

Research Article

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Unraveling the influence of environmental factors on fireweed (*Senecio madagascariensis*) germination and its management implications

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Abstract

Fireweed (*Senecio madagascariensis* Poir.) has invaded and colonized numerous habitats in the coastal areas of southeastern Australia and is a major weed in cultivated lands as well as in poorly grassed, neglected, and highly grazed pastures. To examine the seed germination ecology of two populations (Felton and Gatton) of *S. madagascariensis*, experiments were conducted in the laboratory and screen house. The germination of both populations increased as the alternating temperatures increased from the coolest temperatures (15/5 C) to warmer temperatures (25/15 C). However, the highest temperature regime (35/25 C) resulted in the lowest germination rates. The Gatton population exhibited greater tolerance to higher temperatures, resulting in significantly higher germination (2.4 times) than the Felton population at the highest alternating temperature of 35/25 C. Compared with the Felton population, the Gatton population demonstrated higher tolerance to salt and water stress. In comparison to alternating light and dark periods (12 h each) (97% to 98%), the germination of both populations of *S. madagascariensis* was significantly reduced under complete darkness (24 h) (33% to 39%). A screen house seed burial depth experiment revealed similar emergence of *S. madagascariensis* seedlings between the populations. The maximum emergence (60%) was observed for seeds placed at the soil surface, followed by a dramatic decline in seedling emergence with an increase in depth. No seedlings emerged from a burial depth of 4 cm. With the addition of wheat (*Triticum aestivum* L.) crop residue to the soil surface at rates comparable to 4,000 to 8,000 kg ha⁻¹, seedling emergence of *S. madagascariensis* decreased significantly. Information acquired from this study could be utilized to manage and develop effective weed management strategies for controlling *S. madagascariensis* in different agroecological conditions.

Introduction

Fireweed (*Senecio madagascariensis* Poir.) is a short-lived herbaceous plant native to Madagascar and southern Africa and is known for its strong competition with pasture species. It is poisonous to livestock (particularly cattle and horses) due to the production of pyrrolizidine alkaloids that can cause liver toxicity (Gardner et al. 2006). This invasive plant has spread to several countries, including Australia, Argentina, Brazil, Colombia, Japan, Kenya, Uruguay, the United States, and Venezuela (Egli and Olckers 2017).

In Australia, *S. madagascariensis* was initially discovered in Raymond Terrace, NSW, in 1918 (Radford 1997). It was later found in the Bega Valley, about 650 km south of Raymond Terrace (Sindel et al. 1998). Currently, *S. madagascariensis* is widespread in certain areas of southeastern Queensland, with Logan City, Gold Coast City, and Scenic Rim Regional councils experiencing the worst infestations (Csurhes and Navie 2010). According to climate-based modeling (CLIMEX), the potential range of *S. madagascariensis* could expand farther north into coastal central Queensland and upland areas of the Atherton Tableland in northern Queensland (Csurhes and Navie 2010).

Senecio madagascariensis is known for its rapid growth, high seed production, and efficient seed dispersal (Wijayabandara et al. 2022). On average, a single plant can produce about 230 blooms, with each blossom containing 80 seeds, resulting in a total of 18,000 seeds per plant (Sindel 1986). The seeds have no or a very low level of dormancy. It may quickly spread into various ecosystems through multiple dispersal modes such as wind (Watson et al. 1994), humans and animals, agricultural practices of movement of hay (Sindel et al. 1998), and so on. The seeds are easily dispersed by wind due to being small and lightweight, and aided by a pappus of white hairs (Daniel 1984). Under laboratory storage conditions, seeds can remain viable for up to 5 yr (Alonso et al. 1982).



Management Implications

Senecio madagascariensis (fireweed), which originated from Madagascar and southern Africa, poses a threat to pasture species due to its competitive nature. It is toxic to livestock and has spread to various countries, including Australia. *Senecio madagascariensis* reproduces rapidly, with each plant producing thousands of seeds easily dispersed by wind, animals, and human activities. Control methods primarily involve herbicides. Developing integrated management strategies requires a thorough understanding of weed ecology and biology. Experiments were conducted to assess the impact of environmental factors on the germination and emergence of two *S. madagascariensis* populations (Felton and Gatton). Key findings include:

- Optimal germination occurred at 25/15 C, decreasing at higher temperatures. The Gatton population exhibited higher germination rates at the highest temperature.
- The Gatton population demonstrated greater tolerance to salt and water stress compared with the Felton population.
- Seedling emergence decreased with burial depth, with no emergence at the 4-cm depth.
- Addition of wheat (*Triticum aestivum* L.) crop residue significantly reduced seedling emergence.

