The impact of increased temperatures on germination patterns of semi-aquatic plants

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Abstract

Future climate change predictions indicate that there will be an increase in ambient air temperature. Increases in ambient air temperature will result in a corresponding increase in soil temperature. The consequences of further increases in soil temperature will potentially be detrimental for the soil seed bank of plants in terms of length of dormancy and viability of seeds. This experiment investigated the effect of different exposure temperatures and duration of exposure on the germination of semi-aquatic plant species. Seeds of four species (*Alternanthera denticulata*, *Juncus usitatus*, *Persicaria lapathifolia* and *Persicaria prostrata*) were exposed to temperatures ranging from 25 to 100°C for durations between 1 and 14 days, before being germinated in an incubator for 6 weeks. Germination occurred in all four species after exposure to temperatures ranging from 25 to 60°C. These temperatures appeared to promote germination as the temperature and duration of exposure increased. However, in *P. lapathifolia* and *P. prostrata*, the number of seeds germinating declined when exposed to 70°C and there was no germination for temperatures exceeding this. In contrast, *A. denticulata* and *J. usitatus* only began to decline when exposed to 80°C, with no germination at higher temperatures. These results suggest that soil temperatures exceeding potential threshold temperatures of 70 and 80°C will result in a decline in the number of seeds germinating and may potentially see a change in species distributions. As such soil temperatures are already being experienced throughout Australia, some species may already be close to their thermal threshold.

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Introduction

Globally, climate change is likely to result in the loss of many plant species (Thuiller *et al.*, 2005) as a consequence of rising temperatures that exceed critical thresholds (Dunlop and Brown, 2008). For species that rely on dormant propagules to survive adverse environmental conditions (Brock *et al.*, 2003), increasing temperature may reduce the overall viability and resilience of populations.

For many floodplain and wetland plant species, the production of a large seed bank that can remain viable in the sediment for many years is one mechanism for surviving adverse conditions such as drying and drought (Brock *et al.*, 2003; Nielsen *et al.*, 2013). The majority of viable seeds are found in the top 1–2 cm of the sediments, with viability decreasing with sediment depth (Gleason *et al.*, 2003; Leck and Simpson, 1987; Mott, 1972; Nicholson and Keddy, 1983; Nielsen *et al.*, 2018; van Der Valk and Davis, 1979). During dry periods the seeds on the surface of floodplain and wetland sediments may be exposed to extremes in environmental conditions ranging from sub-zero temperatures to above 70°C (Dexter, 1970). Climate-induced increases in temperature are most likely to influence those seeds that accumulate on the sediment surface; however, these seeds are likely to be resilient to short-term exposure to elevated temperatures (Smith, 2007).

Across many regions of south-eastern Australia, ambient air temperatures are predicted to rise by up to 4°C in response to climate change (CSIRO, 2007; Hughes, 2011; Suppiah *et al.*, 2007). Corresponding to these increases in temperature, there will be an increase in aridity with many wetlands remaining dry for longer periods (Nielsen *et al.*, 2013). Increases in ambient air temperatures have been correlated with increases in sediment temperatures; a 4°C increase in ambient air temperature will result in a 10°C increase in sediment temperature (Ooi *et al.*, 2009; Ooi *et al.*, 2012), although increased temperatures may be mitigated by standing vegetation providing shade, leaf litter, moisture content and sediment type (Harte *et al.*, 1995). Temperature is critical to the persistence and maintenance of seed banks for most plant species (Baskin and Baskin, 2001; Baskin *et al.*, 2004; Walck *et al.*, 2011). Soil temperature can both alter germination rates and impact the effectiveness of dormancy, depending on the species (Brändel, 2004; Nielsen *et al.*, 2015; Santana *et al.*, 2010). Therefore, temperature plays an important role in determining species' distribution (Sheldon *et al.*, 2011). Increasing temperature has been shown to significantly reduce the numbers of seeds germinating (Nielsen

et al., 2015; Pinceel et al., 2018). Higher temperatures caused by climate change could threaten the persistence of seed banks and reduce the resilience of wetland plant communities.

