

Research Article

Cite this article: Asaduzzaman M, Koetz E, Wu H (2020) Germination ecology of dwarf amaranth (*Amaranthus macrocarpus*): an emerging weed in Australian cotton cropping systems. *Weed Sci.* **68**: 612–618. doi: [10.1017/wsc.2020.58](https://doi.org/10.1017/wsc.2020.58)

Received: 21 February 2020
Revised: 24 May 2020
Accepted: 13 July 2020
First published online: 26 August 2020

Associate Editor:

Debalin Sarangi, University of Wyoming


Keywords:

Burial depth; dormancy; emergence; integrated weed management; temperature

Author for correspondence:

Md Asaduzzaman, Research Officer–Weeds, New South Wales Department of Primary Industries, Wagga Wagga, NSW 2650, Australia. (Email: md.asaduzzaman@dpi.nsw.gov.au)

Germination ecology of dwarf amaranth (*Amaranthus macrocarpus*): an emerging weed in Australian cotton cropping systems

Md Asaduzzaman¹ , Eric Koetz² and Hanwen Wu³

¹Research Officer–Weeds, New South Wales Department of Primary Industries, Wagga Wagga, New South Wales, Australia; ²Research Agronomist–Weeds, New South Wales Department of Primary Industries, Wagga Wagga, New South Wales, Australia and ³Principal Research Scientist–Weeds, New South Wales Department of Primary Industries, Wagga Wagga, New South Wales, Australia

Abstract

Dwarf amaranth (*Amaranthus macrocarpus* Benth.) is a problematic broadleaf weed in many crops in Australia; however, no information is available on the germination ecology of this species. Seeds from two populations of this species were collected from Hillston, NSW, Australia (D-P-01), and Yandilla, QLD, Australia (D-P-02). Seeds were germinated at a range of constant (20 to 45 C) and alternating temperatures (30/20, 35/25, 40/30, and 45/35 C day/night). For the constant temperature treatments, the highest germination occurred at 35 C for D-P-01 (89%) and D-P-02 (82%). Germination was higher at the alternating day/night temperature of 40/30 C for both populations D-P-01 (91%) and D-P-02 (85%). Seed germination of both populations was stimulated by light, which indicates a great amount of emergence of *A. macrocarpus* can occur on bare ground such as crop seed beds. Results also revealed that this species tolerates a moderate level of salinity and can germinate in slightly alkaline soil conditions. The emergence of this species was highest (47%) for the seed buried at 0.5-cm depth in grey cracking alkaline soil compared with seed buried at the same depth in acidic red soils. These results suggest that soil inversion by tillage to bury weed seeds below their maximum emergence depth could serve as an important tool for managing *A. macrocarpus*. The results from this study will help in developing more sustainable and effective integrated weed management tactics for the control of this weed and weeds with similar responses in summer cropping systems.

Introduction

Seed germination is a critical phase in the life cycle of a weed, and successful establishment of weeds depends significantly on their ability to germinate, where germination is the result of complex connections between multiple internal and external factors (Bewley and Black 1994; Sohrabi et al. 2016). Environmental factors such as water activate the enzymatic activity required to initiate germination activities (Baskin and Baskin 2014; Bewley et al. 2013). The absence of water can prevent the timely germination of seeds of many weed species, while dormancy mechanisms can control germination in some species (Bewley et al. 2013). Temperature is another critical factor that can regulate the occurrence and speed of germination (Campbell-Martinez et al. 2017; Chauhan et al. 2006; Derakhshan et al. 2014; Nosratti et al. 2017). Soil temperature controls the rate of germination by affecting the seed dormancy levels and the proportion of the enzymatic activities (Bewley et al. 2013). Other environmental factors such as light can stimulate germination of some species; these species are expected to be more prevalent in no-till cropping systems (Cousens et al. 1993). Cultural operations, including tillage or sowing, may bury weed seeds at various depths and thereby affect germination and seedling emergence due to altered accessibility of required moisture, temperature, and light exposure (Buskin and Buskin 1985; Singh et al. 2012). Hence, knowledge about weed seed biology will help identify the mechanisms that trigger germination and provide effective management decisions for targeted weed species (Bhowmik 1997; Singh et al. 2012).

Amaranthus species are among the most troublesome weeds in many crop production systems (Hao et al. 2017). The genus *Amaranthus* has many species—redroot pigweed (*Amaranthus retroflexus* L.), smooth pigweed (*Amaranthus hybridus* L.), Powell's amaranth (*Amaranthus powellii* S. Watson), Palmer amaranth (*Amaranthus palmeri* S. Watson), common and tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer]—all of which are primarily weedy pests in cultivated crops (Horak et al. 1994). The germination ecology of different species of *Amaranthus*, including spiny amaranth (*Amaranthus spinosus* L.), green amaranth (*Amaranthus viridis* L.), purple amaranth (*Amaranthus blitum* L.), and *A. palmeri*, in response to environmental factors has been studied, with germination response thresholds to

