

Research Article

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Seed longevity and germination of the emerging invasive species wavyleaf basketgrass (*Oplismenus undulatifolius*) under varied light regimes

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Abstract

Invasive nonindigenous species pose a serious threat to native biodiversity and ecosystem functioning. Understanding how species' performance varies under conditions in the current and invaded range can help to predict the dynamics of the invading species in its new environment. Plants with the ability to alter growth in response to variation in light conditions may be favored in landscapes that experience frequent disturbance, as these species may be able to exploit a wide range of niches. Seedbank persistence may also play a critical role in successful plant invasion, as extended seed viability may increase the chance of outlasting unfavorable conditions, maintain population genetic diversity, and allow reinvasions. This study investigated seed longevity and the effect of light intensity on germination of wavyleaf basketgrass [*Oplismenus undulatifolius* (Ard.) Roem. & Schult.], a newly established invasive species in U.S. mid-Atlantic forest understories. *Oplismenus undulatifolius* seeds were collected across 5 yr from the original site of introduction in Maryland, USA, and stored in standard lab conditions, then subjected to germination trials under four light conditions in a controlled growth chamber. Seeds remained viable for at least 9 yr, and light intensity did not significantly impact seed germination. Our study demonstrates the importance of evaluating environmental and temporal effects on germination traits, because the scope of surveillance in the field may need to be expanded based on new information about environmental tolerance. Long-term monitoring may also be necessary to effectively control invasive plant populations capable of forming a persistent seedbank.

Introduction

Invasive species contribute markedly to global environmental change, and thus pose an increasing threat to native biodiversity and ecosystem functioning (Mainka and Howard 2010; Singh et al. 2021; Vitousek et al. 1996). After introduction to new environments, nonnative species may aggressively compete with native biota for resources directly through interference competition and indirectly through exploitation competition (Allstadt et al. 2012; Bennett et al. 2011; Gioria and Osborne 2014; Le Louarn et al. 2016). Invasive species can impact disturbance dynamics, including fire, erosion, and biotic disturbance regimes (Gergel and Turner 2017; Mack and D'Antonio 1998). Nonnative pathogens can also be transported with an introduced nonnative species, and thus impose an additional ecological stress on recipient communities (Foster et al. 2021; Smith et al. 2006). Furthermore, recipient ecosystems may be susceptible to modification in nutrient cycling and physical and structural properties in response to the establishment of invasive species (Asner et al. 2008; Johnson et al. 2020; Zhang et al. 2019). As plants are foundations of ecological communities, introduced plant species may be particularly likely to critically threaten ecosystems when they establish and become invasive (Weidlich et al. 2020).

The seed stage is vital in the life history of invasive plants, as successful germination is critical for the initial establishment of new populations (Enders et al. 2020; Gioria and Pyšek 2017; Theoharides and Dukes 2007; Wainwright and Cleland 2013). Emergence timing will determine the first environmental conditions that seedlings experience, and thus abiotic cues that initiate germination will affect plant survival and establishment (Baskin and Baskin 1998; Donohue et al. 2010; Finch-Savage and Leubner-Metzger 2006; Zhang et al. 2014). Light quality and quantity are prominent environmental cues that many plant species with photoblastic seeds use to break enforced dormancy or stimulate germination of nondormant, quiescent seeds (Baskin and Baskin 2004; Côme 1970; Fenner and Thompson 2005). How seeds respond to the light environments encountered in their introduced ranges can dramatically impact establishment success in these new locations (Donohue et al. 2010). For example, if coupled with a rapid growth rate, early emergence in low light conditions may provide a competitive advantage when

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Management Implications

Oplismenus undulatifolius (wavyleaf basketgrass) is an invasive species in U.S. mid-Atlantic forest understories that has spread rapidly since its discovery in 1996 at Patapsco Valley State Park in Maryland, forming dense carpets that may crowd out native species. To better inform early-stage invasive management, we examined the seed longevity and germination of *O. undulatifolius* under four light intensities using seeds from five collection years that had been stored in laboratory conditions. We found that under laboratory conditions, *O. undulatifolius* seed viability remained high for 7 yr, and seeds could successfully germinate after 9 yr. Germination percentage did not differ across the light levels examined. This suggests land managers may need to continue monitoring for *O. undulatifolius* seedlings in treated areas for up to 7 yr, even after complete aboveground removal, to prevent potential reestablishment from seed. Our study demonstrates the importance of early-stage monitoring management before a persistent seedbank is established, because eradication becomes increasingly difficult when population regeneration is possible from seeds as well as vegetative propagules. Further, surveillance for new *O. undulatifolius* seedlings may need to be expanded beyond deep-shade areas, as we observed high germination rates across a wide range of light levels. Thus, seeds that disperse to areas of high light may still be able to germinate, though the ability to persist to reproduction in these high light conditions is less understood. We recommend additional studies on factors affecting growth and survival at later life stages of *O. undulatifolius* to determine its potential range of environmental tolerance and inform effective early detection and response efforts.