While there is evidence that dormant seeds of many terrestrial species can survive for periods of elevated short, rapid increases such as those caused by fire (Auld and Bradstock, 1996; Bradstock and Auld, 1995) or more long-term exposure predicted to occur under climate change scenarios (Ooi et al., 2009; Ooi et al., 2014), it is unknown how long seeds of floodplain and wetland species will remain viable as temperature increases in response to climate change. Therefore, in this study we test the hypotheses that increased temperatures and longer periods of exposure will lead to a decrease in the proportion of seeds germinating.

Methods

Seed collection

Seeds were collected from flowering aquatic and riparian plants predominately from a 100 m reach of the Broken River (−36.517694, 145.95361), Benalla, Victoria, in March 2016. The Broken River is a typical example of a lowland river system in south-eastern Australia. The plants from which seeds were collected are common and widespread within south-eastern Australia and their seeds are commonly reported as occurring in seed banks. For each species to obtain sufficient seeds, between 10 and 15 plants were sampled. Where sufficient seeds were not found, additional seeds were collected from the same species at Wonga Wetlands (−36.068571, 146.854253), Albury, New South Wales. Seeds were well mixed, air-dried at ambient natural temperatures, then placed in ziplock bags and stored at 4°C until commencement of experiments in April.

Seeds from 10 species were initially collected due to their abundance, and therefore, the availability of seeds. Seeds from each of these species were tested for viability using the tetrazolium viability test (TZ test) (Cottrell, 1948). To ensure adequate germination under test conditions only four species with more than 50% seed viability were selected for further assessment. These were Alternanthera denticulata (R.Br), Juncus usitatus (L.A.S. Johnson), Persicaria lapathifolia (L.) and Persicaria prostrata (R.Br.).

Seed preparation

An initial pilot germination trial indicated that retention of the perianth promoted the growth of mould on seeds that caused seed mortality. Therefore, the perianth of all seeds was removed prior to the experiment. Seeds from each species, with perianth removed, were then placed in paper bags until each paper bag (replicate) contained more than 110 seeds.

Experimental design

Seeds were subjected to six temperatures (25, 40, 60, 70, 80 and 100°C) for six time durations (1, 2, 4, 7, 10 and 14 days), creating a total of 36 treatments for each species. Due to the number of seeds required for each species the number of replicates for each treatment was limited to four. In addition, as a reference, four additional replicates of each species were not subjected to any heating. Therefore for each species there were 148 bags of seeds containing a minimum of 100 seeds each (>14,800 seeds per species).

Paper bags containing one replicate (>100 seeds) were randomly allocated to one of the six selected temperature treatments and one of the six duration treatments. Two ovens were used for this experiment, a Thermoline Dehydrating oven (heated to 40, 70 and 100°C) and a Contherm Series Five oven (heated to 25, 60 and 80°C). The ovens were pre-heated and paper bags containing the seeds were placed in random locations within the oven. At the appropriate time interval the bags were removed, and the seeds were prepared for germination.

Germination

One hundred seeds from each replicate were placed onto an agar plate containing a 1.0% agar solution using Difco Bacto-Agar and distilled water, in rows of 10 × 10. The plates were placed inside plastic snap-lock bags to retain moisture and then placed into a Thermoline Scientific Illuminated incubator. To provide a range of germination cues that mimic natural environmental conditions, seeds were incubated at 12/25°C minimum/maximum temperatures on a 12 hour/12 hour light/dark cycle (Baskin and Baskin, 2001; Baskin et al., 2006; Durant et al., 2016; Ooi et al., 2014), with a light spectrum ranging from 400 to 720 nm (Sylvania growth lamps, Sylvania, Australia). Germination temperatures were set to reflect the range of temperatures typically experienced in the region from which the seeds were collected (http://www.bom.gov.au/climate/averages/tables/cw_082002.shtml). To maximize germination success, each agar plate was assessed after 6 weeks and the number of seeds that germinated were counted. Seeds were classed as germinated when the radicle was observed to be emerging (Baskin et al., 2006).

Statistical analysis

Statistical analysis was undertaken using the IBM program SPSS (version 25). A logit transformation was applied to proportion data (% germination), to satisfy the assumptions of statistical tests (Warton and Hui, 2011). Binary logistic regression was used to determine the likelihood chi-square ratio to assess the interaction between temperature and duration of heating on seed germination.

