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Research Article

Seed germination of the invasive succulent *Kalanchoe delagoensis* (Crassulaceae) under controlled conditions of seed age, temperature and light

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Abstract

Invasive alien species frequently possess seed related attributes that contribute to invasion success, such as environmental tolerance, numerous seeds, longevity, rapid germination, and high germination rates, among others. These traits can enhance propagule pressure, thus having important implications for management. The genus *Kalanchoe* contains species widely used in the horticultural trade, but a few have become invasive around the world. We evaluated the performance of *Kalanchoe delagoensis* seeds of different age to determine the probability of generating a seed bank under dark-light conditions and constant/alternating temperature to assess photoblastic response and seed tolerance to temperature. Seeds were sown following a factorial experiment that comprised four seed ages (5, 8, 11 and 13 months after collection), two temperature conditions (25 °C constant and 16/25 °C alternating), and two light conditions (light and darkness) resulting in 16 experimental treatments with 10 replicates each and 50 seeds per replicate. Seeds were positive photoblastic with no germination under darkness conditions. Final germination percentage ranged from 1.8% to 49.4% among treatments but decreased with seed age and the interaction with temperature. Mean germination time ranged from 4.5 to 10.9 days among treatments. Results suggest that *K. delagoensis* seeds germinate rapidly, and have a neutral response to the 16/25 °C alternating temperature in germinability. Seed viability rapidly decreases within the first year after the reproductive season, suggesting that this species would only form a transient seed bank. Avoiding inflorescence maturation and covering or burying seeds will contribute to the depletion of the seed bank over the short term and could provide adequate control of invasive *K. delagoensis* populations.

Key words: invasive alien species, transient seed bank, photoblastism, chandelier plant, seed viability, germinability

Introduction

Soil seed banks in invasive alien species (IAS) can be seen as a source of propagules that increase the chances of germination and time of persistence at any given site (one component of propagule pressure) and has been shown to be a determinant of naturalization and invasion (Gioria et al. 2021). Even though germination rate alone does not seem to be an indicator of invasiveness, factors that influence germination rate could increase the success of IAS in novel environments (Gioria and Pysek 2017). A suite of seed related attributes (e.g., seed longevity, continuous seed production, large reproductive output) have also been proposed as traits that can lead to invasion success (Baker 1974; Moravcová et al. 2015; Gioria and Pysek 2017). Reproductive output and high germination rates are but two components that constitute propagule pressure of IAS found in soil seed banks (Gioria and Pysek 2017) as well as abundant seed production and quick germination (Guerrero-Eloísa 2017; Díaz-Segura et al. 2020; Navarrete-Sauza and Rojas-Aréchiga 2023).

Germination in IAS would be determined in part by intrinsic (germination rates, synchrony, mean germination time, seed longevity), as well as extrinsic biotic and abiotic factors (availability of safe sites, seed predation, temperature, humidity, salinity, and other abiotic conditions). In addition to the intrinsic and extrinsic traits, the timing of germination in transient or persistent seed banks (< 1 year or more than 1 year, respectively) and the factors (environmental or genetic) that determine germination rates will affect the above ground outcome in vegetation and their interactions over time (Savadogo et al. 2016).

The consequences that seed traits of IAS can have on native vegetation will ultimately determine the possibilities for management. In these terms, soil seed banks add to complexity because management must consider strategies to deplete the seed bank for successful long term restoration efforts (Grewell et al. 2019). For example, an early rain promoting an early germination under inadequate abiotic conditions can limit the amounts of seeds available for subsequent invasion, eventually depleting the seed bank of exotic grass species (Gillard et al. 2022).