These findings suggest that understanding seed germination ecology can aid in developing effective weed management strategies. Higher germination rates in the Gatton population indicate potential differences in population dynamics and adaptation to environmental conditions. Knowledge of seedling emergence from various depths and under crop residue cover can inform site-specific management practices for *S. madagascariensis* control in diverse agroecological conditions.

In various soil types and habitats, *S. madagascariensis* can develop different growth habits with different leaf shapes (Ramadan et al. 2010). It is an adaptable weed that spreads quickly into new regions (Sindel 2009). *Senecio madagascariensis* prefers to grow along roads, in animal feeding sites, and near dams and other moist locations (Sindel and Coleman 2012). It can also be found in meadows, riverbanks, and improved grasslands (Bartle et al. 2013). *Senecio madagascariensis* can grow in a range of soil types, including sands and limed soils, but it thrives in well-drained, noncompacted, and fertile soils (Sindel 2009; Sindel et al. 1998).

Various herbicides (e.g., glyphosate, 2,4-D, MCPA, tebutiuron, dicamba, bromoxynil, triclopyr, metsulfuron-methyl, fluroxypyr + aminopyralid, and triclopyr + picloram + aminopyralid) can be used to control *S. madagascariensis* plants (Wijayabandara et al. 2022); however, plants should be sprayed during the early flowering growth stage, which occurs during April (autumn) in Australia, and follow-up treatment is often necessary after 6 mo (Sindel and Coleman 2012). Only limited success has been attained in the biological control of *S. madagascariensis* (Egli and Olckers 2015, 2020; Fynn et al. 2019; Krushelnycky et al. 2018; MaFadyen and Morin 2012; Ramadan et al. 2010). Hence, integrated management of *S. madagascariensis* should be adopted in different regions and seasons.

One must have a good understanding of weed biology and ecology to design an effective weed management program. Studies on seed germination ecology provide important information about

weed emergence, establishment, and seedbank dynamics, knowledge that is vital for any successful weed control program (Chauhan and Johnson 2010; Mahajan et al. 2021). Seed biology knowledge is necessary for developing plant simulation models and implementing an effective weed control program (Nonogaki 2017). Several factors, such as temperature, moisture, light, soil salinity, and burial depth, are known to affect seed germination (Mahajan et al. 2021; Taylorson 1987). To effectively control any weed, accurately estimating when weed seeds will germinate can greatly improve the timing of integrated practices.

Temperature plays a vital role in regulating the timing and speed of seed germination, making it one of the most crucial environmental factors (Baskin and Baskin 1998; Bradford 2002). By influencing seed physiology and breaking dormancy, ambient temperature can affect a seed's ability to germinate. As a result, different weed species and different populations within a weed species exhibit varying behaviors in seed germination and emergence due to their specific temperature requirements (Chauhan et al. 2006a; Presotto et al. 2014; Singh et al. 2021). In New South Wales, Australia, the highest germination rates of *S. madagascariensis* were observed between 15 and 27 C, with significantly reduced germination at lower and higher temperatures (Nelson and Michael 1982). Given that constant temperatures are rare in nature, it is crucial to assess how alternative temperature ranges affect the germination of this weed species. Currently, there is a lack of information regarding the optimal germination temperature range for Queensland populations of *S. madagascariensis*.

Light is a critical environmental factor that influences seed germination (Humphries et al. 2018; Presotto et al. 2014). For instance, common groundsel (*Senecio vulgaris* L.) seeds respond to light and germinate accordingly (Popay and Roberts 1970). Despite the impact of light sensitivity on successful recruitment, many plants exhibit germination that is not dependent on light (Baskin and Baskin 1998). Identifying whether a weed demonstrates positive photoblastic germination allows for the establishment of light-restrictive management techniques, such as mulching with crop residues (Ahmed et al. 2015; Chauhan and Johnson 2008, 2010) or dense crop planting (Bajwa et al. 2016), to efficiently control it. Consequently, retaining crop residues could significantly contribute to an integrated weed management strategy.

When conditions are saline, the salt ions in the soil might impede imbibition by reversing the natural osmotic flow of moisture into the dry seeds. Seed germination of several weed species, such as whitetop or hoary cress [*Cardaria draba* (L.) Desv.] (Rezvani and Zaefarian 2016) and South African lovegrass (*Eragrostis plana* Nees.) (Bittencourt et al. 2017), has been found to be greatly reduced in areas of increased salinity. However, regions at risk will be easier to identify if germination responses to specific soil variables such as salt are known. Such information is not available for *S. madagascariensis*.