environmental factors differing between species (Chauhan and Johnson 2009; Costea et al. 2004; Ghorbani et al. 1999; Guo et al. 2003; Hao et al. 2017; Sellers et al. 2003; Steckel 2004). For instance, among the nine tested *Amaranthus* species, including tumble pigweed (*Amaranthus albus* L.), prostrate pigweed (*Amaranthus blitoides* S. Watson), *A. hybridus*, *A. palmeri*, *A. powellii*, *A. spinosus*, *A. retroflexus*, and *A. tuberculatus*, germination of *A. powellii* exhibited the highest total germination across all temperatures (ranging from 5 to 35 C) compared with the other amaranth species, while *A. blitoides* seed demonstrated the lowest total germination (Steckel et al. 2004). Recently, Hao et al. (2017) demonstrated that *A. viridis* is noticeably less tolerant than *A. retroflexus* and *A. blitum* of the same potential of moisture deficit. Although most of the previous studies have examined certain germination characteristics of different *Amaranthus* species, there is no information available for dwarf amaranth (*Amaranthus macrocarpus* Benth.). *Amaranthus macrocarpus* is considered a summer (December to February) weed in Australia. This species is widely distributed in northeast Australia and is rapidly emerging in other parts of Australia, especially areas with subtropical or tropical weather and well-distributed rain (Manalil et al. 2017). The species can exist in both the irrigated and rainfed cotton (*Gossypium hirsutum* L.) systems of Australia (Charles et al. 2004; Walker et al. 2005; Werth et al. 2013). Previous weed surveys in 2008 to 2009 and 2010 to 2011 by Werth et al. (2013) concluded that this small-seeded species is favored by reduced-tillage systems, which has led to its rapid emergence as a problematic weed. Most importantly, *A. macrocarpus* belongs to the genus *Amaranthus*, a genus with many member species having resistance due to high selection pressure of herbicides, including glyphosate (Vieira et al. 2018). Concern exists that *A. macrocarpus* may also possess attributes of resistance to glyphosate. Our random weed surveys conducted across three seasons from 2016 to 2018 indicated an increase in its prevalence over time in northern Australian glyphosate-based cotton-farming systems. Despite its spread, and the risk of it developing herbicide resistance, the ecology and persistence of this species in different Australian agroecological areas has not been studied. Precise knowledge of the germination ecology of this species in response to different environmental factors is required to develop ideal weed management options. This study was conducted to evaluate the germination response of *A. macrocarpus* under different environmental conditions.

Materials and Methods

Sources of Seeds and Germination Procedure

The mature seeds of *A. macrocarpus* were collected from two different cotton farms in 2017. Seed of the first population (D-P-01) was collected from a southern cotton farm located at Hillston, NSW, Australia (33.50°S, 145.45°E), and seed of the second population (D-P-02) was collected from a northern cotton farm located at Yandilla, QLD, Australia (27.48°S, 151.21°E). Seed with visible damage was removed from the experiments. The seed samples were collected at the seed maturity stage. The preliminary germination study showed that the seeds of both populations were not dormant. All experiments consisted of three replicates of 25 seeds placed on two sheets of filter paper (No. 4 filter paper, Whatman International, Maidstone, UK) in 9-cm petri dishes, unless specified otherwise. The filter paper was moistened initially with 5 ml of test solution or distilled water. After seeds were placed, all dishes were sealed with parafilm (American National,

Greenwich, CT, USA) to prevent desiccation. The petri dishes with treated seeds were kept inside an incubator (Lindner + May, Brisbane, QLD, Australia) at various temperatures. The total number of seeds germinated was determined after 7 d, except in seed burial depth studies.

Germination Response to Temperature

The germination response of *A. macrocarpus* to temperature was evaluated by incubating seeds in growth chambers (Lindner + May) under constant temperatures ranging from 25 to 45 C at 5 C intervals and also under alternating temperature ranges (30/20, 35/25, 40/30 and 45/35 C) in light/dark cycles. The objective of this experiment was to find the optimum temperature conditions for germination. These temperature ranges were selected to reflect the current temperature and projected future variation that might occur in Australia. Based on the results of this study, all succeeding experiments were conducted at 40/30 C day/night temperature with a 12-h photoperiod, as maximum germination occurred at these conditions for both populations.

Germination Response to Light

Seed germination of two populations of *A. macrocarpus* was determined under two light conditions. The first light treatment was a 12-h photoperiod (hereafter “light”), and the second treatment was continuous darkness (hereafter “dark”) in a growth incubator for 7 d under a day/night temperature cycle of 40/30 C. The petri dishes were covered in two layers of aluminum foil to incubate in dark environments as previously proposed by Baskin and Baskin (2014). The relative light germination (RLG) was measured by the formula (Equation 1) proposed by Milberg et al. (2000):

$$RLG = \frac{G_l}{G_d + G_l} \quad [1]$$

where G_l is percentage of germination in the presence of light and G_d is percentage of germination in darkness. RLG represents a range of values from 0 (germination only in the dark) to 1 (germination only with light). Mean germination or emergence time (MGT), which is a measure of the speed of germination or emergence, was calculated after 7 d using the following formula (Equation 2):

$$MGT = \frac{D_n}{D_t} \quad [2]$$

where D_n is the number of seeds that had germinated by n days, and D_t is the number of days counted from the beginning of the germination experiment.

