Chapter 18

Effects of global climate change on regeneration of invasive plant species from seeds

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Introduction and background

Plant species introduced to an area in response to intentional or accidental anthropogenic events are called nonnatives. If these species spread rapidly from introduction sites (Richardson et al., 2000) and have harmful effects on the economy, environment, or health (IUCN (International Union for Conservation of Nature), 2000), they are invasive nonnative species. There are approximately 14,000 nonnative plant species established globally (van Kleunen et al., 2015, 2019) and between 2500 (Pyšek et al., 2020) and 4375 (Pagad et al., 2018) of them are considered to be invasive. Invasive species occur in many plant families, but the Asteraceae, Fabaceae, Poaceae, and Rubiaceae have some of the highest numbers of species (Humair et al., 2015). Invasive plants have a range of reproductive and life-history traits (Perrins et al., 1992; Moles et al., 2008), and documenting the common characteristics among them improves our ability to predict how invasive plants are likely to respond to climate change.

Although some invasive plant species rely entirely on asexual reproduction and others benefit from both sexual and asexual reproduction once established, seeds are important for the introduction of many invasive plants into new environments (Barrett et al., 2008; Beckmann et al., 2011). Invasive plants, like native plants, have variable reproductive strategies under both stable and changing environmental conditions, including those predicted under a changing climate (Aronson et al., 2007; Walck et al., 2011). Ten characteristics of many invasive plants that may give them an advantage over natives in response to climate change are (1) rapid growth rates, (2) tolerance of a wide range of climates and environments, (3) short generation time, (4) prolific and reliable reproduction, (5) small seeds, (6) effective seed dispersal, (7) ability to reproduce with just one parent (self-compatible), (8) nonspecialized germination requirements, (9) effective competitive ability, and (10) effective defenses and/or lack of enemies (Baker, 1974; Whitney and Gabler, 2008; van Kleunen et al., 2010; Clements and DiTommaso, 2011). Plants with a horticultural history may share many traits that may be associated with successful landscaping but also with invasiveness (Nicotra et al., 2010). Many of these characteristics develop through human-mediated selection (Nicotra et al., 2010; Chrobock et al., 2011), but some of them are products of natural selection (Clements and DiTommaso, 2011, 2012). These traits, especially those associated with regeneration from seed (Walck et al., 2011), may give invasive plants an advantage when responding to climate change and make their responses to a changing environment predictable.

Many invasive plant species are predicted to expand their range to higher elevations or latitudes in response to global warming (Cunze et al., 2013; Allen and Bradley, 2016; Panda et al., 2018). For example, seed production of *Pueraria lobata* is limited in colder climates, but its range in the USA north from Kentucky and West Virginia into Ohio, Illinois, and Indiana expanded between 1971 and 2006 (Ziska et al., 2011). Phenotypic plasticity can give plants great flexibility in a changing environment, and thus it is a potential adaptation to new environments (Clements and DiTommaso, 2011; Bhowmik, 2014; Geng et al., 2016; Liao et al., 2016). However, phenotypic plasticity does not require a change in the genetic make-up of a species and may allow some plant populations to persist in situ with low genetic diversity (Benito Garzón et al., 2019). Nonetheless, if phenotypic plasticity increases plant fitness at a low cost to the plant, it may help maintain genetic diversity (Grenier et al., 2016).

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Adaptation of invasive nonnative plants to novel habitats via natural selection is related to high genetic diversity resulting from multiple introductions, mutations, or hybridizations (Dlugosch and Parker, 2008; Zalapa et al., 2010; Ellegren and Galtier, 2016). The lag phase between the introduction and population expansion of many invasive plants may be the time needed for the species to adapt via natural selection (Clements and DiTommaso, 2011, 2012). However, phenotypic plasticity may be advantageous to a species when the environment changes more rapidly than a species can adapt via natural selection. The climate variability hypothesis predicts that species experiencing greater seasonality (e.g., at high latitudes) also will exhibit a greater range of tolerances to changes in environmental conditions, such as temperature, that is, be more phenotypically plastic (Mumladze et al., 2017). *Taraxacum officinalis*, which is invading along a latitudinal gradient in South America, shows increasing phenotypic plasticity with increasing southern latitudes (Molina-Montenegro and Naya, 2012).

Some invasive plant species have lower genetic diversity than their native counterparts, but instead of, or in addition to, phenotypic plasticity, they are epigenetically modified (e.g., by DNA methylation), which leads to rapid adaptation (Richards et al., 2012; Banerjee et al., 2019). Polyploidy is common in plants and having multiple copies of genes fosters significant genomic and epigenetic changes leading to rapid, reversible adaptation triggered by changes in the environment (Pikaard and Mittelsten Scheid, 2014). Such responses also may be reflected in shorter lag phases of population development (Pérez et al., 2006). For example, *Ambrosia artemisiifolia* has developed similar latitudinal clinal patterns in leaf surface area, plant size, growth, phenology, sex allocation, reproductive investment, and dichogamy in its two nonnative ranges (Europe and Australia) as exist in its native North American range. These patterns evolved repeatedly in both introduced ranges over only 100–150 years and under limited genetic variation in the Australian range, providing evidence for rapid adaptation (van Boheemen et al., 2019). A *meta*-analysis of studies on 56 invasive plants comparing phenotypic plasticity with local genetic adaptation concluded that changes in size, fecundity, and biomass allocation were due to phenotypic plasticity and changes in phenology due to local genetic adaptation (Liao et al., 2016).

