# Chapter 7

# Invasive Species and Climate Change

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## Executive Summary

Invasive species present one of the greatest threats to the health and sustainability of ecosystems worldwide. Invasive plants, animals, and diseases are known to have significant negative effects on biological diversity and the ecological structure and functions of native ecosystems. Moreover, the economic cost imposed by invasive species is enormous—the damage inflicted to natural resources and costs of control measures is an estimated $137 billion each year in the United States. Climate change can fundamentally alter the behavior, spread, and harm caused by invasive species and the effectiveness of control methods. If we are to keep pace with and effectively limit the spread and damage caused by invasive species, it is critical to understand and predict how climate change will affect species invasions and the efficacy of the tools used to combat these invasions. To better identify research needs, we review the current state of knowledge pertaining to climate change impacts on several key topics, including invasive plants, their biocontrol, and wildlife disease.

Climate change is expected to alter the distribution and spread of invasive plants but in largely unknown ways. The climate models used to predict future distributions of invasive plants (e.g., cheatgrass) are limited by a lack of knowledge about, and consideration of, the ecology, genetics, etc., of the plant. Moreover, climate change may favor and convert non-native species considered benign today into the noxious weeds of tomorrow, but we are unable to predict which species might be favored. There is evidence that the physiology and competitive ability of invasive plants will be favored more than native plants, particularly in arid ecosystems, but in complex ways that are poorly understood.

Biological control—one of few tools proven effective against widespread invasive plants—will be affected by climate change in a number of ways. Like invasive plants, the range and spread of biocontrol insects are likely to be altered. Of particular concern is the potential for climate change to disrupt the temporal or spatial synchrony between biocontrol agents and their invasive host plants. There is also evidence that climate-induced changes in plant chemistry will alter plant-insect interactions in important ways (e.g., how much an insect eats) and could ultimately affect population levels of insects and invasive plants. However, we know next to nothing about the potential

consequences of these predicted changes for successful use of this powerful management tool.

Climate change can alter wildlife disease dynamics with potentially severe consequences for the affected species and entire ecosystems. For example, increased temperatures and altered precipitation patterns can increase the range and abundance of vector species (e.g., mosquitoes and ticks) and thus the frequency of vector borne disease outbreaks, including West Nile Virus. Climate-induced changes can further promote disease by affecting host susceptibility to infection. However, climate change could limit the spread of some pathogens. Research is needed to understand how climate change will impact disease emergence and spread to prioritize and inform management actions.

Climate change will modify invasive species and the tools used to manage them. Our understanding of how and in what direction climate change will drive such changes is insufficient to adequately predict and respond. However, climate-induced changes are likely to be complex and will need to be examined on a case by case basis until more generalized frameworks can be developed. This review will guide development of important research questions, the answers to which will better position us to devise and apply meaningful management options to address invasive species in both present and future climates.

## Introduction

Biological invasions threaten the integrity of many ecosystems and are considered second only to habitat destruction in their effects on biodiversity and on landscapes as a whole. For example, invasive plants currently infest approximately 100 million acres of land in the United States and are spreading at the rate of several million acres per year. However, climate change has the potential to greatly alter the behavior of invaders and their interactions with other organisms, with important consequences for invaders' management. A better understanding of what these climate-induced changes will be is critical to adapt, develop, and successfully apply management strategies to control invasive species.

Invasive species are defined here as any native or non-native species that causes or is likely to cause social, economic, or ecological harm. This chapter is divided into three sections: the first covers climate change effects on invasive plants and their competitive interactions with other plants. The second deals with potential impacts on biocontrol of invasive plants, including direct effects on biocontrol agents and their interactions with invasive plants. The third summarizes climate change effects on wildlife disease.

## Climate Change Effects on Invasive Plants

Non-native plants are now a common theme of many ecosystems throughout the United States (Pimentel and others 2000), including places established specifically to protect native species and communities (Allen and others 2009). Although the exact number of plants introduced into the United States is unknown, published estimates range from 4000 (Stein and Flack 1996) to 5000 species (Morse and others 1995). In comparison, there are approximately 17,000 species of native plants in the United States (Stein and Flack 1997). At present, only a small proportion of the 4000 to 5000 non-native species are classified as invasive, adversely impacting native species, communities, and ecosystems (Hiebert 1997; Skinner and others 2000). The overall impact of existing invasive species may increase or decrease under several scenarios of global change driven by greenhouse-gas influenced climate change, increasing carbon dioxide ($CO_2$) concentration, increasing nitrogen (N) deposition, and altered disturbance regimes (Dukes and Mooney 1999; Bradley and others 2010). Furthermore, the larger proportion of non-native species considered benign and maintained artificially as ornamentals represent a substantial pool of potentially damaging species should environmental conditions shift in their favor as a result of one or more of the elements of global change (Sutherst 2000).

