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REVIEW

Seed bank persistence and climate change

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Abstract

The strong mechanistic relationship between climatic factors and seed dormancy and germination suggests that forecast climatic changes will significantly affect seed bank persistence. This review focuses on the potential impact of changing temperature, rainfall and fire regimes on the longevity of long-term persistent seed-banks. Currently, there are few studies investigating the mechanistic responses of demographic processes, such as seed-bank dynamics, to forecast climate change. However, from the work that has been published, several key points have been highlighted. First, increased air temperatures will produce significantly higher soil temperatures in open and sparsely vegetated habitats. Some evidence shows that this could accelerate the decline of seed viability and compromise bet-hedging strategies of species in dryland regions. Second, changes to rainfall season may determine the relative success of recruitment, with lower levels of success producing net losses to seed bank longevity. Finally, higher temperatures are likely to produce increased fire frequency, compromising the persistence of plant populations dependent on long-lived seed banks. Improving our understanding of both the mechanistic response and adaptive capacity of seed banks to climate change will provide a solid basis for improved predictions of future species distributions and risk of extinction, particularly in ecosystems subjected to temporally stochastic disturbances. It is necessary to develop functional groups based on key life-history trait responses to changing environmental conditions, to enable broader-scale predictions of distribution and persistence in the future.

Keywords: climate change, drought, fire, global warming, heat wave, long-term persistence, semi-arid, soil seed bank, soil temperature, storage effect

Introduction

The strong mechanistic relationship between climate variables and seed dormancy and germination indicates that forecast climatic changes will inevitably affect seed ecology. Subsequently, this will have an impact on seed banks, which are important for ensuring population persistence, particularly in habitats subjected to variable or stochastic disturbance regimes (Harper, 1977; Fenner and Thompson, 2005). Germination from a seed bank has the potential to be delayed so that seedling emergence coincides with a time when conditions are best for seedling establishment, and recruitment is most needed for re-establishing populations. Hence, seed bank persistence is critical, and maintaining viable seeds between recruitment episodes is the primary role that the seed bank plays. Net losses to the seed bank can occur during this period as a result of either decreasing seed viability, or germination and seedling emergence into unsuitable conditions. In order to predict the long-term consequences of climate change on plant

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species distribution and risk of extinction, particularly in ecosystems where seed bank persistence is critical, it is necessary to link future changes to climate with mechanisms that determine seed bank longevity.

Estimating the demographic responses of plant populations to forecast climate changes is one of the key challenges faced by ecologists today. Until quite recently, correlative bioclimatic models have been the primary method for predicting future species distributions (Pearson and Dawson, 2003; Thomas *et al.*, 2004). These predictions are somewhat limited because important factors, such as dispersal ability and the response of demographic processes to climatic changes, are excluded (Ibáñez *et al.*, 2006). The majority of plant species are considered unlikely to disperse at a rate that can track the rate of rapid climate change (Honnay *et al.*, 2002; Van der Veken *et al.*, 2007; Morin *et al.*, 2008) and, as such, will have to either maintain traits that enable them to persist, or adapt to the new conditions (Skelly *et al.*, 2007). Incorporating demographic response data into future modelling strategies, along with climatic and distributional data, will subsequently contribute to increasing the accuracy of predicted climate change impacts on species, and enable estimation of extinction risk (Keith *et al.*, 2008; Anderson *et al.*, 2009). This approach, however, is currently limited because data on demographic responses of plant species to forecast climate changes are scarce (Akçakaya *et al.*, 2006; Parmesan, 2006; Thuiller *et al.*, 2008). This is surprising considering that climate, and the strong influence it has on plant life-history processes, has historically been the subject of considerable study (Woodward, 1987). In particular, there is currently very little known about the response of seed banks and seed bank persistence to future climatic conditions (Thompson, 2000).

