

Climate change effects on biological control of invasive plants by insects

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Abstract

Because many invasive plants are anticipated to benefit from climate change, the need for effective management strategies will become more pressing in the future. Biological control of invasive plants by insects has been an effective management strategy in many instances, but climate change may substantially alter such systems. Maximizing biological control efficacy with climate change will require predicting responses of the invasive plant in question, its biological control agents, and especially their corresponding interactions. However, because of the wide variety of species-specific plant and insect responses to increased atmospheric CO₂ concentrations, temperatures, extreme weather events, and other climate factors, climate change will likely result in highly variable, system- and geographically-specific effects. Even still, predicted future climates are generally anticipated across systems to alter geographic ranges of invasive plants (and correspondingly their biological agents), reduce host-plant quality, and hasten the phenology of both plants and insects. Some of these anticipated effects on biological control systems can be expected to hamper control efficacy. However, because some of these effects might also increase control efficacy, biological control can still be an effective and important management tool in the face of climate change. Although the variety of insect and plant responses to climate change reported in the literature do not currently allow for strong generalizations to be made as to the best biological control agents or strategies in novel climates, pertinent considerations for selecting effective biological control agents in the future are discussed.

Keywords: CO₂, Warming, Interaction, Phenology, Quality, Host, Agent

Review Methodology: Literature searches in Google Scholar and CAB Abstracts using multiple pertinent combinations of the terms 'climate change,' 'CO₂/carbon dioxide,' 'temperature,' 'biological control/biocontrol,' 'insect(s),' 'plant(s)' and 'invasive' were utilized to find previously undiscovered and recent relevant articles for this review. However, because many sub-topics covered within have received their own recent reviews and/or meta-analyses, redundant comprehensive review and correspondingly exhaustive citation lists were intentionally avoided. Inclusion or omission of any particular citations within is therefore not indicative of relative value/importance to the author.

Introduction

Increased atmospheric CO₂ concentrations and consequent climate changes are primary threats to many ecosystems around the world. Increased temperatures, altered precipitation regimes, and increases in extreme weather events worldwide are expected to drastically alter a multitude of ecosystem functions and processes [1]. One example of such ecosystem alterations with climate change is plant community composition [2], including increased potential for exotic plant invasion [3]. Although patterns have varied among studies, multiple cases of increased plant

invasions with climate change have indeed been shown [4–7]. Because of the anticipated benefits for invasive plants, effective plant management strategies will become increasingly important as the climate continues to change.

Although effects of climate change on invasive plants and their competitors have been explored [8–11], relatively little is known about how climate change may impact trophic interactions of invasive plants. Biological control, or the release of natural enemies such as insects, can be an effective way to mitigate plant invasions in an environmentally sound way through targeted trophic interactions aimed at damaging plants [12]. There have been many

documented instances of biological control success in the literature, many of which have been previously reviewed both qualitatively and quantitatively and in both terrestrial and aquatic systems [12–15].

Climate change is expected to result in widespread effects on insect–plant interactions [16–18] and therefore biological control applications [19]. Because climate can be critical in predicting biological control agent population dynamics [20], any changes to climate may in turn alter control success. The likelihood of climate change effects on biological control success (both positive and negative) to be discussed below indicates that biological control should be increasingly considered and studied in the framework of future climates. Adding to such a challenge, however, is the fact that life histories of most insects are poorly understood, particularly in relation to climate change [21].

This review is structured to highlight the primary aspects of insect and plant ecology and physiology that may be most likely to be altered in ways to either enhance or hamper biological control success as the climate continues to change. Although this review will largely be restricted to producer and consumer trophic interactions given the nature of biological control of plants by insects, note that predators and food webs more broadly will also be impacted by climate change [22], which could certainly affect biological control agent populations and therefore success as well. Even still, relative climate change impacts on biological control systems directly (i.e. agents and target plants) will be the primary focus here. Because several general aspects of plant and insect biology under climate change have already been recently reviewed as cited throughout, such topics will receive neither extensive re-review, nor exhaustive citation lists, in an effort to avoid duplicating the recent work of others. When possible, plant biological control by insect studies specifically will be highlighted, but because biological control in the context of this review is inherently an insect–plant interaction, examples will also necessarily be drawn from general insect and plant literature as well.