Although alterations of climatic patterns will undoubtedly exert a major influence on the distribution of invasive plants (Blumenthal and others 2008; Hellmann and others 2008), studies that report the responses of invasive plants to climate change in an ecosystem context are limited (Dukes and Mooney 1999). However, Bradley and colleagues (Bradley 2009; Bradley and others 2009) have examined the effects of variable future climate scenarios on cheatgrass (*Bromus tectorum* L.) for the interior western United States using bioclimatic envelope modeling approaches based on Atmosphere-Ocean General Circulation Models (AOCGM). Cheatgrass is an invasive winter annual brome species that, along with red brome (*Bromus rubens* L. or *Bromus madritensis* ssp. *rubens* [L.]), dominate millions of hectares of former shrublands in semi-arid and arid habitats throughout the Interior West (Brooks and others 2004; Chambers and others 2007). Both species facilitate their own increase and spread through their effect on fire return frequency (*Bromus* spp. invasions provide abundant, highly flammable fine fuel); cycles of frequent burning can create near-monocultures of these grasses over large areas (Mack and D'Antonio 1998; Brooks and others 2004). Using the climate of the area currently occupied as a guide, Bradley (2009) and Bradley and others (2009) identified major variables that predict cheatgrass presence: annual precipitation, summer precipitation, and spring precipitation, with lesser effects of winter temperature. Modeling potential distribution given current climatic conditions indicated that sizeable areas (Wyoming, for example) may become available as climatically suitable habitat. AOCGM models generally predict that the Great Basin region will experience both reduced total precipitation and reduced spring precipitation, but the models vary widely in their predictions for summer precipitation. Consequently, the outcome of bioclimatic envelope modeling of future cheatgrass distribution is very much dependent on the AOCGM model used; both major increases (45%) and major decreases (70%) in future climatically suitable area have been predicted (Bradley 2009). The high uncertainty of these largely precipitation-based predictions is, in part, due to the inherent difficulty in projecting future precipitation (compared to temperature).

Bioclimatic envelope modeling is a valuable tool for predicting species response to climate change, but these models assume that species distribution is static under a given set of climatic conditions (see Friggens and others, Chapter 1 this volume). Bradley and colleagues (2009) used a presence-only approach that makes no a priori assumptions about the climate unsuitability of areas not known to be occupied, and their model does not take into account the fact that cheatgrass is known to be rapidly expanding its range into novel habitats. These researchers have documented range expansion into montane, extreme salt desert, and warm desert environments, many of which are likely outside the defined bioclimatic envelope (e.g., Ramakrishnan and others 2006; Leger and others 2009; Scott and others 2010). Furthermore, the bioclimatic envelope model as used by Bradley and others (2009) does not take into account another very important fact, namely that not all cheatgrass is created equal. Research has confirmed that the invasion of novel habitats involves unique biotypes (inbreeding lines) of cheatgrass that have suites of adaptive traits that preadapt them to specific environments (Ramakrishnan and others 2004, 2006; Merrill and others, in review).

This genetic variability, combined with highly dispersible seeds, creates the possibility that biotypes preadapted to areas with changed climates could rapidly replace cheatgrass biotypes that have become locally maladapted. This shift would be transparent to a casual observer, as there are few or no morphological markers for identifying these unique biotypes. In essence, these shifts involve evolutionary change in response to climate change, a possibility that is rarely considered and difficult to include in modeling scenarios.

At the plant level, increased atmospheric $CO_2$ concentration has a positive impact on plant photosynthesis and growth, although the relative response varies considerably among species (Hunt and others 1991). Previous research indicates relatively strong responses of invasive plants to elevated $CO_2$ in competition-free environments (Ziska 2003; Dukes 2000), and studies are available that demonstrate higher rates of photosynthesis for invasive plant species when compared to their native counterparts (Pattison and others 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001). However, Dukes (2000) concluded after an extensive review that, while a large number of invasive species respond strongly to elevated $CO_2$, the overall responses were not statistically different from the responses of non-invasive plants within the same functional group.