Another environmental factor influencing seed germination and dormancy is soil water potential (Baskin and Baskin 1998; Bradford 2002). Weeds that can germinate in environments with severe salinity or moisture stress benefit from these conditions, as they prevent the germination of other species (Altop et al. 2023). Low moisture availability in the soil can prolong the dormancy of seeds, because the amount of water is not sufficient for imbibition (Bittencourt et al. 2017). In Spain, osmotic potentials ranging from 0 to -0.3 MPa showed no differences in their impact on the germination of *S. madagascariensis* (Alonso et al. 1982). Comparable data for Australian populations are limited.

The germination and emergence of weed species can be impacted by the depth at which the seeds are buried. In a study conducted in Spain, seedling emergence of *S. madagascariensis* did not occur from seeds buried below 2 cm (Alonso et al. 1982). Photoreactivity may directly affect the establishment and survival of seeds by influencing the maximum depth of the soil from which germination is permitted (Koller 1964). As burial depth increases, photoblastic seed germination decreases. Species that can germinate without light may also be constrained by increased burial, as was the case with the desert weed white horehound (*Marrubium vulgare* L.) (Florentine et al. 2016). Vertical seed distribution in the soil can be affected by tillage (Chauhan et al. 2006b), and weed population dynamics may be influenced by this varying weed seed distribution in the soil profile as they experience differential temperature and moisture conditions (Buhler 1991). It is possible to make suggestions for tillage depths by determining the burial depth from which weed seedlings cannot emerge (Sindel 2009).

The objectives of this study were to determine the effects of various environmental factors such as temperature, light, salt stress, osmotic stress, burial depth, and mulch, on the seed germination and seedling emergence of two populations of *S. madagascariensis* in Australian conditions. Investigation of the germination requirements and responses of *S. madagascariensis* seeds will enable more targeted and sustainable management approaches to be developed to mitigate the spread of this invasive weed.

Materials and Methods

Site Description

Two Australian populations (Felton and Gatton) of *S. madagascariensis* were selected for seed collection. Felton (27.732°S, 151.737°E) is a rural locality in the Toowoomba Region, QLD, characterized by a warm and temperate climate. Summers are prolonged and warm, reaching temperatures of up to 29 C and occasionally exceeding 32 C. Winters, on the other hand, are brief and cold, reaching lows of around 2 C and occasionally dropping below 0 C (BOM 2023). Gatton (27.555°S, 152.334°E) is a locality in the Lockyer Valley Region, QLD, known for its humid subtropical climate. Summers are lengthy, hot, and humid, with temperatures reaching up to 31 C and occasionally exceeding 35 C. These seasons are characterized by high humidity. Winters are short and mild, with temperatures typically around 4 C and rarely dropping below 0 C, featuring predominantly sunny days (BOM 2023). The distance between the two sites is about 70 km. Mature seed heads (seeds dark in color and starting to disperse from plants) from each site were collected during September 2021 and then bulked to obtain experimental samples of Felton and Gatton populations. Seeds were collected from at least 100 plants for each population, with plants distributed over an area of at least 1 ha for each population. Seeds were manually cleaned (separated mature achenes from their pappus), dried in the shade, and kept in airtight containers at room temperature (25 ± 2 C) until used in the experiments (March to July 2022).

General Seed Germination Test Protocol

To evaluate the effect of different environmental factors on seed germination of *S. madagascariensis*, various germination tests were conducted in 9-cm-diameter petri dishes containing a double layer of filter paper (Whatman® No. 1, Maidstone, UK). Each petri plate

contained 25 seeds, distributed equally, and 5 ml of distilled water or a treatment solution was added. To avoid any water vapor loss, petri dishes were placed inside plastic ziplock bags, and then these bags were placed in temperature- and light-controlled incubators (ICCBOD-300, Laboratory Equipment, Marrickville, NSW, Australia). The fluorescent tubes inside the incubator emitted a white light with an intensity of 85 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Studies on the effects of light, salt stress, and water stress were conducted in an incubator that was set at 25/15 C with a 12-h photoperiod, because this temperature range was found to be optimal for seed germination in the temperature experiment (described in the following section). As there was no germination after 35 d of incubation, the number of germinated seeds was counted at that time, and seeds were deemed to have germinated when the radicle was at least 1 mm in size. All experiments were conducted using a randomized complete block design. Each experiment was conducted twice, and each treatment within a run included three replications (therefore, a total of 150 seeds per treatment). The second run started 1 wk after completion of the first run.

Effects of Temperature on Germination

To evaluate the optimal temperature conditions for the germination of *S. madagascariensis* populations, the effect of five different temperatures in a light (12-h)/dark (12-h) environment was analyzed. The five different temperature regimes were 15/5, 20/10, 25/15, 30/20, and 35/25 C, with one incubator for each temperature regime. These temperature regimes were chosen to reflect the temperature conditions present in Australia's eastern cropping regions at different times of the year.

