REVIEW PAPER

Impact of climate change on the invasive traits of weeds

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Invasive weeds degrade ecosystems and are a threat to plant and animal biodiversity. The literature on biological invasions suggests that only 10% of introduced species become invasive in a new host range. Most introduced plants do not become invasive in a new environment. The invasive behavior of a weed depends on the weed's genetic variability, biotic factors, and climatic factors with which it interacts. The climatic factors that affect the invasive traits of weeds include the atmospheric temperature, soil temperature, precipitation, evaporation, and CO_2 concentration. The biological traits that are influenced by a change in any one or more of these climatic factors include the pattern of assimilate partitioning, induction of dormancy or seed germination, herbivore tolerance, propagule production and distribution, variability of plant architecture, photosynthetic rate, and seedbank longevity. The impact of climate change on the invasive traits of certain weed species is reviewed.

Keywords: alien weeds, climate change, invasive traits, weed shift.

Every single organism on the Earth undergoes a struggle for its perpetuation and propagation. The fitter that emerge during the course of the struggle try to dominate over the others in the process of resource sharing and in establishing the scope for their continued success in survival. However, besides the individual's ability or potential to win this race, the external factors that are involved also influence the result to a considerable extent. Although the concept of categorizing weeds and crops involves more of a human psychology than any botanical principle, from the point of view of agricultural production and food security, it is imperative that weeds or plants that are out of place deserve a control, rather than coexistence. The control options are more constrained when plants are non-native with more of an invasive nature and complex biological adaptations. Such plant species or invasive alien plants need to climb up a series of steps or barriers to reach a new area and spread (Williams 2003). These steps could be Entry or Escape, Establish, Expand, Explode, and Entrench. These phases are often influenced by abiotic factors like climate. Such an interaction between the climatic conditions and the individual organism that is in the process of range extension, which comprises the last "three Es", namely Expansion, Explosion, and Entrenchment, either could be a direct impact or an indirect impact. The triggering of the biological traits of the species concerned could be considered as a direct impact. The removal of natural barriers or biotic factors that resist invasion by non-natives or aliens (through climate-related disasters like flood or drought) could be the indirect effects of such interaction. However, the success of a particular species or weed in its invasive potential largely depends on such favor or resistance as offered by the climate in the introduced range, as finishing with enthralling vigor and speed is more important than getting a good head start in any race or competition. Thereby, predicting a weed's invasiveness needs to necessarily consider such of those climatic parameters that would alter its invasive traits.

ATMOSPHERIC TEMPERATURE

Invasive species whose native ranges are warmer than their introduced ranges would be at an advantage as

they withstand hot temperatures better than the natives of that region. Increasing atmospheric temperatures could trigger invasion by some weeds in warm-season crops. A rise in temperature by 3°C of average temperature was shown to enhance the biomass and leaf area of itch grass (*Rottboellia cochinchinensis*) by 88 and 68%, respectively (Patterson *et al.* 1979). The weed also has been reported with projected increases in maximum growth for the mid-Atlantic states in the USA (Patterson *et al.* 1999). This invasive weed, which has caused significant yield reductions in sugar cane in Lousiana (Lencse & Griffin 1991), also has been shown to be competitive in corn, cotton, soya bean, grain sorghum, and rice systems (Lejeune *et al.* 1994). As many of these invasive weeds of the southern USA had their origin in areas that are associated with the warm temperature of a tropical climate, increasing temperatures might accelerate the expansion of these weeds to the northern states. (Patterson 1993). Increasing temperatures also could trigger the northward migration of cogongrass (*Imperata cylindrica*) and witch weed (*Striga asiatica*) (Patterson 1995a). An increase in temperature due to global warming might trigger plant migration that exceeds the rate of the same that was observed in relation to the postglacial period (Malcom *et al.* 2002). This would lead to the preferential selection of plant species with higher mobility. Plant traits that aid their dispersal over long distances are frequent in invasive plants (Rejmanek 1996). Accordingly, these invasive plants would be greatly triggered for migration by increasing temperatures (Dukes & Mooney 2000). A hypothesis predicted the migration of Kudzu (*Pueraria lobata* gaining entry to south-eastern USA from Japan) to northern parts (Sasek & Strain 1990). The weed was shown to be restricted by low winter temperatures of −15°C two decades ago. Recent observations indicated mid-western populations of this weed and this migration from south-eastern USA is attributed to an increase in the minimum winter temperature (Ziska *et al.* 2010).