Studies that experimentally compare the physiological responses of invasive plants to elevated $CO_2$ to their native constituents are limited (Sasek and Strain 1991; Dijkstra and others 2010a; Song and others 2009). In an environmentally controlled experiment involving monocultures of three invasive species and three co-occurring native species, Song and others (2009) reported that elevated $CO_2$ resulted in significantly higher photosynthetic rates and increased biomass for the invasive species compared to the native species tested. Similarly, Sasek and Strain (1991) found that Japanese honeysuckle (*Lonicera japonica*), a non-native species, produced significantly more biomass under $CO_2$ enrichment than did coral honeysuckle (*Lonicera sempervirens*), a related native species. These authors suggested that this may convey an advantage for invasive species under increasing atmospheric $CO_2$, although such responses may differ in diverse, competitive environments (Bazzaz and McConnaughay 1992). For example, Dijkstra and others (2010) evaluated the effects of elevated $CO_2$ on a mix of five native semi-arid grassland species and one invasive plant species under greenhouse conditions. They found that species' responses to elevated $CO_2$ and supplemental water depended on whether the species were grown in a monoculture or in a mixture. Specifically, *Linaria dalmatica*, the invasive species used in that study, responded positively to elevated $CO_2$ when grown in a monoculture but negatively when grown in mixtures that included the five native species.

In mixed species competition, the response of a functional group, including invasive plants, to elevated $CO_2$ may depend upon how $CO_2$ indirectly alters competition for other resources (Bazzaz and McConnaughay 1992; Patterson 1995). Increased $CO_2$ also decreases transpirational water loss, which can improve season-long soil moisture conditions, and invasive species that can take advantage of the additional moisture may become more abundant (Dukes and Mooney 1999). Elevated $CO_2$-induced increases in water use efficiency are predicted to be greater in arid ecosystems because of the increased availability of a very limited resource (Smith and others 2000; Morgan and others 2004). The direct effect of atmospheric $CO_2$ enrichment on annual bromes (cheatgrass and red brome) has been investigated in both greenhouse and free air carbon enrichment (FACE) studies (Smith and others 1987, 2000). The general conclusion from these studies is that annual bromes have a larger positive growth response to $CO_2$ enrichment than associated native herbaceous species, which should increase annual brome competitive advantage as atmospheric $CO_2$ levels increase.

Elevated $CO_2$-induced increases in soil moisture can enhance plant N uptake, which is important for sustained increases in plant productivity associated with increased atmospheric $CO_2$ (Dijkstra and others 2008, 2010a). However, Dijkstra and others (2010b) reported that N availability decreased with increasing $CO_2$-induced soil moisture, while warming increased soil inorganic N and plant N uptake.

Anthropogenic-caused increases in N deposition is a component of global change that receives limited attention with respect to its potential impact on non-forested ecosystems (Vitousek 1994) where slow-growing native species adapted to low nutrient poor soils are likely to be the most impacted by increasing N (Milchunas and Laurenroth 1995; Tilman 1987). Fertilization experiments in N-limited ecosystems demonstrate that increased N concentrates plant diversity into one or a few N-responsive plants (Tilman 1987; Vitousek 1994 and references within), which likely includes many non-native species found in several North American grasslands. Stohlgren and others (1999) reported that much of the variation in non-native species richness could be explained by the total percentage N in the soil; however, more recent research indicates that elevated $CO_2$ could ameliorate the negative effect of N enrichment on species richness (Reich 2009).

In summary, predicting the specific effects of global change on current and potential invasive plants is a significant challenge because the complex matrix of interacting elements associated with global change often produces inconsistent patterns (Bradley and others 2010) and also because invasive plants already represent a significant component of global change (Vitousek 1994). Overall, the evidence indicates that invasive plants will be favored by many of the elements associated with global change. This may be especially true for non-forested ecosystems of the Interior West that are typically water and nutrient limited. However, applying general patterns to specific species invading specific sites is difficult, and more site-specific research is needed in non-forested ecosystems that simultaneously evaluate multiple elements of global change, including the effects of extreme events (Bradley and others 2010). For example, more research is needed on the population genetic structure of both cheatgrass and red brome, including the initiation of large reciprocal seeding experiments to determine whether differences in adaptive phenotypes associated with inbreeding lines that have distinctive marker genotypes result in differential establishment, survival, growth, and fecundity in contrasting environments. Additionally, GSD Ecosystem researchers need to respond to restoration opportunities where the distribution and abundance of invasive plants are contracting because of global change.

## Climate Change Effects on Biocontrol

### *Direct Impacts on Biocontrol Agents*

Biocontrol intentionally reunites, for the purposes of pest population regulation in an invaded or adopted range, the species targeted for control with co-evolved and host-specific natural enemies originating from their common native range. The establishment, abundance, and distribution of invasive plants (weeds) and the co-evolved, host-specific herbivorous insects known as their biological control (or biocontrol) agents are fundamentally mediated by habitat suitability, competition, and natural enemies (Holt and Barfield 2009). Long-term shifts in seasonal temperature and coupled precipitation patterns anticipated under climate change in turn have the potential to alter species abundance and distribution (Walther and others 2009). Studies specifically evaluating how climate change may affect weed biocontrol are scarce (but see Sims-Chilton and others 2010; Watt and others 2010). Under these circumstances, extrapolation from generic ("herbivorous insects" or "invasive species") or multi-trophic (e.g., "host-specific invasive pest" or "rare indigenous species") case studies can be useful. In addition, results reported from studies of invasive or conservation-targeted species are effective for inferring many direct and indirect potential climate change impacts on non-native weeds and their arthropod biocontrol agents.

