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REVIEW ARTICLE

Climate change effect on the efficacy of biological control agents of terrestrial and aquatic invasive weeds

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ABSTRACT

Climate change may affect the weed biology and ability to thrive well in adverse situations in comparison to biocontrol agents used to manage these weeds though biological control methods. The complex interactions between invasive terrestrial and aquatic weeds and their biocontrol agents have challenges under climate change scenarios. Increased climatic parameters like temperature, CO_2 and rainfall have been documented well for increasing the fitness of terrestrial and aquatic weeds in different areas. Some studies have also pointed out the effect of elevated temperature, CO_2 and rainfall on the insect life-cycle and their performance to manage the invasive weeds by the biocontrol agents. Many prediction models based on climatic parameters have been developed in context to the distribution and range expansion of terrestrial and aquatic weeds and also suitability of their biocontrol agents to manage them. In this review, we synthesize and discuss studies describing the potential of biocontrol agents for the management of invasive terrestrial and aquatic weeds under climate change in context to India and the world as well. We also discuss potential methodologies of prediction models that can be used for the fast establishment of biocontrol agents against the invasive weeds under climate change.

Keywords: Aquatic weeds, Biocontrol agents, Biological control, Climate change, CO_2, Invasive weeds, Weed biology

INTRODUCTION

Alein invasive weeds are plant species when introduced to new environments, rapidly multiply and replace native species, causing ecological, economic, and social damage due to unbeatable attributes like rapid growth, high seed production, and environmental adaptability. Species like *Cirsium arvense*, *Lantana camara*, *Parthenium hysterophor*us, *Eichhornia crassipes*, *Pistia stratiotes*, *Salvinia molesta etc.* exemplify this disturbance. *Lantana camara* forms dense thickets that displace native plants and alter fire regimes in tropical forest areas. *Parthenium hysterophorus*, once a weed of non-cropped areas, has become a major weed of cropped areas (Sushilkumar 2014) while *Cirsium arvense* competes with crops and native species for resources in temperate zones. Water hyienth in water bodies develops dense mats on water surfaces, blocking sunlight and oxygen, severely impacting aquatic ecosystems, fisheries, and recreational activities besides being a cause of several drowning cases of men and animals in India and elsewhere (Dar *et al.* 2019, Yigermal and Assefa 2019, Sushilkumar 2011, 2012, 2022). These invasive weed species reduce biodiversity, degrade habitats, and disrupt ecosystem functions in both terrestrial and aquatic environments globally.

Methods like manual or mechanical removal and herbicides are expensive, environmentally harmful and often ineffective on a large scale. Biological control has gained popularity as a more sustainable and eco-friendly solution for managing invasive weeds. Introduction of coevolved natural enemies from an invasive species' home range (classical biological control) has been one of the key methods for suppressing invasive species (McFadyen 1998, Moran *et al*. 2005, Messing and Wright 2006). Biological control uses natural enemies like insects, pathogens, competitive plant species, nematodes or herbivores to manage invasive species through eating, killing or competition. Host specific biocontrol agents are carefully chosen from the native range of weeds to introduce in other countries where that type of weeds has become a menace or to introduce known and proven bioagents from other countries to target invasive weed without harming native plants, animals, or ecosystems (Sushilkumar 2015). Biological control has effectively managed invasive species such as *Opuntia* (prickly pear cactus) from India and many other counties (Sushilkumar 2015) including from South Africa, where *Dactylopius opuntiae*

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(cochineal insect), controlled its spread (Kudakwashe 2021). For aquatic weeds like *Eichhornia crassipes*, bioagent *Neochetina eichhorniae* targets the plant's stems and roots, reducing its growth and expansion. Similarly, *Cyrtobagous salviniae* have been introduced to control *Salvinia molesta* in regions like Southeast Asia including India and Australia, feeding on its fronds to limit its spread (Sushilkumar 2015). These examples highlight the success of biocontrol agents in managing invasive species world over by targeting their specific weaknesses. Success stories of weed biological control in India have been dealt by Sushilkumar (2022).

Biological control offers several advantages over traditional methods, including long-term, self-regulating management of invasive weed species. Once established, biocontrol agents can maintain populations in response to changes in weed numbers, reducing the need for continuous intervention and minimizing environmental risks from chemicals or mechanical methods. It is also more cost-effective for large-scale weed control, especially in resource-limited countries. However, the success of biological control depends on environmental factors, including climate conditions, which affect the survival, reproduction, and efficacy of biocontrol agents. Therefore, climate change may significantly impact the effectiveness of biological control strategies.

Climate change significantly impacts the spread, distribution, growth and ecological impact of invasive weeds in general and alien invasive weeds in particular. Rising temperatures, changed rainfall patterns and increased atmospheric CO_2 can increase the invasiveness of weed species, which in turn disrupt ecosystems, threaten native biodiversity, and cause economic losses in cropped, non-cropped and forest areas. There is prediction of increase of global temperatures which may exceed 1.5°C during 2021 to 2040, particularly under high-emission scenarios (Bacchin *et al.* 2023, IPCC 2023). It has been projected that CO_2 concentrations may increase two to four times higher than those observed in the last 0.8 million years without significant mitigation efforts. This may lead unprecedented climatic changes (Raviraja 2023). According to the Intergovernmental Panel on Climate Change (IPCC), the global atmospheric CO_2 concentration may rise to 730-1000 µmol/mol by the end of the 21st century (Varanasi *et al.* 2015). Further, if emissions remain unchecked, global temperatures could rise by 3.6 to 4.4°C by the end of the 21st century (Adak *et al.* 2023), which may cause severe consequences for, food security, human health and water availability.