Species of the genus *Kalanchoe* are widely used in horticulture, but a few of them have become invasive in a variety of environments worldwide (Wang et al. 2016), including Mexico (González de León et al. 2016; SEMARNAT 2016). Among the species reported as invasive are *K. daigremontiana* (Herrera and Nassar 2009), *K. delagoensis* (Guerra-García et al. 2015), *K. pinnata* (Global Invasive Species Database 2023), and the hybrid *K.* × *houghtonii* (whose parentals are *K. daigremontiana* and *K. tubiflora*) (Herrando-Moraira et al. 2020). In particular, *Kalanchoe delagoensis* Eckl. & Zeyh. is regarded as a weed of difficult control, with noxious effects on native flora and even crops (Sandoval and Martínez 1994; Guerra-García et al. 2018). The very low genetic variation in Mexico suggests that it has spread primarily through clonal growth (Guerra-García et al. 2015). However, infrequent reproductive sexual events are possible, as seeds were found in one population of the Mexican Northeast. Here, we analyze the performance of *K. delagoensis* seeds in order to experimentally determine the probability of generating a seed bank by analyzing both intrinsic and extrinsic factors: by assessing the germination of seeds over time (intrinsic) under controlled conditions and assess the effect of two abiotic, extrinsic factors (light and temperature) on germination.

Materials and methods

Study species. *Kalanchoe delagoensis* is a plant native from Madagascar (Africa) that has become invasive worldwide (Wang et al. 2016) and reported in at least seven states in Mexico (Guerra-García et al. 2015). It is a biennial or short-lived perennial, with simple, slender, cylindrical stems that are usually 1 m tall (Hannan-Jones and Playford 2002; Wang et al. 2016). Reproduction is mainly clonal by producing plantlets (pseudobulbils) at the apex of the leaves (Hannan-Jones and Playford 2002). Flowers are tubular, numerous, with a red to scarlet coloration. *Kalanchoe* species usually flower during winter in their native range (Smith et al. 2023) and in the Tamaulipas (TAMP) population, inflorescences have been observed from late October to January, whereas in the Queretaro (QRO) population from late November to mid-January (CM-P and MC-M *pers. obs.*). Fruits have been observed in February in the QRO population, when seed dispersal begins (K. Ortega and MC-M *pers. obs.*).

Seed collection. We collected post-anthesis inflorescences to search for seeds in two populations from two Mexican states: Querétaro (QRO, 20°41′14″N; 99°48′16″W) in February 2009 and Tamaulipas (TAMP, 22°56′53″N; 99°48′16″W) in March 2010 and 2011. The QRO population was located within the grounds of the Botanical Garden "Ing. Manuel González de Cosío", in the municipality of Cadereyta. This location occurs at the southern end of the Chihuahuan Desert. Vegetation is a xerophilous scrubland, with hot semi-dry climate and summer rains (BS1 kw). Mean annual temperature ranges from 16 °C to 19 °C, and annual precipitation is 550 mm (INEGI 2017a). The TAMP population was located in a secondary xerophytic scrubland, dominated by *Prosopis laevigata*, *Larrea tridentata*, *Jatropha dioica*, and *Castela* sp. Other invasive species in the area are *Kalanchoe daigremontiana* and *Aloe vera*. Climate in the TAMP population is semiarid (BS0hw), with a mean annual temperature between 20 and 22 °C, and annual precipitation of less than 500 mm (Martínez-Ávalos and Suzán-Azpiri 2000; INEGI 2017b). Between 30 and 70 post-anthesis inflorescences from different individuals were collected at each population, inflorescences were dissected in search of seeds inside the carpels. Seeds were found in only one population (TAMP, March 2011) consistent with the lack of seeds reported by Guerra-García et al. (2015). During the first week after collection, seeds were separated from plant debris and stored inside paper bags under laboratory conditions (20 ± 2 °C) until experiments initiated 5 months after harvest.