Bale and others (2002) provided a comprehensive review of key direct effects—insect herbivore development, survival, range, and abundance—as influenced by the increased temperatures predicted under global climate change. Hellmann and others (2008) identified probable consequences of climate change for invasive species and developed testable hypotheses for invasive species responses to specific climate change consequences. Monitoring for changes in the geographic distribution of host-specific herbivorous insect species across latitudinal and elevational gradients was identified as a robust methodology for accurately sensing climate change impacts (Andrew and Hughes 2005; Hodkinson and Bird 1998).

Because many of the plant species targeted for classical weed biocontrol in temperate regions of the United States originated in Eurasia, the simplistic assumption might be made that increasing temperatures in North America will generally benefit biocontrol agents that have been collected from a comparatively warmer native range. Studies evaluating ecological sorting along altitude-influenced thermal gradients indicate that insect physiological responses to temperature, specifically thermal tolerance thresholds, can profoundly affect agent demographics via temperature-mediated fecundity (Dangles and others 2008) and distribution (Hodkinson and Bird 1998). The results of a meta-analysis of insect species range margins suggests that although genetic diversity tends to decline during colonization of new habitats, there could be a positive feedback between range expansion and an increase in traits that accelerate range expansion through adaptations specifically affecting dispersal, metabolic rate, and changes in habitat associations (Hill and others 2011).

Increased temperatures projected under climate change could substantially extend the core area and edge-of-range distributions for both weed biocontrol agents and their host plants, especially for Eurasian species established in northern temperate locales. Thomas and others (1999) determined that a 2 to 3 °C rise in mean spring and summer temperature increased available suitable habitat and the length of time that successional habitat could be occupied, and decreased the effective distance between suitable habitat patches in northern temperate locations. Davis and others (1998) asserted that accurate predictions of species range and abundance cannot be based on physiological response to temperature alone (called "climate mapping") but should also consider climatic influences on species dispersal and inter-specific interactions. Bradley and others (2009) cautioned that climate change could result in contractions of invasive plant ranges as well as range expansions.

The probability that a species will reach locations that have, under the influence of global warming, changed from unsuitable to suitable habitat patches depends on the interaction of dispersal ability and behavioral responses with environmental structural components (Gaston 2009). Fox and others (1999) determined that positive effects of winter warming on St. John's wort (*Hypericum perforatum* L.) would be ephemeral and readily neutralized by a projected increase in summertime herbivory if winter warming was followed by summer drought; the authors concluded that St. John's wort would not likely benefit from the warmer temperatures predicted under global warming, particularly at the northern extent of its range. The guild structure of herbivores colonizing *Acacia falcata* growing within or transplanted at sites 208 km beyond its current range was similar even though the transplant sites were 1.2 and 5.5 °C warmer; this was not the case for the guild structure of herbivores collected from a related host species *A. leptostachya* growing at transplant sites outside the current range (Andrew and Hughes 2007).

The internal temperature of ectotherms, including all plants and most insect species, is regulated by ambient environmental temperature (Gutierrez and others 2008). Ectothermic metabolic rate, dictated by body mass and body temperature, is therefore highly susceptible to alterations in habitat thermal properties (Dillon and others 2010; Gillooly and others 2001). Response to changing climatic conditions is restricted to dispersal, phenotypic plasticity, or adaptation (Holt 1990). Phenological alterations resulting from the increased length of temperate growing seasons can facilitate the development of asynchrony in key interspecific interactions (van Asch and others 2007; Cobbold and Powell 2010; Fabiana and others 2010). Hegland and others (2009) pointed out that asynchrony in insect-plant interactions can be temporal or spatial in nature, and, in extreme cases, could lead to trophic decoupling and food web scale disruptions characterized by a mismatch in abundance of consumers and their food sources.