Effects of Light on Germination

In this experiment, the germination of the two *S. madagascariensis* populations was compared under two conditions: an alternating light (12-h)/dark (12-h) period and complete darkness (24-h) regime. Alternating light/dark-treated seeds were placed in an incubator that was set at 25/15 C with a 12-h photoperiod. For the complete darkness treatment, petri dishes were wrapped with three layers of aluminum foil to ensure that no light penetrated the dishes and then placed in the same incubator as the light/dark treatment.

Effects of Salt Stress on Germination

To measure the impact of salt stress on *S. madagascariensis* germination, 25 seeds of each population were placed in petri plates with 5-ml solutions of 0, 20, 40, 80, 160, and 320 mM sodium chloride (NaCl). The plates were incubated at 25/15 C day/night temperature for 35 d, and then the germination percentage was recorded. These concentration levels were chosen to represent the ranges of soil salinity that exist in different parts of Australia (Rengasamy 2002).

Effects of Osmotic Stress on Germination

To evaluate the impact of water stress on seed germination of *S. madagascariensis*, seeds from both populations were incubated in a wide range of water-deficient conditions, including 0.0, -0.1, -0.2, -0.4, -0.8, and -1.6 MPa. Following the procedure of Michel and Radcliffe (1995), solutions with the necessary osmotic potentials were made using polyethylene glycol 8000 (PEG; Sigma-Aldrich, St Louis, MO 63103, USA).

Effects of Burial Depth on Seedling Emergence

Seeds of both populations of *S. madagascariensis* were used to measure the impact of seed burial depths on emergence. Each 14-cm-diameter plastic pot contained 25 seeds, which were either sown on the top of the soil or at a depth of 0.5, 1, 2, or 4 cm. The pots were kept on benches in a screen house at the Gatton Farms of the University of Queensland. The average maximum and minimum temperatures during the experimental period were 28.7 and 7.0 C, respectively. The soil utilized had a clay loam texture, 2.7% organic matter content, and a pH of 7.2. The soil was passed through a 2-mm sieve and then sterilized to prevent contamination. Control pots without any added seeds were used to ensure that there were no seeds of *S. madagascariensis* in the soil. To maintain an appropriate soil moisture level, pots were regularly subirrigated, and seedlings were only deemed to have emerged when a cotyledon appeared on the soil surface. The trial was terminated at 35 d after seed placement, as no further emergence occurred after that.

Effects of Crop Residue Amount on Seedling Emergence

In the same screen house, 14-cm-diameter plastic pots were used in which 25 seeds of both populations were planted on the soil surface. Chopped, air-dried wheat (*Triticum aestivum* L. 'Spitfire') residue was then spread out at rates equating to 0, 1,000, 2,000, 4,000, and 8,000 kg ha⁻¹. The same soil that was used in the seed burial experiment was used in this experiment. After the experiment began, emerging seedlings were counted at weekly intervals, and the trial was terminated at 35 d after sowing. The results were expressed as a percentage of the seeds sown.

Statistical Analysis

The data were combined across the two experimental runs for further analysis, as ANOVA showed no interaction between the experimental runs and treatments in each experiment (GenStat 21st edition, VSN International, Hemel Hempstead, UK). The degree of significance ($P \leq 0.05$) for each treatment and interactions between factors were determined using ANOVA. Before analysis, the homogeneity of variance and normality of residuals were checked to determine whether there was a need to transform the data. Nontransformed data were used, as data transformation did not enhance the homogeneity of variance. Fisher's protected LSD test was used to separate the means. Graphs were made using SigmaPlot v. 14.5 (Systat Software, Palo Alto, CA, USA).

Results and Discussion

Effects of Alternating Temperature Regimes on Germination

An interaction effect ($P < 0.001$) between day/night temperature regimes and populations was observed for germination (Figure 1). The response of both populations remained similar at 15/5, 20/10, 25/15, and 30/20 C, but diverged at the highest temperature regime (35/25 C). At the lowest alternating temperature regime (15/5 C), 74% and 81% of the Felton and Gatton seeds germinated, respectively. Germination of both populations increased with increasing temperature, reaching maximum germination (98% for Felton and 97% for Gatton) at the alternating temperature of 25/15 C. With further increase in the temperature, germination of both populations decreased, reaching minimum germination of both populations (23% for Felton and 55% for Gatton) at the highest alternating temperature of 35/25 C.