Germination experiments. An experiment under controlled conditions was set up with seeds sown in Petri dishes with 1% bacteriological agar (BIOXON), placed inside a transparent plastic bag in an environmental chamber (Lab-

Line Instruments, Inc., model 844L, IL, USA). The experiment covered a 13-month period to assess how seed germination changed with seed age after collection (5, 8, 11, and 13 months). In addition to seed age, at each germination event (5, 8, 11 and 13 months), temperature and photoblastism were tested. Temperature consisted of two levels: a constant temperature of 25 °C and an alternating temperature (25/16 °C), both with a 12 h photoperiod. Finally, for the light treatment, Petri dishes received the white light from the germination chamber or were kept in complete darkness by covering the Petri dish with two layers of aluminum foil and checked only at the end of the experiment (40 days). This factorial design resulted in 16 treatments (4 age treatments, 2 light conditions, and 2 temperature conditions), each treatment consisted of 10 replicate Petri dishes, each one containing 50 seeds for a total of 8,000 seeds. Petri dishes were checked for germination every second day for 40 days, except for those in the darkness treatments. Germination was considered when the radicle emerged from the seed cover. In order to detect if any seeds that did not germinate under dark conditions maintained the potential to germinate when they were then exposed to light. Petri dishes under the darkness condition were uncovered after 40 days, and seeds were monitored every other day for a further 28.

Data analyses. Final germination percentage and mean germination time (MGT) were obtained using "GerminaQuant for R" (Lozano-Isla et al. 2019). "GerminaQuant for R" is based on the packages GerminaR (Lozano-Isla et al. 2019) and Shiny (Chang et al. 2020), and were run using R 4.2.2 (R Core Team 2022). Mean germination time measured the time taken for a group of seeds to germinate (Kader 2005), and thus provided a measure of the speed of germination. Final germination percentage and mean germination time were analyzed with a two-way ANOVA, having seed age (four levels) and temperature (two levels) as factors with the seeds from the light experiment as none of the seeds under the darkness treatment germinated. Comparisons among the eight treatments were followed up with a Tukey *post hoc* test. Final germination percentage and mean germination time of seeds under darkness and subsequently exposed to light were also analyzed with a two-way ANOVA, with seed age and temperature as factors. We decided to analyze seeds under light and under darkness separately since the period that seeds were imbibed was longer for the darkness treatment, and results were not necessarily comparable.

Results

Seeds were clearly positive photoblastic as no germination was found in the darkness treatment. Final germination percentage of seeds under the light treatment ranged from 1.8 to 49.4%. According to the two-way ANOVA, seed age negatively influenced final germination ($F_{(3,72)} = 71.837$, $P < 0.001$), as well as the interaction between seed age and temperature ($F_{(3,72)} = 4.207$, $P = 0.008$), but temperature solely did not affect final germination ($F_{(1,72)} = 1.956$, $P = 0.166$).