Much of the research conducted in Interior West grasslands, shrublands, and desert ecosystems concerns function and productivity in dryland habitats. The interaction of environmental (e.g., climate change) and anthropogenic (e.g., management practices) drivers profoundly affects dryland function and productivity (Chambers and Pellant 2008). Productivity, in terms of increased plant photosynthesis, biomass, and water use efficiency, is predicted to increase, especially for alien invasive species, in U.S. arid ecosystems under higher atmospheric levels of $CO_2$ associated with climate change (Ziska 2003; Smith and others 2000). Species interactions, and not only direct effects of climate change, were shown to influence grassland productivity and species diversity (Suttle and others 2007). Drylands are susceptible to dominance by non-native transformer species (i.e., species capable of significantly altering ecosystems over a wide area) (Richardson and others 2000). Transformer species such as *Bromus tectorum* (cheatgrass; downy brome) and *Linaria dalmatica* (Dalmatian toadflax) (D’Antonio and others 2004) are targets of biocontrol research by scientists in the GSD Ecosystems Program of RMRS. Biocontrol, used alone or as part of an adaptive integrated weed management strategy, may significantly reduce unintended negative, non-target impacts to surrounding desirable vegetation. Conventional herbicide treatments have been correlated with secondary invasions of weeds such as cheatgrass (Pearson and Ortega 2009) and an increase in the proportion of bare or unvegetated ground (Barnes 2007); the ability of dryland vegetation communities to rebound after herbicide applications is likely to be compromised under climate change and may increase the frequency, intensity, and persistence of desertification. Verstraete and others (2009) paraphrased the United Nations Convention to Combat Desertification definition of desertification as: “any form of degradation in drylands…where degradation refers to a persistent reduction in the bundle of services provided to humans by the ecosystem under considerations, thus encompassing both social and biophysical considerations.”

## *Impacts on Plant-Herbivore Interactions*

The success or failure of biocontrol is largely determined by the outcomes of interactions between individual plants and biocontrol agents (herbivores). That is, herbivory at the individual level can have negative effects on a plant’s growth and reproduction, which can, in turn, impact the abundance, distribution, and dynamics of entire plant populations (Maron and Crone 2006). For biocontrol to be deemed successful, individual herbivory must lead to population-level reductions in the target weed. However, climate change has the potential to fundamentally alter interactions between plants and herbivores, which could alter broader population-level outcomes and the success of biocontrol. Another primary route by which climate change is predicted to affect herbivory is by modifying plant chemistry—the central factor regulating plant-herbivore interactions. Major climate change factors, most notably elevated $CO_2$ and temperature, can potentially affect the susceptibility or resistance of plants to herbivory (e.g., by altering leaf nutrients and defensive compounds); however, little is known about how these changes may affect individual plant-insect interactions or broader community dynamics. A better understanding of how climate change will impact relationships between invasive plants and their biocontrol agents is needed to predict and advance biocontrol efficacy in a rapidly changing climate.

The most obvious way climate change can affect interactions between plants and insects is by altering the basic nutritional value of plants. Most studies show that herbivores consistently respond to $CO_2$-induced changes in their host plants by consuming more foliage (Coviella and Trumble 1999). For example, elevated $CO_2$ generally causes an increase in plant growth (the "fertilizer effect") and increases in the ratio of C:N in plant tissues, which reduces the nutritional quality for N-limited insects (Coviella and Trumble 1999). As a result, insects must eat more to compensate for less N content (Coviella and Trumble 1999; Dermody and others 2008; Johnson and McNicol 2010). Another route by which increased $CO_2$ can affect insect feeding is by increasing sugars in plant leaves. For example, soybean plants grown in elevated $CO_2$ conditions contain 31% more sugars than plants grown in ambient air and, as a result, Japanese beetles (*Popilla japonica*) prefer and consume twice as much foliage from high-$CO_2$ soybeans (Hamilton and others 2005). Drought stress—something predicted to increase dramatically in western North America—can affect virtually every plant nutrient and may encourage herbivore outbreaks (Mattson and Hauk 1987). Such climate-induced increases in insect damage are expected to negatively impact agricultural production by off-setting potential gains in plant productivity due to the fertilizer effect (DeLucia and others 2008). However, the implications for biocontrol, though potentially far reaching, are unknown.

Climate change can also significantly impact plant nutritional value by altering chemical defenses against herbivores. Plant defensive chemistry can have important consequences for plant fitness and populations (Baldwin 1998) and can drive cycles in herbivore populations (Underwood 1999). Elevated $CO_2$, temperature, ozone ($O_3$), and ultra-violet (UV) light are each reported to affect levels of plant secondary chemicals (Bidart-Bouzat and Imeh-Nathaniel 2008). However, available information is limited and dependent on the plant and insect species involved as well as the class of chemicals examined (e.g., C-based versus N-based defenses). For example, elevated $CO_2$, temperature, $O_3$, and UV light can each either increase, decrease, or have no effect on plant defensive chemistry (Bidart-Bouzat and Imeh-Nathaniel 2008). These conflicting studies have hindered attempts to develop general predictions about how climate change will affect plant defensive chemistry and point to the involvement of a host of interacting factors. However, climate-induced changes in chemical defenses can have important consequences for plants and herbivores. For example, quaking aspen trees (*Populus tremuloides*) grown in elevated $CO_2$ and $O_3$, singly and in combination, had altered physical and chemical leaf defenses that led to increased populations of herbivores and pathogens (Percy and others 2002). It was recently discovered that elevated $CO_2$ can disrupt herbivore-induced plant defenses, specifically the production of proteinase inhibitors that interfere with insect digestion, resulting in poorly defended leaves and increased growth and development of herbivores (Zavala and others 2008). Moreover, the reduction of proteinase inhibitors can further reduce plant fitness by increasing herbivore attack on younger leaves, which contributes disproportionately to plant growth (Zavala and others 2009).