Results

For all species, logistic regression revealed a significant interaction ($p < 0.001$) between temperature and duration of exposure (Table 1). For the species A. denticulata there was no change in the proportion of seeds germinating after 14 days at 25 and 40°C. In contrast, exposure to temperatures of 60, 70 and 80°C appears to enhance germination, which was maintained across all time periods for the 60 and 70°C treatments. Although the proportion of seeds germinating in the 80°C treatment was initially enhanced, germination declined substantially after exposure to this temperature for more than 4 days. No seeds germinated when exposed to temperatures of 100°C (Fig. 1).

Juncus usitatus was unaffected between temperatures of 25 and 70°C, with the majority of seeds germinating within this temperature range. At 80°C the proportion of seeds germinating declined as duration of exposure increased, with 50% of seeds not germinating after 14 days of exposure to this temperature. No seeds germinated when exposed to temperatures of 100°C (Fig. 1).

Table 1. Chi-square analysis results for each of the four species

	Likelihood ratio chi-square	d.f.	Significance
Alternanthera denticulata			
Temperature	4867	5	<0.001
Duration	0.00	5	1.000
Temperature × Duration	571	26	<0.001
Juncus usitatus			
Temperature	9352	5	<0.001
Duration	25	5	<0.001
Temperature × Duration	141	26	<0.001
Persicaria lapathifolia			
Temperature	3706	5	<0.001
Duration	0.000	5	1.000
Temperature × Duration	506	25	<0.001
Persicaria prostrata			
Temperature	4739	5	<0.001
Duration	0.000	5	1.000
Temperature × Duration	759	25	<0.001

Germination of *P. lapathifolia* and *P. prostrata* seeds increased after exposure to temperatures between 25 and 60°C and maintained across all exposure periods. For *P. prostrata*, the proportion of seeds germinating after exposure to 70°C declined after 2 days and few seeds were able to germinate after 10 days. Similarly, *P. lapathifolia* was able to germinate after exposure to 70°C for 7 days, but longer durations of exposure decreased germination to 10% (Fig. 1).

In this study, the germination response of the four species to increasing temperature and duration of exposure varied between species and could broadly be classified as three patterns of response:

Response A: Germination remains steady with exposure to temperatures up to 70°C, irrespective of exposure time. Germination is suppressed at higher temperatures with increasing exposure to heat irrespective of time (*J. usitatus*).

Response B: Germination increases at temperatures of 60 and 70°C compared with the lower temperatures. Germination is suppressed at higher temperatures with increasing exposure to heat (*A. denticulata*).

Response C: No difference in the germination of seeds exposed to temperatures up to 60°C. Germination is suppressed at temperatures of 70°C and above and with increasing exposure time (*P. lapathifolia* and *P. prostrata*).

Discussion

In this study we tested the hypotheses that the increasing temperature and duration of exposure leads to a decrease in the proportion of available seeds germinating. Results indicate that for the seeds of all species tested there is a thermal threshold, which results in a decline in the proportion germinating. For some species, temperatures below these thresholds appear to enhance germination, which along with moisture and light, is known to be one of the primary environmental factors that regulates both dormancy and germination (Baskin *et al.*, 2004; Finch-Savage and Leubner-Metzger, 2006).

Physiological dormancy is the most common form of dormancy for the majority of angiosperms and the most common form of dormancy in temperate seed banks (Baskin and Baskin, 2004; Finch-Savage and Leubner-Metzger, 2006). Germination is broken by a range of environmental cues such as changes in temperature (heating/cooling) or chemical stimuli. The breaking of physiological dormancy is reliant on appropriate cues and it is generally accepted that temperature and light regimes are required not only to break dormancy but to promote germination, and that the temperature at which dormancy is broken is dependent on individual species' requirements (Baskin and Baskin, 2001; Brändel, 2004; Finch-Savage and Leubner-Metzger, 2006; Ooi *et al.*, 2014; Steadman and Pritchard, 2004).

The patterns of germination of each species were allocated to three response types. In general, plants in the 'Response A' group will be less susceptible to increasing temperature and duration of exposure compared with those in the 'Response C' group, which were the most susceptible to increasing temperature and duration of exposure. In contrast, the 'Response B' group is an intermediate group, where exposure to increased temperature initially promoted germination, but germination declined with increasing exposure.