Models predict that not all invasive species will perform well across their current nonnative range in response to climate change, although they typically do not account for plasticity or rapid adaptation (Bradley and Wilcove, 2009; Benito Garzón et al., 2019). Geographic ranges of many invasive plants are expected to contract along the southern latitudes in the Northern Hemisphere (Allen and Bradley, 2016). A *meta*-analysis of 204 native and 157 nonnative species by Sorte et al. (2013) found no difference in native versus nonnative terrestrial species (mostly plants) in response to changes in CO_2 and precipitation. However, nonnative species tended to perform better with increased precipitation and CO_2 and native species better with increasing temperatures and decreasing precipitation. In aquatic ecosystems (mostly animals), increased CO_2 and temperature were more inhibitory for native than nonnative species. The authors concluded that the risk of invasion increased if climate change increased the favorability of a site for plant growth, while risk of invasion decreased if sites became less favorable (Sorte et al., 2013).

Combining demography and phenology with climate models helps account for natural selection and rapid evolution and consequently should result in more accurate models about how native and nonnative species are likely to respond to climate change (Chapman et al., 2014; Merow et al., 2017). Optimistically, there may be an unrealized potential of some native plants that have not yet experienced a novel environment to adapt rapidly to climate change (Sow et al., 2018; Thiebaut et al., 2019). Indeed, shifts in geographic range of native species may be shifting their status from native to nonnative, possibly requiring a new definition of "native."

Restoration of ecosystems to a resilient state composed of native plants present prior to any invasion of nonnative species is considered an important initial step in mitigating the effects of global climate change and potential subsequent spread of invasive plants (Bradley et al., 2010; Allara et al., 2012; Chambers et al., 2014). Paradoxically, invaded systems are among the most resilient ones in terms of being able to sustain their altered stable state (Côté and Darling, 2010). Such resilience could be due in part to genetic diversity and subsequent selection or to epigenetic modifications within nonnative populations lacking the genetic diversity to respond to a novel environment. Resilience also likely is related to changes in species composition due to changes in fire frequency and soil nutrient cycling that favor invasives over natives (Gaertner et al., 2014). Moreover, climate-change mitigation efforts may include human-mediated introductions of even more species (including "natives") thought to be adapted to the predicted new climate.

The goal of this chapter is to summarize the literature on invasive plants in relation to climate change and includes (1) mating systems and phenology, (2) sexual reproductive capacity and seed dispersal, (3) seed dormancy, (4) seed germination and viability, (5) soil seed banks, and (6) biotic interactions. Consideration will be given to how each trait and biotic interaction may help ensure survival and spread of invasive species under a changing climate. This information will be linked to restoration efforts with the objective of defining a more informed climate-change mitigation strategy.

Mating systems and phenology

Changes in plant mating systems can impact gene flow, genetic diversity, gene recombination, and effective population size of plants, which in turn may affect the ability of an invasive species to respond to a changing climate (Eckert et al., 2010; Hargreaves and Eckert, 2014). Self-compatible plants are likely to become established outside their native range because they can reproduce from a single individual (Razanajatovo et al., 2016). Pollen development and pistil–pollen interactions are limited by moderate increases in temperature predicted to occur with global climate change, which, in turn, may impact regeneration by seeds (Snider and Oosterhuis, 2011). Disturbance and changes in climate also are associated with pollen limitation either by a reduction in pollinators or mates due to decreased population size; both may increase reliance on self-compatible mating systems and asexual reproduction (Barrett et al., 2008; Eckert et al., 2010). The risk of pollen limitation is higher for dioecious plants, and dioecy is rare in native and nonnative angiosperms (Käfer et al., 2017).

The gynodioecious species *Fallopia japonica* was introduced to the USA with only male sterile (female) plants, but it spread via rhizomes. However, this species has since hybridized with a less invasive nonnative knotweed (*F. sachalinensis*) to form *F.* x *bohemica*, which produces viable seeds, thereby promoting dispersal of the taxon. Although *F. japonica* has low genetic diversity, it is epigenetically diverse. However, *F.* x *bohemica* is 10 × more epigenetically diverse than *F. japonica*. Not only has the mating system of this species complex changed from mainly asexual to both asexual and sexual via hybridization, but the ability to respond epigenetically to stress has also increased its capacity to adapt rapidly (Richards et al., 2012; Gillies et al., 2016).