These results reveal that *S. madagascariensis* seeds may germinate under a range of temperature conditions and may

grow year-round in Australia at low altitudes in subtropical and tropical regions due to this capability. The most favorable temperature regime for germination (25/15 C) aligns with previous findings by Nelson and Michael (1982) and Sindel et al. (1998). Their research revealed that the fastest germination of *S. madagascariensis* occurred between 20 and 25 C, with the highest germination rates observed between 15 and 27 C. Starr et al. (1999) also reported that rainfall and occasionally mild, warm temperatures (15 to 27 C) can help *S. madagascariensis* seed germination. They also observed that the ideal temperature range for germination of *S. madagascariensis* was 15 to 27 C, while most rapid germination occurred between 20 and 25 C. In Australia, most seeds of *S. madagascariensis* germinate from March to July (Sindel 1986), but the main germination period is in April (Sindel and Michael 1996). The long-term temperature data of both sites show a similar temperature range (10.2 to 30.4 C for the Gatton and 10.1 to 26.1 C for the Felton sites) from March to May (BOM 2023) and support these results.

At the highest alternating temperature of 35/25 C, germination of the Gatton population was significantly higher (2.4 times) than that of the Felton population, indicating that the Gatton population was more tolerant to high temperatures when compared with the Felton population. However, in contrast to our results, germination of *S. madagascariensis* has been reported to cease at 35 C or above in Australian conditions (Nelson and Michael 1982).

Effects of Light on Germination

Interaction ($P < 0.001$) between populations and light treatments was observed for the seed germination of *S. madagascariensis*. Higher germination of both populations was noted under light/dark conditions as compared with total darkness. The germination percentage of both populations exceeded 95% (98% for Felton and 97% for Gatton) under light/dark conditions (12 h each), which was significantly higher than the germination of *S. madagascariensis* under complete darkness (24 h) (33% for Felton and 39% for Gatton).

Radford and Cousens (2000) reported that germination of *Senecio* species was maximized in the presence of light as compared with dark conditions. Similarly, Figueroa et al. (2010) observed a differential effect of day length on the germination of *S. vulgaris* populations collected from different locations in the United States. Weed seeds that require light for their germination will emerge when near the soil surface, and these weed species may be more common in no-till cropping systems or non-cropped areas where there is minimal soil disturbance (Chauhan and Johnson 2008).

Many researchers have found that several plant species can significantly increase germination when exposed to light, for example, *S. vulgaris* (Popay and Roberts 1970), *Halocnemum strobilaceum* (Pall.) Bieb. (Qu et al. 2008), and musk thistle (*Carduus nutans* L.) (Han and Young 2013). In a Spanish population of *S. madagascariensis*, light was found to be nonessential for seed germination, but it did stimulate germination (Alonso et al. 1982). Our results also indicate that *S. madagascariensis* prefers light for germination, but some seeds can still germinate in darkness.

Effects of Sodium Chloride on Germination

An interaction ($P < 0.001$) between populations and varying salt concentrations was observed for seed germination of *S. madagascariensis* (Figure 2A). Seed germination decreased with

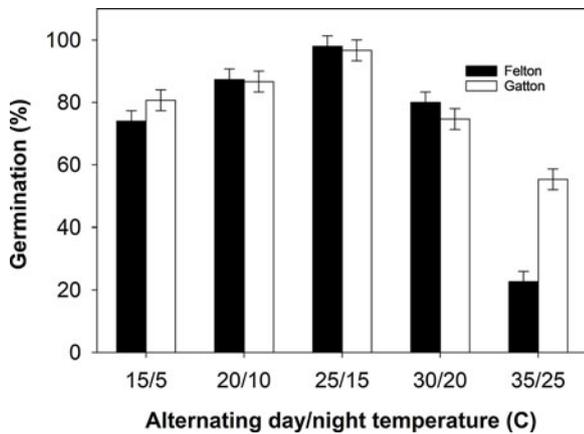


Figure 1. Effect of alternating day (12-h)/night (12-h) temperatures (15/5 to 35/25 C) on the germination of the Felton and Gatton populations of *Senecio madagascariensis*. Vertical bars represent the LSD at 5%.