In general, breaking of physiological dormancy is directly related to temperature, with an increasing proportion of seeds breaking dormancy and germinating as temperature increases (Long *et al.*, 2015). While seeds may survive longer at lower temperatures (Baskin and Baskin, 2004), results from this study indicate that more seeds germinate at higher temperatures and increased duration of exposure until their threshold is exceeded and germination ceases. Although not tested, we assume that the lack of germination is due to a loss of viability (Ooi *et al.*, 2012; Ooi *et al.*, 2014).

In all treatments, it was observed that there were temperatures at which initial germination was higher compared with the reference treatment. This suggests that exposure to heat breaks dormancy, as has been observed in fire-dependent species (Keeley and Fotheringham, 2000; Ooi *et al.*, 2014; Santana *et al.*, 2010). These results suggest that for some wetland plant species (*A. denticulata*, *P. lapathifolia* and *P. prostrata*), exposure to increased temperatures increases the number of seeds released from dormancy, thereby promoting germination. For these three species, germination initially increased with increasing temperature and duration of heating.

This study has demonstrated that although some species can germinate after exposure to higher temperatures, the threshold exposure temperatures for the species tested was found to be around 70–80°C. At exposure temperatures above this, germination declined for all species tested within days of exposure. In contrast to these results, a previous study by Nielsen *et al.* (2015) indicated that sediment temperatures that exceed 50°C (33°C equivalent air temperature) for 14 days will have catastrophic effects on the germination of wetland plants. It is therefore conceivable that if the seeds used in this experiment were exposed to these higher temperatures for longer than 14 days, declines in germination may have occurred. Alternatively the species selected for this experiment may be more tolerant to elevated
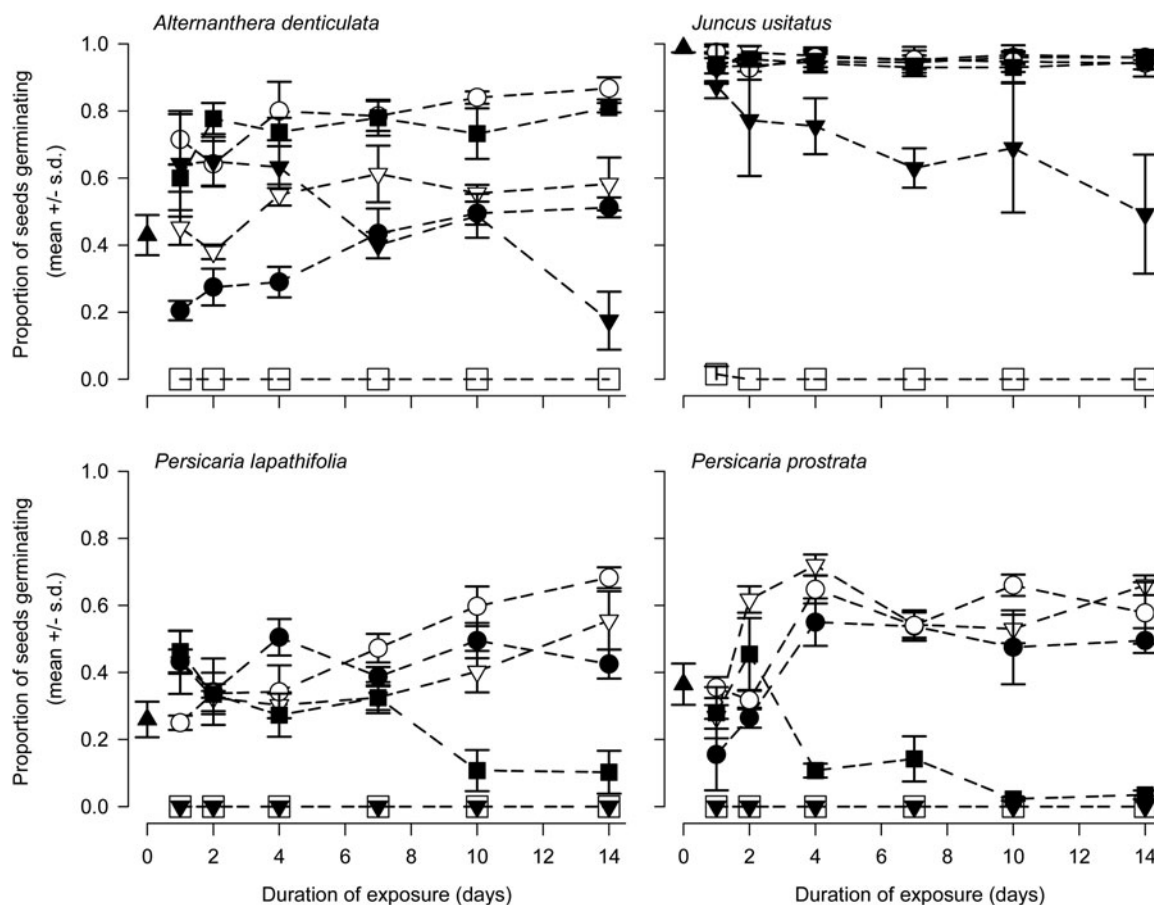
Fig. 1. Mean proportion of seeds of each species germinating after exposure to different temperatures. Symbols represent the temperature to which the seeds were exposed to prior to incubation at 25°C (▲, reference seeds; ▽, 25°C; ●, 40°C; ○, 60°C; ■, 70°C; ▼, 80°C; □, 100°C.