Global warming also impacts the phenology of invasive plant species. In recent decades, earlier flowering has been correlated with increasing temperatures (Ellwood et al., 2013). With increased temperatures, the growing season for plants starts earlier and/or ends later, and if both, is extended in duration. Likewise, longer flowering periods, which may occur with extended growing seasons (Dorji et al., 2020), allow plants to allocate more resources to reproduction and increase time for interaction of flowers with pollinators (Feng et al., 2016). Earlier flowering and phenological changes (e.g., first flowering) due to climate change have been documented. The historical dataset from Concord, Massachusetts, USA, ("Thoreau country") collected between 1851 and 2006 (Primack et al., 2009) shows that the invasive species *Alliaria petiolata*, *Cynanchium louiseae*, *Frangula alnus*, and *Lonicera morrowii* flowered 11 days earlier than native plants (Willis et al., 2010). Although 87% of these species follow predictions based on climate change (e.g., earlier and/or later flowering/budburst), some of them show no change or an opposite trend (Parmesan and Yohe, 2003). In response to a warmer and wetter environment in the lower latitudes of Europe, *Ambrosia artemisiifolia* flowers later, benefitting from larger late-season plants, and the time between pollen maturation and stigma receptivity is shorter than that for plants in its native North American range (van Boheemen et al., 2019).

Phenology of plants also is likely to be impacted by decreased precipitation due to climate change as documented by the response of the invasive annual grasses *Avena sterilis* and *Hordeum spontaneum* to an aridity gradient in their native Israel. With an increase in aridity, length of growing season was shortened and time to flowering decreased, but seed production increased as seed size decreased (Volis, 2007). Furthermore, *Bidens pilosa*, native to temperate and tropical America and a noxious weed in other regions worldwide, has a phenotype that flowers in February or March in the Southern Hemisphere and a phenotype that flowers 1–2 months earlier, both of which occur in its native range. Seeds of both phenotypes give rise to the typical phenotype under favorable growth conditions. The early flowering phenotype produces larger but fewer seeds than the typical-flowering phenotype. Thus, if climate change results in stress during the life cycle, we can expect an increase in abundance of the early phenotype (Gurvich et al., 2004). In contrast, *Lythrum salicaria* is predicted to have an extended growing season even with climate change because it occupies wetland habitats (Colautti et al., 2017).

Not all invasive plant species are expected to benefit from a change in growing season due to climate change. For instance, in the western USA the range of the annual invasive grass *Bromus tectorum* is predicted to decrease due to increases in drought conditions that result in a growing season too short for plant survival and/or reproduction (Bradley and Wilcove, 2009).

Sexual reproductive capacity and seed dispersal

High fecundity and small seed size are traits of many invasive plants (Radford and Cousens, 2000; Goergen and Daehler, 2001; Morris et al., 2002; Whitney and Gabler, 2008). However, plants from large seeds have higher survival (Moles and Westoby, 2004), greater competitive ability, and higher adult fecundity (Moravcová et al., 2007; Germain and Gilbert, 2014) than those from small seeds. The tradeoff between seed size and number is a response to stress such as drought, and species with large seeds are predicted to colonize more stressful habitats than those with small seeds (Muller-Landau, 2010). Variation in seed size of individuals of invasive plant species also occurs across environmental gradients (Cochrane et al., 2015).

Changes in seed mass of plants growing in different levels of stress provide insight into how climate change may affect seed mass. Seed mass increases in environments with consistently low amounts of precipitation, but it can vary if low levels of precipitation are temporally unpredictable (Volis and Bohrer, 2013). In contrast, seed mass of *Ambrosia artemisiifolia* is larger in the warmer, wetter climate of its nonnative European range than in its native North American range (van Boheemen et al., 2019). *Avena fatua, Festuca arundinacea*, and *Lolium multiflorum* tend to produce fewer and smaller seeds when exposed to higher temperatures (Wiesner and Grabe, 1972; Boyce et al., 1976; Peters, 1982). *Microstegium vimineum* tends to produce smaller seeds in relatively dry than in mesic environments within its invasive range (Huebner, 2011). However, there was no effect of increased temperature (1.5/3.0 degrees day/night) and CO_2 (600 ppmv) (combined) over a 6-year period on seed mass of the invasive *Centaurea diffusa* or *Linaria dalmatica* and two associated native grasses (*Bouteloua gracilis* and *Koeleria macrantha*) in Wyoming, USA (Li et al., 2018).

Seed size also may vary across generations, indicating adaptive transgenerational plasticity (Herman and Sultan, 2011). When *Microstegium vimineum* plants from seeds collected from two regions differing primarily in annual rainfall were grown under drought conditions in a greenhouse, plants derived from the drier region produced seeds with higher mass than those derived from the mesic region (Huebner and Waterland, unpublished data). As the maternal environment changes across generations, seed characteristics and responses to environmental cues also may change. Larger seed may confer greater drought resistance (Cochrane et al., 2015), which could support the differential transgenerational response noted for *M. vimineum*.