Modifications to many climatic factors are forecast and include such changes as increases to mean air temperatures, climate extremes and solar radiation, and alterations to rainfall regimes (Salinger, 2005; IPCC, 2007). Both air temperature and rainfall, particularly, interact with other environmental variables, such as soil composition and vegetation type, to provide many of the primary ecological cues for seed germination and emergence from the seed bank. Alterations to these factors will therefore affect seed ecology and subsequent population dynamics (Walck *et al.*, 2011). For example, dormancy for the majority of species is controlled by soil temperature, whereas the timing and magnitude of rainfall can determine the success, or otherwise, of germination and seedling recruitment (Baskin and Baskin, 1998; Fenner and Thompson, 2005). Understanding the demographic response to changing climatic trends and mean conditions is therefore important. More recent progress has also revealed the impact of extreme climate events, which include increases in the frequency, intensity and duration of phenomena such as droughts, storms and heat waves, on the persistence and composition of plant communities (e.g. Jentsch *et al.*, 2007; De Boeck *et al.*, 2010; Royer *et al.*, 2011; Smith, 2011).

The mechanistic responses of demographic processes to forecast climate change are currently poorly understood but are essential to include in predictive models to more accurately ascertain species distributions and risk of extinction in the future. Relatively few studies have focused on the mechanistic responses of seed banks to predicted climatic change. In this review, I will evaluate the impacts of changes to temperature and rainfall on seed bank persistence, focusing on long-term persistent soil seed banks in ecosystems where population dynamics are driven by stochastic environmental factors. These ecosystems are usually already subject to relatively harsh environmental conditions and so demographic processes may already be close to their functional limit. As such, they are a good starting point to investigate the seed bank response to climate change. Additionally, the key life-history stage ensuring persistence of many species in these variable environments is the seed bank. I will also discuss an approach for functionally grouping species by their response to climate change.

Mechanistic impacts of climate factors on seed bank persistence

Increased air temperature

Warming beyond the global mean is expected for all land regions around the world in the 21st century (IPCC, 2007). For many places this will include a mean air temperature increase as well as an increased frequency of extremely high daily temperatures (i.e. 'heat waves'). In most dryland regions, mean summer temperatures are forecast to increase significantly under continued high CO_2 emission scenarios (IPCC, 2007). Large areas of habitat, such as in semi-arid Australia, are predicted to have a daytime temperature increase of more than 4°C in the summer period by the year 2070. Some temperate areas will be subject to significant temperature increases of over 3°C, also during the summer period (CSIRO, 2007).

Forecast higher air temperatures may affect the seed bank via two main mechanisms. First, seedling mortality could increase due to increased evaporation of soil moisture, with subsequent recruitment failure producing a net loss of seeds from the seed bank. For example, in Mediterranean shrubland in Spain, Lloret *et al.* (2004) found that warming and drought conditions related to climate change reduced seedling survival and related species richness. They concluded that species producing fewer seedlings were most susceptible to local extinction and that the different

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responses between species could result in altered community diversity and structure. Second, increased air temperatures would change maternal environment conditions. The association between higher air temperatures experienced by the parent plant and the production of less dormant seeds (Fenner, 1991), particularly when physiological dormancy is the controlling mechanism, means that seeds may be less discerning about when to emerge. Kochanek *et al.* (2010) found that seed longevity of the semi-arid species *Wahlenbergia tumidifructa* was reduced as a result of higher temperatures experienced by the parent plants, and concluded that the species' bet-hedging capability may be compromised under future environmental conditions. The strength of this association is likely to vary between species, however, with Hoyle *et al.* (2008) finding only a small effect of maternal environment on dormancy levels of *Goodenia fasicularis*, a species from a similar semi-arid habitat.

Increased soil temperature

Higher air temperatures mean that temperatures experienced by seeds in the soil are also likely to change, with the degree of increase depending on habitat and vegetation type (Harte *et al.*, 1995). Canopy cover can reduce near-ground solar radiation and subsequently reduce levels of soil moisture evaporation and soil temperature (e.g. Huang *et al.*, 2010; Royer *et al.*, 2011). However, where soil surfaces are exposed to direct sunlight or are only sparsely vegetated, soil temperatures have been shown to increase to remarkable levels. For example, in semi-arid parts of the Negev Desert in Israel, Gutterman and Gozlan (1998) recorded daily maximum air temperatures of approximately 30°C in early summer, and associated soil temperatures of over 50°C just below the surface. Mott (1972) found similar increases in arid Western Australia, with 40°C air temperatures producing corresponding soil temperatures (at 0.5 cm below the surface) of approximately 78°C. In more temperate regions, soil temperatures above 40°C, and sometimes over 50°C, have been recorded in fire-prone regions during summer, either after canopy removal (Auld and Bradstock, 1996) or in unburnt open heathland (Ooi *et al.*, in press).

