Weed Science

cambridge.org/wsc

Research Article

Cite this article: Chahal PS, Irmak S, Jugulam M, Jhala AJ (2018) Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors. Weed Sci 66:738–745. doi: 10.1017/wsc.2018.47

Received: 25 March 2018
Revised: 10 June 2018
Accepted: 27 June 2018

Associate Editor:
Martin M. Williams II, USDA–ARS

Key words:
Decagon; degree of water stress; field capacity; moisture sensors; seed production

Author for correspondence:
Amit J. Jhala, Department of Agronomy and Horticulture, University of Nebraska–Lincoln, Lincoln, NE 68583. (Email: Amit.Jhala@unl.edu)

Evaluating Effect of Degree of Water Stress on Growth and Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors

Parminder S. Chahal[1], Suat Irmak[2], Mithila Jugulam[3] and Amit J. Jhala[4]

[1]Graduate Research Assistant, University of Nebraska–Lincoln, Lincoln, NE, USA, [2]Professor, Department of Biological Systems Engineering, University of Nebraska–Lincoln, Lincoln, NE, USA, [3]Associate Professor, Department of Agronomy, Kansas State University, Manhattan, KS, USA and [4]Assistant Professor, Department of Agronomy and Horticulture, University of Nebraska–Lincoln, Lincoln, NE, USA

Abstract

Palmer amaranth (*Amaranthus palmeri* S. Watson) is the most problematic weed in agronomic crop production fields in the United States. The objective of this study was to determine the effect of degree of water stress on the growth and fecundity of *A. palmeri* using soil moisture sensors under greenhouse conditions. Two *A. palmeri* biotypes collected from Nebraska were grown in loam soil maintained at 100%, 75%, 50%, 25%, and 12.5% soil field capacity (FC) corresponding to no, light, moderate, high, and severe water stress levels, respectively. Water was regularly added to pots based on soil moisture levels detected by Watermark or Decagon 5TM sensors to maintain the desired water stress level. *Amaranthus palmeri* plants maintained at ≤25% FC did not survive more than 35 d after transplanting. *Amaranthus palmeri* at 100%, 75%, and 50% FC produced similar numbers of leaves (588 to 670 plant^{-1}) based on model estimates; however, plants at 100% FC achieved a maximum height of 178 cm compared with 124 and 88 cm at 75% and 50% FC, respectively. The growth index (1.1×10^5 to 1.4×10^5 cm^3 plant^{-1}) and total leaf area (571 to 693 cm^2 plant^{-1}) were also similar at 100%, 75%, and 50% FC. *Amaranthus palmeri* produced similar root biomass (2.3 to 3 g plant^{-1}) at 100%, 75%, and 50% FC compared with 0.6 to 0.7 g plant^{-1} at 25% and 12.5% FC, respectively. Seed production was greatest (42,000 seeds plant^{-1}) at 100% FC compared with 75% and 50% FC (14,000 to 19,000 seeds plant^{-1}); however, the cumulative seed germination was similar (38% to 46%) when mother plants were exposed to ≥50% FC. The results of this study show that *A. palmeri* can survive ≥50% FC continuous water stress conditions and can produce a significant number of seeds with no effect of on seed germination.

Introduction

Water stress is one of the major limiting factors for optimum crop production (Benjamin and Nielsen 2006; Wu et al. 2013). A plant's water stress resistance mechanisms, which include drought avoidance, drought tolerance, drought recovery, or drought escape, allow C_4 plant species to maintain growth and development more than C_3 species under water stress and higher irradiance levels (Lawlor 2013; McLachlan et al. 1993; Steckel et al. 2003; Stoller and Myers 1989). Being a C_4 species, Palmer amaranth (*Amaranthus palmeri* S. Watson) can adapt to water stress conditions using drought tolerance as a mechanism (Ehleringer 1983).

Amaranthus palmeri is the most troublesome weed species in agronomic crop production systems in the United States (Chahal et al. 2015, 2017; Kohrt and Sprague 2017), and its interference can cause significant yield losses in crops, including corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] (Klingaman and Oliver 1994; Liphadzi and Dille 2006; Massinga et al. 2001). *Amaranthus palmeri* and other C_4 species such as spotted mallow (*Malvastrum rotundifolium* A. Gray) can maintain a high photosynthetic capacity and growth under water stress conditions using osmotic adjustment to increase leaf solute concentration, allowing the stomata to remain open longer during conditions of water stress and maintain CO_2 diffusion to chloroplasts (Ehleringer 1983, 1985; Forseth and Ehleringer 1982).

Amaranthus palmeri was historically located in the Sonoran Desert and began spreading to the southern and midwestern United States in recent years (Chahal et al. 2015; Jhala et al. 2014). The spread and dominance of *A. palmeri* over other weed species could be related to its growth characteristics, ability to survive and reproduce under water stress conditions, or evolution of resistance to distinct site-of-action herbicides. *Amaranthus palmeri* biotypes have evolved resistance to herbicides that inhibit microtubule function (Group 3), acetolactate synthase (Group

2), photosystem II (Group 5), 5-enol-pyruvylshikimate-3-phosphate synthase (Group 9), 4-hydroxyphenylpyruvate dioxygenase (Group 27), and protoporphyrinogen oxidase (Group 14) in different states in the United States (Heap 2017).

Amaranthus palmeri, waterhemp [*Amaranthus tuberculatus* (Moq.) J. D. Sauer], and redroot pigweed (*Amaranthus retroflexus* L.) are the most commonly found *Amaranthus* species in Nebraska agronomic crop fields (Vieira et al. 2018); however, they differ in their growth characteristics (Horak and Loughin 2000). *Amaranthus palmeri* has the highest plant dry weight, leaf area, height, growth rate (0.10 to 0.21 cm per growing degree day), and water-use efficiency compared with other pigweed species (Berger et al. 2015; Horak and Loughin 2000; Massinga et al. 2003; Wiese 1968). *Amaranthus palmeri* roots are finer, longer, and greater in number, allowing it to occupy a much larger soil volume and acquire more soil nutrients compared with most crops, especially during conditions of water stress and low fertility (Wright et al. 1999a). In addition, *A. palmeri* is a prolific seed producer, and if left uncontrolled, a single female plant can produce as many as 600,000 seeds (Keeley et al. 1987). With increasing soil water stress, some studies have reported reduced growth and fecundity of different weed species, including *A. palmeri* (Chauhan 2013; Chauhan and Johnson 2010; Sarangi et al. 2015; Webster and Grey 2008). In addition, a few studies have reported the growth response of *A. palmeri* exposed to different durations of levels of water stress for a few weeks and then irrigated back to saturated conditions (Chandi et al. 2013; Paudel et al. 2016). However, *A. palmeri* fecundity and seed germination parameters were not studied. Weed seed germination is an important component of weed management strategies and is influenced by environmental factors such as water availability, light, temperature, and photoperiod during seed development (Baskin and Baskin 1998; Fenner 1991).