Efficient seed dispersal is a trait of many invasive plants (Honig et al., 1992; Vilà and D'Antonio, 1998), and range expansion is likely to be accompanied by long-distance dispersal. The more seeds produced the more likely a few of them will be dispersed to safe sites at a greater distance from the homesite in a changing climate (Clark et al., 2001; Hampe, 2011). Plant migration rates should be $3000-5000\ \mathrm{m\ yr^{-1}}$ to track estimates of climate change rates (Petit et al., 2008). However, most plants, are estimated to expand their ranges $<100\ \mathrm{m\ yr^{-1}}$ (Neilson et al., 2005; Petit et al., 2008; Nogués-Bravo et al., 2018), with a few approaching $610\ \mathrm{m\ yr^{-1}}$ (Parmesan and Yohe, 2003). Long-distance dispersal to new sites tends to favor self-compatibility, especially if marginal populations are small and the likelihood of being able to outcross is low (Hargreaves and Eckert, 2014). Thus, the ability to adapt rapidly may be a more important means of responding to climate change than having both high fecundity and the ability to disperse over long distances.

Since increased CO_2 increases plant height of some invasive species, including *Centaurea diffusa* (Reeves et al., 2015), *Cirsium arvense*, *Euphorbia esula, Sonchus arvensis* (Ziska, 2003; Ziska et al., 2011), and several crop weeds (Ramesh et al., 2017), it is expected that seed dispersal distance via wind will increase. Differences in plant height and capitulum drying time resulting from climate change conditions increased dispersal distance of *Carduus nutans* via wind by 38% (Teller et al., 2016). An increase in stormy weather, with increases in wind duration and speed, also may increase dispersal distance of seeds of both invasive and native species (Ziska et al., 2011). However, Jablonski et al. (2002) found that seed mass but not seed production of agricultural crop weeds increased in response to increasing CO_2.

Seed dormancy

Seed dormancy spreads germination of a cohort of seeds over time and thus the opportunity for seedling establishment over multiple seasons in environmentally unpredictable habitats (Venable and Brown, 1988). Dormancy of a species may differ between native and nonnative ranges, making responses to global change less predictable as species enter novel environments. For example, *Phragmites australis* seeds appear to have acquired physiological dormancy (PD) in its nonnative range, where 50% of seeds are dormant, compared to no dormancy in the native range (Kettenring and Whigham, 2009). Furthermore, seeds of *Cardamine hirsuta* in Japan (where it is invasive) have stronger PD than those from native European strains of the species under warmer temperatures, making it a strict winter annual in its nonnative range (Kudoh et al., 2007; Donohue et al., 2010).

Seeds of many invasive species have either no dormancy or nondeep PD. In nature, nondeep PD is broken either during exposure to summer temperatures or to low (moist) winter temperatures, depending on the species (Baskin and Baskin, 2014). Global warming may negatively impact the PD breaking requirements of species whose seeds require low temperatures and moist conditions in winter for dormancy-break, but impacts on species whose dormancy is broken in summer may be minimal (see Chapter 10). Invasive nonnative plants that require a relatively long period of cold stratification to break dormancy include *Alliaria petiolata* (Merow et al., 2017; Footitt et al., 2018), *Frangula alnus*

(Dukes et al., 2009), *Heracleum mantegazzianum* (Moravcová et al., 2006), and *Prunus serotina* (Phartyal et al., 2009). Temperature increases due to climate change may negatively impact dormancy-break and germination of these species especially in the southernmost part of their range. Effect of climate change on dormancy-break and germination of *A. petiolata* was investigated using a polyethylene tunnel in which temperature was increased by 0 to +4°C (above outside air temperature), depending on position in the tunnel. Warming in winter decreased seedling emergence, but a few seedlings emerged at the warmest end of the tunnel, suggesting adaptation to a warming climate via selection against dormancy is possible for *A. petiolata* (Footitt et al., 2018).

Seeds of *Cardiocrinum giganteum* var. *giganteum* (native of Japan and invading New Zealand) have an underdeveloped embryo that is physiologically dormant, that is, morphophysiological dormancy. To break dormancy of the embryo, a period of warm moist conditions of summer followed by cool moist conditions of autumn and cold moist conditions of winter are required, resulting in an 18–19-month period between dispersal and germination (Phartyal et al., 2012). Any negative effects of climate change on regeneration of this species from seeds likely would be related to decreased soil moisture.

Seeds of several invasive species, especially those in the Fabaceae, have physical dormancy (PY, water-impermeable seed coat). Acquisition of PY is related to seed drying to a certain moisture content, depending on the species (Baskin and Baskin, 2014). It is predicted that decreased precipitation will increase the proportion of seeds in species such as *Acacia saligna* with PY (vs. nondormancy) in temperate regions (Tozer and Ooi, 2014). In contrast, decreased precipitation may decrease seed dormancy breakage for *Mimosa pigra* and *Parkinsonia aculeata*, invaders of Australian wetlands, both of which require a wet-warm period to break PY (van Klinken and Goulier, 2013). Likewise, increased fire frequency and magnitude are possible consequences of climate change (IPCC, 2013, Ooi et al., Chapter 17), and fire can break PY and stimulate germination (Riveiro et al., 2020; Ooi et al., Chapter 17). High summer temperatures can promote dormancy break in some species with PY. Exposure of seeds of *Acacia dealbata*, an invasive shrub in southeastern Australia, to 60°C that mimics soil temperatures associated with climate change broke PY (Passos et al., 2017). Increased temperatures due to climate change could impact these species via subsequent germination and depletion of soil seed banks (Ooi et al., 2014).