individuals are able to overtop neighbors and increase potential light exposure (Carvalho et al. 2021; Makana and Thomas 2005; Weinig 2000). The ability to germinate under a wide range of conditions may also favor invasiveness by increasing potential suitable habitat and the likelihood of establishment in novel environments (Bellache et al. 2022; Ebrahimi and Eslami 2012; Hou et al. 2014; Javaid et al. 2018). Alternatively, narrow germination requirements may promote invasion success by ensuring favorable conditions for seedling establishment, such as through microhabitat selection (Carvalho et al. 2021; Gioria et al. 2018; Kudoh et al. 2007; Makana and Thomas 2005; Marushia et al. 2010; Stromberg et al. 2007; Wainwright et al. 2012). As plants may encounter diverse environmental conditions following initial dispersal to new locations, broad light requirements for germination may strongly influence where invasive plants may be successful, whereas strict light requirements may optimize seedling establishment and growth (Bhatt et al. 2023; Castillo et al. 2013).

Seed longevity for a year or more can also be important for the successful establishment of invasive plant populations, by increasing recruitment opportunities when germination conditions are suitable (Gioria et al. 2021; Simons and Johnston 2006; Venable and Brown 1988). The ability to maintain a reservoir of metabolically inactive individuals in a seedbank allows plant species to employ a bet-hedging strategy to counter suboptimal conditions and can influence the long-term evolutionary potential of populations (Gremer and Venable 2014; Levin 1990). Seedbanks provide a degree of resilience to populations in highly variable or disturbed environments by temporally staggering emergence within a growing season or across multiple years (Evans and Dennehy 2005; Kalisz 1986; ten Brink et al. 2020). Additionally,

persistent seedbanks can facilitate population regeneration and help maintain genetic diversity within a population across generations, which may contribute to invasion success (Abbas et al. 2021; Gioria et al. 2012; Gremer and Venable 2014; Lennon et al. 2021). Seedbanks can reduce vulnerability to local extinctions and potential negative consequences of founder effects, genetic bottlenecks, and small population sizes early in the invasion history (Houle and Phillips 1988; Meimberg et al. 2006; Puillandre et al. 2008; Williams and Fishman 2014). This stabilizing effect of seedbanks results in part from the reserve of historical genetic diversity maintained in dormant seeds, which can supplement current populations experiencing low genetic diversity (McCue and Holtsford 1998; Rees 1993). Consequently, seedbank persistence can affect demographic persistence by promoting local patch reestablishment, as well as providing a source for propagules contributing to range expansion (Abbas et al. 2021; Galatowitsch et al. 2016; Leary et al. 2018).

First discovered in the United States in 1996 near Baltimore, MD (Peterson et al. 1999), wavyleaf basketgrass [*Oplismenus undulatifolius* (Ard.) P. Beauv., Poaceae] is recognized as a high-risk invasive species by the U.S. Department of Agriculture (DCR 2022; USDA 2012). This perennial rhizomatous grass forms dense carpets in the forest understory that may crowd out native herbaceous plants and inhibit the regeneration of native hardwood trees (Beauchamp and Koontz 2013; Bowen et al. 2020). Seeds may also be an important form of long-distance dispersal for *O. undulatifolius* to colonize new habitats. Flowering spikelets with long awns produce an extremely sticky substance that strongly adheres to animals and other objects that brush past the inflorescence, allowing seeds to be transported over long distances (Beauchamp and Koontz 2013).

Oplismenus undulatifolius continues to spread across the U.S. mid-Atlantic region and has been reported in seven states as well as the District of Columbia (EDDMapS 2023; DCR 2022). Patches of *O. undulatifolius* appear restricted to shady conditions that are characteristic of other congeneric species (Charles-Dominique et al. 2018; Middleton 1998; Scholz 1981; Srivastava and Shukla 2016; Xu et al. 2023). As such, light availability may be a factor limiting the spread and distribution of *O. undulatifolius* within its invasive range (Beauchamp and Koontz 2013). However, how large a role photoinhibition has on invasion success, as well as at what life stage light has a critical influence on the performance of *O. undulatifolius*, remains unexplored. In this study, we focused on performance at the earliest life stage of *O. undulatifolius*, as successful germination is a necessary requirement for subsequent population establishment. Specifically, we (1) characterized the capacity of *O. undulatifolius* seeds to germinate under a range of light levels characteristic of those found in U.S. mid-Atlantic forest understories and (2) evaluated how seed viability changed with seed age.