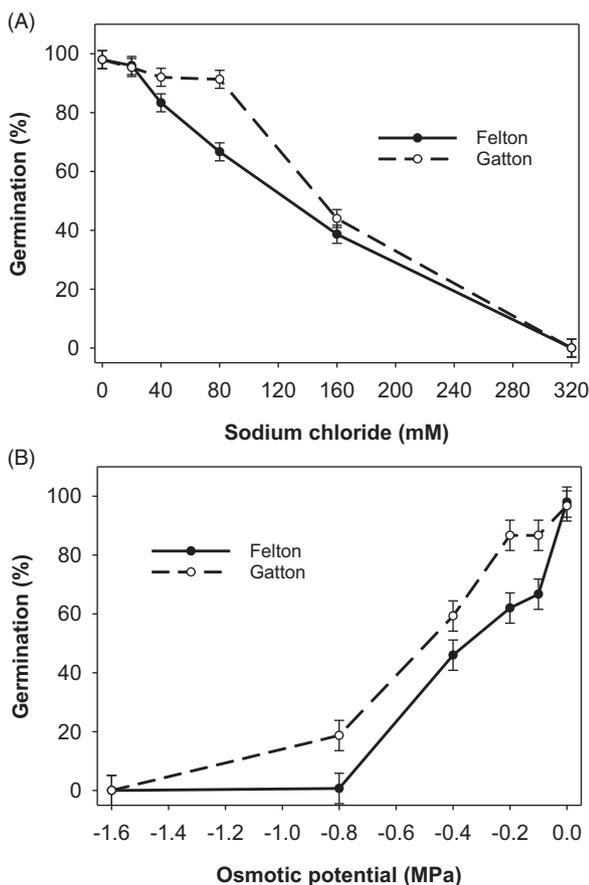


Figure 2. Effect of sodium chloride concentration (A) and osmotic potential (B) on the germination of the Felton and Gatton populations of *Senecio madagascariensis* incubated under alternating light/dark for 35 d at 25/15 C. Vertical bars represent the LSD at 5%.

increasing NaCl concentration from 0 to 320 mM. Both populations germinated similarly (>95%) under the control treatment and at a salt concentration of 20 mM NaCl. As the NaCl concentration increased above 20 mM NaCl, germination of the Felton population was drastically reduced (67%), while the germination of the Gatton population remained unaffected (91%) up to 80 mM NaCl. When the NaCl concentration increased from

80 to 160 mM, significantly lower but similar germination was observed for both populations (39% for Felton and 44% for Gatton), whereas both populations did not germinate at all at 320 mM NaCl.

If the total salt concentration in the soil exceeds 20 mM, then soils are categorized as salt-affected (Abrol et al. 1988). In our study, germination of both populations occurred up to 160 mM NaCl, which suggests that salinity and competition from *S. madagascariensis* may limit crop production, as this weed could grow in highly salinated conditions. Briggs (1978) observed that distinct, geographically isolated forms (topodemes) of *S. vulgaris* from saline sites were more salt tolerant than those from nonsaline habitats.

Osmotic stress and ion toxicity under excessive salinity could affect seed germination (Bliss et al. 1986). Previous research also showed that elevated levels of Cl^- and Na^+ concentrations could affect the process of seed germination, restricting the uptake of essential micronutrients, cellular activity, and energy production (Gupta and Huang 2014). Besides this, osmotic stress, a reaction to an increase in salt content, may change water and nutrient intake as well as hormonal and enzymatic activity in seeds, resulting in poor germination (Thiam et al. 2013). Consequently, in the present study, it is possible that ion toxicity or osmotic stress might have caused germination inhibition at the greatest salt concentration. The results of this investigation suggest that *S. madagascariensis* can colonize those locations that are salt-affected and may further impact crop production.

Effects of Osmotic Potential on Germination

The interaction ($P = 0.002$) between populations and varying osmotic potentials affected the seed germination of *S. madagascariensis* (Figure 2B). In the control treatment (no stress), both populations had similar and maximum germination (>96%). As the osmotic potential decreased below 0 MPa, the germination of the Felton population was drastically reduced, while the germination of the Gatton population remained unaffected up to -0.2 MPa. Significantly lower germination was observed for both populations (46% for Felton and 59% for Gatton) when the osmotic potential decreased further from -0.2 to -0.4 MPa. Additional reduction in the osmotic potential from -0.4 to -0.8 MPa resulted in significantly lower germination of both populations, whereas both populations failed to germinate at -1.6 MPa (Figure 2B). The germination behavior of both populations to water stress was different, and when compared with the Felton population, the Gatton population was found to be comparatively more tolerant of water-stressed situations.

In our study, the highest germination of *S. madagascariensis* in the no-water stress treatment suggests that uniform distribution of rainfall throughout the year in eastern Australia along with irrigated cropping systems could favor the incidence of this weed (BOM 2023). Osmotic potential below -0.2 MPa significantly reduced germination of both populations, which indicates that moist soil is preferred by *S. madagascariensis* for germination. However, Alonso et al. (1982) reported that osmotic potentials ranging between 0.0 and -0.3 MPa did not differ in their effects on the germination of *S. madagascariensis*. They also reported that a sharp decrease in the germination of *S. madagascariensis* seeds occurred due to a decrease in osmotic potential beyond -0.3 MPa.