Seed dormancy is a heritable trait under strong selection pressure (Baskin and Baskin, 2014), and in the invasive *Avena fatua* with dormant and nondormant genotypes it is controlled by multiple genes (Foley and Fennimore, 1998). The dormant genotypes are sensitive to temperature and drought experienced in the maternal environment, with higher germination percentages associated with higher temperatures and more severe drought conditions (Sawhney and Naylor, 1979; Naylor, 1983; Jana and Thai, 1987). The maternal plant environment can influence seed dormancy with higher temperatures and drought often reducing dormancy (Fenner, 1991). Seeds of *Parthenium hysterophorus*, an invasive herb in Australia (and other countries) originating in the New World tropics and subtropics, exhibit greater dormancy when maternal plants are grown under warm conditions, with even greater dormancy associated with seeds produced from plants grown in warm and dry conditions. In response to increasing atmospheric CO_2, warming temperatures, and decreasing moisture, *P. hysterophorus* grows to a larger size at a faster rate, has a shorter life span, produces more seeds, and has more dormant seeds than under normal conditions for growth. These results suggest that this species will perform well in parts of its invasive range where temperatures and drought are predicted to increase (Nguyen et al., 2017).

Seed germination and viability

After dormancy is broken, seeds of many invasive plants, including *Ailanthus altissima, Alliaria petiolata*, (Huebner et al., 2018), *Echium plantagineum* (Forcella et al., 1986), *Microstegium vimineum* (Huebner et al., 2018), *Physalis angulatus, P. philadelphicus* (Ozaslan et al., 2017), *Vulpia bromoides*, and *V. muryos* (Dillon and Forcella, 1984) germinate over a wider range of conditions in their invasive range than associated native species. One of the strongest shared patterns among invasive plants, including *Amaranthus retroflexus* (Ruprecht et al., 2014), *Ambrosia artimisiifolia* (Leiblein-Wild et al., 2014), *Echium plantagineum* (Forcella et al., 1986), *Eragrostis plana* (Guido et al., 2017), *Galinsoga ciliata* (Ruprecht et al., 2014), *Gunnera tinctoria* (Gioria et al., 2018), *Impatiens glandulifera* (Skálová et al., 2011; Ruprecht et al., 2014), *Plantago virginica* (Xu et al., 2019), *Rhododendron ponticum* (Erfmeier and Bruelheide, 2005), *Rudbeckia laciniata* (Ruprecht et al., 2014), *Senecio inaequidens* (Sans et al., 2004; Gioria and Pyšek, 2017), and *Ulmus pumila* (Hirsch et al., 2012) is earlier germination than associated native species, which may enable the invasive plants to grow under reduced competition (Wainwright and Cleland, 2013; Gioria and Pyšek, 2017). In contrast, while nonnative *Taraxacum officinale* had a higher germination percentage than the associated native *T. laevigatum*, this was only true under ideal environmental conditions that ensure seedling survival. *Taraxacum laevigatum* germinated to a higher percentage than *T. officinale* under stressful conditions, whereas a new invader *Taraxacum* *brevicorniculatum* had the highest germination among the three species at all test conditions (Luo and Cardina, 2012). These findings suggest that long-established nonnative plants may lose their ability to adapt quickly to novel environments such as those caused by climate change.

Seeds of *Achillea millefolium*, *Hieracium pilosella*, *Hypericum perforatum* (Beckmann et al., 2011), *Ludwigia peploides* (Gillard et al., 2017), and *Ulex europaeus* (Udo et al., 2017) germinate faster and at higher temperatures in their nonnative-warmer environment than in their native-colder environment, suggesting adaptation to warmer temperatures. Other invasive plant species that appear to be expanding their range into warmer, mesic environments include *Ambrosia artemisiifilia* (Leiblein-Wild et al., 2014), *Berberis thunbergii* (Merow et al., 2017), *Gunnera tinctoria* (Gioria et al., 2018), and *Leucaena leucocephala* (Marques et al., 2020). Rapid germination of species that are shifting their range north (Northern Hemisphere) may be somewhat risky for species intolerant of cold. Risk may be abated for some species by an increase in cold tolerance of seedlings as found for *Ambrosia artemisiifolia* in its nonnative European range (Leiblein-Wild et al., 2014).

Seeds of some invasive species are tolerant of high temperatures and water stress, suggesting that they would not be negatively affected by climate change (Hou et al., 2014). *Tithonia diversifolia* seeds germinated after a 30-day heat treatment at 80°C and about 20% of them germinated at −0.6 MPa (Wen, 2015). Seeds of *Ageratum conyzoides, Conyza canadensis*, and *Crassocephalum crepidioides* germinate over a broad range of temperatures (15°C−30°C), and those of *A. conyzoides* (the most tolerant species) germinated to about 25% at 35°C and 95% at 40/25°C (high temperature for 7 h per day). Seeds of *A. conyzoides* also germinated to 65% at −0.8 MPa, suggesting that germination and seedling establishment were possible under the temperature and water stress conditions of the introduced range in southern China (Yuan and Wen, 2018). Increased temperature enhances germination of seeds of *Oenothera biennis*, *Petiveria alliacea*, and *Syncarpia glomulifera* (Sershen et al., 2017). However, at 0.0 MPa seeds of *Cenchrus ciliaris* germinate to ≥60% at 20°C−40°C but to only about 45% at −0.06 MPa (Tinoco-Ojanguren et al., 2016). Similarly, the combined effects of increased temperature and CO_2 had no impact on seed viability or overall germination percentages but increased germination rates of the invasive species *Centaurea diffusa* and *Linaria dalmatica* (Li et al., 2018).