Although increased atmospheric CO₂ concentrations and corresponding temperature increases will primarily be discussed below, increased frequency of extreme weather events with climate change [1] can also be expected to potentially benefit invasive plants [23] and alter insect–plant interactions [24], including biological control [25]. As such, extreme weather events and their effects on biological control should certainly be considered going into the future as well, especially because drought has been shown to be the most important climate factor (relative to CO₂ and temperature) in driving the success of at least one insect herbivore, *Lochmaea suturalis* Thomson (Coleoptera: Chrysomelidae) in Denmark [24]. However, various extreme weather events such as drought, deluge, hot and cold spells, intense storms, etc., can be speculated to have hard to predict, site/system-specific, and therefore quite inconsistent effects on biological control agents and their target plants. Consequently, the focus of this review is on

the more consistently expected climate change impacts on biological control, beginning with geographic range changes of invasive plants and their biological control agents.

Geographic Range Changes of Invasive Plants and Their Insect Biological Control Agents

As temperatures continue to climb, invasive plants may be able to expand into novel latitudinal and altitudinal ranges, affecting biological control applications by shifting the geographical ranges in which interactions between biological control agents and their target plants occur [16, 26]. As a result, range shifting can clearly change where plants and agents will experience ideal (and non-ideal) temperatures, which could correspondingly alter control efficacy in a site- and system-specific manner based on ideal thermal ranges for the plant and insect in question [25, 26]. Consequently, the most effective biological control agent for a given plant could potentially vary geographically based on if a particular agent performs better in site-specific climates that might be experienced in newly-invaded latitudes or altitudes [26]. As such, ideal thermal ranges of biological control agents should perhaps receive more attention in future studies to best elucidate which agents might be most effective in novel plant populations given the site-specific microclimatic conditions [25].

With the clear possibility for invasive plant range changes under climate change, once released and if established, biological control agents would ideally be able to follow plants into novel locations. This will perhaps be one of the largest assets in continuing to utilize biological control in the face of climate change. However, a multitude of other expected plant chemical and physiological changes with climate change will combine with this potentially novel geographic variability to likely further site- and system-specificity of climate change effects on biological control efficacy. Such additional climate effects on invasive plants and their corresponding effects on biological control agents will be discussed in the following sections.

Invasive Plant Chemistry and Climate Change

Highly varied effects on plants and their interactions with insects have been observed under elevated atmospheric CO₂ concentrations [17, 18, 27–31]. However, one largely consistent effect of carbon fertilization under elevated CO₂ has been reduced host-plant quality, primarily through increases in C:N ratios and carbon based defenses [17, 18, 27, 28, 30, 32, 33]. Although such reductions in plant quality have been shown to result in increased plant consumption (and therefore potentially damage in a biological control context) by insects to compensate for nutritional deficiencies [27, 28, 30, 34], reduced plant preference and performance by insects under elevated CO₂ (as discussed further below) has been shown as well. Note, however,

that increased plant consumption by insects (which itself may not be universal [35]) might not always result in an overall increase in plant damage, as plants may grow relatively more under elevated CO₂ than the increased insect damage mitigates [27]. Clearly, any changes to plants such as lower C:N ratios that reduce successful recruitment of biological control agents into populations would hinder long-term control efficacy, so more research needs to be performed on the tradeoffs of increased feeding damage but potentially lower insect performance and survival on plants grown under elevated CO₂. The currently available literature does not allow for consistent predictions of such tradeoffs to be made, but this will be an important issue with which to contend in future climates. This is particularly true given that trophic interactions and populations of consumers may be more variable and take longer to recover after disturbance with climate change [36].

As with CO₂, elevated temperatures have been reported to show variable effects across plant species and therefore their insect interactions [37]. Among these temperature effects are again reductions in host-plant quality and insect performance [38]. While reduced host-plant quality could again clearly be expected to hinder biological control, consideration of insect traits such as feeding strategy might help mitigate the effects of lowered host quality relative to biological control agent performance. As such, climate change effects on insects (including variability of effects by feeding strategy) will receive attention in the following section.