The impact of temperature changes on floristic composition is through a tilting of the balance towards crops in the process of crop–weed competition. Crop losses due to weeds that are left uncontrolled are considerably higher in southern than in northern USA and this is attributed to the presence of perennial invasive weeds (like itch grass, a severe competitor) that are restricted in the northern states by low winter temperatures (Bunce & Ziska 2000). In Australia, the increase in mean temperature is expected to be associated with the range extension of tropical prickly acacia *Acacia nilotica* to the south (Kriticos *et al.* 2003). Crop–invasive weed competition also could be influenced by the

varying magnitudes of response to the interaction of rising temperatures and floral reproductive ability (Ziska & Reunion 2007).

Higher mean annual temperatures are shown to favor assimilate partitioning towards the root biomass in the introduced exotic species *Prosopis juliflora* in southern India. The greater root biomass of this species aids rapid and robust regeneration after lopping of the shrub for the popular fuel wood purpose that contributes to the livelihood of the rural poor in the drier areas or after the revival of ecological stress conditions, such as drought or submergence (Kathiresan 2006a) (Table 1).

An increase in the shoot biomass due to increasing temperature, though observed, is not as significant as the increase in the root biomass. An increase in the root biomass largely contributes to a weed's ability to tolerate climatic extremes, such as the peak of summer that is associated with a high temperature and water scarcity and the peak of the monsoon winter that is associated with water inundation and flooding. This adaptation favors the weed to predominate over other native flora that are susceptible to any one of the two extremes (Kathiresan 2006a). Hyvonen *et al.* (2010) suggest that climate change, with a particular reference to an increasing temperature, would increase the risk of population establishment of new weed species in the northern regions of Europe. A definite warming trend in Germany is expected to increase the chances for the establishment of species with a higher temperature optimum, such as *Vallisneria* spp., and those intolerant to freezing, such as *Pistia stratiotes*, *Eichhornia crassipes*, and *Salvinia auriculata* (Hussner *et al.* 2010).

SOIL TEMPERATURE

The soil temperature plays a key role in promoting seed germination (Schonbeck & Egley 1980). The soil temperature mainly could serve the purpose of the thermal induction of seed germination. Carpetweed *Trianthema portulacastrum* that is invading irrigated upland ecosystems in several tropical Asian countries is shown to be

Table 1. Temperature regimes and root biomass enlargement in *Prosopis* (Kathiresan 2006a)

Mean annual temperature (°C)	Mean annual increase in root biomass (kg)	Mean annual increase in shoot biomass (kg)
28	1.9	42
30	4.4	47
32	6.2	56

more invasive by virtue of synchronized mass seed germination, coinciding with increasing soil temperatures, in India (Kathiresan 2006b).

A major weed that has been invading irrigated upland agro-ecosystems in several tropical Asian countries is *T. portulacastrum*. This weed is reported to have originated from tropical Africa and has invaded three continents; namely, Australia, Africa, and Asia (Yaduraju *et al.* 1980; Rawson & Bath 1984). A survey that was conducted in different irrigated upland crops in Veeranum Ayacut in Tamilnadu, India, indicated that *T. portulacastrum* is the dominant species in the three crops, sugar cane, sunflower, and gingelly, with Important Value Index percentages of 28.73, 26.83, and 25.99, respectively. (Important Value Index percentages are computed by summing the relative density, relative dominance, and relative frequency of each of the component species in the flora and arriving at their average values as a percentage, as suggested by Sen [1981]). This weed tops the list of the 15 weed species that have been recorded in all these crops in different locations in India (Kathiresan 2004). One of the most important characteristics that is responsible for its invasiveness is the thermal induction of seed germination, with a soil temperature of ~35°C favoring the synchronized and mass germination of seeds, covering the soil as a green carpet. In a field study that was conducted at Annamalai University, it was observed that the increasing soil temperature with the summer months of June and July triggered the mass germination of the seeds of this weed, suppressing the native species. The seeds of this weed undergo dormancy during winter and thermo-induction in order to break the dormancy requires soil temperatures of >35°C (Kathiresan 2006b).