Ooi *et al.* (2009) found a strong linear relationship between measured air and soil temperatures in semi-arid south-eastern Australia and used this relationship to predict future soil temperatures. They found that forecast air temperature increases of approximately 4°C during summer in this region could produce associated increases in soil temperatures of 10°C. As a result, summer soil daytime temperatures were estimated to increase from a current mean of 60°C up to a new predicted mean of 70°C and potentially be sustained for several months. Work in temperate heathland, using a similar predicted air temperature rise, found that soil temperatures could increase by 7°C from the current mean (Ooi *et al.*, in press). The impact of such large temperature increases experienced by seeds in the soil is potentially significant.

In variable environments, seed bank persistence ensures that populations can re-establish after drought or disturbance (Fenner and Thompson, 2005). In ecosystems where plant population dynamics are driven by unpredictable rainfall regimes, non-dormant seeds germinate quickly in response to rain (Holmgren *et al.*, 2006). However, follow-up rains are not always sufficient for plants to complete their life cycle. By incorporating a bet-hedging strategy, where only a proportion of the seed bank germinates as a result of any particular rainfall event, risk of extinction is spread over time (Facelli *et al.*, 2005; Venable, 2007). Decreased dormancy and/or increased levels of germination from the seed bank, resulting from climate change, can subsequently compromise the bet-hedging strategy and have a significant impact on species persistence.

Increased soil temperatures could reduce the proportion of viable seeds within the seed bank by producing temperatures that are lethal to seeds. For instance, Ooi *et al.* (2009) found that sustained higher temperatures related to predicted future summer conditions increased levels of seed mortality for *Tephrosia sphaerospora*, one out of five physically dormant semi-arid species tested. However, although this example shows that there is some potential for this mechanism to compromise seed bank persistence, it may be an exception to the rule for species already occurring in harsh and very hot conditions. Many more examples show that seeds of species from such environments suffer no mortality under sustained very high temperatures (e.g. Tieu *et al.*, 2001; Daws *et al.*, 2007; Ooi *et al.*, 2009; Santana *et al.*, 2010). In these ecosystems, it is therefore likely that future higher soil temperatures would contribute most to net losses to the seed bank by influencing dormancy and germination mechanisms rather than increasing seed mortality.

The relationship between higher temperatures and greater loss of dormancy (e.g. Auld and O'Connell, 1991), or greater levels of germination, provides the underlying basis for a mechanistic impact of forecast increased temperatures on soil seed-bank dynamics. Species with physical dormancy in particular could be susceptible to increased soil temperatures. Physical dormancy, which is imposed by a hard seed coat that is impermeable to water, cannot be reversed once it is broken for the vast majority of species. Thus a loss of dormancy is directly related to seed bank persistence (Fenner and Thompson, 2005). To maintain a persistent soil seed bank, current soil temperatures cannot exceed the threshold for breaking physical dormancy

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of at least some proportion of the seed bank. Ooi *et al.* (2009) found that, under laboratory conditions, dormancy could be broken to significantly greater levels than currently occurs for two out of four physically dormant species from semi-arid south-eastern Australia, after a 3-month dry heat treatment at mean soil temperatures predicted for the end of the 21st century. Dormancy was broken in over 80% of seeds for both species. Santana *et al.* (2010) found a similar result for all six species studied from fire-prone vegetation, with the greatest loss of dormancy related to temperatures produced by summer heat-wave conditions (as determined by Ooi *et al.*, in press) rather than from a mean temperature increase. Although not specifically testing climate change scenarios, Tieu *et al.* (2001) found in their study that long-term dry heat treatments (which appear comparable to soil temperatures and durations likely to occur under current and future conditions) could break dormancy in an increasing proportion of physically dormant *Gompholobium knightianum* seeds.