Insect Biological Control Agents and Climate Change

While increased CO₂ is known to have a multitude of effects on plants, not much evidence currently exists for substantive direct effects of CO₂ on herbivorous insect biology or behavior [16] (although the possibility will not necessarily be discounted here). Most CO₂ effects on herbivorous insects will likely be indirect through changes to plant chemistry as introduced above [30]. These indirect effects could still greatly alter control efficacy, however, but may vary in order/species-specific ways [30] and by insect life history traits such as feeding strategy. For instance, although foliage feeders and leaf miners may be able compensate for plant nutritional changes under elevated CO₂ by increasing intake, larval development times may be delayed and overall abundance can be reduced at least in some cases [28, 30]. Phloem feeding insects, on the other hand, have been not only been shown to maintain performance on elevated CO₂ plants, they have even been found to exhibit decreased development times and overall population growth [30, 32, 39, 40]. Beyond foliage and phloem feeders, adults of a larval seed-feeding biological control agent (*Larinus minutus* Gyllenhal; Coleoptera: Curculionidae) have been shown to prefer elevated CO₂ plants (*Centaurea diffusa* Lam. [Asteraceae]) grown in the

field in Wyoming, USA [41], so plant chemistry (quality) changes may not always be a direct detriment to biological control efforts.

The literature does not currently allow strong predictions or comparisons to be made as to the best insect feeding strategies to use across CO₂-induced plant changes and biological control systems, so it will not be speculated here, for instance, that phloem feeders might be the most effective biological control agents in the future. Especially because foliage feeding insects have been shown to be less affected by drought than phloem feeders [42], CO₂ and other climate effects on biological control systems will be more complicated than can allow for such broad predictions to be made. Furthering the complexity of predicting insect life history traits that may generally maximize biological control efficacy is that different life stages/instars of the same insect species can respond differently to climate [32, 43], as well as evidence that different plant tissues may also respond differently to elevated CO₂ [30].

Unlike CO₂, increased temperatures will have multiple direct and substantive effects on insect biological control agents. First, feeding activity of at least some biological control agents has been shown to increase under elevated temperatures [44], with this pattern being fairly common across many phytophagous insect species in general [37]. While this may clearly be beneficial for increasing plant damage (especially when paired with the potential increase in consumption for nutritional deficiencies), such patterns of temperature effects on insect feeding activity are variable and sometimes negative across insect species, particularly at the highest temperatures (i.e. above 30°C; [37]). In fact, recent work has demonstrated that insect thermal response curves can be highly variable across insect and plant species (even independent of plant nutritional quality), demonstrating that effects may not be as consistent as indicated by previous theoretical studies [37]. Second, beyond feeding rates, additional generations and therefore increased population sizes for multivoltine insects [16, 18], as well as a correspondingly greater frequency of feeding events, might be expected to increase plant damage and therefore control efficacy. Similarly, milder winters in many locations could increase agent survival over winter [16, 45] and therefore help keep biological control agent populations viable. Finally, hastened insect phenology is likely to be the most consistent and perhaps substantial impact of higher temperatures across insect species and their corresponding interactions with their host plants [16, 18]. Consequently, phenology of both plants and insects will receive an entire combined section below, as plant phenology is likewise expected to hasten in future climates [18].

Phenological Changes to Invasive Plants and Their Insect Biological Control Agents

Although inherent variability exists in insect and plant phenologies and whether or not they are matched from an

evolutionary standpoint [46], warmer temperatures are widely anticipated to hasten the phenology of both plants and insects [16, 18]. Such phenological alterations (including potential shifts in invasive plant reproductive strategy [45]) will clearly and may often considerably impact insect–plant interactions such as biological control. Among the consequences of altered phenologies is the potential for decreased synchrony between plant and insect life cycles [16, 18], which could certainly affect the timing and therefore amount of insect damage to plants. Such changes to timing of insect feeding might be particularly exacerbated for insects experiencing additional generations as noted above, with the added generations of insects potentially experiencing plants at different phenological stages than earlier generations in the same year. For biological control applications, reduced plant damage resulting from decreased synchrony between the biological control agent and its target plant would certainly be detrimental to control efforts. However, based on how both the particular plant and insect respond phenologically relative to their evolved starting places, biological control may also be enhanced. For instance, in one recent study, it appears that climate treatment-induced hastened plant phenology resulted in better phenological matching, rather than mismatching, between a biennial weed, *C. diffusa* and its biological control agent, *L. minutus* [41]. In this system, the biological control agents emerge from over-wintering before plant growth is vigorous, so plants with hastened phenology were preferred due to earlier availability and therefore better matching with when adults begin to search out hosts [41].

