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Effect of soil moisture regimes on the growth and fecundity of slender amaranth (*Amaranthus viridis*) and redroot pigweed (*Amaranthus retroflexus*)

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Abstract

Slender amaranth (*Amaranthus viridis* L.) and redroot pigweed (*Amaranthus retroflexus* L.) are increasingly problematic weeds of summer crops in Australia. Water is considered the most limiting factor in an agroecosystem, and water stress adversely impacts the growth and reproduction of plant species. The primary objective of this study was to determine the growth and fecundity of two Australian biotypes (Goondiwindi and Gatton) of *A. viridis* and *A. retroflexus* under water-stress conditions. Four water-stress treatments (100%, 75%, 50%, and 25% field capacity [FC]) at a 4-d irrigation interval were chosen. No difference was observed for growth and seed production between the two biotypes of both species when grown under varying soil moisture regimes. At 100% FC, *A. viridis* produced 44 g plant^{-1} aboveground biomass and 1,740 seeds plant^{-1}. The maximum growth (46 g plant^{-1}) and seed production (3,070 seeds plant^{-1}) of *A. retroflexus* were observed at 100% FC. The growth and seed production of both species were reduced with increased water-stress levels. Both weeds responded to water stress by decreasing the shoot:root biomass ratio. However, *A. viridis* (290 seeds plant^{-1}) and *A. retroflexus* (370 seeds plant^{-1}) were able to produce a significant number of seeds per plant even at 25% FC. Results suggest that both weeds will produce seeds under water-limiting conditions. Therefore, management strategies are required to minimize the growth and survival of weeds in water-deficit conditions.

Introduction

Slender amaranth (*Amaranthus viridis* L.) and redroot pigweed (*Amaranthus retroflexus* L.) are broadleaf annual weeds naturalized in temperate and warm temperate countries of the world, including countries in Africa, Asia-Pacific, and Europe (Holm et al. 1997; Uva et al. 1997; Waselkov and Olsen 2014). *Amaranthus viridis* and *A. retroflexus* are C_4 weeds with aggressive growth habits and are considered the most complex and widespread species of the genus *Amaranthus*, and each species causes monetary losses to crop production globally (Ward et al. 2013). Both weeds have high potential to compete with horticultural and field crops for resources such as light, water, and nutrients (Carvalho and Christoffoleti 2008). A significant yield reduction in many crops has been reported. For example, *A. retroflexus* infestations can reduce soybean [*Glycine max* (L.) Merr.] yield by 38%, depending on its density and time of emergence (Bensch et al. 2003). Multiple resistance in these weeds to acetolactate synthase– and photosystem II–inhibiting herbicides has been reported in many countries; however, there are no reports of the presence of herbicide-resistant biotypes of these weeds in Australia (Heap 2020).

In Australia, crop production is highly dependent on rainfall events, and climatic models have anticipated higher water deficiency in the future (Rengasamy 2002). In the wake of a changing climate, limited availability of water has become the major factor limiting crop production and food security. Weeds respond efficiently to changes in climate and cultural practices, which leads to the dominance of weeds in agricultural ecosystems (Mahajan et al. 2012). Bajwa et al. (2017) stated that drought-tolerant weeds, such as Santa Maria feverfew (*Parthenium hysterophorus* L.), grew vigorously and produced a significant number of seeds even at 50% field capacity (FC). The greater plasticity of weeds enables them to develop well in comparison with crops in a water-restricted environment (Chauhan and Mahajan 2014; Crusciol et al. 2001; Mahajan et al. 2015). Therefore, studying the effect of water stress on weeds could help in formulating better weed management strategies.

Water stress hinders growth, nutrient assimilation, and photosynthesis, ultimately causing a significant reduction in biomass production. Water stress destroys the thylakoid membrane and photosynthetic pigments and reduces chlorophyll content (Anjum et al. 2011). In the presence of water stress, a plant activates its resistance mechanism, such as drought avoidance, drought tolerance, drought recovery, or drought escape (Fang and Xiong 2015). The mechanisms are stronger in C_4 plants than in C_3 plants (Lawlor 2013; McLachlan and Swanton 1993; Stoller and Myers 1989). However, the resistance mechanism of *A. viridis* and *A. retroflexus* to cope with water-stress conditions is not fully understood. C_4 plants maintain a high level of photosynthetic and osmotic modification to boost the concentration of leaf solute, causing the stomata to remain open for a long period during water-stress conditions. This mechanism enables C_4 plants to maintain CO_2 diffusion to the chloroplast (Ehleringer 1983; Forseth and Ehleringer 1982).