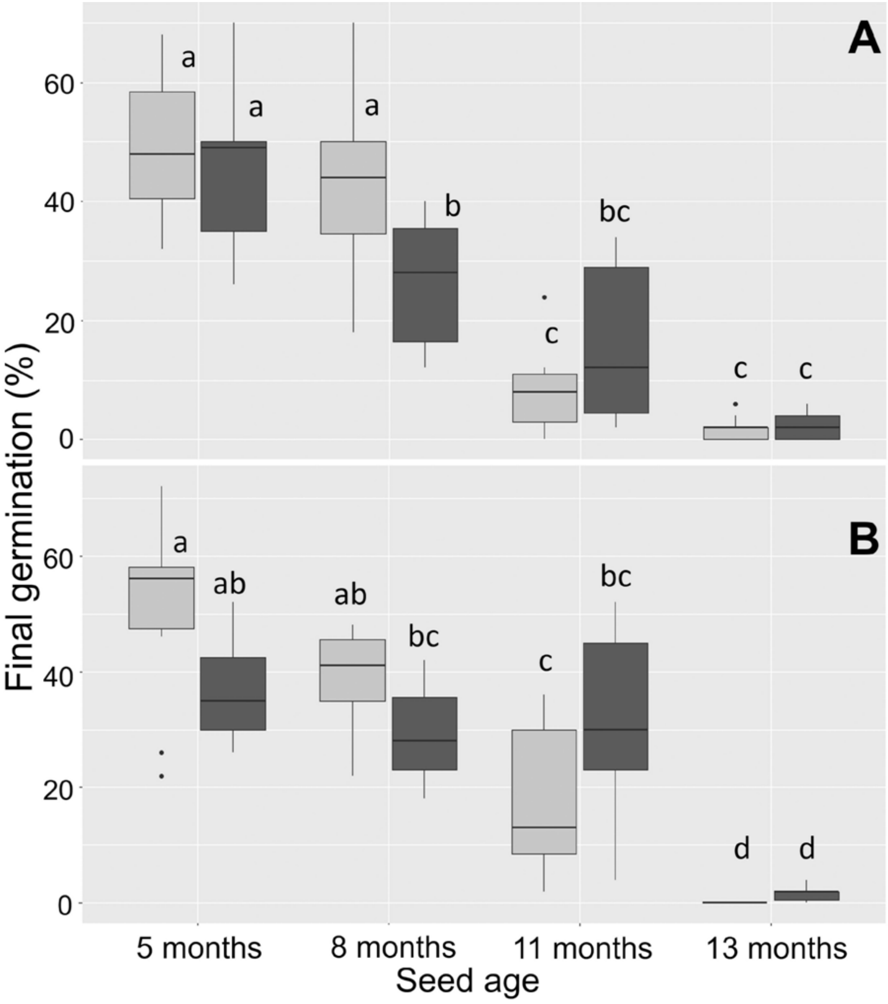

Figure 1. Mean germination percentage of *Kalanchoe delagoensis* seeds under controlled conditions of light, seed age, and temperature. Seeds were sown under light (A) and darkness; seeds under darkness were exposed to light after 40 days of darkness (B). Seeds were sown at four different times after seed collection (Seed age), and under two temperature regimes (light gray = constant temperature, dark gray = alternating temperature). Different letters denote significant differences according to *post hoc* Tukey comparisons.

This represents a loss of 45% in mean germination between youngest and oldest seeds in the experiment over an 8-month period. The highest germination percentage was found for 5 months-old seeds under constant temperature (49.4 ± 3.628%, mean ± s.e.), but decreased significantly with age for 13 months-old seeds under constant temperature to 1.8 ± 0.629% (mean ± s.e.) (Figure 1A). There were significant differences between temperature treatments only for 8 months-old seeds, which accounted for the interaction of the two-way ANOVA (Figure 1A). These results indicate that age is a key factor in the final germination rate, and seeds lose the potential to germinate in a little over a year, increasing the likelihood of a transient seed bank.

Mean germination time of seeds ranged from 4.512 ± 0.074 days (mean ± s.e.) to 10.904 ± 0.225 days across treatments. Germination time of seeds was quick, since the mean germination time in all treatments took 11 days or less but effects were found for age and temperature. Mean germination