Although temperature will most often be implicated in future plant phenological changes, elevated CO₂ has also been shown to accelerate plant phenology by increasing growth in the biennial weed, *C. diffusa*, in the system discussed directly above [41]. Because rosettes of biennial plants typically need to attain a minimum size to flower, larger individuals can flower earlier [47]. Conversely, among perennial species, CO₂ has been shown to have little effect on reproductive phenology [48]. Such results indicate that differences among various plant life histories should also be taken into account when considering phenological consequences for biological control in the future. Further illustrating this point is evidence that beyond reproductive strategy, plant photosynthetic pathways and other traits can alter plant response to climate change [7].

As noted throughout, temperature and CO₂ can affect multiple aspects beyond phenology of both insect and plant biology in various species-specific ways. Because each of these temperature and CO₂ effects on plants and insects can work together to exacerbate or mitigate the effects of the other, studies relying solely on single climate factors should be interpreted with caution when considering climate change implications on a given insect–plant system [17, 18, 49, 50]. As such, multi-factor climate change studies are critical for understanding how biological control

may truly be impacted in the future, examples of which will be discussed below.

Importance of Multi-Climate-Factor Studies/Effects

A relative lack of research exists when considering combined effects of elevated temperature and CO₂ on plant–insect interactions [17, 18, 49, 50] and therefore biological control of plants by insects. While this likely the understandable result of logistical and cost challenges of such studies, multi-factor studies currently are (and will increasingly become) critical for most accurately predicting climate change effects on biological control. Existing multi-factor studies on insect–plant interactions (e.g. that combine both CO₂, temperature or even more treatments) have produced highly variable results [17, 18, 24, 35, 51, 52], again leading to reiterated cautions against broad interpretations of climate change effects from single-factor studies [17, 18, 49, 50].

While single factor studies have provided invaluable information for predicating possible climate change effects on insect–plant interactions, it must not be forgotten that atmospheric CO₂ and temperature are inextricably linked. As an important part of this linkage, CO₂ and temperature can act to either synergize or counteract the effects of each other on plants and their corresponding interactions with insect biological control agents. As one specific example in a biological control context, elevated CO₂ increased success of endophagous larval agents, *Octotoma championi* Baly and *Octotoma scabripennis* Guérin-Ménéville (Coleoptera: Chrysomelidae) by counteracting leaf loss of *Lantana camara* L. (Verbenaceae) induced by warming alone [35]. That is, the addition of CO₂ allowed for water savings by the plant that prevented the leaf loss, which was responsible for reduced survival under warming-only treatments. If this study had focused solely on warming, the negative effects from warming alone may have been exaggerated as compared to the more realistic (and no less positive) results observed under combined elevated CO₂ and temperature. Although the intent here is not necessarily to devalue any previous (or future) single-factor studies, the likelihood that interactive effects of CO₂ and temperature may alter results seen from single-factor studies should certainly be considered going forward. Such multi-effect studies on biological control are indeed possible and have even been performed in field settings [41].

Clearly, it will be critical to include multiple climate factors in future studies to best understand how CO₂, temperature, and other factors such as altered precipitation will interact to change plant and insect phenology, physiology, etc., and how such changes may in turn benefit or hinder biological control efficacy. While antagonistic effects of multiple climate change factors on food webs/trophic interactions [49, 50] and decreased insect performance with increased number of factors have been shown [24],

the above example of CO₂ preventing leaf loss and therefore increasing endophagous larval success over warming alone clearly suggests that interacting climate factors can alter insect–plant interactions in important, but variable and system-specific ways. As a final example, increased temperature has been shown to mitigate the above-noted positive effects of elevated CO₂ on phloem-feeding insects, in this case pea aphids (*Acyrtosiphon pisum* Harris; Homoptera: Aphididae) consuming the legume, *Medicago sativa* L. (Fabaceae) [40], so such interactive effects can clearly be either positive or negative in biological control contexts. With the variety of both synergistic and mitigative as well as direct and indirect effects of CO₂ and temperature on insect–plant interactions, many important considerations will be necessary for selecting and utilizing biological control agents in future climates.

Considerations for Biological Control Agent Selection in Future Climates

The combined geographical, physiological and phenological changes to both biological control agents and their target plants as the climate continues to change may, in effect, create novel biological control systems even among already well-studied and utilized agents. That is, under novel climate conditions and in novel locations, currently effective agents may become less so, and vice versa, so biological control agent selection will likely become even more challenging in the future. Related to this, the goal of elucidating the most effective agent for any given plant may not be as useful a strategy going forward as it has been previously for focusing control efforts. It may well be the case that the most effective biological control agent(s) for a particular plant might vary geographically based on the conditions in a particular plant population, especially when combined with relative phenological and other plant changes that may concurrently vary with site-specific environmental conditions [9]. As such, consideration of multiple agents and multiple aspects of their respective life histories will become increasingly necessary in the future. Adding to this challenge, however, is again the fact life histories for most insects are currently poorly understood (especially in relation to climate change), with even the better known species likely to show geographically specific responses [21]. Because climate change will result in many complicated changes to the biology of both insects and plants, gaining a better understanding of the basic biology of more biological control agents will become ever more critical.

