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Seed germination ecology of leucaena (*Leucaena leucocephala*) as influenced by various environmental parameters

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Abstract

Leucaena [*Leucaena leucocephala* (Lam.) de Wit] is a perennial weed in more than 25 countries, including Australia. Knowledge regarding the seed biology of *L. leucocephala* could help in making weed management decisions. Experiments were conducted to study the effect of hot water (scarification), alternating temperatures, heat stress, salt stress, water stress, and burial depth on seed germination of two populations of *L. leucocephala* collected from Toowoomba and Gatton, Australia. The optimum duration of hot water treatment to break the hard seed coat dormancy was 2 min for both populations. The highest germination (92% to 98%) was recorded at 35/25 C for both populations, and similar germination occurred at 30/20 C. The Toowoomba population recorded greater germination at low temperature (15/5 to 25/15 C) than the Gatton population. Additionally, the Gatton population had higher germination than the Toowoomba population after 5 min of exposure to temperatures of up to 100 C, suggesting that the Gatton population may be more tolerant to heat stress. Germination was completely inhibited at pretreatment (5 min) temperatures of 150 to 250 C. The Toowoomba population recorded 17% greater germination than the Gatton population at a high salt concentration (160 mM NaCl), indicating its greater salt tolerance. At low moisture stress (−0.1 and −0.2 MPa), higher germination was observed in the Toowoomba population than in the Gatton population, whereas germination was similar for both populations at higher water stress levels (−0.4 MPa or lower). Germination was similar for both populations at shallow depths (0 and 1 cm) but higher emergence was recorded for the Toowoomba population at 2 to 8 cm than the Gatton population. Differential germination behaviors of both populations suggest that they adapted differently in their respective local environments. Knowledge gained from this study will help in formulating integrated management practices for *L. leucocephala*.

Introduction

Leucaena [also white leadtree; *Leucaena leucocephala* (Lam.) de Wit] is a shrub or small tree in the Fabaceae family that originated in Mexico and Central America and is now largely distributed throughout the subtropics and tropics (CABI 2021; Dalzell et al. 2006). It is considered a beneficial species in some regions because of its multiple uses, such as nutritional fodder, fuelwood, timber, and shade (Olckers 2011; Shelton and Dalzell 2007; Walton 2003). However, *L. leucocephala* is also categorized as an invasive weed species due to its aggressive growth habit and its ability to invade new areas by forming a dense thicket. It can be found in coastal strands; outskirts of forests; canopy gaps; disturbed and cleared areas; and other ruderal sites like roadsides, abandoned fields, and waste ground (Campbell et al. 2019; Walton 2003). In Australia, *L. leucocephala* is commonly known as cow tamarind, jumbie bean, leadtree, or white leadtree and can be found in southeast, central, and north Queensland.

Leucaena leucocephala is tetraploid and self-pollinated; therefore, a single plant is capable of producing viable seeds. The seeds of *L. leucocephala* possess a hard seed coat and therefore require scarification for germination. They can remain viable in the soil for 10 to 20 yr (Olckers 2011; Raghu et al. 2005; Walton 2003). It can also thrive well in nutrient-limited conditions, especially in low-nitrogen circumstances, because of its nitrogen-fixing ability (De Angelis et al. 2021). All these characteristics of *L. leucocephala* increase its invasiveness (Marques et al. 2014).