Materials and Methods

Experimental Conditions

To investigate the effect of light intensity on *O. undulatifolius* germination, we established a range of light levels in a TC2 walk-in growth room (Environmental Growth Chambers, Chagrin Falls, OH) under long-day conditions (16-h light at 22 C/8-h dark at 18 C) and 50% relative humidity. Four photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) levels were created (Table 1) by increasing the number of overlapping shade cloth layers

Table 1. Comparison of light intensity (mean ± SE) in the growth room experimental conditions and representative field locations where *Oplismenus undulatifolius* is established.

Location	Average light intensity ^a μmol m ⁻² s ⁻¹
Growth room shade treatments ^b	
Full exposure	160.83 ± 4.21 a
1 shade layer	39.63 ± 1.43 b
2 shade layers	8.83 ± 0.63 c
3 shade layers	2.46 ± 0.09 c
Field light conditions ^c	
PINE	8.51 ± 0.96 c
POWH	5.80 ± 1.54 c
ANNA	6.13 ± 1.26 c

^aValues are PPFD (μmol m⁻² s⁻¹) measured with a Li-Cor LI-250A photometer. Means followed by distinct letters are significantly different (one-way ANOVA followed by Tukey's HSD post hoc tests, $F(6, 57) = 746.217$, $P < 0.0001$).

^bGrowth room shade treatments were established by increasing the number of overlaid shade cloth layers ($n = 9-12$ measurements in each shade treatment).

^cLight measurements at three sites in Virginia where *O. undulatifolius* occurs: Piney Grove Preserve (PINE; 36.98932°N, 77.04135°W; $n = 15$); Powhatan State Park (POWH; 37.68427°N, 77.91688°W; $n = 8$); and Lake Anna State Park (ANNA; 38.111°N, 77.831°W; $n = 2$).

(Gemplers, Janesville, WI) suspended by PVC pipe structures constructed within the shelving system of the growth room, such that the top and all four sides of each shelf were enclosed with the shade cloth. PPFD was measured using a Li-Cor LI-250A light meter, LI-190R quantum sensor, and 2003S mounting and leveling fixture (Li-Cor Biosciences, Lincoln, NE). We conducted field surveys of light intensity in June 2021 to determine how these experimental light levels in the growth room compared with conditions in the field (Table 1). Light intensity was sampled at three sites in Virginia (Piney Grove Preserve, $n = 15$; Powhatan State Park, $n = 8$; and Lake Anna State Park, $n = 2$) in established *O. undulatifolius* populations (EDDMapS 2023; DCR 2022). Our two lowest light levels in the growth room were consistent with those found in the field (one-way ANOVA followed by Tukey's HSD post hoc tests, $F(6, 57) = 746.217$, $P < 0.0001$ for light treatment, $P > 0.05$ for three field sites and two lowest light treatments; Table 1).

Seed Source

We germinated seeds from five collection years under four light levels to determine whether seed viability varied with age or light conditions. *Oplismenus undulatifolius* seeds were collected by Vanessa Beauchamp (Towson University, Towson, MD) from the Woodstock region of Patapsco Valley State Park, MD (39.333222°N, 76.782965°W) in 2011, 2012, 2013, 2015, and 2020. We used seeds from this location, because it is the site of first identification (Peterson et al. 1999) and thus may have the most potential for genetic and phenotypic variability. Preliminary studies suggest somewhat greater allelic diversity and heterozygosity in this population than in two more recently established locations (Wu et al. 2018), but how this compares with populations in the native range is currently unknown. Seeds were stored in paper bags at room temperature and ambient humidity after collection, and seed glumes were removed before the experiment.

