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Seed bank dynamics and climate change in semi-arid ecosystems: a focus on physically dormant species

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ABSTRACT

The dynamics surrounding seeds are arguably the most important drivers of population persistence in semi-arid ecosystems. To fully understand plant population persistence and, in particular, to predict the impacts of changing climatic conditions, we need to develop a clearer picture of the ecological consequences of variation in seed dormancy and germination. In this review, I focus on seeds with physical dormancy in semi-arid regions, looking at the mechanistic effects of climate on seed bank dynamics. Both pre-dispersal and post-dispersal environment effects are considered. Knowledge is lacking in the understanding of the effects of changing climate on seed production, dormancy-breaking temperature thresholds, seed longevity and seed vigour. While lessons can be learnt from the broader range of studies conducted in the agricultural sector, there is a limit as to how the results from such studies can be applied to wild species in natural ecosystems. A concerted effort to increase the amount of ecological research in native environments is needed to gain a better understanding of the effects of climate change on biodiversity.

Keywords: seed ecology, physical dormancy, climate change, germination, maternal effects, heat wave, seedling vigour, Fabaceae, Malvaceae.

Introduction

The dynamics surrounding seeds are arguably the most important drivers of population persistence in semi-arid ecosystems. Whilst extensive research has been conducted in many areas of seed biology, especially into dormancy and germination mechanisms (Finch-Savage and Leubner-Metzger, 2006), our knowledge of the variation in these characteristics, and how variation can influence seed bank dynamics, is still somewhat limited. To fully understand plant population persistence and, in particular, to predict the impacts of changing climatic conditions, we need to develop a clearer picture of the ecological consequences of variation in seed dormancy and germination (Walck et al., 2011; Ooi, 2012; Cochrane et al., 2014).

Semi-arid regions are characterised by stochastic rainfall events, and classified according to mean annual rain thresholds and temperature (very broadly between 200 and 600 mm, although at times higher). Rainfall may be seasonal or aseasonal but is sufficient to allow the development of grasslands or savannahs and shrublands, unlike the lower production of biomass in more arid regions (Walter, 1973; Bailey, 1979). Semi-arid regions are generally on the fringes of drier arid areas, with examples occurring in Australia (shrublands, woodlands and grasslands), Brazil (caatinga), Chile (matorral and savanna), the Mediterranean (matorral) and South Africa (savanna and Karoo) (Groves, 1994; Kalin Arroyo et al., 1995; Cowling et al., 1997). Many semi-arid plant communities have dynamics which are driven

by fire as a recurring disturbance (e.g. Hodgkinson, 2002).

Quantifying plant population dynamics presents numerous challenges but is important for making predictions regarding species persistence and extinction risk (Venable, 1989). In ecosystems where population dynamics are driven by stochastic events, such as in arid, semi-arid and disturbance-prone vegetation, the seed bank provides a storage mechanism which ensures that a species can persist after disturbance (Fenner and Thompson, 2005; Baskin and Baskin, 2014). In fire-prone regions, recruitment from the seed bank after fire is the main factor determining subsequent community composition and structure (Lloret, 1998; Keeley et al., 2005), whereas in dryland systems much of the variation in recruitment is driven by a stochastic element to the timing and magnitude of rainfall (Noy-Meir, 1973; Kigel, 1995).

Seed bank dynamics are determined by the seed persistence, the dormancy that species possess, how this dormancy is broken, and the variability in dormancy and germination response (Baskin and Baskin, 2014). Quantifying the variability of dormancy, germination and other seed bank processes in response to specific environmental cues, and assessing whether traits display phenotypic plasticity (Chevin et al., 2010; Nicotra et al., 2010; Long et al., 2015), is essential to accurately predict population dynamics, which has direct application to understanding responses to management regimes or climate (Ooi et al., 2012). Seed persistence and seedling emergence from the seed bank are dependent on a number of interacting event-dependent factors, such as soil warming and available moisture, which are in turn influenced by climatic variation (Walck et al., 2011).