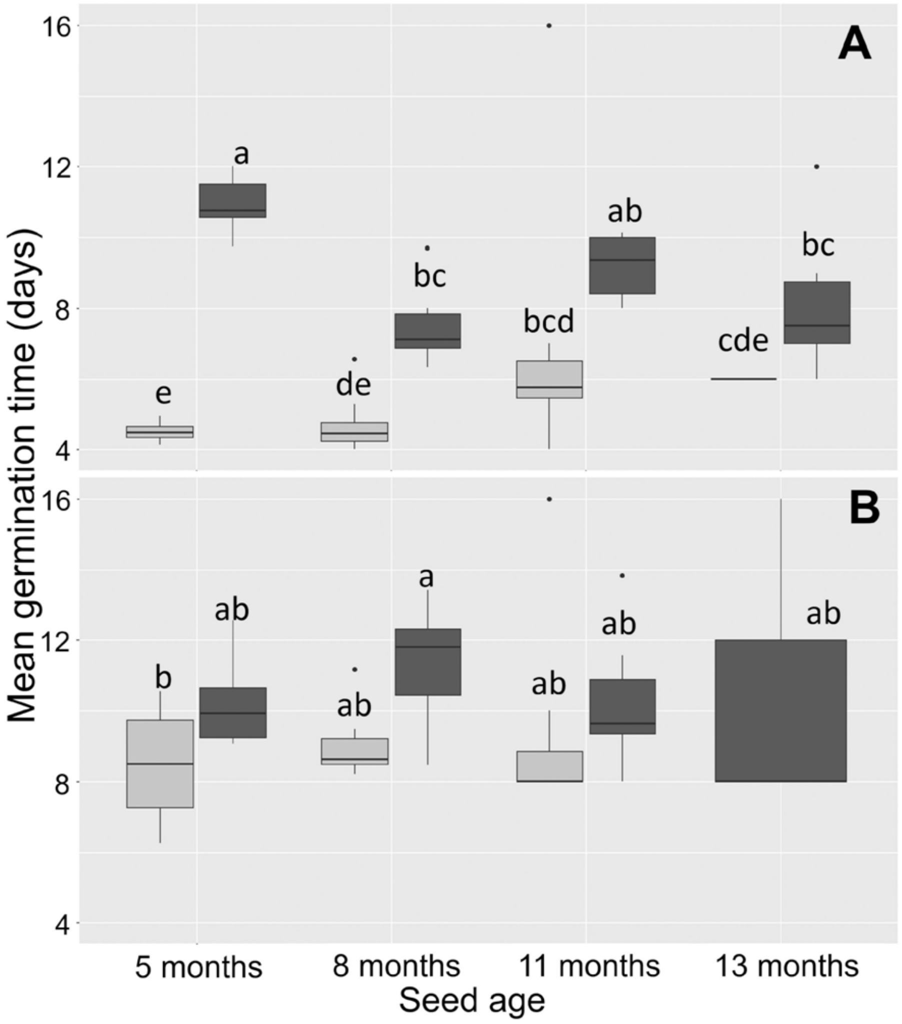

Figure 2. Mean germination time of *Kalanchoe delagoensis* seeds under controlled conditions of light, seed age and temperature. Light grey = constant temperature, dark gray = alternating temperature. Seeds under light conditions (A) and exposed to light after 40 days of darkness (B) Different letters denote significant differences according to *post hoc* Tukey comparisons.

time was significantly different according to age ($F_{(3,72)} = 40.47$, $P < 0.001$), temperature ($F_{(1,72)} = 94.896$, df = 1, $P = 0.002$), and the age × temperature interaction ($F_{(3,72)} = 7.614$, df = 3, $P < 0.001$). Seeds under the alternating temperature tended to have a consistent delayed germination time across seed ages, with a significant difference between temperature treatments of 5 months-old and 8 months-old seeds (Figure 2A). However, as seeds became older, differences in germination time across treatments were less pronounced (i.e., among seed ages of 11 and 13 months, where differences between temperature treatments were non-significant). These results indicate that alternating temperatures delayed germination in younger seeds, but its effect seemed to diminish as seeds aged.

Seeds under the darkness condition did not germinate at all; however, when exposed to light, germination was triggered, which supports the hypothesis that seeds are positive photoblastic. Final germination percentages were similar to those under the light condition (range = 0–50.6%) (Figure 1B).

According to the two-way ANOVA, age and the age × temperature interaction affected final germination ($F_{(3,72)} = 62.130$, $P < 0.001$, and $F_{(3,72)} = 7.284$, $P < 0.001$, respectively), but temperature by itself did not ($F_{(1,72)} = 0.744$, $P = 0.391$). Mean germination time of these seeds ranged between 4.51 ± 0.07 to 10.9 ± 0.23 days (Figure 2B). Only temperature accounted for significant differences in mean germination time among treatments ($F_{(1,72)} = 11.664$, $P = 0.001$); neither age nor age × temperature interaction influenced significatively mean germination time ($F_{(3,72)} = 0.744$, $P = 0.530$ and $F_{(1,72)} = 0.613$, $P = 0.545$, respectively). Seeds that were exposed to light after darkness responded similarly as seeds under light: percentage of final germination diminished as seed age increased, and the interaction of seed age and temperature also affected final germination, but not temperature. These results indicate that seeds that were under darkness and imbibed, increased the period that remained viable and capable of germinate after being sowed (at least 40 days, that was the period that comprised the experiment of darkness). Mean germination time in seeds exposed to light after darkness was reduced, less variable, and was affected only by temperature, compared with seeds under the light treatment (Figure 2). This response of a reduced germination time suggests that seeds could have been imbibed during the darkness period, and when exposed to light, were primed to germinate and germinated faster.