Germination Assays

In summer 2021, seeds were sown on 9-cm-diameter petri dishes containing 20 ml (0.008 g ml⁻¹) sterilized phytoblend agar (Caisson Laboratories, North Logan, UT) in a laminar flow hood to reduce surface contamination. Petri dishes were sealed with 3M

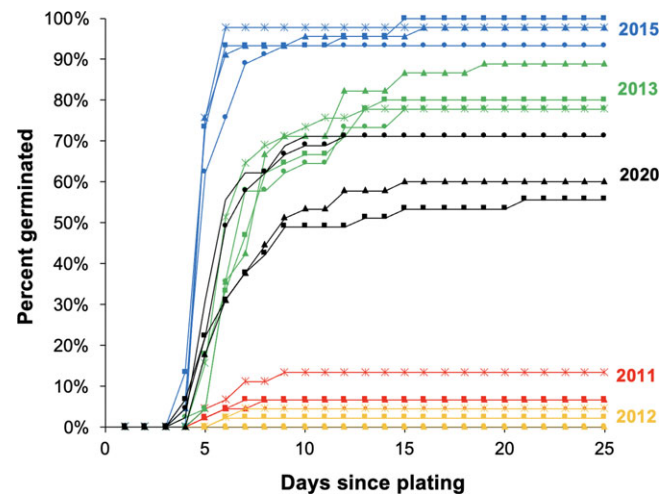


Figure 1. Germination patterns of *Oplismenus undulatifolius* seeds collected in different years (indicated by color) under four light levels for 25 d. Lines indicate total percentage of seeds germinated across three replicate plates for each collection year × light level combination. Light levels: ●, 0 shade layers; ▲, 1 shade layer; ■, 2 shade layers; ✕, 3 shade layers.

Micropore Surgical Tape (Nexcare, 3M Health Care, St Paul, MN) to minimize moisture loss while allowing gas exchange. Within a given light level, three replicate petri dishes were established for each collection year. Each petri dish contained 15 seeds from a single collection year, arrayed in a three by five grid pattern. In total, each of the four light levels contained 15 petri dishes (five collection years with three replicates per year).

Seed germination was recorded as the first day of radicle or shoot protrusion and monitored daily for 25 d. When germinants were counted, petri dishes were kept within the shade structures to prevent potential exposure to ambient light from the growth chamber, as short-duration light exposure can stimulate germination in some species (Milberg et al. 1996). Photometer measurements confirmed that accessing petri dishes within the shade structures this way did not expose seeds to detectable changes in light. Total germination was measured as the percent of seeds that successfully germinated for each petri dish. To test for effects of light level and collection year on total percentage of germination, a two-way ANOVA was performed using jamovi software for Windows (jamovi project 2021), after confirming that the data met model assumptions.

Results and Discussion

The capability to germinate under a range of light levels and after years of dormancy may enable invasive plants to persist in a wide range of environmental conditions and aid expansion beyond native niche limits. In this study, we germinated *O. undulatifolius* seeds of five ages under four light levels, using overlapping shade cloth layers to manipulate light intensity. We found similar rates of germination regardless of collection year or light level, with 99% of all seeds that eventually germinated doing so by 15 d after plating (Figure 1).

We found no significant effect of light level (two-way ANOVA, $F(3, 40) = 0.628$, $P > 0.05$) or interaction with seed age ($F(4, 40) = 0.989$, $P > 0.05$; Figure 2; Table 2) on total germination percentage after 25 d, indicating that *O. undulatifolius* seeds may be light indifferent, at least in terms of the light intensities or quantities

Table 2. Two-way ANOVA for effects of light level and seed age on *Oplismenus undulatifolius* seed germination after 25 d under controlled growth room conditions.

Factor	df	SS	MS	F	P
Light level	3	0.015	0.005	0.628	0.601
Collection year	4	9.029	2.257	293.014	<0.001*
Light × year	12	0.091	0.008	0.989	0.476
Error	40	0.308	0.008		
Total	59	9.443			

*Significant treatment effect: $P < 0.05$.

SS = Sum of squares, MS = Mean squares.

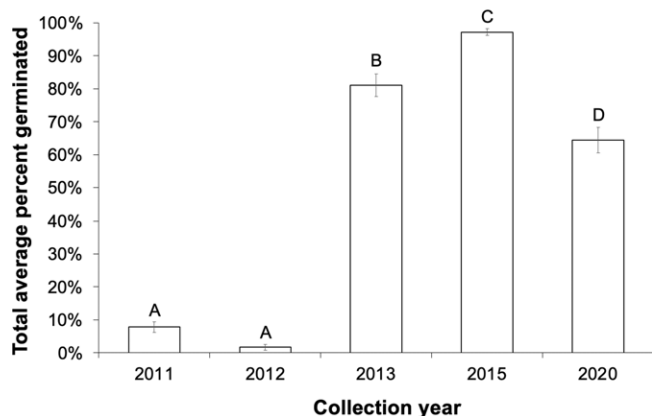


Figure 2. Comparison of total average percent germination in *Oplismenus undulatifolius* seeds collected across years. Means (\pm SE) of percent germinated for all seeds per collection year, pooled across light treatment levels. Bars with unique letters are significantly different from one another ($P < 0.05$). $n = 12$ replicate plates per collection year.