A negative response of seeds of some invasive plant species to increasing temperature and/or water stress suggests that plant regeneration via seeds may be negatively affected by climate change. The palm *Archontophoenix alexandrae* (widely planted in tropical parts of China) can germinate only at temperatures between 20°C and 30°C and is highly sensitive to desiccation, with seed viability decreasing at temperatures above 60°C (Wen, 2019). Seedling emergence and survival of *Oenothera biennis* decreased in response to increasing temperatures (Sershen et al., 2017). *Piper aduncum* seeds did not germinate at constant temperatures above 35°C but germinated at an alternating temperature regime of 40/25°C. Germination of this species was inhibited by water potentials more negative than −0.06 MPa (Wen et al., 2015). Variation in winter precipitation decreased germination of the nonnative *Centaurea solstitialis* (Hierro et al., 2009).

Maternal plant environmental temperatures may impact seed germination, timing, and viability. Responses to elevated temperatures provide insight into how plants might respond to increased temperatures due to climate change. Seeds of *Carduus nutans* plants grown at temperatures moderately higher than those in current field conditions had higher germination percentages and rates than those from plants grown under ambient field conditions (Zhang et al., 2012). *Alliaria petiolata* seeds collected from populations across a latitudinal gradient in North America and sown in a common garden located at a northern latitude exhibited population differences after 13 years of monitoring. Seeds from southern populations had lower germination percentages than those of northern populations. However, after 6 years germination percentages had become more similar, with the southern-population germination percentages increasing, revealing local adaptation. Annual seedling emergence was correlated with spring temperatures, thus phenotypic plasticity also may play a role (Blossey et al., 2017). In a reciprocal seed transplant experiment with *Ludwigia peploides*, an invasive in the Mediterranean region of California (USA) and temperate climates of France, seed viability was higher in the Mediterranean climate seeds exposed to Mediterranean climate temperatures (average 24°C) than the temperate climate seeds exposed to temperate climate temperatures (average 18°C), However, seeds from both provenances germinated faster at 24 than at 18°C (Gillard et al., 2017).

Soil seed banks

Seed banks are a bet-hedging strategy in unpredictable environments (Venable and Brown, 1988). In addition, they may provide a genetic history of invasive plant species evolution. For *Gunnera tinctoria*, a long-established invasive plant in Ireland, the number of alleles, percentage of polymorphic loci, and genetic diversity decreased in seeds found at increasing soil depths. Furthermore, the greatest change (increase) in genetic diversity in the seed bank of this species occurred after the lag time of establishment, when range expansion began (Fennell et al., 2014).

The impact of climate change on seed banks is predicted to decrease the number of seeds in the soil, especially for species whose seeds have PY. For example, a 4°C increase in air temperature, as predicted by climate change for southeastern Australia, may increase soil temperature by about 10°C. Reduced seed viability or increased germination of buried seeds due to soil warming may deplete the soil seed bank (Ooi, 2012). With a 2°C increase in habitat temperature, 75% of the seed bank of *Leucaena leucocephala* was lost (Marques et al., 2020). For *Parkinsonia aculeata*, increases in soil temperature and soil moisture led to a decreased seed bank size via PY-break (van Klinken and Goulier, 2013), while most seeds of *Acacia saligna* in its invasive range lost viability (Cohen et al., 2019).

Invasive species that form persistent soil seed banks may be difficult to control (Marchante et al., 2011). Thus, much attention has been given to seed banks of invasive species (e.g., van Clef and Stiles, 2001; Gioria and Pyšek, 2016; Gioria et al., 2019). However, not all invasive species form large persistent soil seed banks, for example, *Ailanthus altissima* (Kowarik, 1995; Kostel-Hughes and Young, 1998), *Berberis thunbergii* (D'Appollonio, 2006), and *Lonicera maackii* (Luken and Mattimiro, 1991; Luken and Goessling, 1995; Hartman and McCarthy, 2008). Seeds of *Ambrosia artemisiifolia* (Fumanal et al., 2008) and *Ailanthus altissima* (Rebbeck and Jolliff, 2018) buried deeper than 5 cm in their invasive range had increased longevity. Seeds may be buried by disturbance, and they serve as a future seed source. Climate change is predicted to cause habitat disturbances and soil turn-over, which may increase the likelihood of increased seed burial of invasive species and formation of new seed banks (Fumanal et al., 2008).