On top of potentially using different agents geographically, with the variety of species- and even plant tissue-specific [30] phenological and physiological responses to climate change expected, releasing multiple agents in conjunction that can target different plant parts at different times could perhaps be a particularly useful biological control strategy moving forward. There has previously

been some debate in the literature as to whether release of one or multiple agents is more effective, with at least some evidence that multiple agent releases can be more effective in plant biological control applications [53]. In such cases, interactions between agents will clearly need to be evaluated. For instance, predation of one plant biological agent on another (both seed feeders) has been shown, but in the same system, an overall positive effect of multiple other concurrent biological control agents was still observed [54]. Although previous studies have usefully evaluated multiple biological control agents and their relative efficacy for a given invasive plant [e.g. 55, 56], with all the changes expected to both plants and insects in novel climates, multiple agents should not be an overlooked strategy. As such, not only will climatic matching of biological control agents with their target plant (in a particular location) be quite important moving forward [19, 53], matching biological control agents to each other may become increasingly important as well.

Novel climates and therefore novel biological control systems will require land managers to utilize as much information as they can to maintain or hopefully even enhance biological control efficacy. Careful consideration and study of agents' life histories will be critical, especially in relation to the corresponding life history of its target plant. Although this point has been reiterated many times throughout, it is perhaps the crux of this entire review. While the available literature again does not currently make it possible to predict for many (if any) systems, which particular biological control agents may be most effective for a particular plant invasion with climate change, important general considerations for biological control agent selection given the current literature as cited throughout have been summarized in Figure 1.

Beyond the many considerations that will need to be made for matching biological control insects to target invasive plants in the face of climate change, another area of important consideration for the future may be non-target effects. Non-target effects have long been of concern and studied as a key part of selecting biological control agents [12]. In a climate change context, however, consideration of non-target effects even further adds to the already substantive complexity of agent selection. That is, matching plant and agent life histories may need to also include elucidation of any changes to native plants that might increase likelihood of attack by biological control agents. Non-target (native) plants can of course be expected to undergo the same sorts of modifications with climate change that are anticipated for respective invasive plants as described throughout this review. These changes in non-target plant biology, as with their invasive counterparts, may serve to either make non-target plants more or less attractive to biological control agents, at least if they were already within the agent's potential host range. Although non-target effects can be expected to be as variable across systems as all other aspects of biological control described throughout, changes to target host plants