Simberloff (2012) opined that climate change may also influence weeds and natural enemy's species interactions, and biological control agents effectiveness by causing changes in their life-cycle and distribution. Climate change can shift interactions of invasive weeds and biocontrol agents which may cause risks to non-target species (Simberloff 2012).

With the growing concern of climate change and weed invasions, there has been an increase in studies on climate change effects on biocontrol agents, however, our understanding of the response of these plant-herbivore interactions to the full complement of climate-driven changes are still elementary. The aim of this paper is to review the available information of climate change effects on weed biocontrol agents apart from some insight on effect on invasive weeds.

Climate change impacts on terrestrial invasive weeds

Clements and Ditommaso (2011) interpreted those rising temperatures, altered precipitation patterns, and an increase in extreme weather events will likely to facilitate the spread and proliferation of invasive weeds, allowing them to expand into new regions and become more abundant and harmful to the existing ecosystems. Rising temperatures increase growing seasons, accelerating growth and seed production, while enabling weeds to colonize in higher altitudes that were previously unfavorable (Clements and Jones 2021). *Parthenium hysterophorus*, an invasive species in Asia, Africa, and Australia, thrives in disturbed soils and regions with low rainfall. The increase in temperatures and atmospheric CO_2 levels has enhanced its germination and spread, particularly in the cooler regions, where it poses a significant threat to agriculture and public health due to its toxic nature and allergenic pollen (Mao *et al.* 2021).

Chromolaena odorata, native to America, has also spread into parts of Africa and Asia as a result of climate-induced changes in temperature and precipitation (Adhikari *et al.* 2023). This weed has been reported to increase its spread from South India to Central and North India through Chhattisgarh and Madhya Pradesh (Sushilkumar 2015). Likewise, *Mikania micrantha* was never encountered in Central India, but its recent occurrence in Sarni village of Betul district of Madhya Pradesh and near Talpuri lake of Durg district of Chhattisgarh is an indication of its expanding range due to climate change (Sushikkumar, personal observations).

Lantana camara, native to Central and South America, has become a major invasive species in tropical and subtropical regions, forming dense thickets that displace native vegetation and alter fire regimes. Rising temperatures and changing rainfall patterns have accelerated its spread in Africa, Asia, and Australia, complicating biocontrol efforts by increasing its density and resilience (Dar *et al.* 2019). *Carduus nutans*, an invasive weed, has become more aggressive due to warmer temperatures and higher CO_2 levels. These conditions enhance its growth and seed production, increasing competition with native plants and crops, and complicating biocontrol efforts by agents like the *Rhinocyllus conicus* weevil (Keller 2019).

With the increase in temperatures, many invasive weeds may extend their growing seasons and expand their geographic ranges, moving into areas that were previously too cold. For example, earlier *Ageratina adenophora* (Crofton weed) and *Lantana camara* (Lantana) were observed to invade higher altitudes and new temperate zones but hot temperatures now support their growth and reproduction. This tendency has caused the invasion of Lantana for cooler and temperate reasons world over. Such shifts enable these species to invade new habitats and outcompete native flora adapted to cooler climates (Bradley *et al.* 2010, Hulme, 2016).

Increased CO_2 can increase the growth rate, biomass, and reproductive output of species like *Bidens pilosa* (black jack) and *Ipomoea purpurea* (morning glory), allowing them to replace native plants (Ziska and George 2004). Climate change in the form of droughts can benefit drought-tolerant invasive terrestrial weeds like *Chromolaena odorata* and *Parthenium hysterophorus* at the expense of native species that may not be resilient as of them (Sushilkumar 2015).

Climate change has contributed to increased fire frequencies. Lantana has been found responsible for many forest fires in India. This accelerated the spread of Lantana after forest fires in the barren land devoid of other native vegetation. Weeds like *Parthenium hysterophorus* are becoming more difficult to manage in crop fields as climate change extends their growing seasons throughout the year and enhances their resilience. These factors affect crop yields and increase the costs associated with weed management, such as herbicide applications and labor (Sushilkumar and Varshney 2009). Ziska and George (2004) opined that although some aspects of climate change may be viewed as advantageous, the rise in atmospheric CO_2 is not selective as it stimulates the growth of both wanted and unwanted plants.

Effects of climate change in aquatic invasive weeds

Aquatic invasive weeds spread and establishment in new areas may be altered by flood or increased drought. Rahel and Olden (2008) reported that *Cabomba caroliniana* (Carolina fanwort) and *Typha angustifolia* (narrow leaf cattail) benefitted from altered water regimes, allowing them to spread in new or expanded waterways. Similarly, *Salvinia molesta* has expanded its range from its native areas into regions such as India, Southeast Asia, and Australia, driven by rising temperatures and fluctuating water levels. This invasive fern forms dense mats on water surfaces, blocking sunlight and oxygen, which disrupts aquatic ecosystems and outcompetes native plants Expanding range of *Salvinia molesta* in water bodies from South India to central and North India is an alarming indications of climate change on the thriving abilities of this weed (Sushilkumar 2022, 2024).