Biotic interactions of invasive plant species

Evaluating the impacts of climate change on species assemblages in addition to individual species may ensure greater success of mitigation efforts. For example, although the invasive grass *Eragrostis plana* germinated more rapidly and to higher percentages than many of its associated native species when each species was tested separately in Petri dishes, its germination was delayed compared to that of native associated species in mixed-species cultures (Guido et al., 2017). Also, mismatches in timing between flowering and pollinators and between seed maturity and dispersers are likely to increase with climate change (Thomson et al., 2010). Some invasive shrubs may be able to resynchronize interactions more rapidly than native species because of high photosynthetic rates in response to increased length of the growing season (Fridley, 2012). Extended fruiting periods could delay departure of migratory birds or increase the number of broods of potential seed dispersers (Gallinat et al., 2015). Changes in pollinators and seed predators/diseases due to climate change also impact plant regeneration from seeds. A seed predator bruchid beetle (*Acanthoscelides macrophthalmus*) of *Leucaena leucocephala*, an invasive tree in Brazil and other tropical countries, does not injure the embryo but promotes germination by scarifying the water-impermeable seed coat (da Silva and Rossi, 2019). Increases in size of beetle populations due to climate change could increase germination of this species. Similarly, the invasive tree *Triadica sebifera* has higher germination percentages and rates and greater seed longevity after seeds have passed through the gut of birds (Renne et al., 2001).

Some pollinators, seed dispersers, and seed predators of invasive plants are invasive themselves. Thus an important consequence of climate change may be the presence of new animals in a plant community. For example, the red-whiskered bulbul (*Pycnonotus jocosus*), native to southeast Asia and introduced to Mauritius, consumes fruits of *Ligustrum robustum* and *Clidemia hirta*, native to southeast Asia and central and south America, respectively. Gut passage of seeds of these species increased germination success in their introduced habitat in Mauritius (Linnebjerg et al., 2009).

Birds that consume fruits of invasive plants without damaging the seeds serve as long-distance dispersal agents in addition to enhancing germination (Jordaan et al., 2011). Long-distance seed dispersal may be even more direct and easily predicted by the movement of cattle, other livestock, and deer that consume and then defecate seeds of invasives, such as *Acacia nilotica* (Kriticos et al., 2003), *Elaeagnus umbellata, Ligustrum vulgare* (Averill et al., 2016), *Lonicera maackii* (Williams and Ward, 2006; Guiden et al., 2015), *Lonicera morrowii* (Williams and Ward, 2006; Averill et al., 2016), *Rosa multiflora* (Williams and Ward, 2006), *Rubus phoenicolasius* (Williams and Ward, 2006), and *Stellaria media* (Myers et al., 2004). Northward migration in response to global warming in temperate regions may occur relatively rapidly for invasive species whose seeds are consumed by deer, whereas other invasives that deer avoid (e.g., *Alliaria petiolata, Berberis thunbergii*, and *Microstegium vimineum*) are less likely to migrate as fast (Averill et al., 2016).

Increases in extreme climatic events such as drought or flooding as well as increases in winter and nighttime temperatures are predicted to lead to range expansion of several diseases, either alone or in association with range expansion of invasive plants (Anderson et al., 2004). Pathogens associated with mature leaves and leaf litter of *Ageratina adenophora* increase time to germination and decrease germination percentages in China, where the species was established 20−80 years ago, suggesting that it may be accumulating pathogens with time (Fang et al., 2019). These results suggest that a changing environment may reset or reduce this accumulation of pathogens, thus removing enemies acquired by invasives established beyond their typical range.

Fungal effects on seed longevity also could be impacted by a changing climate. *Microstegium vimineum* has relatively high seed mortality due to fungal infections, resulting in longevity of only 2−4 years of seeds buried in the field. Increased precipitation and temperature may accelerate loss of seed viability of this species, potentially leading to no viable seed bank after 2−4 years (Redwood et al., 2018). *Prunus serotina*, an invasive tree in Europe, produces more viable seeds in well-drained, nutrient-poor soils than in moist, rich soils due to combined (negative) effects of fungal pathogens in the wetter soils and its inefficient nitrogen assimilation in nutrient-rich soils (Closset-Kopp et al., 2011). In contrast, seeds of *Ailanthus altissima* (Redwood et al., 2019) and *Alliaria petiolata* (Redwood et al., 2018) do not appear to be impacted by fungal infections, possibly due in part to allelopathic compounds they produce, and the seeds had low mortality when buried in the field. In tropical regions, *Ulex europaeus* occurs only above 1000 m in its invasive range due to high fungal infection in the warmer lower altitudes (Udo et al., 2017). Climate change may increase temperatures at higher elevations, which may increase fungal infections and reduce viability of *U. europaeus* seeds.

Interactions of invasive species with biocontrol agents are likely to change in response to climate change. Currently, the invasive species *Centaurea solstitialis* is controlled by two weevils and two picture-winged flies but only in the northernmost part of its range in Oregon (USA), where a shorter growing season impairs its ability to compensate for the damage done by the agents (Gutierrez et al., 2008). For this species, decreased precipitation due to climate change would decrease plant growth and enhance the effectiveness of control organisms. In the case of *C. diffusa* and its biocontrol agent (a weevil), weevil efficacy increases with elevated CO_2 and temperature. However, elevated CO_2 and temperature promote early flowering of *C. diffusa* resulting in more and larger seeds than in controls under normal conditions. Despite the weevil being able to infest more seeds in response to the earlier reproductive phenology of *C. diffusa*, increased seed predation did not eliminate the positive effects of CO_2 on seed production (Reeves et al., 2015).