Different weed species react to soil moisture stress differently; however, some weeds grow very well, complete their life cycles, and produce considerable amounts of seeds under water-stress conditions (Chauhan and Johnson 2010; Kaur et al. 2016). *Amaranthus viridis* and *A. retroflexus* are common weeds of Australia, and the interaction of these weeds with environmental changes has not been studied extensively. Consequently, it will be essential to explore the impact of various soil moisture levels on *A. viridis* and *A. retroflexus* growth and reproductive potential. Such parameters can also be used to assess and differentiate the invasive potential of different Australian biotypes of *A. viridis* and *A. retroflexus.* Therefore, a study was conducted to evaluate the impact of varied moisture regimes on the growth and reproductive behavior of two Australian biotypes of *A. viridis* and *A. retroflexus*. Such research could guide us in evaluating and comparing the invasiveness of these weeds under future water-limiting climate scenarios.

Materials and Methods

Plant Material

In 2016, seeds of two biotypes of *A. viridis* and *A. retroflexus* were collected from Goondiwindi (28.41°S, 150.23°E; altitude 210 m) and Gatton (27.45°S, 152.21°E, altitude 90 m), QLD, Australia, cleaned thoroughly, and stored separately at room temperature. Seeds from both biotypes of each species were regrown at Gatton to remove the maternal conditions (Mobli et al. 2019), and seeds collected from these plants were used in the present study. No seed dormancy–breaking treatment was used before planting. Seeds were germinated in trays containing commercial Platinum Potting Mix (Centenary Landscaping, NSW, Australia). The potting mix contained biological organic-based products and had a pH of 5.6 and an electrical conductivity of 1.6 dS m^{-1}. Seedlings were transplanted at the 5-leaf stage (4 to 6 cm in height) into black, free-draining pots of a size of 25 cm in diameter and 30 cm in height filled with soil collected from the Gatton farm of the University of Queensland. The soil was air-dried and passed through a 3-mm sieve to establish uniform consistency. Soil texture was heavy clay loam with a pH of 6.7, electrical conductivity of 0.14 dS m^{-1}, and organic matter content of 2.8%. Each pot was filled with 12 kg of oven-dried soil (90 C for 72 h). All pots were supplied with adequate water until the experiment commenced.

Soil Moisture Adjustment

Ten pots containing dry soil were weighed, watered until saturation, covered with a plastic sheet, and left in a shade house. After 24 h, the pots were weighed again to calculate the pot water contents, that is, 100% FC. The 75%, 50%, and 25% FCs were determined based on the fraction of the 100% FC. To reestablish FC in the pots during the study, an appropriate amount of tap water was added to the pots after every 4 d (Bajwa et al. 2017; Chauhan and Johnson 2010). The equation used for the calculation of pot water content is given below (Equation 1):

$$\text{Water-holding capacity} = (W_w - W_d) \times \frac{100}{W_d} \tag{1}$$

where W_w = weight of wet soil and W_d = weight of dry soil.

Experiments

In the summer of 2017 to 2018, a pot study was carried out in a naturally ventilated shade house (mean temperature = 28 C) at the University of Queensland, Gatton, Australia. The experiment was a two by two by four factorial arrangement of species (*A. viridis* and *A. retroflexus*), biotype (Gatton and Goondiwindi), and moisture regime (25%, 50%, 75%, and 100% FC) arranged in a randomized complete block design with three replications. Both *Amaranthus* species (Gatton and Goondiwindi biotypes) were grown at the four different soil moisture levels. The experiment ran for 84 d until the plants were fully matured and seed production had ceased. Plant height and number of leaves, biomass (shoot and root), inflorescence number per plant, and seed number per plant were recorded at maturity. The shoot and root parts (washed to remove the soil particles) were bagged separately and oven-dried for 3 d at 70 C. Afterward, the weight was determined to record shoot and root biomass, and shoot:root biomass ratio. The number of seeds per plant was calculated by taking a sample of 1 g of seed from each plant. The number of seeds in 1 g was counted and multiplied by the total seed weight of each plant. In the summer of 2018 to 2019, the experiment was repeated in the same conditions.