Rising temperatures and changing rainfall patterns create favorable conditions for invasive aquatic weeds like water hyacinth, alligator weed, water fern to grow faster and spread more widely. *Eichhornia crassipes* (water hyacinth) thrives in warmer temperatures, which allows it to proliferate across all over the world including India. Warmer winters reduce natural die-back, enabling it to form dense mats that obstruct waterways, hinder fishing, and disrupt ecosystems (Patel 2012, Datta and Palit 2021, Sushilkumar 2022). For example, water hyacinth thrives more in South India during winter than the North India where its growing points are killed due to die-back symptoms, which reduced its growth drastically. *Najas* spp. and other submerged weeds have been benefited from warmer temperatures allowing it to invade new regions and persist longer in water bodies. (Sharma *et al.* 2020, Sushilkumar 2022).

Water hyacinth and *Salvinia molesta* (giant salvinia) respond positively to elevated CO_2 leading to rapid biomass accumulation (Gupta *et al.* 2020). *Azolla pinnata* (mosquito fern), a highly CO_2 -responsive species, showed increased biomass production in elevated CO_2 environments. This proliferation enables it to rapidly cover the surface of ponds and canals, significantly reducing oxygen levels and blocking sunlight, which impacts the photosynthesis of submerged plants (Gupta *et al.* 2021). *Potamogeton crispus* (curly-leaf pondweed) demonstrates accelerated growth and larger plant mass with higher CO_2 levels (Rajan and Mathew 2019).

Climate-induced droughts can lower water levels in rivers, lakes, and reservoirs, creating shallow, warm waters ideal for invasive submerged weeds like *Hydrilla verticillata, Potamogeton* spp., *Vallisneria* spp. *etc*. Increase and heavy rainfall lead to flooding, which aids the quick dispersal of floating invasive weeds like water hyacinth, *Pistia stratiotes,* and *Alternanthera philoxeroides* (alligator weed) through broken weed fragments and seeds over larger areas, accelerating the colonization of new water bodies and flooded plains. This spread affects agriculture, as these weeds often invade rice paddies and irrigation canals, leading to reduced crop yields and higher management costs (Singh *et al*. 2016). *Salvinia molesta* fast spread and invasion was reported in the rice field in the Bhandara district of Maharashtra state of India with the flood water of Wainganga River during rainy season of 2022 (Sushilkumar, personal observation). Farmers and Agricultural department were worried due to invasion of this aquatic weed in the rice fields.

Current biocontrol scenario of terrestrial and aquatic weeds in India

In India, biological agents, mainly insects have provided excellent biological control of prickly pear *Opuntia elatior* and *O. vulgaris* by *Dactylopius ceylonicus* and *D. opuntiae*; *Salvinia molesta* by weevil, *Cyrtobagous salviniae*; water hyacinth by weevils *Neochetina bruchi, N. eichhorniae* and mite *Orthogalumna terebrantis*; and *Parthenium hysterophorus* by chrysomelid beetle *Zygogramma bicolorata*. Some introduced bioagents did not prove success but providing partial control like of Lantana by agromyzid seed fly, *Ophiomyia Lantanae,* tingid lace bug, *Teleonemia scrupulosa* out of 9 introduced bioagents; *Chromolaena odorata* by *Pareuchaetes pseudoinsulata* and *Cecidochares connexa*; *Ageratina adenophora* by gallfly *Procecidochares utilis*; submerged aquatic weeds such as *Vallisneria* spp. and *Hydrilla verticillata* in fish ponds by grass carp (Sushilkumar 2024).

A tropical American rust fungus (*Puccinia spegazzinii*), collected in Trinidad, was released in India in Assam and Kerala in 2005. Initial symptoms of attack were noticed but it did not prove potential bioagent so far. Despite the rust failing to persist in the field in India and China, the potential of *P. spegazzinii* is recognized by Taiwan, Fiji where it has established and causing significant damage to *Mikania micrantha* (Sushilkumar 2024).

Currently in India, about 32 exotic biological control agents have been introduced against weeds, of which six could not be released in the field, 3 could not be recovered after release while 23 were recovered and established. Based on established results of biological control agents, 7 are providing excellent control, 4 substantial control and 10 partial controls (Sushilkumar 2024). Maximum degree of success by classical biological control agents in India has been reported by Singh (2004) by aquatic weeds (55.5%) followed by homopterous insect pests, a type of sucking insect class (46.7%) and again terrestrial weeds (23.8%).