Germination is the first step in the life cycle of any plant species. A better understanding of germination ecology is always helpful in planning weed control programs. There are many factors that influence the germination of weeds, such as temperature, water stress, salinity, heat stress, and burial depth. Temperature is one important factor that influences seed germination. Information related to the effect of temperature on seed germination of *L. leucocephala* may be helpful to better understand its potential expansion range at both spatial and temporal levels and to devise integrated weed management strategies. However, the literature is very limited for the germination of *L. leucocephala* when affected by a range of environmental conditions. This study was conducted to evaluate the effect of alternating day/night temperature, heat stress, salt stress, water stress, and burial depth on seed germination of *L. leucocephala.*

Materials and Methods

Seed Collection

Seeds of two populations of *L. leucocephala* were collected in August 2020 from Gatton and Toowoomba towns in Queensland, Australia. The geographical coordinates for Gatton and Toowoomba are 27.5571°S, 152.2770°E and 27.5598°S, 151.9507°E, respectively. Gatton is at 94 m elevation from the mean sea level, with an average temperature of 20 C (13 to 27 C) with annual rainfall of 770 mm, while Toowoomba is at 691 m elevation from the mean sea level, with a mean temperature of 18 C (13 to 23 C) with annual rainfall of 725 mm. At least 50 plants of each population were selected for seed collection, and seeds were mixed together for each population. Pods were threshed, and seeds were placed in plastic bags at room temperature until the start of experiments in September 2020.

General Protocol

To evaluate the germination of *L. leucocephala*, 25 seeds were evenly placed in a petri dish (Rowe Scientific Pty Ltd, Brisbane, QLD, Australia) having a diameter of 9 cm. The petri dish contained two layers of Whatman No. 1 filter paper (Whatman, Maidstone, UK) moistened with 5 ml of ionized water/salt solution/polyethylene glycol (PEG) solution. To avoid evaporative water loss, petri dishes were placed inside sealed plastic bags before incubation. An incubator was set at alternating day/night temperatures of 35/25 C in the 12-h light/12-h dark regime, unless otherwise indicated, and petri dishes were placed in the incubator. The seeds were placed in hot water at 90 C for 2 min before the start of each experiment, because this was found to be the optimum period to break the hard seed coat dormancy in the scarification experiment. After 15 d, seed germination was recorded, as there was no further germination after this period in a preliminary experiment. A seed was considered to be germinated when its radical was at least 1 mm in length. Treatments in each trial were replicated three times, and each trial was repeated ($n = 6$).

Experiment 1. Effect of Scarification on Germination

Leucaena leucocephala possesses hard seed coat dormancy. Therefore, a trial was conducted to evaluate the optimum duration of hot water treatment to break its dormancy. Seeds of both populations were immersed in hot water at 90 C in a temperature-controlled water bath for either 2, 5, 10, or 20 min as per the treatment. There was also a control treatment (0 min) in which seeds were not placed in hot water. After the hot water treatment, seeds were placed in petri dishes and incubated at 35/25 C as described earlier.

Experiment 2. Effect of Temperature on Germination

To evaluate the effect of temperature on seed germination of *L. leucocephala*, scarified seeds (2 min at 90 C hot water) of both populations were incubated at five different alternating day/night temperatures. The temperature regimes were 15/5, 20/10, 25/15, 30/20, and 35/25 C with a 12-h light/12-h dark photoperiod. Bags having petri dishes for both populations were placed inside five different incubators according to the treatments. These temperatures regimes were selected to reflect the temperatures occurring in Queensland throughout the year.

Experiment 3. Effect of High-Temperature Stress on Germination

An experiment was conducted to test the effect of high-temperature pretreatment on the germination of *L. leucocephala*. Nonscarified seeds of both populations were placed in an oven at 25, 50, 100, 150, 200, or 250 C for 5 min; 25 C was included as room temperature. These preheated seeds were then placed in an incubator at 35/25 C as described earlier.

Experiment 4. Effect of Salt Stress on Germination

To evaluate the effect of salt stress on the germination of *L. leucocephala*, scarified seeds of both populations were incubated at 35/25 C with solutions of either 0 (control), 20, 40, 80, 160, or 320 mM sodium chloride (NaCl). The required concentrations were prepared using NaCl (Rowe Scientific Pty Ltd) and ionized water. These concentrations were selected because these salt levels are commonly found in various regions of Australia.