Germination Response to Salt Stress

The effect of salt stress on germination of *A. macrocarpus* was determined by placing seeds on filter paper in petri dishes containing 5 ml of 0, 25, 50, 100, 150, and 200 mM sodium chloride solutions (sodium chloride, AR grade, Merck, Melbourne, VIC, Australia). The treatment solutions were prepared by dissolving the required amount of salt (0, 1.5, 2.4, 5.8, 8.8, and 11.7 g of NaCl) in 1 L of de-ionized water (Ahmed et al. 2015; Asaduzzaman et al. 2019; Michel 1983). This range of NaCl concentrations reflects the salinity stress levels determined to exist in the surface of the heavy grey cracking clays (grey vertosols) mainly

Table 1. Soil physicochemical properties of grey cracking and acidic red soils collected from two different cotton farming systems in Australia.^a

Soil type	Location of soil collection	pH	Electrical conductivity	Carbon	Nitrogen	Sulfur	Textural class	Mn	Cu	Zn	Se	Mo	Cd	Pb
			— $\mu\text{S/cm}$ —	—%—				— mg kg^{-1} —						
Grey cracking soil	Whitton, NSW	7.13	159.36	2.3	0.29	0.078	Sandy loam	123	4.5	7.5	0.18	0.21	0.0	6.3
Acidic red soil	Leeton Research Station, Leeton, NSW	5.90	187.29	1.8	0.19	0.007	Sandy loam	110	5.6	8.9	0.19	0.23	0.05	6.7

^aSeeds of both populations of *Amaranthus macrocarpus* were buried at different depths in both soils.

used for cotton production in the northern cropping region of Australia.

Germination Response to pH

The impact of pH on germination of *A. macrocarpus* was evaluated by using four different pH buffer solutions: 4, 6, 8, and 10. The buffer pH solutions were prepared based on a method previously described by Chachalis and Reddy (2000). This range of pH values (4–10) reflects pH values commonly found in Australian soils (Caritat et al. 2011). The final pH value of tested solutions was measured just before solutions were placed in the dishes by using a water-quality pH meter (Model 860033, SPEP Scientific, Frederick, MD, USA) at room temperature.

Emergence Response to Soil Type and Seed Burial Depth

The effect of burial depth on seedling emergence under two different soil types was evaluated in the glasshouse. Two soil types were compared; their properties are presented in Table 1. Before seed burial, 15-cm-diameter pots were filled with soil, irrigated (every alternate day for 2 min with manual sprinkler), and kept for 14 d in a glasshouse. Any seedlings from the soil weed seedbank were removed before the seed burial experiment. A total of 50 seeds of each population were placed separately on the soil surface of the pots and then covered with the same soil to depths 0, 2.5, 5, 7.5, and 10 cm. Pots were initially watered manually with an overhead sprinkler and later with an automated sprinkler irrigation system. Seedling emergence was counted until 21 d, as after that no further emergence was observed.

Statistical Analysis

A randomized complete-block design with three replications was considered for all experiments. Each experiment was repeated after the end of the first run. Data from two runs were pooled, as there was no time by treatment interaction as determined by ANOVA. A three-parameter gaussian model (Equation 3) was fit to the germination values resulting from the constant temperature effect experiment. The model was:

$$y = a * e\{-0.5 * [(x - b)/c]^2\} \quad [3]$$

where a is the height of the curve's peak (maximum germination); b is the position of the center of the peak (the constant temperature required to achieve maximum germination), and c is the width of the curve. An ANOVA was used to assess the effect of alternating temperature on seeds germination. A three-parameter log-logistic (nonlinear) dose-response model (Seefeldt et al. 1995) was fit (Equation 4) for data derived from the salt stress experiment:

$$y = \{[c + (d - c/1 + \exp(b(\log(x) - \log(ES_{50})))]\} \quad [4]$$

In Equation 4, c and d are the lower and upper response against the explanatory variable (salt stress), respectively. The mean response of the control treatment corresponds to the upper limit d . ES_{50} is the effective salt stress level required to reduce germination by 50%, and b is the slope of the curve around ES_{50} . A polynomial regression model (Equation 5) was used to detect the effect of different pH buffer solutions on germination:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 \quad [5]$$

where y is the response variable (% germination) and β_0 is the estimated model intercept. The parameters β_1 and β_2 are coefficients.

The normality and distribution of data were verified by a Shapiro-Wilk normality test. The data variance was also examined by plotting the residuals to confirm homogeneity of variance. The significant differences among treatment means were identified by Tukey's honest significant difference at $P < 0.05$. The R packages DRC (Ritz and Streibig 2008) and AGRICOLAE (De Meddiburu 2017) were used in RStudio (RStudio 2019) for model fitting and summarizing data.

Model Goodness of Fit

The candidate models were assessed based on Akaike's information criteria (AIC) and mean square-root (MSE) values; the nested models were compared using MSE, and the nonnested models were assessed based on the difference of AIC value (if the difference was >2 , then model with the lowest AIC value was selected). Root mean-square error (RMSE) and adjusted R^2 were calculated further to test the goodness of fit for the selected best models, as they are commonly used to estimate model quality (Sarangi et al. 2015; Werle et al. 2014). The RMSE was calculated based on the equation (Roman et al. 2000):

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (p_i - o_i)^2}{n}} \quad [6]$$

where P_i is the predicted value, O_i is the observed value, and n is the total number of observations.

A smaller RMSE value means a better fit to the model due to closer observed and predicted values.