Effect of climate change on physiology and nutritional status of weeds vis-a-vis their natural enemies

It has been documented that biological invasions will be favoured under this new atmospheric regime (Reeves 2017), as exotic weed species are more adapted to take up and use available resources at a faster rate than native communities. Bale *et al*. (2002) examined the direct effects of climate change on insect herbivores and identified temperature as the dominant abiotic factor, which affects development, survival, range and abundance. Photoperiod is the dominant cue for the seasonal synchrony of temperate insects, but their thermal requirements may differ at different times of year. Many studies have shown that increased CO_2 levels in the atmosphere cause significant impacts on photosynthesis, plant productivity (Reeves 2015, Gufu *et al*. 2018) and plant-insect interactions (Cornelissen 2011). Feeding habits of insects may get affected due to changes in nutritional parameters of weeds under high CO_2 (Casteel *et al*. 2012). Study showed that plants including weeds grown under elevated CO_2 inclined to have increased rates of photosynthesis, reduced photorespiration, high C:N which cause overall decrease in plant quality with lower nutritive ratios (Zavala *et al*. 2013, Reeves 2017, Kumar *et al*. 2021). Climate change significantly affects the dynamics between invasive weeds and their biological control agents, with far-reaching implications for ecosystem management (Pyšek and Richardson 2010). In addition to altering weed distribution, climate change can also impact the physiological traits of plants, such as nutrient content and the production of chemical defenses, which make these invasive species more resilient and reduce the effectiveness of biocontrol agents (Finch *et al*. 2021). Increased carbon assimilation may reduce nutrient levels like nitrogen and phosphorus, which are responsible for reducing biocontrol effectiveness (Grutters *et al*. 2016). Increased CO_2 levels can boost the production of defensive compounds in invasive weeds, such as alkaloids and tannins, making them more resistant to biocontrol agents (Kaur *et al*. 2022). For example, *Carduus nutans* increase lignin and carbon-based compounds under elevated CO_2 making it tougher and less palatable to herbivores like the *Rhinocyllus conicus* weevil. This reduces the weevil's feeding efficiency and limits its impact on the weed population (Crawley and Ross 1990). Zhang *et al.* (2016) mentioned that elevated CO_2 levels can alter the biochemical composition of invasive weeds, affecting their nutrient content and chemical defenses.

Climate change can alter water temperature and chemistry, affecting *Salvinia molesta* nutritional content and increasing secondary metabolites. This makes the plant less palatable to biocontrol agents like *Cyrtobagous salviniae*, reducing their feeding rates and effectiveness in controlling the weed (Wahl *et al.* 2021). Higher CO_2 levels can boost secondary metabolite production, such as tannins, lignins, and alkaloids, making plants more resistant to herbivores and biocontrol agents. For example, Parthenium shows increased allelopathic chemicals under elevated CO_2 reducing biocontrol agents' effectiveness (Mao *et al.* 2021).

Effects of climate change on biocontrol agents of terrestrial weeds

With the increase in spread and abundance of an invasive weed species into new regions, the effectiveness of biological control becomes increasingly ambiguous. In some cases, the height and growth of invasive plants may overwhelm the capacity of biocontrol agents to reduce weed populations effectively. Initially, it was found that *Zygogramma bicolorata*, a bioagent of Parthenium was suited to a moderate climate and may not establish in areas experiencing temperature below 15°C and above 35°C (Jayanth and Bali 1993). However, Sushilkumar (2012, 2014, 2015, 2022, 2024) found the effectiveness of these bioagents in many parts of India under extreme climatic conditions. Omkar *et al*. (2008) found that development was fastest with maximum survival at 27°C. They also showed that a lower temperature threshold (lowest average temperature in which, life cycle can sustain well) of 18.5°C and thermal constant (K) of 480.8 degree-day were required to complete the development.

While there are a number of studies predicting the effects of increased CO_2 on plant ecology (Reeves 2017), increased temperature under the same conditions has not received noteworthy attention, especially within the terrestrial environment. It is of utmost importance to ensure constant effectiveness of biological control in the light of climate change as it would be detrimental to the environment and the economy of the country to re-employ previous control measures like the use of chemicals and mechanical and manual removal to manage the weeds. Therefore, it is essential to perceive and predict precisely the response of invasive weeds and their biological control agents to climate change (Reeves 2017).

Terrestrial weed *Parthenium hysterophorus* has invaded about 35 million hectares of land in India (Sushilkumar and Varshney 2009). It has been considered a biggest threat for loss of crop productivity, biodiversity and many health problems in human beings. In spite of thr invincible attributes of Parthenium, its biological control by bioagent *Zygogramma bicolorata,* introduced from Mexico during the 1980s caused huge reduction of the weed and helped in restoration of the biodiversity. Although, it is claimed by the non-believer of biocontrol that the bioagent has done nothing to reduce the intensity of Parthenium. However, in a conservative estimate Sushilkumar (2022) estimated that *Z. bicolorata* has spread and established well in about 25 million hectares out of 35 million infested area of India, which amounts to be about 71% area. The bioagent effectiveness was recorded from low to high temperature regimes from different regions of India. This bioagent controls Parthenium at varied levels from nil to 100% during the rainy season only. Taking only 10% complete control (100%) of the weed, the saving of about Rs. 6.0 billion every year was estimated in terms of herbicides required to control it.