Data Analysis

Data from both species, biotypes, and experimental runs were subjected to ANOVA (GENSTAT 16th ed., VSN International, Hemel Hempstead, UK). Both biotypes of *A. viridis* and *A. retroflexus* (Gatton and Goondiwindi) responded similarly ($P > 0.05$) to the degree of moisture stress. The treatment by experimental run interaction was also not significant in either study; therefore, data from both biotypes and repeats were combined ($n = 12$ for each treatment). After being combined, the data were subjected to ANOVA and means were compared. Fisher's protected LSD mean comparison test at probability 0.05 was used. Figures were plotted using SigmaPlot v. 14 (Systat Software, San Jose, CA, USA).

Results and Discussion

Water stress had a significant effect ($P < 0.001$) on the growth and seed production of *A. viridis* and *A. retroflexus* (Table 1), and the highest effect on the plant's growth and seed production was observed at 25% FC (Figures 1–6).

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Table 1. ANOVAs for various plant parameters of two biotypes of *Amaranthus viridis* and *Amaranthus retroflexus* at maturity.[a]

Source	Degree of freedom	Plant height	Leaves	Inflorescences	Seeds	Shoot biomass	Root biomass	Shoot:root ratio
	—df—	—cm—	—no. plant^{-1}—			—g plant^{-1}—		
				P value				
Replication	11	0.26	0.30	0.35	0.60	0.16	0.50	0.21
Species	1	<0.001	<0.001	<0.001	<0.001	<0.001	0.37	0.57
Water treatment	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Species × water treatment	3	<0.001	<0.001	<0.001	<0.001	0.01	0.52	0.15
Error	77							

[a]Both biotypes of *A. viridis* and *A. retroflexus* from Gatton and Goondiwindi, QLD, Australia, responded similarly (P < 0.001) to water-stress levels. The treatment by experimental run interaction was also not significant in either study; therefore, data from both biotypes and runs were combined.

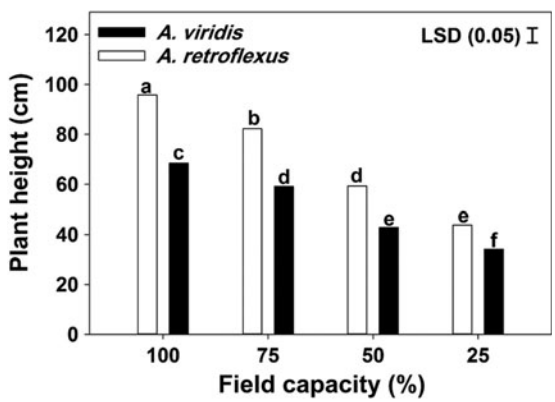

Figure 1. The effect of soil moisture on plant height of *Amaranthus viridis* and *Amaranthus retroflexus*. Moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bar represents LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

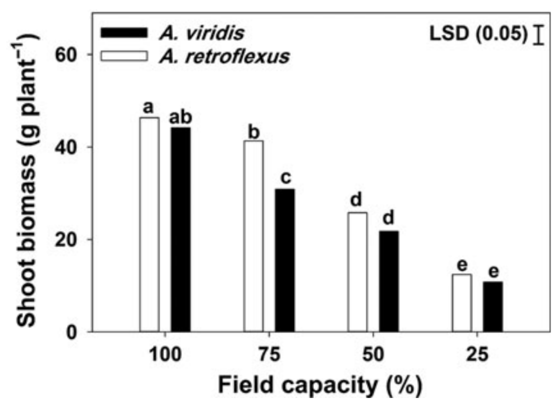

Figure 3. The effect of soil moisture on shoot biomass of *Amaranthus viridis* and *Amaranthus retroflexus*. The moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bar represents LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