The production and release of volatiles—airborne chemical compounds emitted by plants—is another important hallmark of plant-herbivore interactions that is expected to be affected by climate change (Yuan and others 2009). These airborne chemicals can significantly impact the fitness of plants and insects by serving as foraging cues for organisms that are beneficial to plants, such as predators and parasites of herbivores (De Moraes and others 1998) or by directly repelling herbivores (De Moraes and others 2001). Volatiles can also convey information about a plant's identity and location to harmful organisms (or beneficial organisms in the case of biocontrol insects) such as herbivores (De Moraes and others 2001; Runyon and others 2006). Climate change can alter the biological functions of plant volatiles with largely unknown consequences (Yuan and others 2009). For example, drought and elevated $CO_2$ can increase emission of volatile terpenoids, which could increase plant apparency to herbivores or perturb attraction of herbivore natural enemies (Mattson and Hauk 1987; Himanen and others 2009). Increases in $CO_2$ have been shown to increase volatile production by soybean plants, which seemingly act as a super stimulus that may elicit an exaggerated feeding response in herbivores (O'Neill and others 2010). Conversely, $O_3$ can react with and rapidly degrade certain volatiles in the atmosphere (Pinto and others 2007). Elevated temperature has long been known to increase plant volatile emission rates (Guenther and others 1993), indicating a general increase in plant volatiles under a warmer climate with unknown but likely profound impacts on ecological interactions between plants and insects (Yuan and others 2009). It is unlikely these changes could lead biocontrol insects to shift to non-target plant species; biocontrol insects are highly host-specific and rely on species-specific chemical cues (e.g., the presence/absence of compounds) to locate and feed. However, our poor current state of knowledge about such potential climate change impacts does not allow us to rule this possibility out.

In summary, we know alarmingly little about how climate change will impact the relationship between plants and insects, despite the profound implications for agriculture and biocontrol. The limited knowledge available indicates that responses are highly variable and dependent on the species involved. Many herbivores will alter how much they eat in response to climate-induced changes in plant nutrition and plant defensive chemistry; yet, we know next to nothing about what this might mean ecologically or economically. If biocontrol is to keep pace with and remain effective in a changing climate, increased funding is needed to:

- Determine how climate change will affect the nutrient content of invasive plants and what impact these changes will have on biocontrol agents.
- Evaluate effects of climate change on the defensive chemistry of invasive plants and determine how these changes impact biocontrol agents.
- Develop a conceptual framework to understand and predict how climate-induced changes will alter broader population- and landscape-level outcomes of biocontrol.
- Develop effective tools and techniques to best use and adapt biocontrol to manage invasive plants in a changing environment.

This is an opportunity to advance our basic understanding of the ecology of plant-insect interactions and the conditions under which herbivory translates into meaningful changes in plant populations—fundamental ecological questions that hold great promise for managing invasive plants in present and future environments. Moreover, because climate-induced changes in western North America—much of which is dominated by grasslands, shrublands, and deserts—have generally outpaced change elsewhere (Overpeck and Udall 2010), biocontrol is likely to be affected first and most severely there. As such, the GSD Ecosystems Program is well positioned to take on the research needed to adapt and respond to future environmental changes.

## Climate Change Effects on Wildlife Disease

Disease is a natural process in wildlife communities that, under normal circumstances, acts to regulate communities and interactions. However, when disease dynamics are altered by wildlife manipulations (translocations, hunting, and commercial trade) and lead to new pathogen-host interactions, disease often becomes a destructive force. In general, invasive species, and in particular, vectors and pathogens, can destabilize natural communities and irrevocably change ecosystem structure and function with severe economic and environmental consequences (Crowl and others 2008). Wildlife managers and conservation biologists have become increasingly concerned with the rise in emergence of many serious diseases, including plague (*Yersinia pestis*) encephalitis, canine distemper, and West Nile virus (Daszak and others 2001; Deem and others 2000; Gubler and others 2001).