Studies evaluating a plant's response to water stress are often performed under greenhouse or controlled environmental conditions, with the plants growing in pots to maintain them at a certain water stress level for a limited time or throughout the growing period. The most common approach used to maintain desired water stress level in previous studies has been to weigh the pots to determine water loss from the soil and then add the desired amount of water (Chandi et al. 2013; Chauhan 2013; Chauhan and Johnson 2010; Earl 2003; Sarangi et al. 2015). Because it is not possible to separately determine the weight of the plant growing in the pot when using this method, plant weight is normally included along with the weight of soil and water, resulting in inaccurate information regarding the actual amount of water present in the pot soil. This could result in an error during rewatering, especially as plants grow larger. Additionally, this method is labor intensive and time-consuming, because all the pots must be weighed at regular intervals until the end of the study. The labor required for weighing and watering the pots can be reduced by using soil moisture sensors such as Decagon 5TE (Decagon Devices, 2365 NE Hopkins Court, Pullman, WA 99163) or Watermark (Irrometer Company, 1425 Palmyrita Avenue, Riverside, CA 92507) sensors. These sensors are very accurate in determining moisture stress in real time. Therefore, moisture sensors would allow researchers to measure soil moisture content more frequently and maintain the water stress level within a narrow, predetermined range (Irmak et al. 2016). The Decagon 5TM sensor is a frequency-domain reflectometry sensor that measures soil water content directly as a percent volume and performs well in loam and silt loam soils (Paudel et al. 2016; Zhu 2016). The Watermark granular matrix sensor measures soil matric potential in kilopascals (kPa) or centibars (cb) and converts the matric potential outputs to soil water content through developed soil-specific soil–water retention curves (Saxton and Rawls 2006). No information is available regarding the growth and fecundity of *A. palmeri* exposed to different water stress levels throughout its growing period. The objective of this study was to determine the effect of degree of water stress on growth, fecundity, and seed germination of *A. palmeri* biotypes from Nebraska using soil moisture sensors.

Materials and Methods

Plant Materials

Amaranthus palmeri seeds were collected from two different production fields located in Thayer County and Fillmore County, NE, and were stored in separate paper bags in a refrigerator at 4 C in the dark for 5 to 6 mo until used in this study. Seeds from both biotypes were planted in germination trays containing potting mix (Berger BM1 All-Purpose Mix, Berger Peat Moss, Saint-Modeste, QC, Canada), and seedlings were later transplanted in 72-cell germination trays and kept under greenhouse conditions. Seedlings of 6 to 8 cm in height were transplanted into round, free-draining black plastic pots (20-cm diameter and 30-cm height) containing 10 kg of finely ground loam texture soil with 1 plant pot^{-1}. Each pot was filled with dry soil, and the soil was lightly tapped from the top using a wooden block to ensure homogeneous soil bulk density within and between the pots. Pots were watered lightly every other day to avoid transplant shock until the initiation of water stress treatments at 7 d after transplanting (DAT). The study was conducted in a greenhouse at the University of Nebraska–Lincoln that was maintained at a 28/24 C day/night temperature, and plants were supplied with 24–8–16 commercial plant fertilizer (Miracle-Gro® Water Soluble All Purpose Plant Food, Scotts Miracle-Gro Products, 14111 Scottslawn Road, Marysville, OH 43041) in irrigation water every 14 d throughout the study period. Overhead metal-halide lamps with 600 mmol photon m^{-2} s^{-1} light intensity were used to provide supplemental light in the greenhouse to maintain a 16-h photoperiod. Treatments were arranged in a randomized complete block design with four replications, and the experiment was repeated in time under the same greenhouse conditions as described above.

Soil Water Content

The soil used in this study was collected from a field near Lincoln, NE, with no known history of herbicide usage for the last 10 yr. The soil was a Crete silt loam texture (fine, smectitic, mesic Pachic Udertic Argiustolls) with a pH of 7.7 and particle size distribution of 37% sand, 19% clay, 44% silt, and 1.9% organic matter content. The permanent wilting point and saturation point values of the soil were 12.8% and 44.6% volumetric, respectively. The soil had a bulk density of 1.2 g cm^{-3} and a field capacity (FC) of 33.5% by volume based on soil test reports, and an FC of 28% by weight calculated using the following equation (Hillel 1998):

$$\theta_g = \theta_v / \rho_b \qquad [1]$$

where θ_g is the percent gravimetric soil water content, θ_v is the percent volumetric soil water content, and ρ_b is the soil bulk density in grams per cubic centimeter.