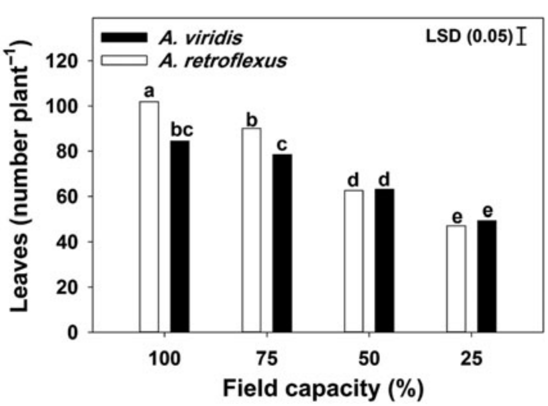

Figure 2. The effect of soil moisture on number of leaves of *Amaranthus viridis* and *Amaranthus retroflexus*. The moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bar represents LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

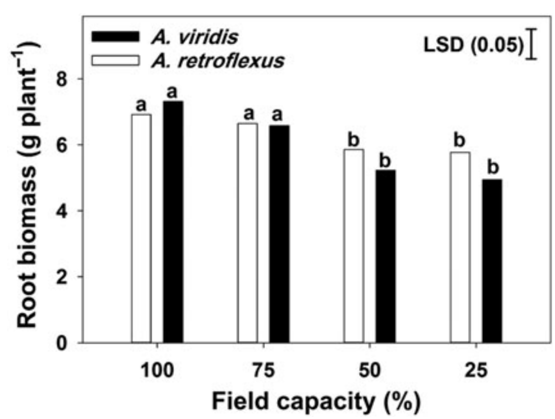

Figure 4. The effect of soil moisture on root biomass of *Amaranthus viridis* and *Amaranthus retroflexus* as described by a linear model. The moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bar represents LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

Plant Height

The effect of species, water treatments, and their interaction was significant (P < 0.001) on plant height of *A. viridis* and *A. retroflexus* (Table 1). Maximum height achieved by *A. viridis* and *A. retroflexus* plants was 83 and 106 cm, respectively (Figure 1). Compared with the no water stress treatment (100% FC), plant height of *A. viridis* was reduced by 14%, 37%, and 50% at 75%, 50%, and 25% FC, respectively. The corresponding reductions in plant height for *A. retroflexus* were 14%, 38%, and 54%, respectively.

Number of Leaves per Plant

Species, water treatments, and their interaction significantly affected the number of leaves (Table 1). In both weed species, the maximum number of leaves was produced in the 100% FC

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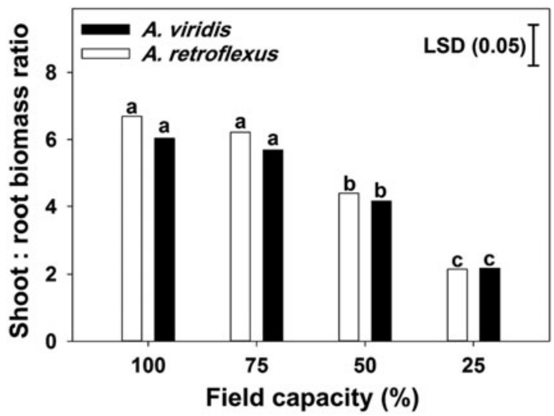

Figure 5. The effect of soil moisture on shoot:root biomass ratio of *Amaranthus viridis* and *Amaranthus retroflexus*. The moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bar represents LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