Results and Discussion

Germination Response to Temperature

There was a significant ($P < 0.05$) interaction between temperature and population on total germination of *A. macrocarpus*. Each population had a similar response in the constant temperature

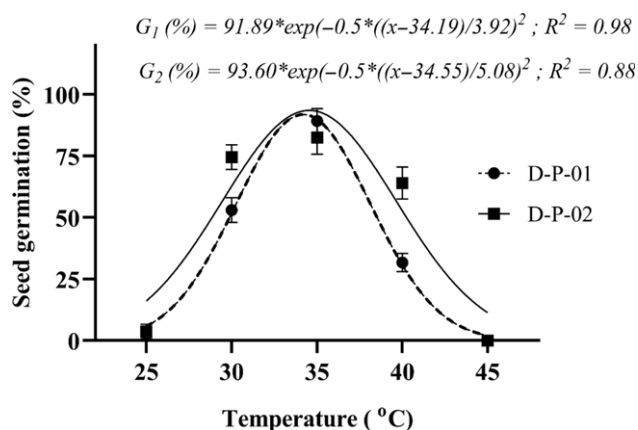


Figure 1. Effect of constant temperatures on germination of *Amaranthus macrocarpus* for 7 d. Data were pooled from six petri dishes (experimental units) and fit into a three-parameter gaussian model with goodness of fit $R^2 = 0.98$ and 0.88 for two different population D-P-01 and D-P-02, respectively. The solid and dotted lines represent a three-parameter gaussian model, and dots and boxes with vertical bars show the observed means (\pm SE) of the germination. The calculated root mean-square error values for D-P-01 and D-P-02 are 2.6 and 3.5, respectively

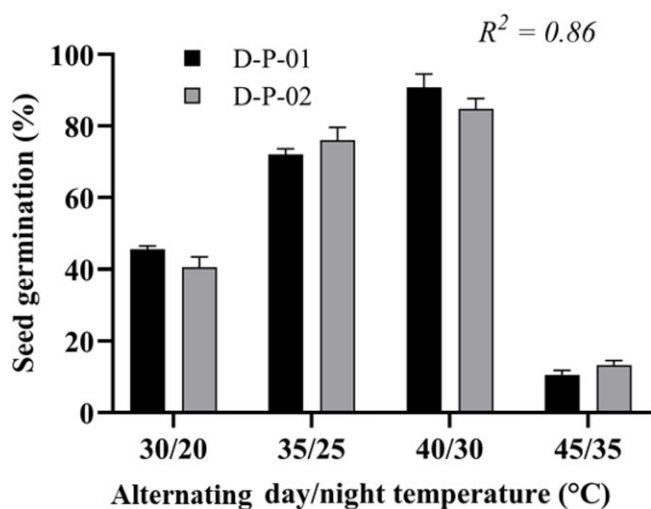


Figure 2. The effect of alternating temperature (day/night) on germination of two populations (D-P-01 and D-P-02) of *Amaranthus macrocarpus* for 7 d. Data were pooled from six petri dishes (experimental units). The solid bars show the observed means (\pm SE) of the germination (% germination; $P < 0.05$, ANCOVA). The calculated root mean-square error values for D-P-01 and D-P-02 are 10.7 and 9.40, respectively.

experiment, with both not germinating below 20 C. Greatest germination in this experiment was achieved for both populations at 35 C (89% and 82% for D-P-01 and D-P-02, respectively) (Figure 1). *Amaranthus macrocarpus* germination at high temperatures enables the species to grow under hot Australian conditions. Seeds of this species will not germinate in winter in the field and will remain dormant until late spring to summer. This could explain the higher infestations of *A. macrocarpus* in the warmer cotton-cropping systems. Similarly, mature *A. palmeri* seeds remain dormant during autumn and winter (< 20 C) and become nondormant during summer (Jha et al. 2008; Jha and Norsworthy 2009). When temperatures were cycled (Figure 2), germination at 40/30 C resulted in maximum germination (91% and 85% for D-P-01 and D-P-02, respectively) followed by 35/25 C (72% and 76% for D-P-01 and D-P-02, respectively). Germination decreased

significantly when cycled at 45/35 C. The alternating temperatures 40/30 C resulted in maximum germination (91% and 84%) for both populations (D-P-01 and D-P-02, respectively). Higher germination at alternating temperatures than at constant temperatures in both populations indicates that both day and night temperatures influence germination of *A. macrocarpus*. The stimulation of germination by alternating temperatures has also been reported for other *Amaranthus* species (Baskin and Baskin, 1977, 1998; Gallagher and Cardina 1998a, 1998b; Guo and Al-Khatib 2003; Leon and Owen 2003; Steckel et al. 2004). Temperature fluctuations like alternating temperature regimes have been shown to reduce dormancy, decrease time to onset of germination, and increase germination rates in *Amaranthus* species (Jha et al. 2010; Oladiran and Mumford 1985; Thomas et al. 2006; Weaver 1984), because alternating temperatures are most similar to diurnal temperature responses and can break seed coat-imposed physical dormancy of seeds (McKeon and Mott 1982).

Germination Response to Light

A significantly ($P < 0.001$) greater number of seeds germinated under light/dark conditions than under complete darkness. More than 90% germination was recorded for both populations under the 12-h light/dark cycle (Table 2). Significant ($P < 0.018$) differences were observed between populations for seed emergence under the dark condition. Germination in constant dark conditions was 17.5% and 12% for populations D-P-01 and D-P-02, respectively. This demonstrates that *A. macrocarpus* is photoblastic and light can stimulate germination. There was a significant ($P < 0.0013$) difference between populations for RLG, with mean germination being higher for D-P-02 (0.88) than D-P-01 (0.84). This ecological distinction is especially vital in the case of small-seeded species like *A. macrocarpus*, because they have restricted resources, and seeds buried deeply in the soil will not emerge successfully (Fenner and Thompson 2005; Pons 2000). Milberg et al. (2000) reported that light response and seed mass coevolved as an adaptation to ensure the germination of small-seeded species, particularly when they are near the soil surface. The difference between populations in terms of germination rate under dark conditions might be due to the influence of different maternal environments during the seed development stage. Inhibition of germination in the dark indicates that tillage and mulching may play a key role in reducing germination of *A. macrocarpus* in cropping fields by burying or covering seeds until seed death occurs. This is consistent with Kigel (1994), who reported that most species of *Amaranthus* respond to light, and the response level varies among species (Cristaudo et al. 2007; Gallagher and Cardina 1998a).