Experiment 5. Effect of Water Stress on Germination

The effect of osmotic potential on germination of *L. leucocephala* was evaluated by placing scarified seeds of both populations in the incubator at 35/25 C in solutions of either 0, −0.1, −0.2, −0.4, −0.8 or −1.6 MPa osmotic potential. Solutions with different concentrations were prepared following the procedure of Michel and Radcliffe (1995) by dissolving PEG 8000 in distilled water.

Experiment 6. Effect of Burial Depth on Emergence

To evaluate the effect of burial depth on the emergence of *L. leucocephala*, 50 scarified seeds (2 min at 90 C hot water) of both populations were planted in plastic pots having a diameter of 20 cm. The pots were filled with the field soil collected from the Gatton research farm of the University of Queensland. Before the pots were filled, the soil was sieved through a 3-mm sieve. The texture of the soil was clay loam with 33% sand, 46% silt, and 21% clay with 2.6% organic matter. Seeds were either placed on the soil surface (0 cm) or buried at depths of 1, 2, 4, or 8 cm (15 pots per population by 2 experimental runs). For maintaining optimum moisture, the pots were placed in plastic trays filled with water and then placed inside the incubator set at alternating day/night temperatures of 35/25 C in the 12-h light/12-h dark regime. Water was added manually to these trays every third day to maintain an optimum level of moisture.

Experimental Design and Statistical Analyses

Petri dishes were the experimental unit in Experiments 1 to 5, and pots in Experiment 6. The statistical design used in all the experiments was a randomized complete block design with three replications. Each replication was arranged on a different shelf in the incubator and considered a block. All experiments were repeated, and the second run was started within a month after the completion of the first run. In each experiment, there was no interaction between experimental runs and treatments; therefore, the data were pooled across the two experimental runs for ANOVA (Genstat 2021). Before analysis, the variance of the data was visually checked for the homogeneity of variance. The data of both

Table 1. ANOVA results for the effect of population and/or treatment on seed germination (%) (Experiments 1–5) or seedling emergence (%) (Experiment 6) of *Leucaena leucocephala*.

Source of variation	Degree of freedom	Experiment 1	2	3	4	5	6
		F-ratio (P value)					
Population	1	6.3 (0.016)	112.3 (<0.001)	64.4 (<0.001)	17.6 (<0.001)	6.8 (0.013)	56.0 (<0.001)
Treatment	4	1228.4 (<0.001)	425.7 (<0.001)	149.0 (<0.001)	42.2 (<0.001)	333.0 (<0.001)	262.4 (<0.001)
Population × treatment	4	326.9 (<0.001)	21.7 (<0.001)	11.1 (<0.001)	15.7 (0.048)	2.7 (0.045)	3.3 (0.019)
Error	45						

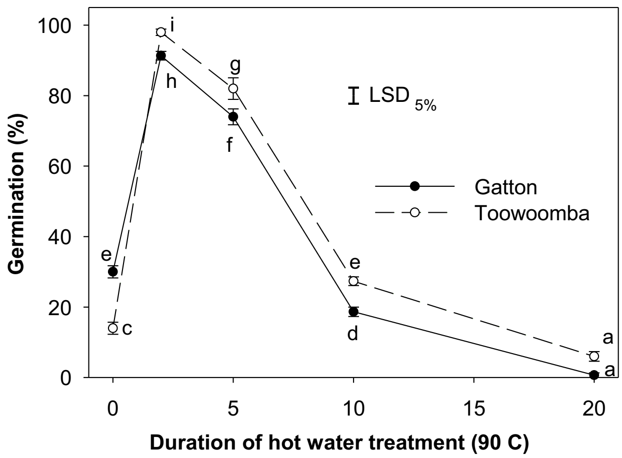

Figure 1. Effect of hot water treatment (90 C) for different times (minutes) on seed germination of *Leucaena leucocephala* populations (Gatton and Toowoomba). Means are shown with SEs, and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