In this review, I focus on seeds with physical dormancy (also known as ‘hard-seededness’) in semi-arid regions. Physical dormancy is maintained by the majority of species in dominant families such as the Fabaceae, Chenopodiaceae, Convolvulaceae, Malvaceae, Cistaceae, Rhamnaceae and Sapindaceae and is a key mechanism controlling seed bank dynamics in fire-prone and arid systems (Fenner and Thompson, 2005; Merritt et al., 2007; Ooi, 2007; Ooi et al., 2009; Baskin and Baskin, 2014). Seeds

with physical dormancy have an impermeable coat that prevents water uptake which; once the seed coat and thus dormancy has been broken, it cannot be reversed (Baskin et al., 2000). As such, measuring the proportion of dormancy loss in physically dormant seed lots is a good proxy for estimating seed bank decline and provides a mechanism with which we can directly assess some of the potential impacts of increased temperatures and changing rainfall regimes on seed bank persistence (Ooi et al., 2014).

The aim of this review is to examine the potential impacts of climate change on seed bank dynamics in semi-arid regions. I intend to highlight several key areas where research has been conducted, as well as to identify key knowledge gaps. I will focus on the mechanistic effects of climate on seed bank dynamics, and divide these effects broadly into (1) those that occur on seed banks that result from the environmental conditions experienced by seeds while still developing on the maternal plant (pre-dispersal environment). And (2), I review the potential effects that occur while seeds are in the soil (post-dispersal environment), as well as the effects that this may have on seedling survival. Changes to the levels of seedling mortality are strongly connected with seed bank dynamics, because failed seedlings equate to a net loss to the seed bank. Interactive effects between the pre- and post-dispersal environment on seeds are highly likely, and could potentially have additive impacts on seed bank dynamics that are yet to be fully understood.

Seed bank dynamics in semi-arid plant communities

Dryland ecosystems cover approximately 40% of the earth’s land surface and include arid, semi-arid and hyper-arid classes (UNEP, 1991). Semi-arid regions occur across most continents. They are defined by their levels of aridity, with rainfall a key driver of vegetation dynamics, as well as their temperature extremes. Rainfall is erratic and highly variable over space and time (Evenari, 1984). Subsequently, recruitment also occurs intermittently and seeds of many species can persist for years or even decades.

Many semi-arid plant communities are characterised by a combination of long-lived perennial shrubs and trees, along with short-lived ephemeral species (*sensu* Noy-Meir,

1973). Perennial species appear to have a high variability with regards to the longevity of seed bank persistence, and although many have long-term persistence (e.g. Auld, 1995), they can depend on annual seed input to maintain seed bank size. For annuals or short-lived ephemeral species, population dynamics are more sensitive to the inherently unpredictable rainfall regimes, with germination occurring rapidly in response to pulses of rainfall (Holmgren et al., 2006). However, if rainfall episodes that initiate germination are not sufficient, or there are no adequate levels of moisture in follow-up rains to allow annuals to complete their life-cycle, then successful seed production may be episodic, and germination failure can rapidly cause depletion of the seed bank (Jurado and Westoby, 1992; Ooi et al., 2009). Such species rely on persistent, long-lived seed banks, to ensure that viable seeds are available to take advantage of sporadic rainfall events (Guterman, 1994; Pake e Venable, 1996; Facelli et al., 2005). Seed banks therefore have two clear roles in semi-arid environments. Firstly, they have to respond rapidly, with fast germination and seedling growth, to best take advantage of the sporadic rain. Secondly, they need to retain a proportion of seeds as a residual seed bank as a bet-hedging strategy (Philippi, 1993; Guterman and Gozlan, 1998; Venable, 2007).

Climate change and pre-dispersal effects on seeds

Plants can adjust to climate change via phenotypic plasticity or adaptation through natural selection (Nicotra et al., 2010). Plasticity itself is partially genetically controlled and heritable, and a proportion of this variation can therefore contribute to producing a plastic response. However, we currently have little understanding of the variability in trait response for perennial species in wild populations or their potential to adjust to climate change. In long-lived species, those dependent on adaptation of traits via natural selection to adjust to future environmental conditions may be at a disadvantage due to the pace of projected climate change (Ooi, 2012). The maternal environment can play a significant role in altering seed characteristics, and subsequently how seed bank dynamics will operate.

