Biology and Management of Problematic Crop Weed Species

Edited by

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Chapter 2

Amaranthus spp.

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Introduction

Genus *Amaranthus* is a genetically diverse group of herbaceous C4 plants that are found in warm to temperate regions around the world. *Amaranthus* spp. are widely found in North America and Europe, but have also been introduced in South America, Africa, China, and Australia (Assad et al., 2017). The number of species in *Amaranthus* genus is disputed and the estimates range from 60 (National Research Council, 1984) to 75 species (Ward et al., 2013). The *Amaranthus* genus has also been described as having untapped potential as a food resource; three grain amaranth species (*A. hypochondriacus* L., *A. cruentus* L., and *A. caudatus* L.) are grown as food crops in mountainous regions of South America (Pederson et al., 1990). When roasted and milled, the seeds of *Amaranthus* spp. are edible and rich in protein, whereas the leaves are high in Ca, Fe, and vitamin A (Becker et al., 1981). Despite these benefits, *Amaranthus* genus is known for having some of the most common and troublesome weeds in the world, including *A. palmeri* S. Wats (Palmer amaranth), *A. tuberculatus* (Moq.) Sauer (waterhemp), and *A. retroflexus* L. (redroot pigweed).

The *Amaranthus* genus contains both monoecious and dioecious weed species. The genus is composed of three subgenera, with 10 dioecious species in the subgenus Acnida (Steckel, 2007), whereas monoecious species fall into subgenera *Albersia* and *Amaranthus* (Mosyakin and Robertson, 2008). Notable monoecious species include *A. powellii* S. Wats (Powell's amaranth), *A. retroflexus*, and *A. hybridus* L. (smooth pigweed) (Assad et al., 2017). Dioecious amaranths include *A. palmeri* and *A. tuberculatus*. The dioecious biology of these two species

combined with wind pollination allows them to maintain high levels of genetic variation, which plays a key role in the adaptation to diverse environmental conditions.

Identification of *Amaranthus* spp.

The species within the *Amaranthus* genus share several morphological and developmental characteristics. Leaf shapes tend to fall into one of the three categories: rounded (e.g., *A. blitoides* S. Wats, and *A. alba* L.), lanceolate (e.g., *A. tuberculatus* and *A. arenicola* I.M. Johnst), and ovate (e.g., *A. palmeri, A. spinosus* L., and *A. retroflexus*). The length of the petiole can be used to differentiate *A. palmeri* from other species, as the length of the petiole on *A. palmeri* is longer than the length of the leaf blade (Fig. 2.1). Additional characteristics for species identification include the presence or absence of pubescence on stem and leaves, with dioecious species such as *A. palmeri* being glabrous to sparsely hairy. Watermarks are present on some species (e.g., *A. palmeri*) but should not be used for the identification as they are not present all the time (Fig. 2.1).

Identifying characteristics of some key *Amaranths* (see Fig. 2.1):

Amaranthus hybridus: monoecious; glabrous or sparsely pubescent stem; ovate-shaped alternate leaves, wavy leaf margin; terminal panicles of numerous slender, cylindrical spikes, and slightly prickly.

Amaranthus palmeri: dioecious; glabrous stem and leaves; ovate-shaped alternate leaves, mature leaves have a petiole longer than the leaf blade; female bracts long, thick, and stiff.

Amaranthus retroflexus: monoecious; pubescent stem and leaves; alternate leaves, ovate, veins with trichomes on underside; large red taproot; spikes in thick inflorescence.

Amaranthus spinosus: monoecious; stems with two very sharp and stiff spines at most nodes; ovate leaves.

Amaranthus tuberculatus: dioecious; glabrous stem and leaves; glossy lanceolate alternate leaves.

FIGURE 2.1 Plants of weedy *Amaranthus* spp. (A) *A. palmeri*, (B) *A. tuberculatus*, (C) *A. retroflexus*.

Herbicide resistance mechanisms

Herbicide resistance in the *Amaranthus* genus is common, with the rapid spreading of herbicide-resistant *A. palmeri* and *A. tuberculatus* populations in the last 20 years (Heap, 2020). These herbicide-resistant traits include resistance to multiple herbicide sites of action caused by a variety of mechanisms including point mutation and metabolic resistance. The acetolactate synthase (ALS) inhibitor resistance is widespread and is generally conferred by target-site mutations in *A. palmeri* (Kohrt and Sprague, 2017; Küpper et al., 2017), *A. tuberculatus* (Chahal et al., 2015; Schultz et al., 2015), and *A. retroflexus* (Nandula et al., 2020). Resistance to protoporphyrinogen oxidase (PPO) inhibitors is also caused by target-site changes, conferred either by amino acid deletion (Lillie et al., 2019; Nie et al., 2019; Salas et al., 2016; Sarangi et al., 2019) or substitution (Nie et al., 2019; Salas-Perez et al., 2017; Varanasi et al., 2018).