The study included five soil water stress treatments: 100%, 75%, 50%, 25%, and 12.5% of the soil FC corresponding to no,

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press

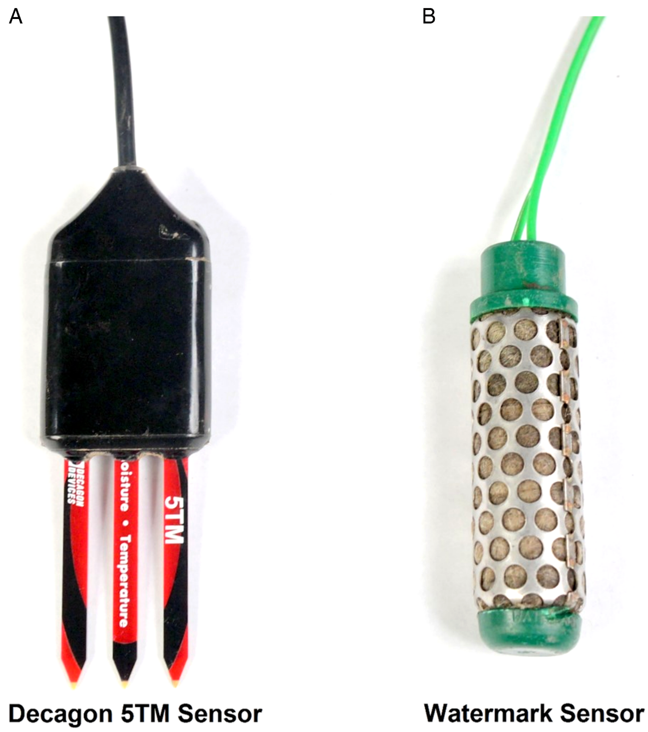

Figure 1. Soil moisture content in pots was measured using (A) Decagon 5TM and (B) Watermark soil moisture sensors to determine degree of water stress on growth and fecundity of *Amaranthus palmeri* biotypes in a greenhouse study conducted for 77 d after transplanting at the University of Nebraska–Lincoln.

light, moderate, high, and severe water stress levels, respectively (Sarangi et al. 2015). Soil water content in the pots was measured using Decagon 5TM and Watermark soil moisture sensors (Figure 1A and B). To convert the Watermark sensor–measured matric potential values to volumetric water content, a retention curve was developed for this specific experimental soil using the Soil-Water Characteristics Software (v. 6.02.74) developed by Saxton and Rawls (2006), which calculates soil hydraulic properties from soil textural properties (Irmak et al. 2016; Rawls 1983; Rawls et al. 1998; Saxton et al. 1986). The retention curve equation is:

$$\mathrm{SWC} = [(-5.818 \times \ln(\mathrm{SMP})) + 51.228] \quad [2]$$

where SWC is the percent volumetric soil water content and SMP is the soil matric potential measured by the Watermark sensor in kilopascals.

The Watermark sensor operates at a range of 0 to 239 kPa (Irmak and Haman 2001; Irmak et al. 2016), which is an effective range of soil-water status for most agricultural soils and corresponds to saturated to 58% of the volumetric FC conditions in this study. Therefore, this sensor was used to measure soil water content for the 100% and 75% FC treatments, and Decagon 5TM sensors were used for the 50%, 25%, and 12.5% FC treatments. A Watermark sensor was installed vertically 10- to 12-cm deep in each pot for the 100% and 75% FC treatments, and a Decagon 5TM sensor was installed vertically at the same depth in each pot for the 50%, 25%, and 12.5% FC treatments. Because the soil has a gravimetric FC of 28%, 2.8 L of water (28% of 10 kg soil) was added per pot at 7 DAT to maintain 100% gravimetric FC. Similarly, 2.1 (75% of 2.8 L), 1.4 (50% of 2.8), 0.7 (25% of 2.8), and 0.35 (12.5% of 2.8) L of water was added to maintain 75%, 50%, 25%, and 12.5% soil FC, respectively, with a range of ±2% set for all water stress treatments. Soil moisture data from Watermark and Decagon data loggers were recorded twice a day, and the required amount of water was added evenly on top of the soil to maintain soil FC.

A preliminary study was conducted under the same greenhouse conditions described earlier to compare the efficacy of the Decagon 5TM and Watermark sensors in the pots. Both sensors were installed 10- to 12-cm deep in the same pot filled with 10 kg soil with a total of 6 pots and 2.8 L of water added to each pot to maintain 100% soil FC. Soil moisture data were recorded from the data loggers 1 d after watering, and the results suggested that volumetric FC values recorded from Decagon and Watermark loggers corresponded very closely with the volumetric FC of soil provided by the soil test report (unpublished data).

Data Collection

Amaranthus palmeri height, number of leaves per plant, and growth index were determined at 7-d intervals starting from 21 DAT until plants were harvested upon maturity at 77 DAT. Growth index can be defined as a quantitative indicator of plant growth rate used to compare plants grown under different soil water conditions and was calculated using the following equation (Irmak et al. 2004; Sarangi et al. 2015):

$$\mathrm{GI}(cm^3) = \pi \times (w/2)^2 \times h \quad [3]$$

where w is the width of the plant calculated as an average of two widths, one measured at the widest point and another at 90° to the first; and h is the plant height measured from the soil surface to the last stem node at the top.

Upon maturity, all leaves were removed from each stem to measure the total leaf area for each plant using a leaf area meter (LI-3100C Area Meter, Li-Cor, Lincoln, NE 68504). Seed heads were collected from female plants, and seeds were cleaned with a seed cleaner. Plant stems were cut from the soil surface and roots were removed from the pots; stems and roots were washed with water in a container and air-dried for 24 h. The leaves, shoots, and roots from each plant were stored separately in paper bags and oven-dried at 65 C for 7 d. The aboveground and root biomass were weighed. The number of seeds produced per female plant from each water stress treatment were calculated by dividing total seed weight per plant by an average weight of four samples of 200 seeds plant^{-1}. Seeds were stored in the refrigerator at 4 C in the dark for 4 to 5 mo. To determine the germination percentage of seeds, 200 seeds from each female plant were placed on a piece of moist Whatman No. 4 filter paper (GE Healthcare UK, Amersham Place, Little Chalfont, Buckinghamshire HP7 9NA, UK) in a petri dish. All petri dishes were stored for 21 d in a growth chamber maintained at a 35/28 C day/night temperature with a 16-h photoperiod, and an appropriate amount of water was added every 2 d to keep the filter paper wet. Fluorescent lamps were used to produce a light intensity of 85 mmol m^{-2} s^{-1}. The total number of seeds germinated was counted and converted to percent germination compared with the number of seeds placed in each petri dish.