Linking regeneration by seeds with climate change mitigation

Estimated rates of climate change may exceed the limits of adaptation and migration by both nonnative and native species, and thus assisted migration of plants is proposed as a potential solution (Vitt et al., 2010). Mitigation in the form of preemptively transplanting native species to their predicted future habitats will depend on knowledge about native as well as nonnative species mating systems, seed production, seed dormancy, germination requirements, soil seed banks, and avoidance of mismatches among positively or negatively interacting organisms (Seglias et al., 2018). Furthermore, manipulation of growth conditions of maternal plants during seed development by temperature, nutrients, and photoperiod such that dormancy is increased may help ensure long-term establishment of transplanted native species (Sharif-Zadeh and Murdoch, 2000).

It should be noted that range-shifting native species may be acting like invasive plants, colonizing novel environments with potential negative effects (Wallingford et al., 2020). Interactions between native and nonnative species may disrupt once-established native species assemblages that could survive major climatic events such as a drought. This has been demonstrated experimentally in field mesocosms of one, three, and six native species by adding one of two nonnative invasives, *Lupinus polyphyllus* or *Senecio inaequidens*. *Senecio inaequidens*, which is drought tolerant, outcompeted the natives even without drought, but the negative effect of *L. polyphyllus* on the native community depended on drought stress (Vetter et al., 2020).

Future research needs

Of the thousands of plants recognized as invasive globally, we have information about the effects of climate change on regeneration by seeds on less than 10% of them, and the studies typically are focused on only a few reproductive traits. There also may be geographic biases, with more research on invasive plants in North America and Oceania than elsewhere. Nonetheless, some patterns are evident, that is, more invasive species responding to climate change with decreased seed dormancy, earlier germination, and increased germination percentages (Fig. 18.1).

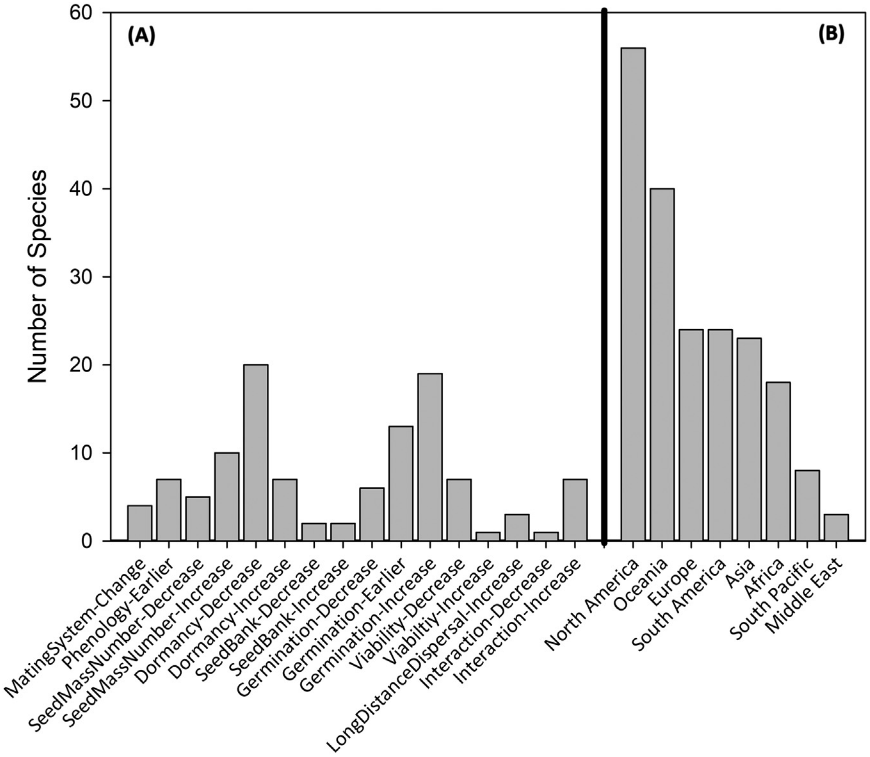

FIGURE 18.1 (A) Summary of number of invasive nonnative species that increase, decrease, or change (earlier or later) in mating system, phenology, seed mass/number, dormancy, seed bank, germination, viability, and interactions with other species. (B) Number of invasive species in each region for which response to climate change has been studied. Oceania includes Australia, New Zealand, Melanesia, Micronesia, and Polynesia.

Based on information summarized in this chapter, there is a need for research on the following aspects of the biology of invasive plant species:

- response of more nonnative invasives to climate change over a broad array of reproductive traits;
- impact of climate change on reproductive traits of assemblages of nonnative and native plant species;
- potential for success of applying climate change mitigation efforts; and
- potential for both native and nonnative plants to adapt rapidly to a changing climate.

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