Germination Response to Salt Stress

Germination was reduced when NaCl concentration increased from 25 to 200 mM, and neither population germinated at 150 mM NaCl (Figure 3). Only 5% and 15% germination was observed at 100 mM NaCl for D-P-01 and D-P-02, respectively. A three-parameter log-logistic model described the relationship between germination of *A. macrocarpus* and salt concentration. The corresponding concentrations for 50% inhibition of maximum germination were 34 and 41 mM NaCl for D-P-01 and D-P-02, respectively. The differential response in germination according to populations, with germination of D-P-02 being less affected, suggests that some adaptation to saline conditions is present in this population. However, this needs to be clarified by examination of

Table 2. Germination of *Amaranthus macrocarpus* when incubated at 40/30 C alternating day/night temperature for 7 d.^a

Population	Location ^b	Germination trait			
		Germination under light conditions	Germination under dark conditions	Relative light germination	Mean germination
D-P-01	Hillston, NSW, Australia	93a	17.5b	0.84a	2.5a
D-P-02	Yandilla, QLD, Australia.	91a	12.0a	0.88b	1.71b

^a A significant difference ($P < 0.05$) was observed between populations in response to light effect. Mean values are presented with different lowercase letters (a and b).

^b Sample sites were georeferenced with a GPS.

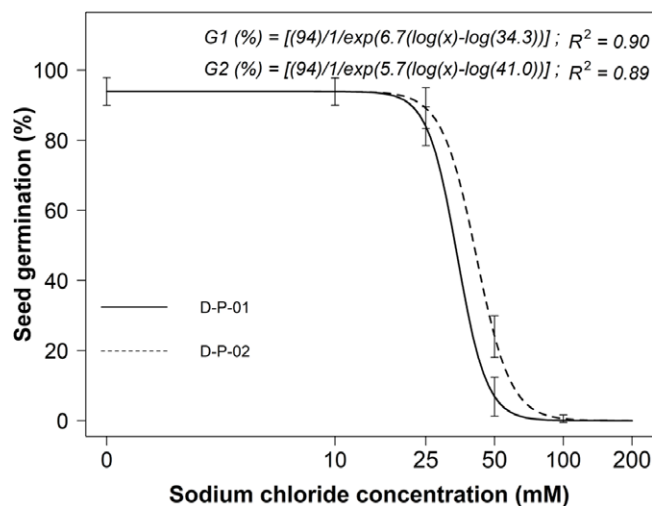


Figure 3. The effect of sodium chloride on the germination of *Amaranthus macrocarpus* incubated at 40/30 C alternating day/night temperature for 7 d. Data were pooled from six petri dishes (experimental units) and fit into a three-parameter log-logistic model with goodness of fit $R^2 = 0.90$ and 0.89 for the two different populations D-P-01 and D-P-02, respectively. The solid and dotted lines represent a three-parameter log-logistic model, and dots and boxes with vertical bars show the observed means (\pm SE) for the germination. The calculated root mean-square error values for D-P-01 and D-P-02 are 2.34 and 6.50, respectively.

more populations collected from both northern and southern Australia. The population sourced from the northern Australia (D-P-02) appears to be more able to establish in moderate to highly saline conditions from 50 to 150 mM compared with the population collected in the south (D-P-01). Previously, Hao et al. (2017) reported germination significantly decreased with 100 mM for *A. spinosus*, 50 mM for *A. viridis*, and 150 mM for *A. blitum*. However, in our study, germination significantly decreased with respect to the control (0 mM) at 50 mM for both populations, suggesting *A. macrocarpus* is more sensitive to NaCl than the species described by Hao et al. (2017).

Germination Response to pH

Germination followed a quadratic response to increasing levels of pH, and seeds of both populations exhibited broad adaptability, germinating across a wide range of soil pH conditions (Figure 4). Germination was about 60% for both populations in acidic conditions (pH 4). The highest germination was observed in pH 7 buffer solution at 91% and 93% for D-P-01 and D-P-02, respectively, and after that declined at pH 8 and pH 10, although more than 70% of seeds germinated for both populations at pH 8. Both populations had about 70% germination at pH 10. In this study, we found that

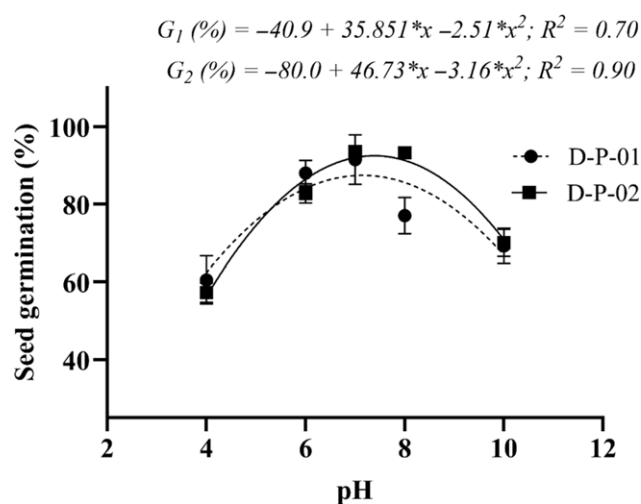


Figure 4. The effect of buffered pH solutions on germination of *Amaranthus macrocarpus* incubated at 40/30 C alternating day/night temperature for 7 d. Data were pooled from six petri dishes (experimental units) and fit into a quadratic polynomial regression model with goodness of fit $R^2 = 0.70$ and 0.90 for the two different biotypes D-P-01 and D-P-02, respectively. The solid and dotted lines represent the polynomial regression model fit to the data. Dots and boxes with vertical bars show the observed means (\pm SE) for the germination. The calculated root mean-square error values for D-P-01 and D-P-02 are 6.74 and 5.78, respectively.

