country are scarce.

Reductionist experiments have almost exclusively been used to study individual invasive species in agroecosystems, usually involving a single crop. However, to adequately assess the utility of experimental data on invasive species establishment it becomes necessary to “scale-up” from the plot level (with one or two variables) to a geospatially significant area involving multi-variable interactions. Because methodological considerations make studying multi-trophic interactions for long-term, large-scale experiments difficult, models are frequently used to determine species dynamics and demographics in relation to anthropogenic climatic change at geographically relevant regions. Many of these models use a simplistic approach to species interactions usually focusing on single-host plant climatic interactions (e.g. Julien et al. 1995; Wharton and Kriticos 2004). To be able to forecast invasive species demographics on a geographical scale would require a means to assess multi-species interactions with respect to predation, competition, and facilitation—data which is rare or absent from the current literature. Some initial efforts are underway to address this, including a temperature by carbon dioxide experiment examining competition and invasion in rangelands (Jack Morgan, USDA-ARS, personal communication). Additional field experiments as well as data sharing and data synthesis between experimentalists and modelers are needed.

While monitoring and regional scale assessments of potential invasive threats is obviously critical, it is also useful to establish temporal demographic baselines in

order to determine potential climatic “tipping points” in invasive species populations within an agricultural system. The dynamics of any pest population are likely to ebb and flow over time, but identification of population demographics that represent a significant, non-recovering disruption in crop production are needed in regard to climate extremes of temperature, precipitation, etc. Therefore, invasive collection data should be upgraded to include dates of species capture so as to make temporal comparisons of projected climate uncertainty with stable climate baselines, typically 1961–1990 (IPCC 2007).

Management Better forecasting is obviously critical. New technical innovations or research that improves existing technology is also greatly desired such as the development of specific spectral signatures for an invasive agricultural species could allow for early detection; the development of temporally sensitive GIS maps that show distribution for a given agricultural invasive; and the incorporation of specific information technologies that signal potential invasive threats would be invaluable. Unfortunately, at present state and county data are inadequate for rigorous spatial analyses—especially at the landscape scale. Overall, improving forecasting methodologies as well as technical innovations could help to identify sources, pathways and destinations of invasive species. Such efforts would provide invaluable information for land managers who will need to re-evaluate invasive species threats for a given agricultural system with climatic change.

Even if we know what invasive species to expect, how will climate change alter the management strategies designed to eradicate, control or manage invasives? For example, if rising CO₂ affects the efficacy of chemical control (Archambault 2007), what measures should be taken to increase herbicide effectiveness? How will chemical control for other invasives be affected? How can agricultural managers compensate, given their past reliance on chemical control measures, for invasive species? Will pesticide resistance increase or decrease with the occurrence of extreme climatic events and/or rising CO₂? Do we need to develop new chemical control measures? If temperature or climate increases root to shoot ratio in invasive perennial weeds (e.g. Canada thistle, Ziska et al. 2004) and there is potentially greater spread of roots and asexual infestation, is tillage, with the potentially greater spread of roots and asexual infestation, the best management strategy? For biological management, how will differential response to climate or host response to rising CO₂ alter predator–prey relationships? Will migratory patterns of predator–prey relationships be altered, with greater fecundity of the invasive species? Should greater attention be paid to the restoration of native habitats around agricultural fields to prevent or minimize invasion? Are there cultural measures (e.g. washing of all vehicles to prevent seed movement) that should be mandated in all agricultural sectors? How should integrated pest management (IPM) strategies change to reflect these concerns?

Little research has been directed to address these questions or to assess the likely threats to agricultural productivity, in spite of the recognition that CO₂ and climate change are likely to enhance the spread of invasive species in both managed and unmanaged systems (e.g. Harvell et al. 2002). Given the potential for rapid anthropogenic climatic change, attention needs to be given to these invasive management issues in order to accelerate testing and adoption of new agricultural management

approaches if we want to minimize the impact of invasive insects, disease and weeds. To date, such efforts are lacking.