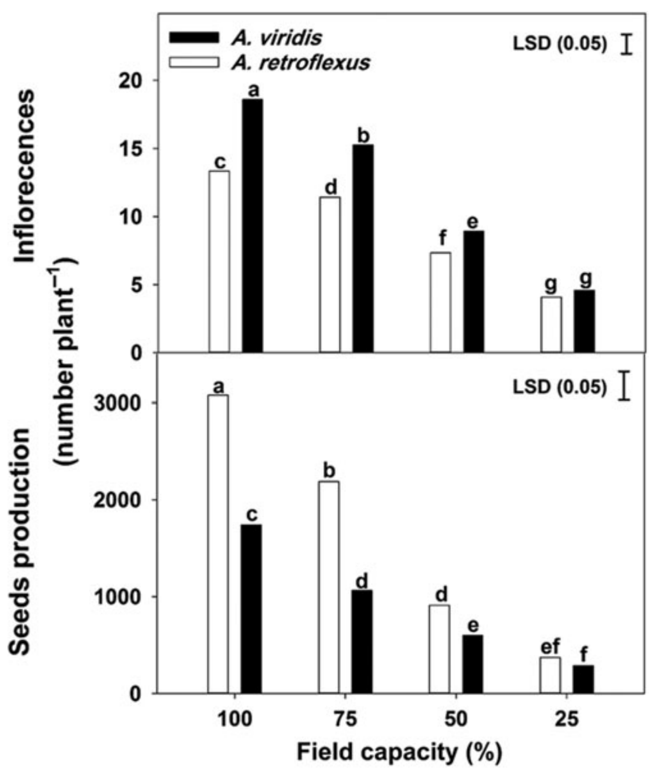

Figure 6. The effect of soil moisture on number of inflorescences and seeds of *Amaranthus viridis* and *Amaranthus retroflexus*. The moisture content was kept at 100%, 75%, 50%, and 25% of field capacity (FC). Vertical bars represent LSD at probability 5%. Data were pooled over biotype and experimental runs ($n = 12$). Letters above bars show group differences between means.

treatment (Figure 2). Leaf production by *A. viridis* and *A. retroflexus* plants was inversely proportional to the water stress applied to the plant. The maximum number of leaves produced by *A. viridis* and *A. retroflexus* plants at 25% FC was 53% and 54% fewer than that of plants at 100% FC, respectively.

Biomass

Although species, water treatments, and their interaction significantly ($P < 0.05$) affected shoot biomass, only the effect of water treatment on root biomass was significant ($P < 0.001$) (Table 1). Shoot and root biomass of both species declined with increasing water stress (Figures 3 and 4). The highest shoot biomass of *A. viridis* (44 g plant^{-1}) and *A. retroflexus* (46 g plant^{-1}) was observed at 100% FC. At 25% of FC, the shoot biomass of *A. viridis* and *A. retroflexus* plants were reduced by 76% and 73%, respectively, compared with the shoot biomass at 100% FC. No differences were observed between root biomass at 100% and 75% FC. At 50% FC, the root biomass of both species was decreased by 22% in comparison with 100% FC; however, no differences were observed between root biomass at 50% and 25% FC.

In the rainfed Australian agricultural system, plants may experience severe water-deficit conditions with changes in rainfall patterns (longer dry conditions and sporadic distribution). Soil moisture plays a key role in weed establishment, growth, and regeneration (Chauhan and Johnson 2010). Weed species respond phenologically and physiologically to different levels of water availability (Bajwa et al. 2017; Chauhan and Johnson 2010). However, the impact of drought conditions on plants depends largely upon plant species and timing, extent, and duration of drought (Stout and Simpson 1978). In the current study, although growth and seed production of *A. viridis* were lower than for *A. retroflexus*, both weed species responded similarly to moisture stress.

In the current study, a sharp decline in *A. viridis* and *A. retroflexus* plant height, number of leaves, and biomass production was observed at 25% FC in comparison to 100% FC. It seems that severe water stress resulted in the reduction of fitness, as both weeds produced lower biomass, but could not completely inhibit the growth and seed production of these species. Sarangi et al. (2016) reported that high water stress (25% FC) could reduce the growth index of waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer] by 43% in comparison with no water-stress conditions (100% FC). Studies on other *Amaranthus* species (Palmer amaranth [*Amaranthus palmeri* S. Watson], grain amaranth [*Amaranthus cruentus* L.], and *A. tuberculatus*) showed that severe moisture stress hindered their growth but could not completely inhibit their vegetative growth (Moore and Franklin 2011; Moran and Showler 2005; Olufolaji and Ojo 2010; Sarangi et al. 2016).

Shoot:Root Biomass Ratio

Only the effect of soil moisture was significant ($P < 0.001$) on shoot:root ratio of *A. viridis* and *A. retroflexus* (Table 1). The shoot:root biomass ratio declined with increasing water-stress levels (Figure 5). The shoot:root biomass ratio of both species was similar between 75% and 100% FC. In both species, the highest decline in the shoot:root biomass ratio was observed at 25% FC. At 25% FC, the shoot:root biomass ratio of both species was reduced by 67% in comparison with 100% FC.