Climate change may indirectly affect biocontrol of weeds by the way of its direct influence on the reproduction, survival, distribution and behavior of bioagents especially insects (Sujayan and and Karuppaiah 2016). Successfully adapted and established bioagents may also get affected due to climate change. For example, feeding efficiency of *Zygogramma bicolorata* on Parthenium was reportedly decreased at the optimal temperatures above 27-30^{0}C (Kumar *et al.* 2021). Changed quality of parthenium weed leaves in elevated CO_2 and temperature levels resulted in the increase of consumption, slower food conversion rates, increase in developmental period with reduced reproduction efficiency of *Z. bicolorata* (Kumar *et al.* 2021). Their findings indicated that the reproduction efficiency of *Z. bicolorata* is likely to be reduced as the climate changes, despite increased feeding rates exhibited by grubs and adult beetles on parthenium weed foliage. Sushilkumar *et al.* (2018) studied the effect of elevated CO_2 and temperature in combination and separately on the efficacy of *Z. bicolorata* on

Parthenium amidst the blackgram crop in open top chambers (OTC). They found low nitrogen content in elevated CO_2 foliage while carbon content was higher in elevated CO_2 foliage. C: N ratio was considerably higher in elevated CO_2 foliage. Elevated CO_2 foliage had higher polyphenol content too, compared to ambient CO_2. Mean population counts revealed maximum population (adults/plant) of *Z. bicolorata* during 6th and 7th weeks in the chambers having elevated CO_2 alone or elevated temperature alone while it was high during 7th to 8th week in the chambers having both elevated CO_2 and elevated temperature, but in ambient chamber, population increased in 8th to 9th weeks. This showed that alone high temperature and high CO_2 induced high egg laying and early development while under combination of temperature and CO_2, population increased was delayed.

Chidawanyika *et al.* (2017) studied heat tolerance in biocontrol agent *Z. bicolorata* through multiple experiments. The results showed the effects of heat waves on the performance and survival of biocontrol agent, which may influence its effectiveness on *Z. bicolorata*. The authors also emphasized the importance of different methodologies when studying heat tolerance. In contrast, the sap-sucking bug *Dactylopius opuntiae* Cockerell (Dactylopiidae) had reduced fitness under elevated CO_2 which resulted in the target weed, *Opuntia stricta* Haw. (Haw.) (Cactaceae), taking on average three weeks longer to die than plants exposed to the same initial density of the agent at current CO_2 concentration (Venter *et al*. 2022). The efficacy of biocontrol of *O. stricta* in South Africa may therefore be reduced in future (Venter *et al*. 2022). The physiological impacts of agents under different climate change scenarios could have important management implications and is an understudied area of research where more effort is warranted.

The effectiveness of *Cactoblastis cactorum* (moth) as a biocontrol agent for *Opuntia* spp. depends heavily on temperature. Warmer temperatures can enhance the insect's life-cycle speed, potentially increasing its population. However, extreme heat may disrupt its reproduction and reduce survival rates, decreasing overall efficacy (Sutherst *et al.* 2007) whereas *Dactylopius ceylonicus* (cochineal insect) also exhibits temperature-dependent development. Climate-driven temperature increase can either improve its efficacy by increasing feeding rates or hinder it if temperatures exceed tolerance levels, impacting the spread and density control of *Opuntia dillenii*. The bioagent *Zygogramma bicolorata*, is an effective biological control agent of *Parthenium hysterophorus* in India and Australia and many other countries. Adult beetles diapause in soil during December to May. As a result, there is delay in its effectiveness on the plant that reaches to flowering and seed production by the time the beetle is able to build up its population after emerging from diapause. Sushilkumar and Ray (2010) conducted a study to explore possibilities of diapause aversion by temperature regulation. They found that exposure of newly emerged adults to heat treatment of 35°C and to low temperature of 10°C could reduce diapause in *Z. bicolorata*. It was suggested to use low temperature as a medium for the storage of the mass reared beetles for a long time without having negative effect on their longevity and fecundity.

Zygogramma bicolorata (Mexican beetle) performs best in moderately dry conditions, and heavy rainfall can limit its effectiveness by reducing its activity and survival rates. Climate change-induced rainfall variability may lead to fluctuations in beetle populations, affecting its capacity to control *Parthenium* effectively (McFadyen 1992). In the Assam state of India, senior author released many thousand adults of *Zygogramma bicolorata* during 2015 to 2017, but only mild establishment of the bioagent was observed in Guwahati and no establishment was found yet (Sushilkumar 2014, 2022). Excessive rainfall and moisture were considered one of the limiting factors in this case.

Higher CO_2 levels may increase the growth rate of *Chromolaena odorata,* making it more challenging for *Pareuchaetes pseudoinsulata* (moth) and *Cecidochares connexa* (gall fly) to keep pace with its growth. Enhanced plant biomass under elevated CO_2 could demand higher agent populations to achieve similar control effects as before, reducing the per capita impact of the agents (Stiling and Cornelissen 2007). *Procecidochares utilis* (gall fly), which is used for biocontrol of *Ageratina adenophora,* may experience altered reproductive cycles under climate change. Rising temperatures may accelerate its development, potentially increasing its population in the short term but potentially leading to fewer generations over the year as reproductive timing is disrupted (Wang *et al.* 2013).