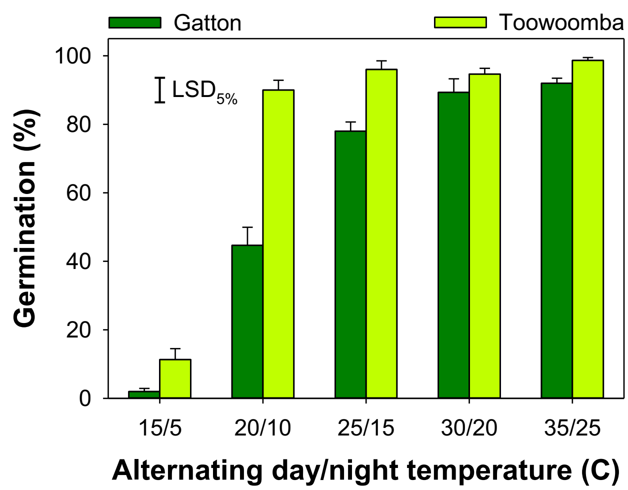

Figure 2. Effect of alternating temperature regimes (15/5 to 35/25 C) on seed germination of *Leucaena leucocephala* populations (Gatton and Toowoomba). Means are shown with SEs, and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

populations were subjected to ANOVA, and the interactions between population and treatment were separated using the LSD test at the 5% level of significance. The graphs were created using SigmaPlot v. 14.0 (Systat Software, Inc., San Jose, CA, USA).

Results and Discussion

Experiment 1. Effect of Scarification on Germination

An interaction was observed for germination between population and duration of hot water treatment (Table 1). Seed germination of *L. leucocephala* was low for both populations without scarification, and the Toowoomba population recorded 50% less germination than the Gatton population (Figure 1). Germination was significantly enhanced by scarifying the seeds with hot water at 90 C. The maximum germination (>90%) was recorded after 2 min of hot water treatment for both populations. After this duration of scarification, germination was decreased, and only 0% to 6% germination was observed after immersing seeds in hot water for 20 min at 90 C. Several studies have reported that hot water treatment is quite effective in overcoming the seed dormancy in *L. leucocephala* (Koobonye et al. 2018; Sharma et al. 2008; Tadros et al. 2011; Yousif et al. 2020).

Seed germination was increased after 2 min of scarification because the hot water treatment helped in breaking the hard seed coat primary dormancy by softening the seed coat. Weed species with hard seed coats such as Venice mallow (*Hibiscus tridactylis* Lindl.), velvetleaf (*Abutilon theophrasti* Medik.), and spurred anoda [*Anoda cristata* (L.) Schltdl.], are known to persist in the soil for a long period of time, as the process of scarification is very slow in natural conditions (Chauhan 2016; Horowitz and Taylorson 1985; Solano et al. 1976). Natural scarification depends on many factors, such as variations in temperature and moisture conditions and predation activities by rodents, insects, microorganisms. Therefore, it is difficult to eradicate *L. leucocephala*, as soil seedbanks can remain viable for at least 10 yr (Walton 2003).

Experiment 2. Effect of Temperature on Germination

An interaction was found for germination between temperature and population (Table 1). The highest germination (92% to 98%) was recorded at 35/25 C and germination was found to be similar at 30/20 C for both populations (Figure 2). But at low temperatures (15/5 to 25/15 C), the Toowoomba population recorded greater germination than the Gatton population. Such a differential response between the two populations might be due to the lower mean temperature at Toowoomba, which could have made *L. leucocephala* more adaptable at low temperatures compared with Gatton. These results are also in line with Hwang et al. (2010), who reported the highest germination of *L. leucocephala* at 35 C.