Statistical Analysis

Amaranthus palmeri height (cm), number of leaves per plant, growth index (cm^3), aboveground and root biomass per plant (g), total leaf area per plant (cm^2), and number of seeds per female plant from both *A. palmeri* biotypes were subjected to ANOVA

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press

using the PROC GLIMMIX procedure in SAS v. 9.3 (SAS Institute, Cary, NC 27513). *Amaranthus palmeri* biotypes, water stress treatments, and experimental runs were considered fixed effects in the model, and blocks were considered random effects. No significant experimental run by treatment or biotype by treatment interaction was observed; therefore, data were combined over two experimental runs and *A. palmeri* biotypes. Before analysis, data were tested for normality and homogeneity of variance using a Shapiro-Wilk goodness-of-fit test and Levene's test in SAS. The normality and homogeneity of variance assumptions were met; therefore, no data transformation was required. Where the ANOVA indicated treatment effects were significant, means were separated at $P \leq 0.05$ with Tukey-Kramer's pairwise comparison test to reduce type I error for series of comparisons.

A four-parameter log-logistic function was fit to number of leaves per plant, plant height, and growth index data using the 'drc' package c (drc 2.3, Christian Ritz and Jens Strebig; R 3.1.0, Kurt Hornik, online) in R statistical software (R Foundation for Statistical Computing, Vienna, Austria) (Knezevic et al. 2007):

$$Y = c + \left\{ \frac{d}{1 + \exp[b(\log x - \log e)]} \right\} \quad [4]$$

where Y is the number of leaves per plant, plant height, or growth index; x is the days after transplanting; c is the estimated minimum number of leaves per plant, plant height, or growth index; d is the estimated maximum leaves per plant, plant height, or growth index; e is the time taken to achieve 50% of leaves per plant, plant height, or growth index; and b represents the relative slope around the parameter e. A t-test was used to determine whether the water stress treatments significantly affected minimum and maximum plant height, number of leaves per plant, or growth index; rate of change of plant height, number of leaves per plant, or growth index with time; and time taken to achieve 50% of maximum plant height, number of leaves per plant, or growth index.

Results and Discussion

Water stress treatments at 100%, 75%, and 50% FC did not affect the number of leaves produced (534 to 626 leaves plant^{-1}) as estimated by the four-parameter log-logistic model (Table 1; Figure 2A). In contrast, Sarangi et al. (2015) reported a greater number of *A. tuberculatus* leaves produced at 100% FC (231 leaves plant^{-1}) compared with 75% FC (185 leaves plant^{-1}) and 50% FC (161 leaves plant^{-1}). Chauhan and Abugho (2013) reported 134 to 147 leaves plant^{-1} for spiny amaranth (*Amaranthus spinosus* L.) at 100% and 75% FC compared with 104 leaves at 50% FC. *Amaranthus palmeri* plants at 75% and 100% FC took 53 to 56 d to produce 50% of the maximum number of leaves compared with 60 d at 50% FC. Similarly, *A. spinosus* at 75% and 100% FC took 30 to 32 d to produce 50% of the maximum number of leaves compared with 26 d at 50% FC (Chauhan and Abugho 2013). *Amaranthus palmeri* maintained at 25% and 12.5% FC did survive only up to 35 DAT, and the four-parameter log-logistic model did not provide a good fit for the number of leaves per plant, plant height, or growth index; therefore, data are not presented.

Amaranthus palmeri height was reduced with increasing levels of water stress as estimated by the log-logistic model. *Amaranthus palmeri* maintained at 100% FC achieved a maximum height of 178 cm compared with 124 and 88 cm at 75% and 50% FC, respectively (Table 1; Figure 2B). Similarly, Chandi et al. (2013)

Table 1. Parameter estimates and test of lack of fit at 95% level for the four-parameter log-logistic function[a] fit to *Amaranthus palmeri* leaves per plant, plant height, and growth index under different degrees of water stress in a greenhouse experiment conducted for 77 d after transplanting at the University of Nebraska–Lincoln.

Water stress treatment[b,c]	c[c,d]	d[c,d]	e[c,d]	b[c,d]	Lack of fit[e]
		———Leaves plant^{-1}———			
100% FC (no water stress)	103 ± 17 a	626 ± 65 a	53 ± 2.6 a	−6.6 ± 1.6 a	0.6
75% FC (light water stress)	82 ± 18 a	567 ± 58 a	56 ± 2.3 ab	−7.0 ± 1.8 a	0.7
50% FC (moderate water stress)	73 ± 14 a	534 ± 69 a	61 ± 2.4 b	−9.5 ± 3.2 a	0.4
		———Plant height (cm)———			
100% FC (no water stress)	35 ± 3 a	178 ± 6.5 a	50 ± 1.3 a	−5.3 ± 0.6 a	0.3
75% FC (light water stress)	30 ± 2.4 a	124 ± 5.6 b	54 ± 1.5 a	−6.5 ± 1.0 a	0.4
50% FC (moderate water stress)	27 ± 2.7 a	88 ± 7.6 c	53 ± 3.0 a	−5.3 ± 1.3 a	0.7
		———Growth index (cm^3)[f,g]———			
100% FC (no water stress)	0.2 ± 0.06 a	1.2 ± 0.1 a	46 ± 2.1 a	−6.7 ± 2.2 a	0.9
75% FC (light water stress)	0.06 ± 0.007 a	1.4 ± 0.7 a	67 ± 21 a	−3.8 ± 1.8 a	1.0
50% FC (moderate water stress)	0.06 ± 0.007 a	1.1 ± 0.2 a	82 ± 12 a	−3.4 ± 1.1 a	0.5

[a] $Y = c + \{d - c/1 + \exp[b(\log x - \log e)]\}$, where Y is the number of leaves per plant, plant height, or growth index; x is the days after transplanting; c is the estimated minimum number of leaves per plant, plant height, or growth index; d is the estimated maximum number of leaves per plant, plant height, or growth index; e is the time taken to achieve 50% of leaves per plant, plant height, or growth index; and b represents the relative slope around the parameter e.
[b] Abbreviation: FC, field capacity.
[c] *Amaranthus palmeri* maintained at 25% and 12.5% soil FC did not survive more than 35 DAT, and the four-parameter log-logistic model did not provide a good fit for number of leaves per plant, plant height, or growth index; therefore, data are not presented for 25% and 12.5% FC.
[d] Means within columns with no common letter(s) are significantly different at $P \leq 0.05$.
[e] A test of lack of fit at the 95% level was not significant for any of the curves tested for the water stress treatments, indicating that the fitted model was correct.
[f] Growth index $= \pi \times (w/2)^2 \times h$, where w is the width of the plant calculated as an average of two widths, one measured at the widest point and another at 90° to the first; and h is the plant height measured from the soil surface to the last stem node at the top.
[g] Values presented for estimated minimum (c) and maximum growth index (d) are divided by 10^5.