In the current study, none of the populations germinated at -1.6 MPa; however, at an osmotic potential of -0.8 MPa, the Felton population had negligible germination (<1%), but the

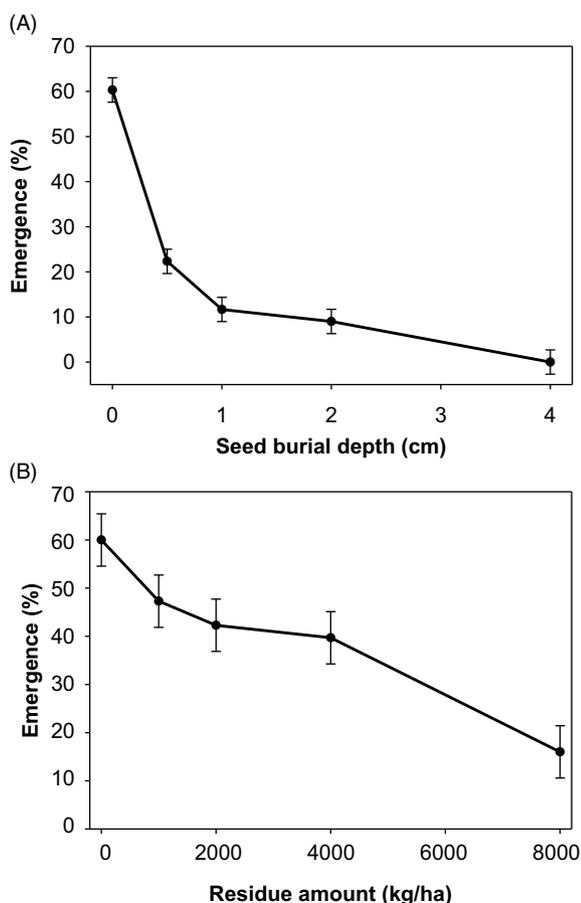


Figure 3. Effect of burial depth (A) and residue amount (B) on the seedling emergence of *Senecio madagascariensis*. Data were averaged across populations. Vertical bars represent the LSD at 5%.

Gatton population had 19% germination. Alonso et al. (1982) also reported that germination of some *S. madagascariensis* seeds occurred at osmotic potentials as low as -1.0 MPa. These results suggest that high osmotic stress (-0.8 MPa) can be tolerated by the Gatton population; thus the Gatton population would have the ability to adapt to water-stressed situations. The ability of the Gatton population to germinate under relatively dry conditions demonstrates that it can survive in dryland agriculture systems, although its germination would be favored by moist conditions that prevail in conservation agriculture systems (Oryokot et al. 1997).

Effects of Seed Burial Depth on Seedling Emergence

Both populations of *S. madagascariensis* exhibited similar ($P > 0.05$) emergence behavior when sown at different burial depths; therefore, the data were averaged across populations (Figure 3A). The emergence of *S. madagascariensis* decreased with the increase in burial depth. More than 60% of *S. madagascariensis* plants emerged when seeds were planted on the surface (0-cm depth). Emergence decreased with an increase in the burial depth from 0 to 1 cm; however, similar emergence was observed at burial depths of 1 and 2 cm. No emergence was observed from the 4-cm burial depth.

The depth from which a seedling emerges may depend on seed size; larger seeds can emerge from greater burial depths due to greater carbohydrate reserves (Baskin and Baskin 1998) as

compared with smaller seeds. Weeds with small seeds, like *S. madagascariensis*, may not emerge from deep burial depths because they may not have enough energy to support hypocotyl elongation. Boyd and Van Acker (2003) also reported that seedling emergence in several weed species decreased due to an increase in burial depth. Four species of *Amaranthus* were studied for the impact of their seed size on emergence; the lightest species (spiny amaranth [*Amaranthus spinosus* L.]) had an ideal burial depth that was noticeably shallower than the heaviest species (slender amaranth [*Amaranthus viridis* L.]) (Hao et al. 2017). For many small-seeded weed plants, emergence decreases with an increase in burial depth (Mahajan et al. 2018; Manalil et al. 2018), because it takes more energy to reach the soil surface. Hence, seeds that are buried deep in the soil profile have low success rates of emergence and establishment. African mustard (*Brassica tournefortii* Gouan), cheese weed (*Malva parviflora* L.), and annual sowthistle (*Sonchus oleraceus* L.) had similar seedling recruitment depths under minimum-tillage and no-till systems (Chauhan et al. 2006b). These are all small-seeded species that, under either tillage regime, failed to emerge from deeper depths.