It was interesting to note that germination of the Toowoomba population was similar from 20/10 to 35/25 C, but for the Gatton population, germination was higher only at 30/20 and 35/25 C compared with other temperatures. These results indicate the greater adaptation of the *L. leucocephala* population from Toowoomba under a wide range of temperatures, and thus this population can germinate equally throughout the spring, summer, and autumn

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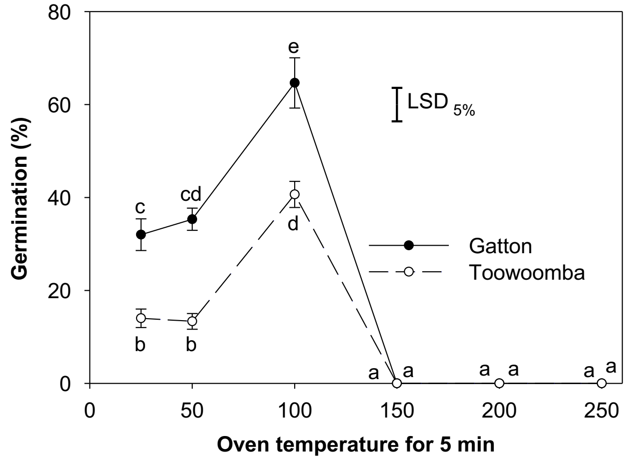

Figure 3. Effect of high-temperature pretreatment for 5 min (C) on the germination of two populations (Gatton and Toowoomba) of *Leucaena leucocephala.* Means are shown with SEs, and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

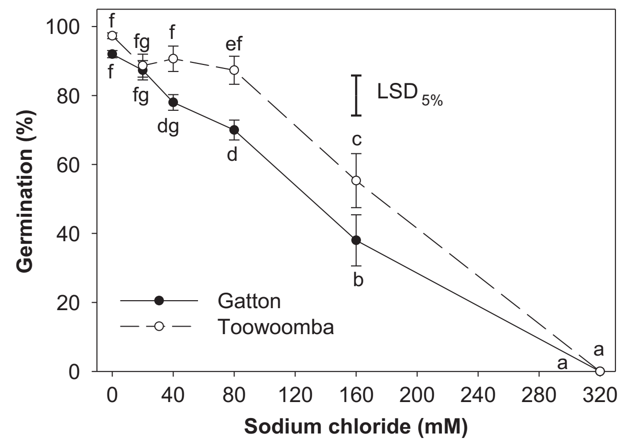

Figure 4. Effect of sodium chloride concentration on germination of two populations (Gatton and Toowoomba) of *Leucaena leucocephala*. Means are shown with SEs, and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

seasons in eastern Australia. Scarified seeds were used in this study, but the scarification process under natural conditions depends on many biotic and abiotic factors, which may make slow process. Seeds of *L. leucocephala* could germinate year-round based on the scarification status and moisture availability in the soil.

Experiment 3. Effect of High-Temperature Stress on Germination

The interaction between the population and the high pretreatment temperature for *L. leucocephala* germination was significant (Table 1; Figure 3). Both populations did not germinate after the exposure to pretreatment temperatures of 150 to 250 C, but higher germination was observed at lower oven temperatures. The Gatton population had higher germination than the Toowoomba population up to a pretreatment temperature of 100 C, suggesting that the Gatton population may be more tolerant to heat. This might be due to the higher mean temperature experienced at Gatton than at Toowoomba.

Seed germination of both populations increased with increasing oven temperature, and maximum germination was observed at 100 C pretreatment. Because nonscarified seeds were used in this experiment, the results suggest that a mild fire may stimulate germination of *L. leucocephala.* Similar results have been reported in sweet acacia [*Vachellia farnesiana* (L.) Willd. & Am.] and *Mimosa invisa* Mart. (Chauhan and Johnson 2008; Chauhan et al. 2021). Germination was completely inhibited at 150 to 250 C for both populations, suggesting that burning at 150 C or greater may be a useful tool to manage *L. leucocephala*, especially when seeds are present on the soil surface or at shallow depths (Willis et al. 2003). Exposure of seeds to fire desiccates the seed coat or damages the embryo and thus inhibits germination (Van de Venter and Esterhuizen 1988).