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press

reported 5% to 15% reduction in the height of 15 *A. palmeri* biotypes under water stress conditions employed for 3 to 9 d compared with no water stress. Sarangi et al. (2015) also reported an *A. tuberculatus* height of 163 cm at 100% FC compared with 146 and 115 cm at 75% and 50% FC, respectively, in a greenhouse study. However, *A. spinosus* produced the greatest height of 128 to 137 cm at 100% and 75% FC compared with 73 cm at 50% FC (Chauhan and Abugho 2013). The model estimated that *A. palmeri* grown at 100%, 75%, or 50% FC took a similar number of days (50 to 54 DAT) to achieve 50% of maximum height. *Amaranthus palmeri* at 100% FC had greater growth index compared with 75% and 50% FC at 21 to 70 DAT based on the fitted model curve (Figure 2C); however, the maximum growth index did not vary (1.1×10^5 to 1.4×10^5 cm^3 $plant^{-1}$) among 100%, 75%, and 50% FC treatments (Table 1; Figure 2C). In contrast, Sarangi et al. (2015) reported the highest growth index of *A. tuberculatus* (4.4×10^5 cm^3 $plant^{-1}$) at 100% FC compared with 75% (3.1×10^5 cm^3 $plant^{-1}$) and 50% FC (1.5×10^5 cm^3 $plant^{-1}$), possibly because of greater width of *A. tuberculatus* plants compared with *A. palmeri*.

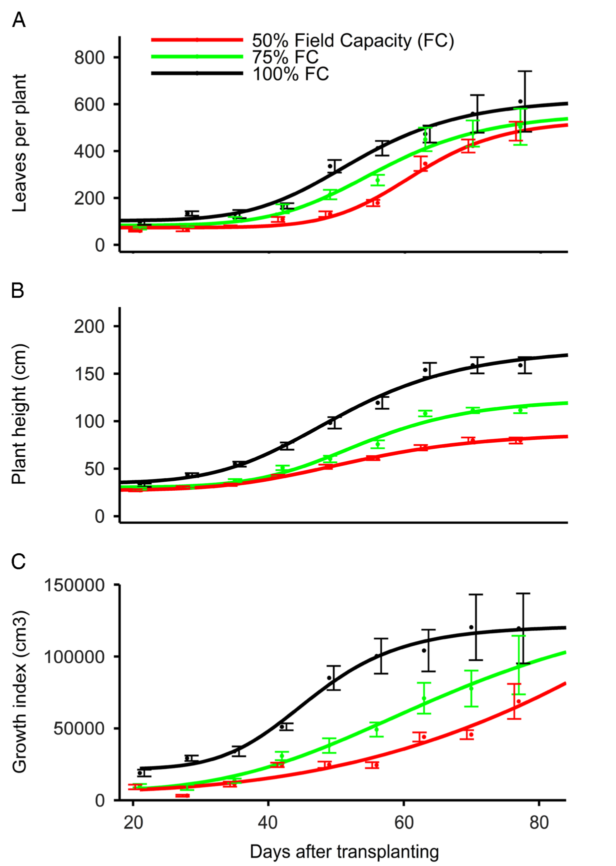

Figure 2. Effect of degree of water stress on (A) leaves per plant, (B) plant height, and (C) growth index of *Amaranthus palmeri* in a greenhouse study conducted for 77 d after transplanting at the University of Nebraska–Lincoln. The 100%, 75%, 50%, 25%, and 12.5% field capacity (FC) treatments were considered as no, light, moderate, high, and severe water stress level, respectively. *Amaranthus palmeri* maintained at 25% and 12.5% soil FC did not survive more than 35 d after transplanting, and the four-parameter log-logistic model did not provide a good fit for number of leaves per plant, plant height, or growth index; therefore, curves are not presented for 25% and 12.5% FC.

Amaranthus palmeri maintained at 25% and 12.5% FC died without producing seeds; therefore, only root, leaf, and stem biomass data collected at 35 DAT are presented (Table 2). The permanent wilting point of soil used in this study was 12.8% by volume, corresponding to 46% FC; therefore, the soil water available at 25% and 12.5% FC was below the permanent wilting point and could have resulted in plant death. Plants maintained at 100% FC were the tallest; therefore, they produced the greatest dry stem biomass of 22.3 g $plant^{-1}$ compared with 13.3 to 15 g $plant^{-1}$ at 75% and 50% FC and 3.4 to 3.8 g $plant^{-1}$ at 25% and 12.5% FC. The total leaf area per plant was not significantly different (571 to 693 cm^2 $plant^{-1}$) at 100%, 75%, and 50% FC. In contrast, *A. tuberculatus* produced the greatest leaf area at 100% FC compared with 75% and 50% FC (Sarangi et al. 2015). The leaf area of plants exposed to 25% and 12.5% FC is not presented, because plants did not survive, and leaves were dry and rolled up. Similarly, dry leaf biomass was similar (5.4 to 6.4 g $plant^{-1}$) among 100%, 75%, and 50% FC at harvest; however, 25% and 12.5% FC plants had only 1.2 to 1.4 g leaf biomass $plant^{-1}$. *Amaranthus palmeri* at 100% FC produced the greatest total aboveground biomass of 38.3 g $plant^{-1}$ at 100% FC compared with 25 to 27.6 g $plant^{-1}$ at 75% and 50% FC and 4.8 to 5.0 g $plant^{-1}$ at 25% and 12.5% FC (Table 2). Water stress treatments, except for 25% and 12.5% FC (0.6 to 0.7 g $plant^{-1}$),

Table 2. Effect of degree of water stress on *Amaranthus palmeri* biomass, seed production, and seed germination in a greenhouse experiment conducted for 77 d after transplanting at the University of Nebraska–Lincoln.