SOIL MOISTURE

Invasive weeds of rangelands, like cheat grass (*Bromus tectorum*) and yellow star thistle (*Centaurea solstitialis*), depend largely on the available soil moisture for seed germination. Prolonged or heavy winters that greatly enrich the soil moisture favor increased seed production in both species (Patterson 1995a). Interestingly, both species are also drought-adapted. Cheatgrass has adapted for drought evasion by a shorter life span; whereas, a deeper root system helps star thistle to endure drought, compared to native species. An increase in snowfall or changes in snowfall variability is suggested to exacerbate the invasion of forbs in mixed-grass prairie ecosystems, which in turn could influence the forage availability (Blumenthal *et al.* 2008). Soil moisture stress promoted greater herbivore tolerance for the invasive *Alternanthera*

philoxeroides and decreased it for the native congener *Alternanthera sessilis* in China (Sun *et al.* 2010).

PATTERN OF RAINFALL AND EVAPORATION

The rainfall and evaporation pattern of a region influences the weeds directly by interrupting the physiological functions that are involved in the process of seed dormancy and germination and by imparting seed mortality due to excessive drying or soaking. These effects are transferred through the soil moisture status. The indirect impacts could be through the displacement of seeds or propagules by runoff, scorching with the removal of the soil cover, and mobility of nutrients for better stand establishment.

Global warming directly results in rising sea levels due to the melting of ice caps and the natural expansion of sea water as it becomes warmer. Consequently, areas adjoining the coast and wetlands could be flooded frequently and the distribution pattern of monsoon rains gets altered with more intense downpours, storms, and hurricanes. On larger populations, precipitation extremes could tilt the weed–crop competition in favor of invasive weeds that would be reflected in declining crop productivity (Patterson 1995b). The meteorological data that are available at Annamalai University, at the tail end of the Cauvery River delta region of Tamil Nadu State, India, show that the average annual rainfall during the last 20 years has increased by 233 mm, compared to the average of the previous 10 years (1588 and 1355 mm, respectively), while the rate of annual evaporation has come down by 453 mm (1700 and 2153 mm, respectively) (Table 2). A phytosociological survey of the floristic composition of weeds in this region reveals the recent invasion of the wetland rice fields by the alien invasive weeds *Leptochloa chinensis* and *Marsilea quadrifolia* (Table 3). These two weed species dominated over the native weeds, such as *Echinochloa* spp. (*Echinochloa crus-galli* and *Echinochloa colona*) and

Table 2. Rainfall and evaporation pattern in the tail end of the Cauvery River delta, India

Time	Annual rainfall (mm)	Annual evaporation (mm)	Number of wet years (†)
1981–1990	1355	2153	2
1991–2000	1483	1898	5
2001–2010	1588	1700	5

†>10% of annual precipitation.

Table 3. Floristic composition of the weeds in rice fields that were irrigated by channels in the Cauvery River delta, India (Importance Value Index, %)(Kathiresan 2011)

Weed species	Channel I		Channel II		Channel III	
	1990	2010	1990	2010	1990	2010
Echinochloa spp.	25.56	7.93	28.48	8.01	27.52	4.02
Leptochloa chinensis	22.74	30.41	24.81	29.85	23.64	32.17
Cyperus rotundus L.	17.23	12.50	22.28	17.25	17.01	4.80
Sphenoclea zeylanica	2.02	6.28	0.68	2.17	1.68	7.24
Marsilea quadrifolia	1.46	39.61	0.63	41.84	0.46	40.32

others, by virtue of their amphibious adaptation to the alternating flooded and residual soil moisture conditions that have been prevalent during recent years in this region (Yaduraju & Kathiresan 2003; Kathiresan 2006b).