Some of the recent reports suggested that cytochrome P450- or GST-driven metabolic resistance was found in *Amaranthus*. This includes resistance to 4-hydroxyphenylpyruvate dioxygenase (HPPD) inhibitors (Kaundun et al., 2017; Oliveira et al., 2018a,b) and Photosystem-II inhibitors (Huffman et al., 2015; Peterson et al., 2017; Vennapusa et al., 2018). Resistance to synthetic auxinic herbicides (such as dicamba and 2,4-D) is also metabolically mediated (Figueiredo et al., 2018; Shyam et al., 2019), although an *A. palmeri* population that was resistant to 2,4-D did not show resistance to Dicamba (Kumar et al., 2019).

Glyphosate, which inhibits the activity of 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) through competitive inhibition, is the most widely used herbicide worldwide. The resistance mechanism of *A. palmeri* to glyphosate is notable, as this weed has developed resistance to glyphosate through the duplication of the *EPSPS* gene and overexpression of EPSPS enzyme (Gaines et al., 2010). *Amaranthus tuberculatus* displays both *EPSPS* gene duplication (Lorentz et al., 2014) and target-site Pro-106-Ser substitution (Bell et al., 2013; Molin et al., 2016; Nandula et al., 2013). Reduced glyphosate absorption and translocation have also been reported to impart nontarget site resistance to glyphosate in *A. palmeri* (Dominguez-Valenzuela et al., 2017; Nandula et al., 2012).

Genetics, interspecific hybridization, and gene flow

The chromosome count of *Amaranthus* genus varies by species, where $2n = 32$ or 34 (Murray, 1940). Estimates of genome size within the *Amaranthus* genus previously ranged from 930 Mb in *A. palmeri* to 1.39 Gb in *A. tuberculatus* (Rayburn et al., 2005), but more recent studies estimated the genome to be around half this size. *Amaranthus hybridus* has a genome size of 504 Mb (Montgomery et al., 2020), whereas *Amaranthus hypochondriacus* L.

(Prince-of-Wales Feather) has a genome size of 466 Mb with an estimated 48% of the genome being repeated elements (Clouse et al., 2016). The two important agronomic weed species fall on opposite ends of the spectrum when it comes to genome size: *A. palmeri* has one of the smallest genomes in this genus, estimated at only 422 Mb, whereas *A. tuberculatus* is the largest, at 675 Mb (Kreiner et al., 2019; Montgomery et al., 2020).

Hybridization and gene flow between *Amaranthus* species have been observed, both in greenhouse and field studies. *Amaranthus tuberculatus* is reported to form hybrids with *A. palmeri* (Steinau et al., 2003; Trucco et al., 2007; Wetzel et al., 1999), *A. hybridus* (Tranel et al., 2002; Trucco et al., 2005a,b), *A. powellii*, *A. retroflexus*, and *A. spinosus* (Murray, 1940). *Amaranthus palmeri and A. spinosus* are close relatives, sharing many genetic similarities including chromosome count ($2n = 34$) and genome size (Rayburn et al., 2005; Wassom and Tranel, 2005), so it is unsurprising that they can also form hybrids (Gaines et al., 2012; Molin et al., 2016). The interspecific hybridization success rate of *Amaranthus* spp. is low and varies by species, with *A. tuberculatus* $\times$ *A. hybridus* rates estimated under field conditions from 0.4% to 2.3% (Trucco et al., 2005b) whereas *A. palmeri* $\times$ *A. spinosus* rates were $< 1.4\%$ (Gaines et al., 2012).

A major concern is that their ability to form hybrids offers the potential for herbicide resistance traits to be transferred between species through introgression (Jhala et al., 2021). Observed examples of this include a Trp574Leu substitution in *A. palmeri* that confers resistance to ALS-inhibitors being transferred to an *A. spinosus x A. palmeri* hybrid (Molin et al., 2016). In a greenhouse study, Franssen et al. (2001b) reported that gene flow occurred between *A. tuberculatus* and *A. palmeri* at a low frequency and that transferred the ALS resistance traits. Oliveira et al. (2018b) conducted field experiments in Nebraska, United States, to determine interspecific and intraspecific transfer of metabolism-based HPPD resistance in dioecious *Amaranthus* species. In this study, gene flow was detected using a resistant *A. tuberculatus* population with enhanced mesotrione (a HPPD herbicide) detoxification via cytochrome P450 enzymes and the results showed that 0.1% hybridization between *A. tuberculatus* and *A. palmeri* occurred under field conditions.

Description of major weedy *Amaranthus* spp.