These examples illustrate the ways, climate change affects biocontrol efficacy, including shifts in temperature, water availability, and CO_2 levels. Adaptation strategies in biocontrol may need to account for these men-driven challenges to maintain effective control over invasive weed species in India and elsewhere.

Effects of climate change on biocontrol agents of aquatic weeds

Reproduction and development of *Cyrtobagous salviniae*, a bio-control agent of *Salvinia molesta* may get affected due to rising temperature (Allen *et al.* 2014). Decreased plant palatability of alligator weed (*Alternanthera philoxeroides*) under drought has reportedly caused reduction in population growth of its bio-agent *Agasicles hygrophila* suggesting that drought can reduce the biological control of alligator weed indirectly by interrupting plant–insect interaction (Wei *et al.* 2015). Climate change may shift interactions of invasive plants, herbivorous insects and native plants, potentially affecting biological control effcacy and non-target effects on native species.

Lu *et al.* (2015) showed how climate warming affects the impacts of a multivoltine introduced biocontrol beetle *Agasicles hygrophila*, an effective biocontrol agent of aquatic and terrestrial weed *Alternanthera philoxeroides* on the non-target native plant *Alternanthera sessilis* in China. In field surveys across a latitudinal gradient covering their full distributions, they found beetle damage on *A. sessilis* increased with rising temperature and plant life history changed from perennial to annual. Experiments showed that elevated temperature changed plant life history and increased insect overwintering, damage and impacts on seedling recruitment. These results suggest that warming can shift phenologies, increase non-target effect magnitude and increase non-target effect occurrence by beetle range expansion to additional areas where *A. sessilis* occurs. This study highlights the importance of understanding how climate change affects species interactions for future biological control of invasive species and conservation of native species. Further, they interpreted that because *A. philoxeroides* will also expand its range further North China in response to warming, and the plant tolerates cold better than *A. hygrophila*, the overall effect of biocontrol may be weak in higher latitude.

Henriksen *et al*. (2018) studied effects of elevated CO_2 on the invasive weed *Alternanthera philoxeroides* and the biocontrol beetle *Agasicles hygrophila*. The authors explored the impacts of elevated CO_2 on the interactions of a plant invader and its biocontrol beetle in terrestrial and flooded conditions. The results suggested that elevated CO_2 will have minor effects on the efficacy of this biocontrol agent

In one of the studies, Reddy *et al.* (2019) compared four biotypes of the weevil, *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), a biocontrol agent of water hyacinth (*Eichhornia crassipes*) and found variation in tolerance to cold among populations. They suggested that the introduction of *N. eichhorniae* from Australia into northern California would result in climate matching between source and release environments and increase the distribution and densities of weevils, and by this improve biocontrol efficacy.

Spread of water hyacinth bioagent namely *Neochetina bruchi, N. eichhorniae* and mite *Orthogalumna terebrantis* has been found in water bodies all over India infested with the water hyacinth from their first release sites of Bangaluru (Karnataka state) during 1980s. This has happened due to their movement through flood water from one river to another river and water channels. Now these bioagents are common along with the water hyacinth, however, their impacts vary region to region and water bodies to water bodies under different climatic conditions (Sushilkumar 2011, 2020). Water hyacinth has become the worst aquatic weed all over India, but under North-East and Kerala situation, water hyacinth has assumed a serious problem worth to consider. Many scientists opined that bioagent *Neochetina* spp. are not effective to control the weed. However, there are spectacular success stories of biological control of water hycienth from all over India like Karnataka, Madhya Pradesh, Manipur, Uttar Pradesh, Bihar, Andhra Pradesh, Tamil Nadu states, *etc*. experiencing warmer to extreme temperature regimes (Sushilkumar, 2011, 2024). It has been proved that for successful biological control of water hyacinth, perennial nature of water bodies is essential. Biological control of water hycienth cannot be expected in rivers and running water channels where, population build-up of bioagent is impossible owing to washing away of the existing population along with weed during flood in the rainy season. This is the reason that bioagents is not effective against water hyacinth in the water channels and rivers. Intentional systematic release of the bioagents in appropriate numbers in suitable water bodies can bring spectacular success (Sushilkumar 2024).

Reductions in light may cause oxygen depletion beneath floating invasive macrophyte mats alter submerged plant, plankton, invertebrate, and vertebrate communities (Coetzee *et al.* 2014). For example, severe invasion of *Salvinia molesta* in 900-hectare reservoir in Sarni village of Betul district of Madhya Pradesh in India caused depletion of earlier dominated submerged weed *Hydrilla verticillata* and other flora and fauna especially fishes, which subsequently lead unemployment to inhabiting fisheries communities around the reservoir (Bhagitath 2024, Sushilkumar 2024). Similarly, Paper *et al.*

(2023) investigated the role of current (400 ppm) and projected (800 ppm) CO_2 concentration on another free-floating aquatic weed, *P. crassipes*, growth with and without two of its biocontrol agents, the leaf-chewing *Cornops aquaticum* Brüner (Orthoptera: Acrididae) and the phloem-feeding *Megamelus scutellaris* Berg (Hemiptera: Delphacidae). The study showed that herbivory by *C. aquaticum* was consistent across CO_2 conditions, but the feeding by *M. scutellaris* increased at the elevated CO_2 level suggesting that, at predicted elevated CO_2 concentrations, the successful biocontrol of *P. crassipes* might rely on phloem-feeding insects (Paper *et al.* 2023).