Experiment 4. Effect of Salt Stress on Germination

A significant interaction was observed for germination between populations and salt concentrations (Table 1; Figure 4). Both populations had similar germination at low NaCl concentrations (0 and 20 mM). Germination decreased with increased NaCl concentration for both populations, but at higher salt concentrations (40, 80, and 160 mM), the Toowoomba population recorded greater germination than the Gatton population. At 160 mM NaCl, only 38% germination was recorded for the Gatton population, while 55% germination was observed for the Toowoomba population. These results clearly suggest that the Toowoomba population is more tolerant to salt stress. Germination was completely inhibited for both populations at 320 mM.

Agboola (1998) conducted an experiment to study the effect of several saline solutions on the seed germination of six tropical forest tree species in Nigeria. Findings similar to those presented here were also reported in that study, and only 5% germination of *L. leucocephala* occurred at 200 mM NaCl. In our study, both populations behaved differently under varying concentrations of NaCl. This differential response might be due to genetic variability or varied adaption to the local environment. Higher germination of the Toowoomba population than the Gatton population at high NaCl concentration indicates the potential for the Toowoomba population to spread in the salt-affected areas of Australia.

Experiment 5. Effect of Water Stress on Germination

The interaction between population and osmotic potential for *L. leucocephala* germination was significant (Table 1; Figure 5). Germination was similar for both populations under no water stress conditions. At low moisture stress (−0.1 and −0.2 MPa), the Toowoomba population had higher germination than the Gatton population, whereas germination was similar for both populations at a higher water stress level (−0.4 MPa). No seeds germinated at −0.8 MPa or lower osmotic potential.

Our results suggest that germination of scarified seeds of *L. leucocephala* is sensitive to water stress conditions and that more germination may occur at relatively high levels of soil moisture conditions. Similarly, Felix et al. (2018) reported that seeds of *L. leucocephala* have poor tolerance to water stress. They found that germination capacity was reduced with decreasing water potential beyond −0.3 MPa. Hwang et al. (2010) tested the germination of *L. leucocephala* populations collected from Taiwan and found that the plant's water requirement for germination is high. They observed that germination of *L. leucocephala* seeds decreased

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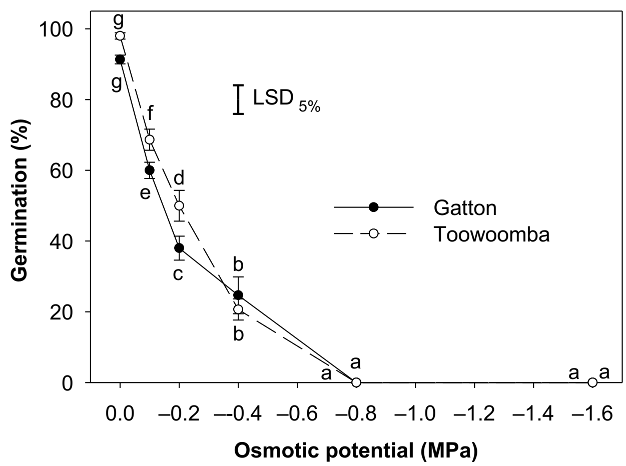

Figure 5. Effect of osmotic potential on germination of two populations (Gatton and Toowoomba) of *Leucaena leucocephala.* Means are shown with SEs, and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