Leptochloa chinensis (Fig. 1) owes its invasive behavior to a longer life span that extends in to the relay crop of mung bean after transplanted rice. These two crops differ widely in the soil conditions, with transplanted rice surviving in inundated water, whereas mung bean thrives in residual soil moisture that is ≤30%. *Leptochloa chinensis* shows an adaptation to both the extremes of soil moisture that in turn depends on the monsoon rains, within the same generation. Frequent floods favor the perpetuation of *M. quadrifolia* (Fig. 2) (Kathiresan 2011). In these rice tracts, weed control has been taken up uniformly by the manual pulling of weeds traditionally, without any herbicide use or use of other weed control methods in rice. Hence, the scope for the influence of disturbance by human activities does not arise. Furthermore, weeds like *Cyperus rotundus*, an invasive weed that occurs in upland rice, also with sporadic

occurrence in lowland rice, are suppressed by the increasingly water-logged conditions of lowland rice.

Wetlands are more prone to weed invasions, in part because they serve as landscape sinks that accumulate materials resulting from both terrestrial and wetland disturbances (excess water, debris, nutrients, sediments, salts, and other contaminants). Opportunities that make wetlands more prone to weed invasions are that the riparian habitats are subjected to flood pulses and inflows from surface water. Habitats that are fed by surface water are low in species richness and the inhabitants are low in quality, with the coefficient of conservatism scoring <5. Studies in Wisconsin, USA, show that wetlands with a history of hydrological disturbance show more widespread invasions (Zedler & Kercher 2004). Despite the emphasis on increased influxes as causing disturbance, it also has been observed that some invasives are abundant where the regions have reduced flood flows. Both increased and decreased runoff will alter wetland water regimes and the floristic composition could be invaded by floating weeds like *E. crassipes* under inundation and *Ipomoea aquatica* under a semi- or completely dry situation in the water sheds

Fig. 1. *Leptochloa chinensis* in transplanted rice.

Fig. 2. Dominance of *Marsilea quadrifolia* in lowland rice.

of southern India (Kathiresan 2011). The greater spring-time moisture that is associated with El Niño events could trigger the range expansion of cheat grass (Bradley & Mustard 2005). Weeds that are constrained by rainfall, such as *Eupatorium riparium*, can expand if rainfall increases in some areas (McFadyen 2008).

A soil moisture status with an available soil moisture percentage of between 40 and 60 is observed to favor the seed germination of the invasive weed *Parthenium hysterophorus*, whereas an available soil moisture of >80%, coinciding with the winter months, or <40%, coinciding with the peak of summer, is detrimental (Kathiresan *et al.* 2005). The soil moisture status is influenced by the rainfall, as well as the evaporation, pattern of the microclimate concerned. The absence of or dismal rainfall (<30 mm) from March to May, coupled with higher rates of daily evaporation that range from 4 to 8 mm per day, results in a water deficit status of the microclimate during this part of the year, which ultimately results in a depleted soil moisture status of <40%.

In Australia, seedling survival and growth are favored by a high soil moisture status, whereas seed germination is suppressed in *Acacia nilotica* (Kriticos *et al.* 2003). An interannual amplified response to rainfall by non–native cheat grass, dominating the ecosystems in the Great Basin, USA, is observed to be distinct from the native shrub; that is, bunch grass (Bradley & Mustard 2005). Altered precipitation, increases in snowfall, and variability in the snowfall might exacerbate its invasion in the mixed-grass prairie. Increased snow favors the biomass production of *Centaurea diffusa* and *Linaria paniculata* (Blumenthal *et al.* 2008).

Overall, an altered pattern of precipitation, with a variable quantity and distribution pattern, coupled with changes in the evaporation pattern is likely to influence an array of biological traits of invasive weeds, including germination, plant size, seed production, and distribution of water-borne propagules.