Water stress had a significant impact on the shoot and root biomass of both weed species, and consequently, the shoot:root biomass declined. Likewise, in *A. tuberculatus* and junglerice [*Echinochloa colona* (L.) Link] (C_4 plants), the lowest shoot:root biomass ratio was observed at a high water-stress condition (Mahajan et al. 2019; Sarangi et al. 2016). Studies showed that some drought-tolerant plants respond to drought conditions by reducing aboveground vegetation to avoid shoot dehydration and increase water-use efficiency (Ogburn and Edwards 2010; Tardieu 2013). Although changes in the shoot:root biomass ratio could be a criterion for explaining a plant's response to drought conditions, biochemical and molecular studies are required to elucidate the mechanism of drought tolerance in a plant (Ali et al. 2009; Fang and Xiong 2015).

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Inflorescences and Number of Seeds per Plant

The effect of species, water treatments, and their interaction was significant ($P < 0.001$) for the number of inflorescences and seed production of *A. viridis* and *A. retroflexus* (Table 1). The number of inflorescences and seeds per plant of both species declined with increasing water stress (Figure 6). Compared with 100% FC, 52% and 45% reductions of the maximum number of inflorescences of *A. viridis* and *A. retroflexus* were observed at 50% FC, respectively. Similarly, the maximum number of seeds of *A. viridis* and *A. retroflexus* was reduced by 66% and 70% at 50% FC in comparison with 100% FC, respectively. At 100% FC, *A. viridis* and *A. retroflexus* produced 3,070 and 1,740 seeds plant^{-1}, respectively. Although seed production was strongly affected by soil moisture, even at 25% FC, *A. viridis* and *A. retroflexus* plants produced 290 and 370 seeds plant^{-1}, respectively.

Seed production is the major contributor in weed infestations, as even a small number of seeds per plant can cause a major infestation in the subsequent crop season. In the current study, despite a high biomass reduction in *A. viridis* and *A. retroflexus*, both weeds produced a significant number of seeds per plant, even at 25% FC. A similar reduction in seed production of *E. colona* and *A. tuberculatus* has been reported as a result of increased water-stress levels (Mahajan et al. 2019; Sarangi et al. 2016). It could be concluded that drought-tolerant species can sustain their reproductive growth even at a high level of soil moisture stress. Despite high seed retention of *Amaranthus* species at crop maturity and a high potential for control of their seed by harvest weed seed control strategies, these weeds should be managed at the earliest stage due to high competition for resources and their large seed production in drought conditions (Sarangi et al. 2016; Schwartz et al. 2016; Schwartz-Lazaro et al. 2017).

In the present study, severe water stress after *A. viridis* and *A. retroflexus* establishment reduced the growth and seed production of these weeds, but both weeds completed their life cycles. Both biotypes of *A. viridis* and *A. retroflexus* from Gatton and Goondiwindi responded similarly to water stress. Similarly, Sarangi et al. (2016) observed no significant differences between growth and seed production of *A. tuberculatus* biotypes under different water-stress levels. Gioria and Pyšek (2017) and Bajwa et al. (2018) have claimed that different responses of weed biotypes to environmental stress could be attributed to maternal conditions during plant development and genetic diversity between biotypes. In the current study, the effect of maternal conditions on seeds was removed by growing both biotypes in the same environment, and it could be concluded that a similar response of these biotypes to moisture stress was an innate trait.

Both weeds have an aggressive growth habit and are capable of high biomass production, factors that impact crop growth and yield due to severe competition for resources in the critical weed-free period (Horak and Loughin 2000). Patterson (1995) reported that water stress has a significant impact on the critical weed-free period in different crop species. Furthermore, it has been reported that POST herbicide efficacy in *Amaranthus* species may be influenced by water-stress conditions (Slabbert and Krüger 2011). Although our results showed that these weeds could be troublesome in water-stress conditions, the competitiveness, fitness, and responses of these weeds to management strategies under drought conditions should be assessed. Comprehensive knowledge of the response of these *Amaranthus* species under water-stress conditions is essential to develop integrated weed management tactics for these species.

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