Disease introductions in wildlife populations usually occur at domestic-wildlife interfaces or are related to translocation efforts. Wildlife disease outbreaks are commonly associated with increased proximity to humans and domestic animals (Deem and others 2000). Multispecies land use, such as occurs in buffer zones where domestic and wildlife share grazing lands, is thought to facilitate disease spread (Daszak and others 2001; Deem and others 2000). However, the primary mechanism for disease spread is translocation (Deem and others 2000). Translocations have multiple consequences for disease management, including an increased risk of exposure of wildlife to new diseases present in new location or unintentional introductions of disease vectors or carrier species (Deem and others 2000). Recent translocations of the white-tailed deer (*Odocoileus virginanus*) resulted in the spread of the lungworm *Parelaphostronglyus tenuis* to Wassa Island, Georgia (Davidson and others 1996). Similarly, reintroduction of a confiscated desert tortoise (*Gopherus agassizii*) infected with mycoplasmosis in Las Vegas Valley led to the spread of that disease in native populations (Jacobson and others 1995), and the transport of infected carcasses was associated with the spread of canine distemper in the Southwest (Davidson and others 1992; Deem and others 2000). The zebra mussel (*Dreissena polymorpha*) is an invasive species whose impact has been amplified through its status as a carrier of the roundworm parasite, *Bucephalus polymorphus*, which can also infect many freshwater cyprinid fish (Crowl and others 2008). Among the invasive diseases currently known to occur in the Interior West, plague, canine distemper, brucellosis (*Brucella* spp.), chronic wasting disease, bovine tuberculosis (*Mycobacterium bovis*), whirling disease (*Myxobolus cerebalis*), and West Nile virus have considerable negative impacts on wildlife population (Bengis and others 2002; Clinton and others 2010; Githecko and others 2000; Longstreth and Wiseman 1989; Mason 2008).

Global warming will impact many wildlife disease patterns, particularly vector-borne diseases (Daszak and others 2001; Harvell and others 2002; Patz and others 2000; Keesing and others 2006; Rosenthal 2009). Local climatic conditions are thought to play an important role in determining disease emergence (Githeko and others 2000; Harvell and others 2002; Hofmeister and others 2010; Lafferty 2009), and global warming is predicted to lead to range expansions of many vector species and increase the frequency of vector borne disease outbreaks (Epstein 2001; Harvell and others 2002). Issues associated with wildlife translocations and their roles in disease emergence are also expected to increase under future climate scenarios (Deem and others 2000). Among other effects, increases in temperature are expected to positively influence the spread of disease by decreasing overwinter mortality of many arthropod vectors and parasites (Harvell and others 2002) and increasing vector and pathogen developmental rates (Wilcox and Gubler 2005). Within the Interior West, the spread of diseases such as West Nile virus and Lyme disease may be encouraged by increases in mean temperature and humidity, which will open up new zones for their mosquito and tick vectors (Deem and others 2000). In higher elevations, warmer temperatures may contribute to the spread of chytrid fungus (*Batrachochytirum dendrobatidis*) among amphibians (Pounds and others 2006; Rohr and Raffel 2010). Furthermore, amphibian host susceptibility may increase as heat stress and high UV-B affect immune response (Harvell and others 2002; Martin and others 2010). Rising water temperatures are likely to exacerbate ongoing issues with the introduced agent of whirling disease, *Myxobolus cerebalis* (Mason 2008; Longstreth and Wiseman 1989). Increases in host breeding season may contribute to the spread of *Ophryosystis elektroscirrha* (protozoal infection) in monarch butterflies (Harvell and others 2002). Of the exotic diseases present in the Interior West, plague and West Nile virus are the most susceptible to climate-related changes in distribution and incidence. Disease distribution and incidence may also increase if wildlife is translocated as part of assisted migration projects being developed to lessen negative climate change impacts (McDonald-Madden and others 2011).

Changes to precipitation regimes will influence the availability of favorable habitat for vectors that rely on water bodies and, in turn, influence the establishment of disease in new areas (Gubler and others 2001; Patz and others 2000). Reduced precipitation might limit breeding sites for many mosquito vectors but could also lead to conditions, such as overcrowding at limited water holes, increased water temperatures, and more organic matter, that are conducive to disease spread, particularly for waterborne diseases such as avian cholera and pox (Friend and Franson 1999). Precipitation also affects intermediate and reservoir hosts by influencing important food resources (Dazak and others 2001). Changes in the overlap of species due to phenological effects of changing temperature and precipitation regimes have consequences for host, reservoir, and vector populations and may lead to new disease issues (Harvell and others 2002; Hofmeister and others 2010; Patz and others 2000). Changes to the timing of host migrations may also influence the risk of disease exposure for some wildlife populations and lead to novel host-pathogen interactions.