Water stress treatment[a]	Stem biomass[b]	Leaf biomass[b]	Aboveground biomass[b]	Root biomass[b] $plant^{-1}$	Total leaf area $plant^{-1}$ [b,c]	Number of seeds $plant^{-1}$ [b,d]	Seed germination[b,d]
	———g $plant^{-1}$———				cm^2	no. $plant^{-1}$	%
100% FC (no water stress)	22.3 a	6.4 a	38.3 a	3 a	571 a	41,696 a	46 a
75% FC (light water stress)	15 b	5.8 a	27.6 b	2.4 a	693 a	18,796 b	39 a
50% FC (moderate water stress)	13.3 b	5.4 a	25 b	2.3 a	616 a	14,835 b	38 a
25% FC (high water stress)[c,d]	3.8 c	1.2 b	5 c	0.7 b	—	—	—
12.5% FC (severe water stress)[c,d]	3.4 c	1.4 b	4.8 c	0.6 b	—	—	—

[a]Abbreviation: FC, field capacity.
[b]Means within columns with no common letter(s) are significantly different at $P \leq 0.05$.
[c]Plants maintained at 25% and 12.5% FC did not survive more than 35 d after transplanting, and leaves were dried and rolled up; therefore, total leaf area is not presented.
[d]Plants maintained at 25% and 12.5% FC died without producing seeds; therefore, the number of seeds per plant and seed germination data are not presented.

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press

did not affect the root biomass production (2.3 to 3 g plant^{-1}). In addition, *A. palmeri* root length at 100%, 75%, and 50% FC was similar (unpublished data). This demonstrates that *A. palmeri* under light to moderate water stress would be able to efficiently acquire water from soil and quickly exhaust the soil water available to crops (Wright et al. 1999a, 1999b).

Amaranthus palmeri at 100% FC produced the highest number of seeds (41,696 plant^{-1}) compared with 75% and 50% FC (14,835 to 18,796 plant^{-1}). Similarly, *A. tuberculatus* produced the highest number of seeds at 100% FC (34,450 seeds plant^{-1}) compared with 27,775 seeds plant^{-1} at 75% and 10,194 seeds plant^{-1} at 50% FC (Sarangi et al. 2015). In contrast, Chauhan (2013) reported greater seed production of itchgrass [*Rottboellia cochinchinensis* (Lour.) Clayton], a C_4 grass species, at 75% compared with 100% FC. *Amaranthus palmeri* seed germination was similar (38% to 46%) at 50% to 100% FC. Similarly, seed germination of *A. tuberculatus* (Sarangi et al. 2015) and junglerice [*Echinochloa colona* (L.) Link] (Chauhan and Johnson 2010) did not differ when mother plants were maintained at 25% to 100% FC under greenhouse conditions. In contrast, previous studies have reported increased seed germination or reduced dormancy of different weed species, including *A. retroflexus*, when the mother plant was grown under water stress conditions compared with no water stress (Benech-Arnold et al. 1992; Karimmojeni et al. 2014; Peters 1982).

Amaranthus palmeri at 100%, 75%, and 50% FC took a statistically similar number of days (45 to 56 DAT) to reach flowering during the study (unpublished data). Early flowering might limit the production of photosynthates in plants, resulting in reduced growth and seed production (Shitaka and Hirose 1998), and *A. palmeri* plants at 75% and 50% FC did not initiate flowering early in the season and produced the same number of leaves per plant, leaf area, and leaf biomass as plants under no water stress. Plant growth parameters, including leaf area, leaf cuticle thickness, or number of leaves per plant, might play an important role under varying soil water stress levels in determining herbicide efficacy by affecting herbicide interception and absorption in plants (Zhou et al. 2007).

Practical Implication

This is the first study, to our knowledge, evaluating response of *A. palmeri* to the degree of water stress by using soil moisture sensors to measure soil water content in the pots more frequently to maintain precise levels of water stress throughout the growing period. *Amaranthus palmeri* height and stem biomass were more sensitive to water stress than leaf number, leaf biomass, or total leaf area per plant. *Amaranthus palmeri* under light (75% FC) to moderate (50% FC) water stress allocated fewer photosynthates to the stem and produced the same leaf number, total leaf area, and root biomass as nonstressed plants. Water stress might also reduce or increase the critical weed-free period in various crops infested with different weed species compared with saturated conditions (Coble et al. 1981; Jackson et al. 1985). The growth characteristics of *A. palmeri* at different water stress levels could indicate its competitive ability under water stress conditions (Bond and Oliver 2006; Horak and Loughin 2000; Radosevich et al. 1997), and this information may be useful for evaluating weed–crop interaction using competition models (Knezevic et al. 1999; Sarangi et al. 2015).

Amaranthus palmeri biotypes used in the study were collected from growers' fields under continuous corn production in Thayer County, NE, and corn–soybean rotation in Fillmore County, NE, and the growth characteristics of *A. palmeri* observed in this study could vary if *A. palmeri* biotypes were collected from different cropping systems or rotations: for instance, Bravo et al. (2017) reported greater height and biomass of *A. palmeri* biotypes collected from tall-statured crops such as corn compared with shorter-canopy crops such as vegetables. The results observed in this study could also vary under field conditions, because *A. palmeri* plants were not able to grow to their full potential due to limited pot size under greenhouse conditions. In addition, a single *A. palmeri* plant was grown in each pot without any inter- or intraspecific competition; however, plants growing with crops might produce flowers earlier or later in the season depending on the competitive nature of the crops (Bolmgren and Cowan 2008; Franks et al. 2007). Additionally, water stress treatments were imposed throughout the growing season in this study, and timing of water stress can also play an important role in determining *A. palmeri*'s growth response (Chandi et al. 2013). Therefore, *A. palmeri* grown under field condition will have better chance of survival and higher seed production due to limited periods of water stress compared with continuous water stress conditions in this study. Previous research has shown reduced control of different weed species, including *A. tuberculatus*, with POST herbicides when grown under high soil water stress conditions, due to reduced herbicide retention, absorption, or translocation (Lubbers et al. 2007; Morrison et al. 1995; Ruiter and Meinen 1998; Skelton et al. 2016; Zhou et al. 2007). Therefore, more research needs to be conducted regarding herbicide efficacy on *A. palmeri* plants under varying water stress levels.