Seed production

Seed production can be an important determinant of eventual seed bank size. In semi-arid plant communities production tends to display a rainfall associated increase (e.g. Gutiérrez et al., 2000). Changes to rainfall, or more specifically, reduced rainfall during seed production could therefore reduce total seed input to the seed bank. Another key projected change is temperature, both via mean increases per year and by the number and duration of extreme heat wave events. High temperatures, even for relatively short durations during seed development, can have negative effects on seed fill for many agricultural species with physical dormancy (e.g. Spears et al., 1997; Hampton et al., 2013). This focus of research on seed fill at high temperatures in the agricultural sector is due to the importance of seed yield for food production (Vadez et al., 2012). Lessons learnt from this sector need to be applied to more studies in natural systems if we are to get a clearer picture of plant population dynamics and model future persistence under climate change with a mechanistic understanding of processes (Keith et al., 2008).

There has been considerable research devoted to investigating the effects of increasing levels of CO₂ on seed production, and it has been hypothesised that a productivity increase from CO₂ fertilisation could offset any loss of yield due to other factors such as those described above. Evidence for the effects of CO₂ on production of physically dormant seeds however has been mixed. For example, Miyagi et al. (2007) found that under laboratory conditions, legume species increased seed production under higher levels of CO₂ and related this to the ability for such species to both fix nitrogen and increase levels of nitrogen acquisition. However, all species tested were crops, with ample supplies of nutrients. Perhaps more relevant to natural systems, Thürig et al. (2003) found that species of Fabaceae within nutrient-poor calcareous grasslands did not increase seed production under increased CO₂. They concluded that this was because seed production can only be increased with a suitable supply of phosphorous (Stocklin and Korner, 1999), and suggested that a lack of

increased seed production is due to a general phosphorous limitation exacerbated at elevated levels of CO₂ (Rogers et al., 2009). This suggests that the often low phosphorous levels of many semi-arid ecosystems may limit any increase in seed production under increased CO₂ for physically dormant species.

Maternal environment effects on physical dormancy: temperature and rainfall

General trends in patterns of dormancy variation have been the subject of considerable study (Fenner and Thompson, 2005; Cochrane et al., 2014), however, much of this is biased heavily by the large volume of research on annual species from cool temperate climates. One such generalisation is that dormancy decreases with increasing parental environment temperature (Fenner, 1991). However, evidence from Ooi et al. (2012) and many agricultural studies suggests that the opposite is true for physically dormant seeds. The study of plasticity in physical dormancy has usually focussed on whether dormancy is present or not. For species with physically dormant seeds, the role that the environment plays in controlling the temperature thresholds required to break dormancy is a much more important question (Hudson et al., 2015; Liyanage e Ooi, in press). This is an important process to understand because it is a key determinant of seed bank response to climate change.

Increased soil temperatures projected under climate change during hot summer days can have a negative impact on the persistence of physically dormant seed banks (Ooi et al., 2009; Ooi et al., 2012). In fire-prone vegetation, loss of physical dormancy between fires results in seeds germinating from the seed bank, but no successful recruitment (e.g. Auld, 1986; Whelan, 1995; Tozer and Bradstock, 1997) and therefore a net loss and seed bank decline. However, plasticity of temperature thresholds in response to seed development temperatures would provide populations with a mechanism to adjust to projected summer temperature increases. Future work in semi-arid regions is necessary to gain a clearer understanding of the effects of temperature, not only on levels of initial dormancy, but on the temperature thresholds that break dormancy. These can be either fire-related or summer related temperatures.

The effects of rainfall on physical dormancy has also focused mainly on effects on the initial levels of dormancy expressed by the seed progeny (Hudson et al., 2015), with drier conditions producing seed lots with a higher proportion of dormant seeds (e.g. Hill et al., 1986). This trait, again, needs to be tested using wild species under more natural conditions, with a focus on how dormancy thresholds are effected, before we are able to make broader conclusions with regards to ecological outcomes.