However, climate change may not always lead to an expansion of disease and could, in fact, decrease some disease threats. Increased temperatures can reduce adult survivorship of vectors (Harvell and others 2002) and limit transmission of certain diseases such as plague that have upper critical temperature thresholds (Githeko and others 2000). Entomophatogenic fungi in insects (some biocontrol agents), coldwater disease in salmon, and avian cholera in waterbirds (*Pasteurella multocida*) may decline as temperatures rise (Harvell and others 2002). Warming may limit the spread of chytrid and iridoviruses, which rely on cool, moist conditions, in amphibian populations in warmer climates. Hot, dry conditions may impede fungal development and enhance insect immune response (Martin and others 2010). Perhaps to the benefit of some biocontrol efforts, warmer temperatures are expected to reduce the cold-induced mortality of the nuclear polyhedrosis virus *Lymantria dispar* on gypsy moth egg cases (Harvell and others 2002). However, the direction of disease response depends on local conditions and the inherent limitations of the disease agents (Githeko and others 2000). Commonly, pathogens limited by winter mortality show predicted range contractions in the south and corresponding expansions to northern areas (Haile 1989). Ultimately, many diseases may shift rather than experience an absolute change in their area (Lafferty 2009). Identifying if and how climate change will impact specific ecosystems, populations, and pathogens is a critical step toward informing management agency actions with respect to disease emergence.

Wildlife disease becomes a Forest Service issue when it affects threatened and endangered species and human use of Forest Service lands and when management of forest lands can mitigate the introduction or expansion of invasive disease. We need to implement research and build expertise to address invasive disease issues and facilitate actions that allow us to manage rangelands for biological diversity, health, and sustained and enhanced use by our stakeholders. Research needs to focus on mitigating the potential effects of invasive disease on threatened and endangered species to prevent further population declines, identify populations at risk due to inherent susceptibilities or increased exposure (migrating species, species in buffer zones), and identify the important interactions (climate, species interactions, and land use practices) that affect ecosystem integrity and invasibility. In addition, wildlife disease has socioeconomic effects when it relates to human use of land and to human health issues (e.g., zoonotic diseases such as plague, hanta virus, Lyme disease, and West Nile virus).

Specific research needs that address the strategic goals of the Forest Service mission are:

- Identify disease threats to threatened and endangered species.
- Identify disease risk for critical habitats, particularly breeding and migratory stopover sites. Analyze risk factors for species and management units and for translocation or assisted migrations.
- Assess economic and socioeconomic issues related to emergent wildlife disease.
- Identify and monitor susceptible/at risk populations.
- Determine how current and proposed management (e.g., restoration) activities affect disease invasibility of ecosystems or basic health parameters of wildlife populations.
- Determine if certain practices are more or less likely to favor the spread of disease.
- Evaluate the effects of management actions for mitigating disease impacts.

Many diseases affect species present or dependent upon grassland habitats and new diseases will further threaten these populations. Many species, such as the desert tortoise and sagebrush grouse, are already endangered and attention must focus on preventing further population decline. The GSD Ecosystems Program is able to address many relevant research questions with expertise in human resources, disease, soil and invasive species. The diversity of sites and ecosystems available in the GSD region puts scientists in this program in a unique position to address some if not all of these issues and to be able to satisfy recent calls for regional-level monitoring (see Crowl and others 2008) and analysis of disease emergence and spread. If applied successfully, these efforts might also be used effectively in other systems and ranger stations. Current activities with the black footed ferret (*Mustela nigripes*) (Rapid City Lab), which are highly susceptible to plague and canine distemper, are one way the GSD Program can develop a more aggressive and comprehensive disease-oriented research. Furthermore, many activities related to current RMRS research, particularly as they pertain to grazing; human-domestic, animal-wildlife interfaces; and restoration activities are also highly relevant to disease prevention and management issues.

In addition to building upon its own expertise and initiating new research, researchers in the GSD Program need to engage opportunities to work with other programs and agencies with ongoing research relevant to species of interest to the Forest Service (e.g., USGS/BLM SAGEMAP project for the greater sage-grouse, which is threatened by West Nile virus). The recent spread of white-nose syndrome illustrates the devastating impact of introduced disease and points to the critical importance to establish networks and cooperation in anticipation of disease emergence. The recent finding of white-nose syndrome in the cave bat (*Myotis velifer*) in Oklahoma is a troubling predictor that this western bat species could soon bring white-nose syndrome to the western United States. As this disease potentially impacts over half the species endemic to United States, the inevitable spread of this disease is an impending crisis requiring immediate action. Forest Service researchers should have a role in identifying research needs and intervention strategies managing white-nose syndrome.

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