Author ORCIDs. Mithila Jugulam, http://orcid.org/0000-0003-2065-9067; Amit J. Jhala, http://orcid.org/0000-0001-8599-4996.

Acknowledgments. The authors gratefully acknowledge Ian Rogers, Adam Leise, and Murtaza Nalwala for their assistance in this project. We acknowledge the Nebraska Corn Board for partial funding of this study. No conflicts of interest have been declared.

References

Baskin CC, Baskin JM (1998) Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. 1st ed. San Diego: Academic. 666 p

Benech-Arnold RL, Fenner M, Edwards PJ (1992) Changes in dormancy level in *Sorghum halepense* seeds induced by water stress during seed development. Funct Ecol 6: 596–605

Benjamin JG, Nielsen DC (2006) Water deficit effects on root distribution of soybean, field pea and chickpea. Field Crops Res 97:248–253

Berger ST, Ferrell JA, Rowland DL, Webster TM (2015) Palmer amaranth (*Amaranthus palmeri*) competition for water in cotton. Weed Sci 63:928–935

Bolmgren J, Cowan PD (2008) Time–size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. Oikos 117:424–429

Bond JA, Oliver LR (2006) Comparative growth of Palmer amaranth (*Amaranthus palmeri*) accessions. Weed Sci 54:121–126

Bravo W, Leon RG, Ferrell JA, Mulvaney MJ, Wood CW (2017) Differentiation of life-history traits among Palmer amaranth (*Amaranthus palmeri*) populations and its relation to cropping systems and glyphosate sensitivity. Weed Sci 65:339–349

Chahal PS, Aulakh JS, Jugulum M, Jhala AJ (2015) Herbicide-resistant Palmer amaranth (*Amaranthus palmeri* S. Wats.) in the United States—mechanisms of resistance, impact, and management. Pages 1–29 in Price A, ed. Herbicides, Agronomic Crops, and Weed Biology. Rijeka, Croatia: InTech

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press

Chahal PS, Varanasi VK, Jugulam M, Jhala AJ (2017) Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) in Nebraska: confirmation, EPSPS gene amplification, and response to POST corn and soybean herbicides. Weed Technol 31:80–93

Chandi A, Jordan DL, York AC, Burton J, Milla-Lewis SR, Spears J, Whitaker JR, Wells R (2013) Response of herbicide-resistant Palmer amaranth (*Amaranthus palmeri*) accessions to drought stress. Int J Agron. 10.1155/2013/823913.

Chauhan BS (2013) Growth response of itchgrass (*Rottboellia cochinchinensis*) to water stress. Weed Sci 61:98–103

Chauhan BS, Abugho SB (2013) Effect of water stress on the growth and development of *Amaranthus spinosus*, *Leptochloa chinensis*, and rice. Am J Plant Sci 4:989–998.

Chauhan BS, Johnson DE (2010) Growth and reproduction of junglerice (*Echinochloa colona*) in response to water-stress. Weed Sci 58:132–135

Coble HD, Williams FM, Ritter RL (1981) Common ragweed (*Ambrosia artemisiifolia*) interference in soybeans (*Glycine max*). Weed Sci 29:339–342

Earl HJ (2003) A precise gravimetric method for simulating drought stress in pot experiments. Crop Sci 43:1868–1873

Ehleringer J (1983) Ecophysiology of *Amaranthus palmeri*, a Sonoran desert summer annual. Oecologia 57:107–112

Ehleringer J (1985) Annuals and perennials of warm deserts. Pages 162–180 in Chabot BF, Mooney HA, eds. Physiological Ecology of North American Plant Communities. New York: Chapman and Hall

Fenner M (1991) The effects of the parent environment on seed germinability. Seed Sci Res 1:75–84

Forseth IN, Ehleringer JR (1982) Ecophysiology of two solar tracking desert winter annuals. Oecologia 54:41–49

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci USA 104:1278–1282

Heap I (2017) Herbicide Resistant Palmer Amaranth Globally. http://www.weedscience.org/Summary/Species.aspx. Accessed: November 9, 2017

Hillel D (1998) Environmental Soil Physics. San Diego: Academic. 771 pp

Horak MJ, Loughin TM (2000) Growth analysis of four *Amaranthus* species. Weed Sci 48:347–355

Irmak S, Haman DZ (2001) Performance of the Watermark granular matrix sensor in sandy soils. Appl Eng Agric 17: 787–795

Irmak S, Haman DZ, Irmak A, Jones JW, Campbell KL, Crisman TL (2004) Measurement and analysis of growth and stress parameters of *Viburnum odoratissimum* (Ker-gawl) grown in a multi-plot box system. HortScience 39:1445–1455

Irmak S, Payero JO, VanDeWalle B, Rees J, Zoubek G, Martin DL, Kranz WL, Eisenhauer D, Leininger D (2016) Principles and Operational Characteristics of Watermark Granular Matrix Sensor to Measure Soil Water Status and Its Practical Applications for Irrigation Management in Various Soil Textures. Lincoln, NE: Nebraska Extension Circular EC783. http://extensionpublications.unl.edu/assets/pdf/ec783.pdf. Accessed: October 30, 2017

Jackson LA, Kapusta G, Schutte Mason DJ (1985) Effect of duration and type of natural weed infestations on soybean yield. Agron J 77:725–729

Jhala AJ, Sandell LD, Rana N, Kruger GR, Knezevic SZ (2014) Confirmation and control of triazine and 4-hydroxyphenylpyruvate dioxygenase-inhibiting herbicide-resistant Palmer amaranth (*Amaranthus palmeri*) in Nebraska. Weed Technol 28:28–38

Karimmojeni H, Bazrafshan AH, Majidi MM, Torabian S, Rashidi B (2014) Effect of maternal nitrogen and drought stress on seed dormancy and germinability of *Amaranthus retroflexus*. Plant Species Biol 29: e1–e8. 10.1111/1442-1984.12022.