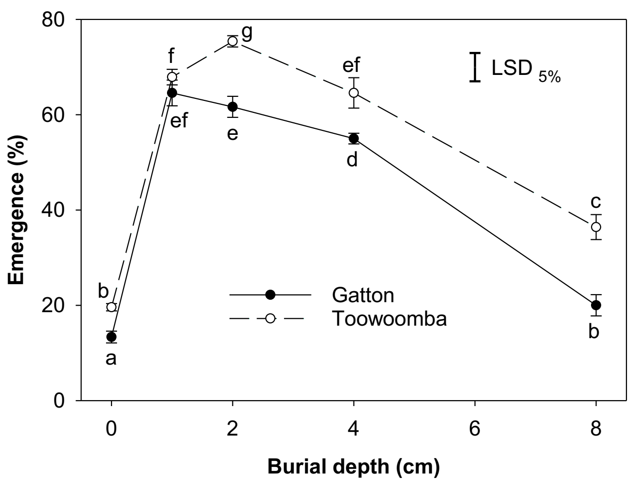

Figure 6. Effect of seed burial depth on seedling emergence of two populations (Gatton and Toowoomba) of *Leucaena leucocephala*. Means are shown with the standard errors and the LSD bar (at a 5% level of significance) shows the interaction between population and treatment. Means with the same lowercase letters are statistically similar with each other.

with decreasing osmotic potential from 0.0 to −0.4 MPa, and no germination was observed at osmotic potentials lower than −0.4 MPa. Germination inhibition of both the Gatton and Toowoomba populations of *L. leucocephala* under low water potential may increase their survival by encouraging dormancy until favorable moisture conditions are available (Fernando et al. 2016).

Experiment 6. Effect of Burial Depth on Emergence

A significant interaction between population and burial depth was observed for seedling emergence (Table 1; Figure 6). Emergence was similar for both populations at shallow depths (0 and 1 cm), but greater emergence was recorded for the Toowoomba population at 2, 4, and 8 cm when compared with the Gatton population. The differences in the emergence of *L. leucocephala* populations might be due to genetic and climatic variability based on geographic location. Akinola et al. (1999) also reported high emergence (70%) of the Peru-type *L. leucocephala* when seeds were sown shallowly. Results indicate that shallow tillage might increase the emergence of *L. leucocephala* because of optimum emergence (65% to 75%) at 1- to 2-cm depths.

Low emergence (13% to 19%) from the surface could be due to seed decay after scarification or lack of moisture. Only 20% to 36% emergence was recorded at the 8-cm depth. This might be because seedlings die and decompose following the exhaustion of food reserves in the seed before the seedlings can emerge from the soil. Furthermore, reduced aeration might also contribute to the poor emergence of *L. leucocephala* at greater depths. Hwang et al. (2010) compared the emergence of Salvadoran and Hawaiian types of *L. leucocephala* (found in the islands of Taiwan) under variable burial depths. They reported 70% and 45% emergence from the surface and 42% and 18% emergence at 5 cm depth for Salvadoran and Hawaiian types, respectively. The larger seed size of the Salvadoran compared with the Hawaiian type might be the reason for its greater emergence.

In summary, seeds of *L. leucocephala* can germinate over a wide range of environmental conditions. The Toowoomba population showed greater germination under low day/night temperatures, high salt concentration, high water stress, and deep burial depths in comparison with the Gatton population. The Gatton population was found to be more tolerant to high temperatures and recorded greater germination at 100 C compared with the Toowoomba population. As water stress adversely affected seed germination, *L. leucocephala* may have higher chances of germination under plant residue systems, where more water is conserved in the soil.

The Toowoomba population of *L. leucocephala* was found to be relatively tolerant of water and salt stress conditions. Therefore, the Toowoomba population may compete better than the Gatton population in problematic soils and under water stress conditions. The emergence of *L. leucocephala* was greatest from the shallow depth (2 cm), and seedlings emerged even from an 8-cm depth, suggesting that shallow tillage might increase the emergence of *L. leucocephala*. The variable response of both populations to temperature, heat stress, water stress, and salt stress conditions suggest that populations of *L. leucocephala* may have undergone differential adaptation in their local environments. Therefore, the two populations of *L. leucocephala* may differ in their invasiveness potential. Results of this study will help in better understanding the germination ecology of *L. leucocephala* and devising integrated management strategies to limit its further spread.

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