germination of *A. macrocarpus* varied over a range of pH values; however, germination was optimal in neutral to alkaline pH environments. Our findings also support the similar response previously observed in *A. retroflexus* and *A. blitum*, which had higher germination response at higher pH values (Hao et al. 2017). This implies that high germination potential and adaptability to a wide range of pH values might play a key role contributing to population establishment and colonization in new areas. Such rapid distribution of this species can be an additional management issue for a newly affected areas.

Emergence Response to Soil Type and Seed Burial Depth

There was a significant ($P < 0.005$) difference for both different soil types and different burial depths in limiting seed germination. The percent emergence of *A. macrocarpus* was greater in heavy grey cracking soil than in acidic red soils, ranging from 0% to 47% and 0% to 36%, respectively (Figure 5). However, there was no significant ($P > 0.05$) difference between populations for seed emergence as affected by soil types and burial depths. The maximum mean number for seed emergence occurred at 0.5-cm depth in both soils, with 47% and 36% emergence for grey and acidic red soils, respectively. Seed emergence of *A. macrocarpus* was different

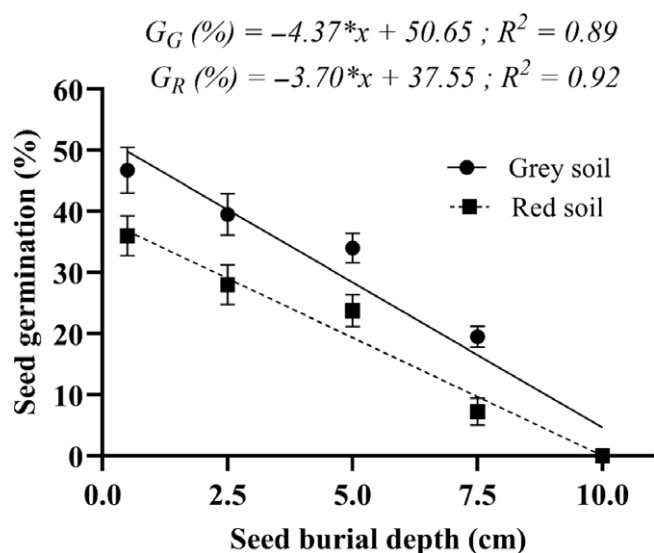


Figure 5. The effect of burial depth in two different soils (red and grey) on germination of seeds of *Amaranthus macrocarpus* buried for 21 d. Data were pooled from six pots (experimental units) and fit into a linear regression model with goodness of fit $R^2 = 0.89$ and 0.92 for the two different biotypes D-P-01 and D-P-02, respectively. The solid and dotted lines represent a linear regression model fit to the data, and dots and boxes show the observed means (\pm SE) for the germination. The calculated root mean-square error values for grey and red soil are 5.40 and 3.06, respectively.

within a range of soil burial depths (0.5 to 7.5 cm) in both soils, and seedbank depletion is slower in red soil than in grey soil, possibly due to different soil physiochemical properties, including pH, nitrogen, sulfur, and organic carbon content (Table 1). At 7.5-cm depth, less than 10% of seed emerged in the acidic red soil, and observed emergence was 0 at a depth of 10 cm in either type of soil. Small-seeded weeds, such as other *Amaranthus* species, can only germinate from shallow soil depths of 0.5 to 2.5 cm (Baskin and Baskin 1998; Benech-Arnold et al. 2000; Buhler et al. 1996; Gallagher and Cardina 1998a; Ghorbani et al. 1999; Leon and Owen 2003; Oryokot et al. 1997). In our current study, we found that seedling emergence on the soil surface was lower than germination observed in controlled conditions such as petri dishes in the presence of light. This difference could be due to poor soil–seed interaction or greater unavailability of moisture on the soil surface than on the filter papers.

Based on the results of our experiment, we conclude that the germination potential of *A. macrocarpus* under a wide spectrum of environmental conditions is likely to make it a persistent weed. *Amaranthus macrocarpus* could be troublesome in reduced or no-tillage cropping systems of Australia. However, tillage practices that bury seeds by turning over the topsoil are potential options to inhibit the emergence and growth of this species. Integrated weed management tactics, including mulch or stubble retention, can also reduce seed germination (Steinsiek et al. 1982). Because *A. macrocarpus* germinates well under cotton's preferred pH range (5.5 to 8.0), altering soil pH is not a plausible weed management strategy for this weed species. Therefore, more work needs to be conducted to determine the optimal soil pH for controlling *A. macrocarpus* in cotton-cropping systems, as a pH below 5.5 will significantly limit the availability of some nutrients to the crop and will likely reduce crop vigor, competitiveness, and yield.

Our results will support growers in developing effective management strategies for this weed species. Seed collections of *A. macrocarpus* from other locations in Australia may have

different responses to environmental conditions because of biological diversity in populations.