Keeley PE, Carter CH, Thullen RJ (1987) Influence of planting date on growth of Palmer amaranth (*Amaranthus palmeri*). Weed Sci 35:199–204

Klingaman TE, Oliver LR (1994) Palmer amaranth (*Amaranthus palmeri*) interference in soybeans (*Glycine max*). Weed Sci 42:523–527

Knezevic SZ, Horak MJ, Vanderlip RL (1999) Estimates of physiological determinants for redroot pigweed. Weed Sci 47:291–296

Knezevic SZ, Streibig JC, Ritz C (2007) Utilizing R software package for dose-response studies: the concept and data analysis. Weed Technol 21:840–848

Kohrt JR, Sprague CL (2017) Herbicide management strategies in field corn for a three-way herbicide-resistant Palmer amaranth (*Amaranthus palmeri*) population. Weed Technol 31:364–372

Lawlor DW (2013) Genetic engineering to improve plant performance under drought: physiological evaluation of achievements, limitations, and possibilities. J Exp Bot 64:83–108

Liphadzi KB, Dille JA (2006) Annual weed competitiveness as affected by preemergence herbicide in corn. Weed Sci 54:156–165

Lubbers MD, Stahlman PW, Al-Khatib K (2007) Fluroxypyr efficacy is affected by relative humidity and soil moisture. Weed Sci 55:260–263

Massinga RA, Currie RS, Horak MJ, Boyer J Jr (2001) Interference of Palmer amaranth in corn. Weed Sci 49: 202–208

Massinga RA, Currie RS, Trooien TP (2003) Water use and light interception under Palmer amaranth (*Amaranthus palmeri*) and corn competition. Weed Sci 51:523–531

McLachlan SM, Swanton CJ, Weise SF, Tollenaar M (1993) Effect of corn-induced shading and temperature on rate of leaf appearance in redroot pigweed (*Amaranthus retroflexus* L.). Weed Sci 41:590–593

Morrison RG, Lownds NK, Sterling TM (1995) Picloram uptake, translocation, and efficacy in relation to water status of Russian knapweed (*Acroptilon repens*). Weed Sci 43:34–39

Paudel R, Grantz DA, Vu HB, Shrestha A (2016) Tolerance of elevated ozone and water stress in a California population of Palmer amaranth (*Amaranthus palmeri*). Weed Sci 64:276–284

Peters NCB (1982) Production and dormancy of wild oat (*Avena fatua*) seed from plants grown under soil water stress. Ann Appl Biol 100:189–196

Radosevich S, Holt JS, Ghersa C (1997) Weed Ecology: Implications for Vegetation Management. New York: Wiley. Pp 278–301

Rawls WJ (1983) Estimating soil bulk density from particle size analyses and organic matter content. Soil Sci 135:123–125

Rawls WJ, Gimenez D, Grossman R (1998) Use of soil texture, bulk density and slope of the water retention curve to predict saturated hydraulic conductivity. Trans Am Soc Agric Eng 41:983–988

Ritz C, Streibig JC (2016) Analysis of Dose-Response Curves. https://cran.r-project.org/web/packages/drc/drc.pdf. Accessed: January 20, 2018

Ruiter HD, Meinen E (1998) Influence of water stress and surfactant on the efficacy, absorption, and translocation of glyphosate. Weed Sci 46:289–296

Sarangi D, Irmak S, Lindquist JL, Knezevic SZ, Jhala AJ (2015) Effect of water stress on the growth and fecundity of common waterhemp (*Amaranthus rudis*). Weed Sci 64:42–52

Saxton KE, Rawls WJ (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Sci Soc Am J 70:1569–1578

Saxton KE, Rawls WJ, Romberger JS, Papendick RI (1986) Estimating generalized soil water characteristics from texture. Trans Am Soc Agric Eng 50:1031–1035

Shitaka Y, Hirose T (1998) Effects of shift in flowering time on the reproductive output of *Xanthium canadense* in a seasonal environment. Oecologia 114:361–367

Skelton JJ, Ma R, Riechers DE (2016) Waterhemp (*Amaranthus tuberculatus*) control under drought stress with 2,4-dichlorophenoxyacetic acid and glyphosate. Weed Bio Manag 16:34–41

Steckel LE, Sprague CL, Hager AG, Simmons FW, Bollero GA (2003) Effects of shading on common waterhemp (*Amaranthus rudis*) growth and development. Weed Sci 51:898–903

Stoller EW, Myers RA (1989) Response of soybeans (*Glycine max*) and four broadleaf weeds to reduced irradiance. Weed Sci 37:570–574

Vieira BC, Samuelson SL, Alves GS, Gaines TA, Werle R, Kruger GR (2018) Distribution of glyphosate-resistant *Amaranthus* spp. in Nebraska. Pest Manag Sci. 10.1002/ps.4781

Webster TM, Grey TL (2008) Growth and reproduction of Benghal dayflower (*Commelina benghalensis*) in response to drought stress. Weed Sci 56:561–566

Wiese AF (1968) Rate of weed root elongation. Weed Sci 16:11–13

Wright SR, Jennette MW, Coble HD, Rufty TW Jr (1999a) Root morphology of young *Glycine max*, *Senna obtusifolia*, and *Amaranthus palmeri*. Weed Sci 47:706–711

Wright SR, Coble HD, Raper CD Jr, Rufty TW Jr (1999b) Comparative responses of soybean (Glycine max), sicklepod (Senna obtusifolia), and Palmer amaranth (Amaranthus palmeri) to root zone and aerial temperatures. Weed Sci 47:167–174

Wu D, Qu JJ, Hao X, Xiong J (2013) The 2012 agricultural drought assessment in Nebraska using MODIS satellite data. Pages 170–175 in Proceedings of the 2nd International Conference on Agro-Geoinformatics. Fairfax, VA: Center for Spatial Information Science and Systems

Zhou J, Tao B, Messersmith CG, Nalewaja JD (2007) Glyphosate efficacy on velvetleaf (*Abutilon theophrasti*) is affected by stress. Weed Sci 55:240–244

Zhu Y (2016) Performance of Frequency-Domain and Time-Domain Reflectometry Soil Moisture Sensors in Coarse- and Fine-Textured Soils. MS dissertation. Lincoln, NE: University of Nebraska–Lincoln. 83 p

https://doi.org/10.1017/wsc.2018.47 Published online by Cambridge University Press