Discussion

We found that seeds of the highly clonal *K. delagoensis* have moderate rates of germination under controlled conditions of seed age, light, and temperature. Seeds of *K. delagoensis* were positive photoblastic, as they strictly required light to germinate. The most influential factor in the final germination rate was seed age, as young seeds had the highest percentage of germination and were able to germinate within two days. Alternating temperature solely did not affect germination percentage but delayed it.

Final germination percentage of *K. delagoensis* in our experiment was significantly lower than conspecifics coming from their native range (e. g. *K. daigremontiana* seeds showed from 60 to 80% of germinability under light conditions and temperatures ranging between 15 to 25 °C) (Seed Information Database 2023) and the highly invasive hybrid, *Kalanchoe* x *houghtonii* from Mexico (that showed up to 92% of germinability) (Seed Information Database 2023). However, the percentage of germination we obtained was greater than for other species of the genus from populations in their invasive range. For example, in *K. pinnata* from the tropical dry forest in Veracruz, Mexico, sexual reproduction was extremely low, and a high percentage of the seeds were non-viable (< 4% of viability). In turn, authors estimate that the germination rate of *K. pinnata* seeds was less than 1% (González de León et al. 2016). In South America, final germination of *K. daigremontiana* seeds was only 12% (Herrera and Nassar 2009). A major difference between

K. delagoensis and these two latter congenerics is the frequency of seed production. Seed production has been shown to be infrequent in *K. delagoensis* in Mexico (Guerra-García et al. 2015), and it may soften the high germination rate as a strategy in the invasion process. This variation in germination success could be related to the storage conditions of the seeds, since in those cases of high germination rate seeds were stored under freezing conditions (Seed Information Database 2023), and we stored seeds at 20 ± 2 °C. It could also suggest variation in germination success among populations, as reported for other invasive species (Podda et al. 2018), which is an issue that deserves further exploration.

Many invasive plants produce large numbers of small seeds, that require light to germinate, and are able to germinate rapidly (Wainwright and Cleland 2013; Gioria and Pyšek 2017). Seeds of *K. delagoensis* fit in this ruderal syndrome—ruderal plants inhabit areas of low-stress and high disturbance, and have traits that increase colonization ability, such as a high seed production and high rate of vegetative growth, among others (Baker 1974)—as they are small (less than 1 mm) (Hannan-Jones and Playford 2002), numerous, positive photoblastic, and germinate rapidly. Although we were not able to estimate seeds per plant, other studies indicate that *K. daigremontiana* can produce up to 16,000 seeds per plant (Herrera and Nassar 2009), and our field observations indicate that seeds are also profusely produced in *K. delagoensis*. Mean germination time of *K. delagoensis* in all treatments occurred within 11 days or less; this means that germination under field conditions occurs rapidly once seeds have favorable conditions, suggesting a potential advantage of opportunistic germination.

The most influential factor analyzed in the germination of *K. delagoensis* seeds was seed age, that is, the time elapsed from seed collection to seed germination. The youngest seeds of *K. delagoensis* (5-months-old seeds in our experiment) had the highest germination rates suggesting that recently produced seeds would very likely increase seedling availability. Although we did not obtain the germination percentage in freshly collected seeds, it was very likely higher than the one obtained for 5 months old seeds following germination behavior of other exotic seeds (Navarrete-Sauza and Rojas-Aréchiga 2023) that showed no dormancy and high germinability for fresh seeds. Germination decreased significantly with age as seeds with 11 and 13-months gave lower germination percentages, which suggests a loss of viability over a short time period. Since flowering at the site of TAMP began in late October (CM-P *pers. obs.*) and seeds were collected in March at both populations, we infer that seeds were produced between November and February. Inflorescences were collected in February and March, and seeds abundantly fell from them. Thus, seed viability rapidly decreases within the first 13–18 months after seed production. This loss of viability through time was also found in *K. daigremontiana* (Herrera and Nassar 2009). The rapid decline of germination suggests that *K. delagoensis* is more likely to form a transient seed bank (< 1 year) (De Souza Maia et al. 2006). For management purposes, the rapid loss of seed viability indicates that this species has a low probability of forming a persistent seed bank, and hence long-term, sexual propagules do not represent an important component of propagule pressure for the expansion of *K. delagoensis*. Management strategies can rapidly deplete the seed bank within a couple of years if covered with leaf litter or other material to reduce light and the increased time in soil will lead to a loss of viability over time and thus depletion of the seed bank (Abbas et al. 2023).