9 Recommendations for research: knowledge gaps and future research directions

9.1 Standardize

1. Terminology of what distinguishes an “invasive” from a “non-indigenous” from an “exotic” from a “noxious” species can be confusing and misleading. The National Invasive Species Council’s (NISC) Invasive Species Advisory Committee (2006) offered a useful definition of invasive species. The scientific community should refer to this and other authoritative sources to develop a consistent use of these concepts and definitions.
2. Scientists should derive a set of agreed-upon criteria that can be used to classify an invasive species, and apply those criteria uniformly. For example, Canada thistle is listed as a noxious weed for 33 states, but is not listed as a federal noxious weed—as are a number of state invasive agricultural weeds (see Table 1, Ziska and George 2004). Such a “piecemeal” approach of federal and state laws and agencies came into being in response to isolated invasive species introductions and is now inadequate to address the extent of current and future biological globalization. ARS criteria can be the basis for states and federal policy maker’s reevaluation of their lists of invasive weeds.
3. Any invasive species is part of a larger biological system, and climate change can be expected to not only affect the individual but the system in a complex unpredictable fashion. At present one group of individuals keeps track of invasive plants, another of pathogens, another of aquatic species, etc. ARS could promote the establishment of a national mechanism (similar to that of the Centers for Disease Control) to coordinate the spatial and temporal observations regarding invasive species introductions.
4. While the threat of climate change with respect to invasive species biology is widely appreciated among scientists in agricultural and ecological fields, the complexities and often-conflicting interactions among long-term climate, short-term weather, other environmental conditions, pest biology, and host–parasite relationships cause uncertainties among experts. It is to be expected, then, that the implications may be completely unknown to policy makers and other non-experts. If policy makers are to make science-based decisions, experts must make concerted efforts to communicate effectively what is known, as well as the uncertainties, to the public. Such efforts may include the current ARS research on invasive species and agriculture. If scientists fail to relate their findings to real-world pressing needs, there is a risk that important decisions will not rest on key information.
5. Include invasive species in any national assessment of climate change on agriculture. We are unaware of any global change model which incorporates the effects of rising CO₂ and/or human-induced climate change on invasive agricultural species. No data on the limitations imposed by invasive species are included in the national assessment regarding the impact of climate change on agricultural productivity (NAST 2000). As we have demonstrated in this review,

- it seems likely that invasive species will certainly be influenced by climatic change, with significant negative consequences for U.S. agriculture. Any current quantification of climate change impacts on agricultural productivity without taking into account the effect of invasive species is incomplete and inaccurate. The community of scientists working on pest biology should be assertive in emphasizing the need for data and expertise to assist groups involved.
6. A separate quantification of endemic and invasive pest damage on agricultural productivity can be made at a future date by ARS. Accurate information regarding probable impacts is necessary in any long-term strategy regarding mitigation and adaptation of agriculture to climate change.
 7. Some studies are available for invasive species (e.g., pathogens) that can be viewed as threats to U.S. national security. Most research at the project level is framed in terms of a small number of species at specified locations. Such an approach leads to a fragmentary knowledge base. Pest biologists should design and conduct research that addresses the scientific uncertainties and begin to concentrate on the larger, overarching themes of invasive species biology; i.e., the basic science that can lead to unifying principles (e.g. resource-enemy release hypothesis, Blumenthal 2006) that is fundamental to long-term, sustainable solutions.
 8. ARS should establish a centralized data repository that can facilitate global information exchange in regard to invasive species. Given the interdependence of the global food supply, the issue of climatic change and invasive agricultural species must be seen as both international and interdisciplinary. Data compilation, standardization, contrast and comparison within federal agencies, states, universities, trading partners, and international organizations must become part of a sustainable information infrastructure. One example along such lines is the potato late blight disease simulation network established by the IGBP Global Change and Terrestrial Ecosystems (GCTE) and Global Initiative for Late Blight (GILB), whose goal is to develop an operational platform for simulating global change drivers on late blight intensity and potato yields on a global scale (Hijmans et al. 2000). Such examples can serve as potential prototypes to enable ARS researchers to provide land managers with the information needed to adapt agriculture to global climate change including the mechanistic bases for climate drivers, the demographic indicators of species invasions and the strategies and tools needed to eradicate or manage new invasive species outbreaks.

10 Conclusions

The rate of introduction of invasive pests in agriculture will continue to increase in proportion to globalization, trade and climate change. Economically, because of productivity losses, the current impact of these invasive species in agriculture is in the billions of dollars per year (e.g. Pimental et al. 2000), with global losses over a trillion dollars (Oerke and Dehne 2004). Given the critical role of the USDA in food production and food security, it is essential to determine those underlying climatic causes associated with invasive species damage. Biologists recognize that for many invasives, the lack of naturalized enemies in their introduced range means that their populations will be limited almost exclusively by climate. Yet, climate is changing,

due in large part to human influence (IPCC 2007). Hence, climatic change associated with weather extremes, precipitation, temperature and carbon dioxide is certain to extend the range and impact of agricultural invasive species.

There is an urgent need to assess the vulnerability of agriculture to climate-induced changes in invasive species biology. Vulnerability can be defined as the measure of the potential impacts of a given change, minus the adaptive capacity to respond to that change within the system being affected (Sutherst et al. 2007). In this paper we have provided illustrative examples regarding how global climate change and rising carbon dioxide can and will alter the vulnerability of agriculture to invasive species. We also emphasize that the information needed to fully assess the vulnerability of the U.S. food supply to such threats is lacking.

In the larger context of climate change and agriculture, and with the realization in recent years that human activity has, and will continue, to provide a greater degree of uncertainty in climate and food security, it is necessary that the American agricultural science community continue their diligence in sustaining the United States as a world leader in supplying plentiful, nutritious, safe food. We need to identify and adopt measures to ensure the productivity, sustainability and safety of American agriculture in an uncertain climate. The research gaps and recommendations in this paper are effective actions to begin addressing a complex, multi-faceted scientific challenge for agriculture, food production and national security.

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