Increased soil temperatures may also compromise seed bank longevity for species with germination cued to gap detection. Seeds can respond via an increase in the maximum temperature experienced or to an increase in the amplitude of diurnally fluctuating temperatures (e.g. Thompson and Grime, 1983; Bullock, 2000). Premature germination produced by heat-wave-induced temperature rises, rather than a gap, could mean seedlings would emerge into conditions unsuitable for recruitment, with a subsequent reduction in seed bank longevity. For example, during heat-wave events at nine sites across Europe, daily maximum air temperatures increased by between 7°C and 9°C above the long-term mean, whereas daily minimums increased by between 2°C and 5°C (De Boeck *et al.*, 2010). The corresponding increase in daily amplitude could therefore exceed 5°C. The level of impact of such air temperature increases on soil conditions and plant population dynamics will depend on the density of the canopy cover (see Royer *et al.*, 2011). However, the growing understanding of the role that future extreme events could play suggests that further investigation of this mechanism is warranted.

Rainfall

Changes to rainfall regimes are very likely to occur in the future, with decreases in mean rainfall levels forecast for most dryland and fire-prone ecosystems, including southern Africa, Mediterranean Europe, south-western USA and Australia (IPCC, 2007). Changes to the timing and supply of rainfall are also predicted, with the risk of summer drought increasing in Mediterranean Europe and Australia (Kirono *et al.*, 2011). Studies investigating changes to the timing of rainfall have primarily focused on phenological impacts to plant populations. Surprising results have arisen from the interaction between temporal shifts in the onset of first rainfall and species-specific germination temperatures, causing subsequent changes to species composition (e.g. Levine *et al.*, 2008; Kimball *et al.*, 2010). However, the greatest risks to seed bank persistence are likely to result from more sporadic rainfall or frequent droughts, combined with increased temperatures, leading to a greater probability of failed germination and seedling mortality. Miranda *et al.* (2009) quantified the drought conditions necessary to have an impact on species diversity in a semi-arid plant community in Almeria (Spain). Under forecast drought conditions, they showed that a rainfall reduction of greater than 25% reduced both productivity and species diversity.

Fire frequency

Species from fire-prone regions are some of the most dependent on persistent and very long-lived seed banks and physical dormancy is the dominant dormancy type (Baskin and Baskin, 1998; Ooi, 2007). The majority of species with soil-stored seed banks have dormancy and/or germination cued to the passage of fire. For example, physically dormant seeds have a hard, impermeable seed coat which is rendered impermeable via heat shock from the fire (Auld and O'Connell, 1991). Although physically dormant species display little response to smoke, many other species with different seed dormancy types increase levels of germination after the application of smoke cues, particularly after a period of burial (e.g. Baker *et al.*, 2005; Ooi *et al.*, 2006; Merritt *et al.*, 2007). A germination response to fire cues ensures that seedlings emerge into the post-fire environment, the primary window for successful recruitment. Obligate-seeders, which are defined as species that have above-ground adult plants killed by fire, are particularly dependent on the seed bank to replace individuals killed by fire and to ensure that populations persist. Seed banks therefore have to be maintained between fire events, via annual seed input from mature individuals, and then germinate after fire has occurred. After the passage of fire, residual seed banks vary, but can often be very low (Auld and Denham, 2006). Subsequent fires must therefore not occur before the new cohort of individuals reaches maturity and replenishes the seed bank, and hence fire frequency is one of the most important drivers of population dynamics in fire-prone vegetation (e.g. Regan *et al.*, 2010). Fire frequency is forecast to increase considerably under both moderate and high continuing CO_2 emission levels (Pitman *et al.*, 2007), posing a threat to species dependent on long-

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lived seed banks and the community composition of fire-prone ecosystems generally. Those species most at risk will be obligate-seeding species with long primary juvenile periods.

Functional grouping as an approach for predicting future distribution of species

With a greater understanding of the mechanistic responses of critical demographic processes, such as seed-bank dynamics, to climate change, we can move towards a greater predictive ability for determining species persistence by using functional groups. Classifying species into functional groups has provided a robust framework for predicting the response of plant populations to disturbance. For example, in fire-prone regions, plant species are broadly categorized as either obligate-seeders, if individuals are killed by fire, or resprouters, if adult plants have some ability for vegetative regrowth and can survive fire (e.g. Pausas *et al.*, 2004). Knowledge of the disturbance response type can subsequently enable prediction of persistence under different fire regimes for a large number of species, as well as providing a strong framework for reducing variability in species distributions models (Syphard and Franklin, 2010).