ELEVATED CARBON DIOXIDE CONCENTRATION

Elevated CO_2 stimulates the invasive traits of non-native species more than native species sympatric in the region under controlled environmental conditions. The average elevated (E) : ambient (A) ratio (the ratio of final biomass at E:A CO_2 when the CO_2 concentration is doubled) is inferred as 1.82 in non-native species, whereas it is 1.28 in native species (Sasek & Strain 1991). Among the Great Basin grasses, the non-native *B. tectorum* showed an E:A ratio of 1.54, while the

native grasses recorded only 1.31 (Smith *et al.* 1987). The E:A ratio of non-native *Rhododendron ponticum* was reported as 1.59, against 1.12 in the native understory plants of a Swiss forest (Hattenschwiller & Korner 2003). The mechanisms that contribute to a better response by invasive species to elevated CO_2, compared to native species, have been reported as: (i) plant architectural differences by virtue of the leaf area (Sasek & Strain 1991; Huxman & Smith 2001; Ziska 2003); and (ii) an altered reproductive allocation with particular reference to the incorporation of carbon and nitrogen in seeds and increased differential abundance in community seed rain (Huxman *et al.* 1999; Smith *et al.* 2000).

The stimulation of biomass production by 46% in response to a doubled CO_2 concentration by six different invasive species has been reported (Ziska 2003). The response of these species (in terms of increased biomass) to the natural increase of atmospheric CO_2 by 30% during the 20th century, averaging 110%, is significantly higher than the native species. This is construed as probable evidence for the fact that many plant invasions during the last century have been triggered by rising CO_2 levels. Besides increased branching and leaf area, higher pollen production from ragweed (*Ambrosia artemisiifolia*), which is detrimental to human health (Ziska & Caulfield 2000), and higher spine production in *Cirsium arvense* (Ziska 2002) also have been reported. The response to elevated CO_2 by three invasive species *Mikania micrantha*, *Wedelia trilobata*, and *Ipomoea cairica* has been compared with the native *Paederia scandens*, *Wedelia chinensis*, and *Ipomoea pes-caprae* in China by Song *et al.* (2009). The average increase in the photosynthetic rate of the invasive species was 67.1%, against 24.8% in the native species. An average increase in the total biomass also was greater for the invasive species (70.3%) than for the natives (30.5%). The benefit of increased atmospheric CO_2 concentration was shown to increase the recruitment of five woody legumes *Acacia farnesiana*, *Gleditsia triacanthos*, *Leucaena leucocephala*, *Parkinsonia aculeata*, and *Prosopis glandulosa*, with the greatest benefit to *Parkinsonia* and *Prosopis*. This is attributed to increased drought tolerance by virtue of enhanced seedling survivorship and by reduced gross depletion of soil moisture (Polley *et al.* 2002).

PROCESS OF SEED DORMANCY AND GERMINATION

Dormancy is defined as an internal condition of the seed that impedes its germination under otherwise adequate hydric, thermal, and gaseous conditions (Benech

Arnold *et al.* 2000). Seed dormancy is a complex mechanism that influences the time of emergence of a weed population. However, dormancy could not exclusively determine the persistence of a seed (Thompson *et al.* 2003). Seed dormancy is stated to be a cryptobiotic state, manifested by a particular form of cessation of growth (Suthar *et al.* 2009).

Seed characteristics, such as dormancy, from an individual plant can vary greatly depending on the mother plant and the environmental conditions. This is because the seed coat is made from the plant tissue of the mother plant and the environmental conditions during seed maturation influence the seed coat's hardiness; for instance, in *Medicago lupulina* (Fenner & Thompson 2005). The soil temperature and water status play a vital role in breaking dormancy and triggering germination (Sauer & Struik 1964). Exposure to light briefly during land preparation also triggers weed seed germination (Wesson & Wareing 1968). Two of the environmental changes that promote germination, involving light signals, have been observed as: (i) soil disturbance by agricultural operations; and (ii) gap openings in dense canopies. In several species, exit from dormancy is completed only after the seeds have been exposed to fluctuating temperatures. Nine different parameters of diurnal temperature cycles are attributed to stimulating germination. They are: the number of cycles, their amplitude, maximum temperature, minimum temperature, duration of exposure under maximum temperature, duration of exposure to minimum temperature, rate of warming, rate of cooling, and the timing of the cycles regarding the start of imbibition. An alteration in any of these without reflecting on at least one another is not possible. Evidence also has been shown by the fact that not all of these characteristics have an active role (Benech Arnold *et al.* 2000). In *Chenopodium album*, the breaking of the dormancy response can increase from an amplitude of as little as 2.4°C up to ~15°C (Murdoch *et al.* 1989). Saturated soil moisture or flooding inhibited the seed germination of Texasweed (*Caperonia palustris*) and temperatures that fluctuate between 30 and 40°C were found to be optimum for germination (Koger *et al.* 2004).