Acknowledgments. We thank Cotton Research Development and Corporation (CRDC) and NSW Department of Primary Industries for funding this research. We are grateful to Cotton Info for their support in tracing weed populations. The authors declare that they have no known conflict of interest that could have appeared to influence the work reported in this paper.

References

- Ahmed S, Opeña JL, Chauhan BS (2015) Seed germination ecology of dove weed (*Murdannia nudiflora*) and its implication for management in dry-seeded rice. *Weed Sci* 63:491–501
- Asaduzzaman M, Koetz E, Rahman A (2019) Factors affecting seed germination and emergence of button grass (*Dactyloctenium radulans*) (R.Br.) P.Beauv. *Weed Biol Manag* 19:85–92
- Baskin CC, Baskin JM (1998) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego: Academic Press. Pp 27–200
- Baskin CC, Baskin JM (2014) *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. San Diego: Academic Press. 1573 p
- Baskin IJ, Baskin CC (1977) Role of temperature in the germination ecology of three summer annual weeds. *Oecologia* 30:377–382
- Baskin JM, Baskin CC (1985) Seasonal changes in the germination responses of buried witchgrass (*Panicum capillare*) seeds. *Weed Sci* 34:22–24
- Benech-Arnold RL, Sánchez RA, Forcella F, Kruk BC, Ghersa CM (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Res* 67:105–122
- Bewley JD, Black M (1994) *Seeds: Physiology of Development and Germination*. New York: Plenum Press. 421 p
- Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) *Seeds: Physiology of Development, Germination and Dormancy*. New York: Springer. 392 p
- Bhowmik PC (1997) Weed biology; importance to weed management. *Weed Sci* 45:349–356
- Buhler DD, Mester TC, Kohler KA (1996) The effect of maize residues and tillage on emergence of *Setaria faberi*, *Abutilon theophrasti*, *Amaranthus retroflexus*, and *Chenopodium album*. *Weed Res* 36:153–165
- Campbell-Martinez G, Thetford M, Miller D, Perez HE (2017) Follicle maturity, seed size, temperature and photoperiod effects on seed germination of *Asclepias humistrata* (sandhill milkweed). *Seed Sci Technol* 45:523–539
- Caritat P, Cooper M, Wilford J (2011) The pH of Australian soil: field results from a national survey. *Crop Pasture Sci* 49:173–182
- Chachalis D, Reddy KN (2000) Factors affecting *Campsis radicans* seed germination and seedling emergence. *Weed Sci* 48:212–216
- Charles G, Taylor I, Roberts G (2004) The impact of the cotton farming system on weed succession: implications for herbicide resistance and adoption of an integrated weed management approach. Pages 410–413 in Sindel BM, Johnson SB, eds. 14th Australian Weeds Conference, Wagga Wagga, NSW. Sydney: Weed Society of New South Wales
- Chauhan BS, Gill G, Preston C (2006) Factors affecting seed germination of little mallow (*Malva parviflora*) in southern Australia. *Weed Sci* 54:1045–1050
- Chauhan BS, Johnson DE (2009) Germination ecology of spiny (*Amaranthus spinosus*) and slender amaranth (*A. viridis*): troublesome weeds of direct-seeded rice. *Weed Sci* 57:379–385
- Costea M, Weaver SE, Tardif FJ (2004) Biology of Canadian weeds 130. *Amaranthus retroflexus* L., *A. powellii* S. Watson and *A. hybridus* L. *Can J Plant Sci* 84:631–668
- Cousens RD, Baweja R, Vaths J, Schofield M (1993) Comparative biology of cruciferous weeds: a preliminary study. Pages 376–380 in Proceedings of the 10th Australian and 14th Asian-Pacific Weed Conference. Brisbane: Weed Society of Queensland
- Cristaudo A, Gresta F, Luciani F, Restuccia A (2007) Effects of after-harvest period and environmental factors on seed dormancy of *Amaranthus* species. *Weed Res* 47:327–334
- De Meddiburu F (2017) agricolae: statistical procedures for agricultural research. R package v.1.3-2. <https://cran.r-project.org/web/packages/agricolae/index.html>. Accessed: April 20, 2019