At its simplest, climate change could also be considered as a large-scale disturbance, which can result in varying effects at the regional and population scale, and functionally grouping species demographic responses to climate change will enable broader-scale predictions of distribution and persistence. It is therefore necessary to develop functional groups based on key life-history trait responses to changing environmental conditions. Recent studies support the idea that using the response of life-history stages or traits to climate change, rather than taxonomic affiliation (e.g. Morris *et al.*, 2008), will provide the best approach for identifying the species that are most sensitive to future climate variability.

In order to develop functional groups, and because there are limited data on the mechanistic response to climate change, it will be necessary to conduct more experimental work to establish the variation in response for different species. Although generating this data may seem to be a large undertaking, especially considering the limited time-scale available, there are potentially vast amounts of data already in existence that could be used to help bridge the knowledge gap relatively rapidly. For instance, in the case of seed bank persistence and physically dormant species, studies exist that have identified temperature thresholds for breaking dormancy, using a range of temperatures for numerous species (e.g. Auld and O'Connell, 1991; Tieu *et al.*, 2001; Santana *et al.*, 2010). Although the focus of these studies may not have been on the response of species to climate change, they provide useful information for identifying groups of species that have low temperature thresholds, or that may be more sensitive to increased temperatures.

Concluding remarks

It is important to link future environmental changes with potential mechanistic effects on life-history stages that are critical for plant species persistence, to more accurately predict the ecological consequences of climate change (Parmesan, 2006; Keith *et al.*, 2008). Improving our understanding of mechanistic impacts of climate change on seed-bank dynamics will therefore provide a basis for more accurate predictions of future species distributions and risk of extinction, particularly in ecosystems subjected to temporally stochastic disturbances. This may be best approached by implementing a modelling framework which incorporates regional climatic changes, current species distribution and responses of key demographic processes.

A high level of importance is therefore also placed on determining which life-history stage is actually critical for population persistence so that it can be targeted for assessment in future studies. In this review I have focused on seed banks in dryland and disturbance-prone environments because seed bank longevity is key in variable habitats. However, under less variable conditions, seed banks may play a less important role (Fenner and Thompson, 2005). Experimental data from studies conducted in more stable habitats with regular rainfall patterns have tended to back this up. Akinola *et al.* (1998) found little effect of soil warming for seed banks of species from limestone grassland in Buxton (UK). Similarly, Dalgleish *et al.* (2010) found that the potential impacts of climate change on short-lived mixed-grass prairie species in Kansas (USA) would be largest at the recruitment stage, and that seed banks played a minimal role for the majority of the species studied. Understanding the response of seed banks to climate change in these habitats is therefore less urgent than, perhaps, understanding the dynamics of seedling survival or seed production.

Climate change is very likely to have a significant impact on species that are dependent on long-lived seed banks, and the degree of impact will vary between species. To better prepare and manage for future threats to biodiversity, we have to identify those species and habitats that are most vulnerable to decline. As outlined in this review, this will require an assessment of their ecological response to future climate scenarios. Additionally, we will also need to

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assess species' abilities to adapt to future conditions either by plastic ecological responses or evolutionary responses (Petrů and Tielbörger, 2008; Williams *et al.*, 2008). For species dependent on long-lived seed banks, their adaptive capacity will depend on several factors, including the length of generation time, the amount of time between recruitment events and the levels of change required to adapt to new conditions. For example, some species with seed bank persistence regulated by temperature may have traits that are plastic enough to cope with mean temperature increases, or be able to adapt because of the constant, albeit relatively rapid, rate of increase. However, adapting to a new set of climatic extremes, such as sporadic heat-wave events, may be more difficult because of the stochastic nature of such extreme events (Ooi *et al.*, in press). Furthermore, although there is some evidence for relatively rapid evolutionary adaptation in response to climate change, particularly for insects, this is unlikely to be the case for the majority of species (Parmesan, 2006; Williams *et al.*, 2008).

Fenner and Thompson (2005) stated that while seed bank persistence appears to be mainly a species trait, the experimental evidence currently in existence suggests that it can be modified by environmental conditions. This is supported for long-term persistent seed banks by a few studies (e.g. Funes *et al.*, 2003; Ooi *et al.*, in press). However, the level of environmental modification forecast under climate change provides a strong incentive for further experimental study investigating both the mechanistic responses and the adaptive capacity of seed bank persistence in relation to changing environmental conditions. Studies investigating these variables are still surprisingly scarce, but are essential for predicting species persistence and managing biodiversity in the future.

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