The germination and emergence of a weed species can be impacted by the depth at which seeds are buried. Similar to our study, in a previous study, seedling emergence of *S. madagascariensis* did not occur below a depth of 2 cm (Alonso et al. 1982). The trait of responsiveness to light may directly affect the establishment and survival of seeds by influencing the maximum soil depth from which germination is permitted (Koller 1964). As burial depth increases, photoblastic seed germination decreases. In light-dependent weed seeds, seed burial has been shown to drastically limit seedling emergence, such as that of eclipta [*Eclipta prostrata* (L.) L.] (Chauhan and Johnson 2008) and doveweed [*Murdannia nudiflora* (L.) Brenan] (Ahmed et al. 2015).

In contrast to our results, Alonso et al. (1982) observed no seedling emergence of *S. madagascariensis* below 2 cm. The cause of these disparate results in the two investigations could be different experimental conditions, genetic variations, or adaptations to localized climatic conditions. The findings of our study indicate that *S. madagascariensis* would emerge more frequently under farming practices that follow no-till systems (i.e., no burial of seeds); however, deep tillage could reduce its emergence. Hence, deep and inversion tillage could be used as a weed management approach to burying the seeds of *S. madagascariensis* below 4-cm depth.

Effects of Crop Residue Amount on Seedling Emergence

Both populations of *S. madagascariensis* exhibited similar ($P > 0.05$) emergence behavior when sown under different amounts of crop residue; therefore, data were averaged across populations (Figure 3B). The addition of crop residue inhibited *S. madagascariensis* seedling emergence. In the absence of residue, cumulative seedling emergence was highest (60%) and then fell dramatically to 47% when crop residue was applied at a rate of $1,000 \text{ kg ha}^{-1}$. With the additional residue of up to 4 Mg ha^{-1} , seedling emergence of *S. madagascariensis* was unaltered. At 8 Mg ha^{-1} of residue, there was only 16% seedling emergence of *S. madagascariensis*.

Crop residue may reduce weed emergence by releasing allelochemicals, decreasing light transmittance, changing soil moisture, reducing oxygen availability, and increasing daily soil temperature amplitude (Chauhan and Johnson 2010; Nikolic et al. 2021; Teasdale 1993). Teasdale (1993) proposed that light was

more crucial for weed control by hairy vetch (*Vicia villosa* Roth) residue than allelopathy or physical impedance. Reduced seedling emergence may be caused by the residue cover acting as a physical barrier. Crop residues have been reported to help prevent the establishment of numerous weeds (e.g., Mohler and Calloway 1992). However, it may be necessary to apply greater amounts of residue than those typically found in fields to significantly reduce weed populations. In our investigation, the addition of 1,000 kg ha⁻¹ of residue led to a 12% reduction in the germination of *S. madagascariensis*, which may be a representation of straw residue left over from a rainfed wheat crop. Nikolic et al. (2021) also reported that velvetleaf (*Abutilon theophrasti* Medik.), common lambsquarters (*Chenopodium album* L.), and *S. oleraceus* had 12% to 56% lower emergence with residues of maize (*Zea mays* L.) and wheat (0.31 to 0.92 kg m² for maize and 0.18 to 0.53 kg m² for wheat) than without residues. Similarly, crop residue of 6,000 kg ha⁻¹ reduced seedling emergence of *E. prostrata* by 68% to 91% (Chauhan and Abugho 2013; Chauhan and Johnson 2008) and *A. spinosus* by 57% to 77% (Chauhan and Abugho 2013; Chauhan and Johnson 2009).

Retaining crop residues on soil surfaces could, in general, result in a reduced need for weed control measures, which would lower production costs (Nikolic et al. 2021). Additional field validation studies are needed to determine the residue quantity required to suppress *S. madagascariensis* emergence. For farmers who use organic farming techniques, or in conservation agriculture, this could be useful (Chauhan and Johnson 2010). However, it will be crucial to find a balance between the amount of residue needed to suppress weeds and the amount that would not prevent crop establishment (Chauhan and Johnson 2010).

In summary, the seed germination of both populations of *S. madagascariensis* was similar and maximized (>97%) at 25/15 C alternating temperatures, and seeds also germinated at temperatures ranging from 15/5 to 35/25 C. Both populations had maximum germination rates (>97%) in light/dark regimes; however, in the total absence of light, significantly lower germination (45%) was observed. The Gattton population was more tolerant to salt- and water-stress conditions compared with the Felton population. Seedling emergence of *S. madagascariensis* was found to be maximum for seeds placed on the soil surface, and no emergence was recorded from the 4-cm depth. The emergence of *S. madagascariensis* decreased drastically with the addition of wheat crop residue at 4,000 to 8,000 kg ha⁻¹. The results of our study highlight some of the key factors that have led to *S. madagascariensis* becoming a widespread and problematic weed in parts of Australia. The knowledge gained from this research may be used to develop and apply efficient management strategies for controlling *S. madagascariensis* under various agroecological conditions.

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