- Derakhshan A, Gherekhloo J, Vidal RA, De Prado R (2014) Quantitative description of the germination of little seed canarygrass (*Phalaris minor*) in response to temperature. *Weed Sci* 62:250–257
- Fenner M, Thompson K (2005) *The Ecology of Seeds*. Cambridge: Cambridge University Press. 260 p
- Gallagher RS, Cardina J (1998a) Phytochrome-mediated *Amaranthus* germination I: effect of seed burial and germination temperature. *Weed Sci* 46:48–52
- Gallagher RS, Cardina J (1998b) Phytochrome-mediated *Amaranthus* germination II: development of very low fluence sensitivity. *Weed Sci* 46:53–58
- Ghorbani R, Seel W, Leifert C (1999) Effects of environmental factors on germination and emergence of *Amaranthus retroflexus*. *Weed Sci* 47: 505–510
- Guo P, Al-Khatib K (2003) Temperature effects on germination and growth of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*Amaranthus palmeri*), and common waterhemp (*A. rudis*). *Weed Sci* 51:869–875
- Hao JH, Lv SS, Bhattacharya S, Fu JG (2017) Germination response of four alien congeneric *Amaranthus* species to environmental factors. *PLoS ONE* 12: e0170297
- Horak MJ, Peterson DE, Chessman DJ, Wax LM (1994) Pigweed identification: a pictorial guide to the common pigweeds of the Great Plains. Manhattan: Kansas Cooperative Extension Service Publication S80. 12 p
- Jha P, Norsworthy JK (2009) Soybean canopy and tillage effects on emergence of Palmer amaranth (*Amaranthus palmeri*) from a natural seed bank. *Weed Sci* 57:644–651
- Jha P, Norsworthy JK, Riley MB, Bridges W Jr (2008) Acclimation of Palmer amaranth (*Amaranthus palmeri*) to shading. *Weed Sci* 56:729–734
- Jha P, Norsworthy JK, Riley MB, Bridges W Jr (2010) Annual changes in temperature and light requirements for germination of Palmer amaranth (*A. palmeri*) seeds retrieved from soil. *Weed Sci* 58:426–432
- Kigel J (1994) Development and ecophysiology of amaranths. Pages 39–73 in Paredes-Lopez O, ed. *Amaranth Biology, Chemistry, and Technology*. Boca Raton, FL: CRC Press
- Leon RG, Owen MDK (2003) Regulation of weed seed dormancy through light and temperature interactions. *Weed Sci* 51:752–758
- Manalil S, Werth J, Jackson R, Chauhan BS, Preston C (2017) An assessment of weed flora 14 years after the introduction of glyphosate-tolerant cotton in Australia. *Crop Pasture Sci* 68:773–780
- McKeon GM, Mott JJ (1982) The effect of temperature on the field softening of hard seed of *Stylosanthes humilis* and *S. hamata* in a dry monsoonal climate. *Aust J Agric Res* 33:75–85
- Michel BE (1983) Evaluation of the water potential of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. *Plant Physiol* 72:66–70
- Milberg P, Andersson L, Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Sci Res* 10:99–104
- Nosratti I, Abbasi R, Bagheri AR, Bromandan P (2017) Seed germination and seedling emergence of Iberian starthistle (*Centaurea iberica*). *Weed Biol Manag* 17:144–149
- Oladiran JA, Mumford PM (1985) The stimulation of seed germination by temperature and light in agronomic *Amaranthus* species. *Biochem Physiol Pflanz* 180:45–54
- Oryokot JOE, Murphy SD, Swanton CJ (1997) Effect of tillage and corn on pigweed (*Amaranthus* spp.) seedling emergence and density. *Weed Sci* 45: 120–126
- Pons TL (2000) Seed responses to light. Pages 237–260 in Fenner M, ed. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd ed. Wallingford, UK: CABI Publishing
- Ritz C, Streibig JC (2008) *Nonlinear regression with R. useR! series*. New York: Springer. 144 p
- Roman ES, Murphy SD, Swanton CJ (2000) Simulation of *Chenopodium album* seedling emergence. *Weed Sci* 48:217–224
- RStudio (2019) *RStudio: Integrated Development Environment for R. Version 1.2.1335*. Boston, MA: RStudio
- Sarangi D, Irmak S, Lindquist JL, Knezevic SZ, Jhal AJ (2015) Effect of water stress on the growth and fecundity of common waterhemp (*Amaranthus rudis*). *Weed Sci* 64:42–52
- Seefeldt SS, Jensen SE, Fuerst EP (1995) Log-logistic analysis of herbicide dose-response relationship. *Weed Technol* 9:218–227
- Sellers BA, Smeda RJ, Johnson WG, Kendig JA, Ellersieck MR (2003) Comparative growth of six *Amaranthus* species in Missouri. *Weed Sci* 51:329–333
- Singh A, Kaur R, Kang JS, Singh G (2012) Weed dynamics in rice-wheat cropping system. *Global Biol Agri Heal Sci* 1:7–16
- Sohrabi S, Ghanbari A, Rasehd Mohassel MH, Gherekhloo J, Vidal RA (2016) Effects of environmental factors on *Cucumis melo* L. subsp. *agrestis* var. *agrestis* (Naudin) Pangalo seed germination and seedling emergence. *S Afr J Bot* 105:1–8
- Steckel LE (2004) *Pigweeds in Tennessee*. University of Tennessee, Knoxville, TN. 3 p
- Steckel LE, Sprague CL, Stoller EW, Wax LM (2004) Temperature effects on germination of nine *Amaranthus* species. *Weed Sci* 52:217–221
- Steinsiek JW, Oliver LR, Collins FC (1982) Allelopathic potential of wheat (*Triticum aestivum*) straw on selected weed species. *Weed Sci* 30:495–497
- Thomas WE, Burke IC, Spears JF, Wilcut JW (2006). Influence of environmental factors on slender amaranth (*Amaranthus viridis*) germination. *Weed Sci* 54:316–320
- Vieira BC, Samuelson SL, Alves GS, Gaines TA, Werle R, Kruger GR (2018) Distribution of glyphosate-resistant *Amaranthus* spp. in Nebraska. *Pest Manag Sci* 74:2316–2324
- Walker SR, Taylor IN, Milne G, Osten VA, Hoque Z, Farquharson RJ (2005) A survey of management and economic impact of weeds in dryland cotton cropping systems of subtropical Australia. *Aust J Exp Agri* 4:79–91
- Weaver SE (1984) Differential growth and competitive ability of *Amaranthus retroflexus*, *A. powellii* and *A. hybridus*. *Can J Plant Sci* 64:715–724
- Werle R, Sandell LD, Buhler DD, Hartzler RG, Lindquist JL (2014) Predicting emergence of 23 summer annual weed species. *Weed Sci* 62:267–279
- Werth J, Boucher L, Thornby D, Walker S, Charles G (2013). Changes in weed species since the introduction of glyphosate-resistant cotton. *Crop Past Sci* 64:791–798