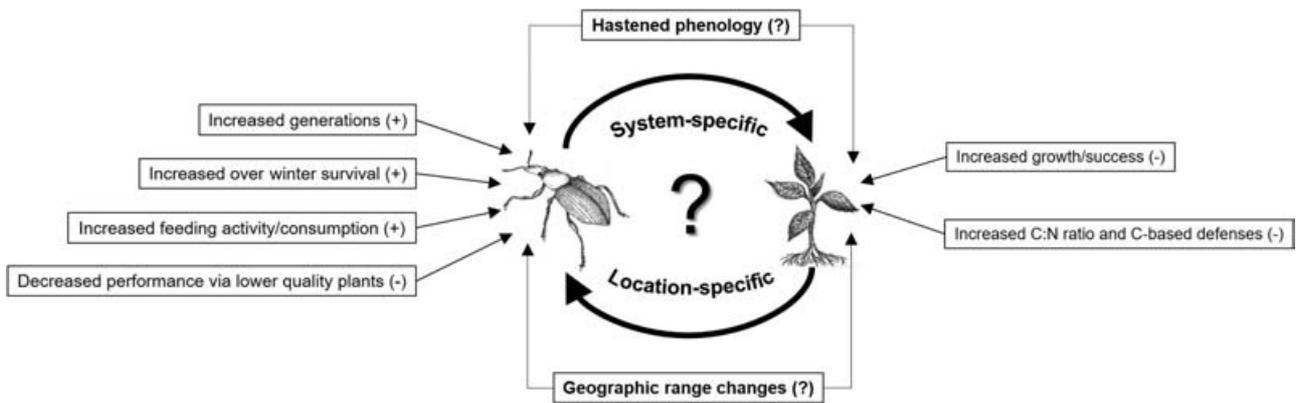


Figure 1. Summary diagram of primary direct and indirect climate change effects on biological control agents and their target plants. Signs associated with each effect indicate the generally anticipated influence on biological control efficacy, but given the highly species- and/or location-specific responses to climate change, signs/influences will not be ubiquitous across systems (and may even be reversed). Hastened phenology and geographic range changes for both agents and plants are bolded to indicate their relatively large and more consistent role in affecting biological control systems in the future, particularly given that they will likely interact with other effects shown to further alter control efficacy. Biological control agents with life history traits that best match not only novel climatic conditions, but also consequent host-plant modifications with climate change will be critical to elucidate in the future.

that may make them less desirable or palatable to biological control agents, along with changes to non-target plants that might make them more palatable, could correspondingly cause agents to switch hosts (or at least more readily accept non-target hosts) and increase non-target effects.

Although the notion of potential host switching with climate change is certainly speculative at this point given the paucity of studies that currently exist on this topic, at least one study has indeed shown increased non-target effects on plants in the field with climate change [45]. In this study, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae), a biological control agent for the invasive plant, *Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae), in China was shown to increase damage on native, non-target *Alternanthera sessilis* L. with warming. This increased damage was concurrent with a major shift in *A. sessilis* from annual to perennial, so combined potential changes to both target and non-target plants, especially in biological control systems with non-target plants that are geographically and phylogenetically near to a given invasive plant in question, should be carefully considered as biological control agents are selected in future climates. As with other aspects of this review, broad generalizations cannot yet be made as to when and where non-target effects might be increased, but practitioners may be wise to consider if any nearby native plants may be phylogenetically related enough to an invasive plant in question to potentially be impacted by climate changes and corresponding biological control agent activity.

Conclusion

Given the anticipated benefits for invasive plants, maintaining or enhancing biological control efficacy (while

minimizing non-target effects) in the future will require adaptation to climate change. Aiming to predict future biological control efficacy will necessitate understanding not only the climate sensitivities of target (and non-target) plants and their agent(s), but especially the climate sensitivity of their interactions. Various life histories of both plants and insects will be impacted in different ways by increases in CO₂, temperature, and other climate factors such as extreme weather events, adding greatly to this challenge. Especially because the multitude of anticipated climate effects may be geographically-specific, many more multi-factor and location-specific studies are needed to best understand how particular biological control systems may respond to climate change. Even still, although substantive phenological, physiological and geographic changes to insect–plant interactions are expected as the climate continues to change, these changes may not all be detrimental to biological control efforts. In fact, such changes may even increase success in some instances, so biological control can and should continue to be an important strategy for invasive plant mitigation in future climates.

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Climate change has increased pest population and their damage potential by expanding distribution, enhancing survivability and allowing to develop the adaptability of insect pest. Rising temperature, modified precipitation patterns, disturbed gaseous composition of atmosphere etc. are causing the change in population, mobility, behavior of insect pest. As the complexity of climate variables have direct concern in agri-culture, the major impacts on agriculture is inevitable. As in agriculture, climate change can intervene in normal plant physiologies like photosynthesis, respiration, transpiration, nutri-ent uptake, mineral balance, ionic exchange etc. As well as, climate change can interfere crop production via modification of popula-tion and function of pests and pathogens. Classical biological control of invasive plants using host specific insects from invaders's native range is a powerful and highly selective tool for mitigating weed spread and impacts. However, climate change may affect multiple factors that determine the efficacy of this important management tool. Future environmental conditions likely include elevated atmospheric levels of carbon dioxide (CO₂) and temperatures, coupled with reduced or altered patterns in precipitation. Subsequent experiments will measure the interactive effects of elevated CO₂ on host plant-herbivore interactions. These will initially focus on determining if and how host plants grown under elevated CO₂ might influence the biology and efficacy of approved and candidate weed biocontrol agents. Climate change is any significant long term change in the expected pattern, whether due to natural variability or as a result of human activity. Environmental conditions play a key role in defining the function and distribution of plants, in combination with other factors. Changes in long term environmental conditions that can be collectively coined climate change are known to have had enormous impacts on current plant diversity patterns; further impacts are expected in the future. It is predicted...