Baso *et al.* (2021) conducted a study to investigate the effects of elevated atmospheric CO_2 (800 ppm) on the biological control of four invasive aquatic weeds (*Azolla filiculoides, Salvinia molesta, Pistia stratiotes* and *Myriophyllum aquaticum* and their respective biological control agents *Stenopelmus rufinasus, Cyrtobagous salviniae, Neohydronomus affinis,* and *Lysathia* sp. in South Africa. They found an overall increase in biomass production and C:N across all species at elevated CO_2, both in the presence or absence of biological control, although C:N of *M. aquaticum* and biomass of *A. filiculoides* with herbivory were not consistant with this trend. Insect feeding damage was reduced by elevated CO_2, except for *S. molesta*. Thus, they found different responses to CO_2 increase, but the general trend suggested that these species will become more challenging to manage through biological control in future.

Cyrtobagous salviniae (*Salvinia* weevil) depends on specific water conditions to effectively manage *Salvinia*. Drought conditions resulting from climate change can reduce water levels, causing habitat desiccation that negatively impacts weevil survival and reduces efficacy in weed control. Conversely, if water bodies become overly flooded, weevil populations may disperse more widely but may not be concentrated enough to control the weed effectively (Julien *et al.* 1999). Sushilkumar (2024) emphasized that for effectiveness of biocontrol agent of water hyacinth *Neochetina* spp., perennial water bodies are one of the important factors after release of bioagents. Water bodies which are dried during summer seasons may affect the pupation process of *Neochetina* spp., because pupation of weevils occur amidst the roots and if roots are anchored in the soil during drought conditions, life cycle will be hampered hence, no success in biological control of water hyacinth may be achieved.

The efficacy of *Neochetina eichhorniae* and *Neochetina bruchi* (water hyacinth weevils) is affected by climate-induced shifts in seasonal patterns. Warmer winter temperatures could disrupt weevil diapause (hibernation period), leading to fewer weevils being ready to control *Eichhornia crassipes* in spring. Moreover, warmer conditions might accelerate the growth of water hyacinth, requiring higher weevil densities to achieve similar levels of control (Tipping *et al.* 2014).

Prediction model to assess effectiveness of bioagent over the weeds in their expanding range

Van and Pichancourt (2015) used matrix models to explore the effects of a biocontrol agent *Evippe* spp. on an invasive shrub *Prosopis* spp. under different climatic conditions. The results showed that plant population dynamics are sensitive to rainfall due to changes in the longevity of the agent adults. Both biocontrol herbivory and changing climate have a strong influence on the invasive shrub and need to be

Dhileepan and Senaratne (2009) mapped the widespread distribution of *P. hysterophorus* and *Z. bicolorata* using CLIMEX modelling and suggested that besides India and Pakistan, this biocontrol agent may be released to *P. hysterophorus* invaded areas of the countries including Bangladesh, Sri Lanka and parts of Nepal. Despite extensive research on *P. hysterophorus and Z. bicolorata* in India, Australia, Africa, Pakistan, *etc*. no serious effort through modelling, other than CLIMEX (Dhileepan and Senaratne 2009, King 2008) has been made to describe the suitable climatic conditions for establishment of *Z. bicolorata* for the management of *P. hysterophorus*. These models have predicted the whole South India including Kerala, coastal areas of Odisha (20.95°N, 85.10°E), West Bengal and whole North-East region of India climatically highly suitable for the establishment of *Z. bicolorata*. However, during ground survey, *Z. bicolorata* was not even recovered from Thrissur, Kerala (10.53°N, 76.21°E); Mohanpur, West Bengal (23.66°N, 88.23°E) and Jorhat, Assam (26.75°N, 94.20°E) in spite of several releases made during 2001–2017 by Sushilkumar (2015, 2022). So far, we have recovered only negligible to moderate establishment of *Z. bicolorata* in Kozhinjampara, Kerala (10.74°N, 76.83°E); Birbhum (West Bengal) and Guwahati (Assam) through ground survey. To predict suitable sites for the establishment of *Z. bicolorata*, an attempt was made by Gharde (2019) to develop statistical models based on ground information so that favorable release sites may be identified. Models were developed using data on climatic variables like temperature, rainfall and relative humidity of the rainy season (July to October) instead of annual mean, when the *Z. bicolorata* remains most active and influences establishment in the subsequent mild season (February to March) and next rainy season. In contrary to CLIMEX Model of King (2008) and Dhileepan and Senaratne (2009), Gharde *et al* (2019) models predict only negligible to moderate establishment of *Z. bicolorata* in Kerala, coastal areas of Odisha, West Bengal and north-east region of India. CLIMEX model on the basis of lower EI values (11–30 and 30–50) predicted Central and North India less suitable while Gharde *et al*. (2019) model predicted these areas moderately to highly suitable for establishment of *Z. bicolorata*. It was understood from the results that although rainfall and relative humidity do not play a significant role if taken individually but their interaction with minimum temperature play a substantial part to predict the establishment. The incorporating of four months climatic data of temperature, rainfall and relative humidity in this model, provide more precise information about the possible establishment of *Z. bicolorata*. Gharde *et al.* (2019) concluded that a site experiencing climate with indices values of average minimum temperature ranging 24.2–26.2°C and rainfall between 191.2–257.3 mm during July to October would be highly suitable for setting up the *Z. bicolor*ata population in the region. It was inferred from the results that sites with very high weighted average rainfall (>514 mm indices value) with MMIN are not suitable for establishment of *Z. bicolorata*. Gaharde *et al.* (2019) models might be useful to decide the most suitable sites for release and establishment of *Z. bicolorata* in India as well as in other parts of the world with similar climatic conditions. The comparative evaluation of these two prediction model based on climate variables clearly reflected that many times, for a particular biocontrol agent, annual mean climatic parameters are not suitable to fit in the predetermined climatic software to predict the suitable areas for the establishment of biocontrol agents. Prediction models for the suitable establishment of bioagent should always be tested with ground verification.