temperatures than those that were germinating from the sediment used by Nielsen *et al.* (2015).

Understanding the germination of seeds under differing temperatures is important to evaluate the potential impacts of climate change on seed dormancy. Seed dormancy allows many plants to disperse in time and avoid adverse environmental conditions such as elevated temperatures that seeds are potentially exposed to during periods of drought (Brock *et al.*, 2003). The results from this study suggest that under predicted climate change scenarios of increased frequency and duration of extreme heat events (CSIRO, 2007), seeds may be exposed to temperatures for durations that exceed their thermal tolerance and reduce the ability of seeds of some plants to persist. Projected climate scenarios predict potential increases in air temperature up to 4°C (Hughes, 2011), and for every 1°C increase in the maximum daily temperature there is an approximate 1.5°C increase in sediment temperature (Ooi *et al.*, 2009; Ooi *et al.*, 2012). This poses a risk for seeds that remain dormant in sediment seed banks. Temperatures approaching 50°C have been recorded in south-eastern Australia, which would equate to a sediment temperature of 75°C which is likely to influence seed survivorship. Therefore, the temperatures used in this study are likely to occur in inland Australia.

Temperatures have been recorded from floodplain sediment in floodplain forests of south-eastern Australia and more arid regions that have exceeded 65°C (Dexter, 1970; Mott, 1972; Ooi *et al.*, 2009). It is likely that germination of many species may

already be impacted by the high sediment temperatures experienced. With future climate scenarios predicting increases in the frequency, duration and intensity of extreme weather events such as heatwaves, fire and drought and an overall increase in temperature and decrease in rainfall, it can be expected that dormant seeds from wetland and floodplain plants present in sediments will become increasingly exposed to temperatures during dry periods. Exposure to temperatures that exceed species' thresholds (IPCC, 2014) will reduce the numbers of plants germinating and potentially result in the loss of species from the sediment seedbank.

Increasing sediment temperatures, however, will favour and select for species in response group 'A', such as *J. usitatus* that are capable of germinating across a broad range of temperatures. Such selection pressure will potentially result in a change in communities associated with changes in species richness and abundance (Gleadow and Narayan, 2007; Sheldon *et al.*, 2011; Walck *et al.*, 2011).

In response to increasing temperature as a consequence of climate change, many terrestrial species have the potential to shift in range to suit their thermal needs (Hughes, 2003; McKenney *et al.*, 2007). Fragmentation of the riverine-floodplain landscapes will cause a decline in the availability of suitable habitats (Nielsen and Brock, 2009). Even though plants have the potential to disperse over long distances, either by wind (Soons, 2006) or birds (Figuerola and Green, 2002), the likelihood of seeds or other propagules establishing in suitable habitats may be poor. Indeed,

local environmental factors are likely to a more important influence on plant communities than dispersal ability (Campbell and Nielsen, 2014; Soons and Ozinga, 2005). The inability of plants to establish in new habitats will lead to local extinctions and losses in biodiversity (Qiu et al., 2010; Sheldon et al., 2011).

This study demonstrates that predicted increases in temperature associated with climate change will impact on a species' ability to survive unfavourable conditions, reducing their capacity to respond when more favourable conditions occur, and thereby undermining the natural resilience of these systems (Brock et al., 2003; Pinceel et al., 2018).

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