Temperature and rainfall effects on subsequent seed vigour

Very little work on wild species has been conducted investigating the effects of the maternal environment on subsequent seed vigour. However, it is a very commonly studied factor in agricultural systems (Hampton et al., 2013). For example, increased temperature during seed fill has been tested extensively on crops such as soy bean (*Glycine max*), with results showing a loss of seed vigour (e.g. Spears et al., 1997). Conversely, there is little evidence to suggest that moisture stress during seed development has any negative effects on subsequent vigour in either soy beans, faba beans (*Vicia faba*) or peanuts (*Arachis hypogaea*) (Ramamoorthy and Basu, 1996; Ghassemi_Golezani and Hossein-Mahootchy, 2009). Poor seed vigour usually translates to lower rates of germination and seedling growth. If similar outcomes were applied to natural systems, it is likely that slower growth would have an impact on the competitive ability of the effected species. An example of this is currently being studied in two species from fire-prone Australia, with wild species appearing to undergo considerable loss of vigour (Ooi, unpublished data). Furthermore, a slower rate of germination is likely to limit the capacity for species to take advantage of short periods of soil moisture typical of arid and semi-arid ecosystems (Stevens et al., 2014). Temperature may also directly influence seedling survival, either by exceeding physiological limits of species, or increasing the amount of evaporation, meaning higher mortality, even for seedlings adapted to fast growth (Stevens et al., 2014).

Post-dispersal effects on seeds in the seed bank

Increased temperature

Temperature is the main factor controlling physical dormancy in semi-arid and arid zone species (Mott, 1972; Baskin and Baskin, 2014). Increasing treatment temperatures alleviate dormancy in increasing proportions of any seed lot (Martin et al., 1975; Ooi et al., 2009; Rangel et al., 2015). In fire-prone regions, physical dormancy is often overcome by a short duration heat shock related to the passage of fire, resulting in a flush of germination (Auld e O'Connell, 1991; Keeley, 1991). Both mechanisms contribute to the maintenance of long-lived seed banks, by ensuring that germination is either delayed until the onset of favourable conditions (i.e. during a rainfall event which provides sufficient moisture for recruitment, or after a fire), or that the seed bank does not germinate all at once (Baskin and Baskin, 2014; Fenner and Thompson, 2005).

From a bet-hedging perspective, for physically dormant species, the effects of temperature have direct relevance to seed bank persistence, because increasing temperatures experienced in the soil may alleviate dormancy in a greater proportion of seeds. In a laboratory study testing dormancy-breaking response under current and projected future soil temperatures, Ooi et al. (2009) found that two of the four physically dormant species tested from semi-arid Australia germinated at much greater levels under future conditions. A smaller but still positive response was found by Pérez-Sánchez et al. (2011) in Mexico, although much higher levels of initial non-dormancy were prevalent. Even a small increase in loss from the seed bank could affect seed bank longevity by committing higher proportions of seeds to germinate during low rainfall events with little follow-up rain. In recent work, Auld e Ooi (unpublished data) have found that increased loss from the seed bank of 20% can increase extinction risk of an *Acacia* species in fire-prone Australia by five times.

Changes to rainfall regimes on recruitment from the seed bank

For many semi-arid regions, climate change projections indicate that rainfall is

likely to become increasingly sporadic in the future in regions including Australia, Brazil, Israel, the United States and many parts of Africa (IPCC, 2007). Furthermore, increases in temperature (see above), will contribute to higher evaporation rates, leading to even greater fluctuations in available soil moisture (Stevens et al., 2014). As rainfall becomes more erratic, this increases the likelihood of 'false start' rains, where rainfall levels are enough to initiate germination but not to allow recruitment of the seedling. This will place a greater importance on seed bank strategies, including spreading germination over time (i.e. bet-hedging), and/or retaining a residual seed bank.

Additionally, higher levels of erratic rainfall and soil moisture variability will also produce a greater chance of seeds undergoing wet-dry cycles, without reaching sufficient moisture levels to initiate germination (Long et al., 2015). Once physical dormancy is broken, the seed must first become imbibed with water in order for the germination process to begin (Baskin and Baskin, 2014). Wet-dry cycles causing the hydration-dehydration of seeds in the seed bank are therefore more likely, however, very few studies have tested these effects on seeds in natural environments (Fenner and Thompson, 2005).