used in our study. This was somewhat unexpected based on characterization of *Oplismenus* as a shade-tolerant genus (Charles-Dominique et al. 2018; Middelton 1998; Srivastava and Shukla 2016). While our experimental low light levels (Table 1) simulated field conditions, the two high light levels (160.83 and $39.63 \mu\text{mol m}^{-2} \text{s}^{-1}$) were much brighter than typical conditions we measured at locations within Virginia forest understories where *O. undulatifolius* is currently found. However, these brighter conditions may be more typical of light conditions that seeds could encounter in light gaps or forest edges near established patches. Thus, *O. undulatifolius* may be physiologically capable of at least initially colonizing a wider range of light environments than predicted based on observed patch distributions, but does not persist in those locations due to poor competitive ability in those open habitats (Grime 1977; Kepner and Beauchamp 2020; Liancourt et al. 2005). Future studies on the effect of different light conditions on subsequent life stages are imperative to predict its potential geographic distribution in the invaded range for effective monitoring and management (Cheplick 2005; Qi et al. 2014; Svriz et al. 2014; Warren et al. 2011).

We expected to see negative photoblastism in *O. undulatifolius* seeds, based on predictions that light availability restricts the distribution of this species (Beauchamp and Koontz 2013). However, our finding that germination percentage did not differ across the four light levels is not unusual among photoblastism studies with invasive plants (Ebrahimi and Eslami 2012; Greenberg et al. 2001; Tinoco-Ojanguren et al. 2016). For example, light intensity did not affect the proportion or timing of germination in

the invasive vine Oriental bittersweet (*Celastrus orbiculatus* Thunb.), although seedlings could also establish in dense shade and grow rapidly when exposed to high light conditions (Greenberg et al. 2001). Indeed, numerous introduced plant studies identified positive photoblastic seeds that exhibit an increase in germination when exposed to high light conditions, which may enhance performance in disturbed areas (Bittencourt et al. 2017; Cervera and Parra-Tabla 2009; Lamsal et al. 2019; Leal et al. 2013; Mwendwa et al. 2020; Qi et al. 2014). However, germination requirements and shade tolerance at later life stages may be uncoupled (Figueroa and Lusk 2001). As such, additional studies are warranted to understand whether the observed germination indifference to light intensity is more broadly characteristic of invasive shade-tolerant grasses like *O. undulatifolius*.

Seeds may respond differently to various aspects of light environments (Lindig-Cisneros and Zedler 2001; Veldman and Putz 2010). For example, invasive canarygrass (*Phalaris arundinacea* L.) seeds displayed positive photoblastism to light quality (photon irradiance: white and red light) and quantity (no germination in the absence of light) but were light indifferent to photoperiod (Lindig-Cisneros and Zedler 2001). Thus, while our results suggest *O. undulatifolius* may be insensitive to light quantity across our experimental light levels, other attributes of light known to promote germination in some species, such as absorption of red light or photoperiod regimes, could be more important cues to break dormancy or release nondormant seeds from quiescence (Baskin and Baskin 1998; Baskin and Baskin 2004; Bhatt et al. 2020; Han et al. 2022; Mathews 2006). Likewise, other abiotic factors known to influence germination, such as temperature and salinity, may also act as potential environmental filters constraining the establishment of *O. undulatifolius* in the invaded range at the seed stage (Bangle et al. 2008; El-Keblawy and Al-Rawai 2005; Ottavini et al. 2019; Tinoco-Ojanguren et al. 2016).