An available soil moisture percentage of >60% or <40% is deleterious for the sprouting of *P. hysterophorus* seeds, whereas monthly average temperatures of >34°C are also detrimental (Kathiresan *et al.* 2005). The breaking of seed dormancy due to accumulated heat units and thermo-induction of seed germination, resulting in mass or synchronized weed germination and establishment, has been observed to be one of the key factors that contributes to the invasive ground cover of *T. portulacastrum* (Kathiresan 2006b). Increasing heat in the

top soil due to an increasing atmospheric temperature from 35°C onwards during the summer months of April, May, and June triggered its mass germination and higher seedling emergence from June to August. A neutral pH was reported to be favorable for the germination of *Solanum nigrum* (Suthar *et al.* 2009). While the flooding of farmlands was observed to depress the sprouting of the old seeds of corn weed, it also was observed to trigger the germination of fresh seeds (Oyewole & Ibikunle 2010).

SEEDBANK LONGEVITY

Germination and stand establishment are not imminent once weed seeds get dispersed from the mother plant. The seed bank serves as a repository, where these seeds get collected and ensure future populations, for the annual and perennial weeds that reproduce exclusively by seeds. However, those seeds that remain dormant or viable in the seed bank are extremely difficult to manage as they are buried and environmental factors, such as soil temperature, soil moisture, and exposure to light during land disturbance, play a vital role in regulating their emergence pattern (Schonbeck & Egley 1980). Climate-related disasters, such as flood or drought, could influence the addition of weed seeds to the seed bank because higher seedbank additions in the fallow fields of Canada have been attributed to the absence of a competitive crop (Archibold & Hume 1983).

Only a few of the seeds that enter the seed bank are successful in serving as a source of reinfestation. Most of them could die, decompose, or be predated on. The mortality of wild oat (*Avena fatua*) seed increased by ≤88% with an increasing soil moisture over a period of 2 years (Mickelson & Grey 2006). Once weed seeds enter the seed bank, they sense and interact with several factors in the surrounding environment. As a result, either they become dormant or get triggered for germination (Gulden & Shirtliffe 2009).

FUTURE NEEDS

1 Scientists with expertise in matching climate parameters with the invasive traits of weeds should publicise their knowledge base with information that already has been well understood, as well as the uncertainties that need to be explored.
2 Funding for these studies needs to be encouraged under the aegis of climate change-related agencies, organizations, and frameworks.
3 Policy-makers should include invasive weeds in any national, regional, or global assessment of climate change on agriculture.

4 Weed species that are favored under a specific combination of the climatic parameters that could result in due course might be predicted based on climate-resilient weed risk scores. These climate-resilient weed scores have to be newly included in the Weed Risk Assessment Questionnaire. Such scores need to be computed based on the weed traits that would respond to changes in climatic parameters, such as the CO_2 level, temperature regimes, precipitation pattern etc.

CONCLUSION

Several-thousands of alien species have become established in different parts of the world over the past couple of centuries. One in seven has become invasive. The success of an introduced weed in getting established and behaving invasively often depends on the climatic parameters with which it interacts. Accordingly, the impact of climate change on the invasive traits of weeds ultimately could be reflected in varied dimensions of resource and biodiversity conservation, as well as agricultural production.

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