Iris pseudacorus originally from Europe has historically invaded North America, China and Japan, and more recently spread through Argentina, South Africa and Australia, where it is now a target for biological control. In this regard, climatic suitability can be used to model the potential distributions of weeds and their candidate agents, both in space and time, thus allowing to identify areas at risk of invasion and predict where agents will be able to establish long-term. Minuti *et al* (2023) modelled the present and future (2040–2060) climatic suitability of *I. pseudacorus* and its candidate agents using the software MaxEnt. They predicted North America and eastern Asia, climatically suitable for *I. pseudacorus* but found very low suitability of its bioagent across these regions, further decreasing under future climatic conditions.

Sun (2017) studied climatic suitability like elevated temperature, CO_2 and high rainfall on biological control candidates for ragweed management in Europe. This modelling study compared the suitability of six biocontrol candidates with regard to their expected range overlap with the plant invader in the introduced range. The authors advocated this approach as a first cost effective pre-release assessment before more elaborate and time consuming experiments.

Future of biological control in India in context to climate change

In spite of failure of many bioagents, we should be optimistic and enthusiastic to do more introduction of known effective bioagent, which have shown promising results in suppression of weeds like water hyacinth, alligator weed, *Pistia, Parthenium, Mikania, Chromolaena etc*. in the countries of their introduction. Many of such bioagents have not been introduced yet in India, which need immediate attention. Some of these like *Listronotus setosipennis, Stobaero concinna, Buccalatrix parthenica, Epiblema strenuana, Puccinia abrupt* on *Parthenium;* a flea beetle *Agasicles hygrophila* for alligator weed *Alternanthera philoxeroides; Sameodes albiguttalis Warren (Lepidoptera: Pyralidae)* on water hyacinth, *Neohydronomous affinis (Hustache)* on *Pistia stratiotes, Heteropsylla spinulosa* (Homoptera: Psyllidae) on *Mimosa diplotricha* have been effective in controlling growth of the weed in many areas in USA and Australia (Sushilkumar 2024). Some of the suggestions are listed below:

1. In India, relatively little work has been done on new introduction of bioagents against weeds after 1980s. Therefore, there is a great scope of introduction of natural enemies against invasive weeds of terrestrial and aquatic situations.
2. Weeds like C. *odorata, A. adenoforum, M. micrantha* and *Mimosa diplotricha* have assumed serious status in forestry plantations and now spreading their tentacles to agricultural and wastelands. There is urgent need to explore the introduction of new bioagent against these weeds.
3. In India, there is great scope of introduction of some well proven exotic insect enemies like dipterous leaf minor *Coteomvze lanatanae* from Australia and noctuid *Neogulea esula* from Hawaii against *Lantana.*

4. Many alien weeds are great problems in protected forests. The problem may be reduced by release of proven bioagents under classical biological control. The authorities of protected areas such as National Parks do not give permission to release bioagents in the pretext of ban to introduce exotics in PA, while the bioagent has been introduced in the country by due permission of Government. It is also true that in due course, an introduced bioagent will reach on its suitable host inside the protected areas, without man's efforts. This need retrospection by the forest authorities to hasten the biological control process.
5. There are known bioagent, which have shown promising results in suppression of weeds like water hyacinth, alligator weed, *Pistia etc*. in the country of their introduction. Many of such bioagents have not been introduced yet in India, which need immediate attention. Some of these are : *Listronotus setosipennis, Smicronyx lutulentus, Stobaero concinna, Buccalatrix parthenica Epiblema strenuana Puccinia abrupta* on Parthenium; alligator weed flea beetle *Agasicles hygrophila* for alligator weed *Alternanthera philoxeroides*; *Sameodes albiguttalis* Warren (Lepidoptera: Pyralidae) on water hyacinth, *Neohydronomous affinis* (Hustache), *Pistia stratiotes* , *Heteropsylla spinulosa* (Homoptera: Psyllidae) on *M. diplotricha* has been effective in controlling aquatic growth of the weed in many areas in USA.

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