Introduced species are often exposed to novel climatic conditions in their new ranges or released from competitive biotic constraints encountered in their native ranges. Rapid evolutionary change in response to these new local conditions may facilitate expansion of introduced species beyond conditions characteristic of their native range, particularly when population differentiation follows climatic gradients in the introduced range (Blossey et al. 2017; Quiroga et al. 2018; Zhang et al. 2022). Indeed, recent studies have found evidence of population differentiation in seed germination requirements of invasive Johnsongrass [*Sorghum halepense* (L.) Pers.] (Fletcher et al. 2020) and garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavare & Grandel] that suggests adaptive shifts in the germination niche that maximizes germination across the invaded North American ranges. Similarly, the realized niche of *O. undulatifolius* may be expanding in North America to include sunlit environments previously thought to be unsuitable based on distribution in its native range. Although light conditions in the field can vary within a single day, this study demonstrates that *O. undulatifolius* has the capacity to germinate in continuous shade as well as under extended exposure to high light intensity. Hence, our results suggest *O. undulatifolius* may also be able to successfully germinate in the field under much brighter conditions than forest understories typical of where it has already been detected in the U.S. mid-Atlantic. Additional studies are needed with seeds sourced from populations spanning the current geographic range, as well as from different microsites (e.g., deep forest understory vs. peripheral patches at forest edges) to test for adaptive changes in germination response to light environment across the invaded range.

We found that some seeds from all collection years successfully germinated under each light level, albeit with varying levels of success (Figure 1). Although total germination differed across collection years, that is, with seed age, at least one seed from each collection year showed successful protrusion of a radicle or shoot. Thus, *O. undulatifolius* seeds are capable of remaining viable for at least 9 yr after storage in standard laboratory conditions. We also found a significant effect of collection year on total germination percentage (two-way ANOVA, $F(4, 40) = 293.014$, $P < 0.001$; Figure 2; Table 2), with germination percentage of seeds collected from 2011 and 2012 significantly lower than that of the younger seeds (Tukey's HSD post hoc test, $P < 0.001$; Figure 2). While the decrease in seed germination in these two seed age groups could be an artifact of maternal effects, temperature and precipitation in 2011 and 2012 were not notably different from the other collection years in the geographic region from which these seeds were sourced (Supplementary Table S1). Similarly, seed storage conditions are unlikely to have influenced relative differences in germination percent across collection years, as all seeds were collected and stored under comparable conditions. These results suggest a potential for high seed viability in *O. undulatifolius* for approximately 7 yr, at least under laboratory storage conditions.

Seed longevity has been found to vary widely across invasive plants (Redwood et al. 2018; Schoeman et al. 2010; Wijayratne and Pyke 2012). While a recent study found seed viability in *A. petiolata* to persist for at least 13 yr in some populations (Blossey et al. 2017), the extended seed viability we observed in *O. undulatifolius* is particularly notable among invasive grasses, many of which show only short-term persistence or transient seedbanks (Humphries and Florentine 2022; Martins 2006; Redwood et al. 2018; Williams et al. 2016). Certainly, our seed storage conditions undoubtedly influenced seed longevity estimates. Laboratory storage is generally more benign compared with soil conditions, where seeds are exposed to complex interacting factors and stochastic events such as risk of predation, infection, and intolerable environmental conditions (Dantas-Junior et al. 2018; Long et al. 2015; Redwood et al. 2018; Wijayratne and Pyke 2012). Even under laboratory settings, loss of viability generally occurs more rapidly under room temperature conditions (as used in this study) than refrigeration (Solberg et al. 2020). However, many members of the Poaceae exhibit relatively short-term viability across different laboratory storage strategies (Solberg et al. 2020), so our observed 7-yr seed viability of *O. undulatifolius* is indeed notable. Additionally, other longevity studies (Bangle et al. 2008; Blossey et al. 2017; Humphries and Florentine 2022; Solberg et al. 2020) also use seed storage at room temperature, and thus provide reasonable comparisons for the observed seed longevity in *O. undulatifolius*. While storage under laboratory conditions may not simulate the full environmental complexity seeds experience in the field, it still provides a useful first assessment of seed longevity. It would be interesting to explore whether this lengthy seed viability in *O. undulatifolius* persists under field conditions. Nevertheless, long-term monitoring and management of *O. undulatifolius*-infested sites may be warranted for up to 7 yr or more, when the potential for successful germination remains high.

Based on the long duration of seed viability under laboratory conditions, we encourage land and natural resource managers to continue long-term control and monitoring efforts for *O. undulatifolius* even after aboveground removal to detect and treat subsequent seedlings. Furthermore, the observed indifference of *O. undulatifolius* germination to light intensity in this study has important management implications. Because light level does not

appear to be a major constraint on germination, seedling establishment and range expansion may be promoted outside previously expected environmental conditions. Understanding seed responses to environmental conditions, as well as the capacity for long-term dormancy, is necessary when forecasting performance of invasive species that are colonizing new habitats. Considering the capability of *O. undulatifolius* to spread by seed (Beauchamp and Koontz 2013), studies on this life stage are essential to make effective management decisions and predict areas that are at high invasion risk.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/imp.2023.27>

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