Hydration-dehydration cycling of seeds is a technique commonly applied in agriculture (seed priming), and produces seeds with a faster germination rate, as well as a greater rate of emergence (Snapp et al., 2008). Research conducted on annual pasture legumes have tested the physiological limits of seeds to priming and found that the longer the period of drying between imbibition events, the more likely that germination rates slow and that viability decreases (e.g. Jansen and Ison, 1994). The length of time the seed is imbibed prior to drying can also play a major role in subsequent germination success (Fenner and Thompson, 2005). For example, a study on mung beans found that the longer the seeds were exposed to a wet period before subsequent desiccation, the higher the mortality of seeds (Hong and Ellis, 1992), a result due to germination progressing to the point of radicle emergence during hydration, essentially a 'point of no return' in the

germination process. Preliminary work on wild species in Australia has begun to examine the limits to successful germination after wet-dry cycling, with the length of the drying period significantly increasing seed mortality (Ooi et al., unpublished data). Future work will need to incorporate a broader range of species and habitat types before we get a clear picture of the ecological consequences of wet-dry cycles and their effects on seed bank dynamics.

Conclusions and future research

A strong mechanistic relationship exists between climate variables and the formation and retention of seed dormancy, and the germination characteristics of seeds (Harper, 1977; Fenner and Thompson, 2005). It is therefore inevitable that projected climatic changes will affect seed ecology (Ooi, 2012). Projections for future climates in semi-arid regions include significant increases to temperature, carbon dioxide, and rainfall variability, as well as increased frequency and severity of extreme events such as heat waves, drought and fire. Understanding the ability of seed banks to cope with such changes means that we need to understand the effects of climate change on a range of seed traits and characteristics, including seed production, dormancy and germination requirements. This has led to a number of studies focused on variation in dormancy levels, particularly in the agricultural sector where the effects on seed yields and vigour are important for food production under a changing climate (Hampton et al., 2013). However, while lessons learnt from the agricultural sector can be applied to studies of wild species, in particular by informing the directions that some research can take, there needs to be a concerted effort to increase the amount of research conducted on natural systems to try and gain a better understanding of the effects of climate change on biodiversity.

As we attempt more experiments and interpret them with regards to projected climatic changes, we need to remain cautious that we examine the results in the context of the ecosystems in which we are studying. For example, a number of recent papers testing the effects of increased temperatures on seed traits have found that germination increases, and this is reported as a positive outcome for a species.

As shown in this review, greater germination under future climates does not necessarily mean greater recruitment, and in regions such as the semi-arid and other rainfall-limited habitats, it is just as likely to be detrimental for population persistence. The levels of dormancy loss is a characteristic that has evolved over time in a particular environment, with the seed bank balancing between providing enough seeds for a chance of recruitment, and retaining an adequate seed bank in case of initial cohort failure. We therefore need to be careful in the way that we interpret results from such studies, and think about how they sit within the broader context of the plants life cycle and the environmental conditions in which they exist.

Predicting the long-term impacts of climate change on plant species distribution and risk of extinction, particularly in ecosystems where seed bank persistence is critical, is necessary to link future changes to climate with mechanisms that determine seed bank longevity. It is important not only to identify the patterns of change that occur as a direct result of climatic changes (e.g. Ooi et al., 2009), but also to examine whether dormancy or germination requirements change as a result of the maternal environment during seed development. For example, one of the key questions to ask with regards to physically dormant species is; can warmer or drier conditions of the maternal environment produce seeds that are more resilient to subsequent warmer conditions during the germination stage? Furthermore, what other effects of the maternal plant environment can buffer species against future climatic changes in the post-dispersal environment? Hudson et al. (2015) stated that while it is difficult to identify whether the source of phenotypic variation in offspring traits are the result of genetic diversity or maternal environmental plasticity, it is still possible to quantify the plasticity of responses. This is one of the key goals for future studies investigating the impact of climate change on mechanistic responses of plant processes in the future.

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