The alternating temperature of 16/25 °C did not consistently affect germination of *K. delagoensis*, as it diminished germination percentage only in 8-months old seeds and it significantly increased the mean germination time for young seeds. This neutral response of germinability to alternating temperatures indicates that *K. delagoensis* may have the ability to germinate under warm and colder conditions. This ability may contribute to its invasive potential towards tropical and subtropical areas, as reported by Wang et al. (2016). More extreme temperatures could affect germination by delaying time to germinate or diminishing germination (Bhatt et al. 2023). Identifying these lower and upper temperature thresholds for germination can help define the range of temperatures a species will tolerate (Bhatt et al. 2023), and in the case of IAS, the width of its ecological niche.

The positive photoblastic response of *K. delagoensis* seeds supports the fact that it would only form a transient seed bank, as buried seeds that remain more time beneath the soil could not germinate in the absence of light. Other studies on germination of IAS have shown that light is a common requirement, possibly linked to the small seed size (Lamsal et al. 2019; Bhatt et al. 2023). Management of IAS with seed banks has shown to be quite complex and challenging. Given the germination traits found on *K. delagoensis*, a management strategy of populations with seed production should focus on depleting the transient seed bank during the first 18 months after seed production. Seeds in darkness during 40 days and then exposed to light were able to germinate similarly to seeds under light and even quicker, demonstrating that darkness did not induce secondary dormancy so shading patches would only postpone germination. This depletion of the seed bank may involve tossing the soil so that *K. delagoensis* seeds having light germinate continuously during this first year and a half. After germination, an opportune mechanical control of the plants is mandatory, before plants become reproductive and produce seeds to avoid the establishment of plantlets through asexual reproduction (Guerra-García et al. 2018; Arroyo-Cosultchi et al. 2022).

Germination traits that would contribute to the process of invasion of *K. delagoensis* are the profuse seed production, the high germinability of young seeds, and the rapid germination. In contrast, viability of seeds during a year and a half, as well as the limited events of sexual reproduction, are factors that certainly restrict the recruitment of individuals to populations through seeds and reduce genetic variation. The finding of seeds of *K. delagoensis* has been extremely rare in Mexico (Guerra-García et al. 2015). We lack information on the mating system of the species, in order to know whether the seeds are the product of cross-pollination or selfing, or if pollinator services are required at all to set seeds. Our finding of *K. delagoensis* seeds in this Mexican population suggests that sporadic events of sexual recruitment may occur in the invasive range of the species. In contrast with other *Kalanchoe* species with low germination rates, we found that *K. delagoensis* seeds reach high percentages of germination when they are young. However, these results may vary across the invasive range of *K. delagoensis*, or in comparison with populations in its native range, as found in other invasive plants (Podda et al. 2018). Further studies that incorporate mating system, pollinators, and dispersal strategies, which incorporate more populations as well, are needed in order to have a more comprehensive scenario of the sexual strategy of this invasive species and provide information for a better future management of its populations.

Authors' contribution

CMP – investigation and data collection, data analysis and interpretation, writing original draft; AVHG – investigation and data collection; MRA – sample design and methodology, data analysis and interpretation, writing original draft; MCM – review and editing; JG – research conceptualization, sample design and methodology, funding provision, writing original draft, review and editing.

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