Amaranthus palmeri

Native to the southwestern United States, *A. palmeri* has been ranked as the most troublesome weed in agronomic cropping systems in the United States (Ward et al., 2013). In the last few decades, human activities such as agricultural development and seed and equipment transportation have led to the spread of *A. palmeri* to the northern United States (Culpepper et al., 2006). Since the first report of *A. palmeri* in Virginia in 1915, it has become one of

the most problematic weeds in agronomic cropping systems in the United States (Chahal et al., 2017).

Growth and seed production

Amaranthus palmeri has a high photosynthetic rate leading to a high growth rate and considerable biomass accumulation compared with other *Amaranthus* species (Ehleringer, 1983; Jha and Norsworthy, 2009). *Amaranthus palmeri* leaves are oriented in a perpendicular fashion to incoming sunlight (Fig. 2.1), allowing the plant to absorb maximum light to fix the carbon at a faster rate (Ehleringer and Forseth, 1980). *Amaranthus palmeri* is a prolific seed producer (Keeley et al., 1987) and has been found to survive and produce a high number of seeds even under moisture-stressed situation (Chahal et al., 2018). Keeley et al. (1987) reported that a female *A. palmeri* plant can produce 200,000−600,000 seeds. Schwartz et al. (2016) reported that Palmer amaranth growing in soybean [*Glycine max* (L.) Merr.] field can produce as high as 800,000 seeds per female plant. Seed production of *A. palmeri* grown without crop competition can exceed one million seeds per plant (Keeley et al., 1987). *Amaranthus palmeri* seeds are usually dispersed by gravity forces; however, dispersal via irrigation, plowing, mowing, harvesting, birds, and mammals has been documented in multiple studies (Costea et al., 2004, 2005).

Competitiveness and yield loss

Continuous emergence pattern of *A. palmeri* throughout the growing season leads to season-long crop interference (Jha and Norsworthy, 2009). *Amaranthus palmeri* interference can cause substantial yield losses in agronomic crops (Fig. 2.2). Uncontrolled *A. palmeri* has caused yield losses as

FIGURE 2.2 Herbicide-resistant *A. palmeri* and *A. tuberculatus* competing with soybean in a production field in Nebraska, United States.

high as 91% in corn (*Zea mays* L.) (Massinga et al., 2001), 54% in cotton (Morgan et al., 2001), and 68% in soybean (Klingaman and Oliver, 1994). Bensch et al. (2003) reported 79% soybean yield loss at a density of 8 plants/m^2 in Kansas, United States. Early emergence (0−1 week after soybean emergence) and establishment of *A. palmeri* have been shown to reduce soybean yield compared to late emergence (2−8 weeks after soybean emergence) (Korres et al., 2019). *Amaranthus palmeri* at 1.58 plants/m^2 resulted in 38%−63% grain yield loss in sorghum (*Sorghum bicolor* L.) (Moore et al., 2004). In a study conducted at North Carolina, United States, Burke et al. (2007) reported that *A. palmeri* decreased the canopy diameter of peanut (*Arachis hypogaea* L.) and caused 28% and 68% yield loss at densities of 1 and 5 plants/m of peanut row, respectively, and interfere with the peanut harvesting.

A recent multilocation/year study conducted in Nebraska, United States, reported that the critical period of weed (including *A. palmeri*) removal in soybean was delayed from V1-V2 to V4-R5 using preemergence (PRE) herbicides such as saflufenacil + imazethapyr + pyroxasulfone and saflufenacil + imazethapyr (Knezevic et al., 2019). However, in the absence of a PRE herbicide, the critical time of *A. palmeri* removal evaluated at 5% soybean yield loss occurred at V1 and V6 soybean growth stages that was equivalent to the 194 and 480 growing degrees days (GDD) in 2018 and 2019, respectively (de Sanctis et al., 2021).

Reproductive biology

Amaranthus palmeri is a dioecious species; male (pistillate) and female (staminate) flowers are produced on separate plants (Mosyakin and Robertson, 2008). Male inflorescences can be distinguished from the female flower as they lack the sharp, stiff bracts that subtend female flowers and thus have a softer feel (Mosyakin and Robertson, 2008). Flowering in *A. palmeri* usually starts in summer and continues into fall. Keeley et al. (1987) reported that flowering of *A. palmeri* is influenced by day length; shorter days hasten flowering, which in turn, reduces plant size and number of seeds. Male *A. palmeri* plants produce wind-dispersed pollen grains (Borsch, 1998; Franssen et al., 2001a) and pollen-mediated gene flow from herbicide-resistant to susceptible *A. palmeri* has been reported under field conditions (Sosnoskie et al., 2012) thus the transfer of herbicide resistance alleles (Jhala et al., 2021).

Herbicide resistance

Glyphosate-resistant *A. palmeri* was first reported in Georgia (Culpepper et al., 2006), and since then, 27 other states in the United States have documented the presence of this weed as of 2020 (Heap, 2020). *Amaranthus palmeri* has evolved resistance to at least eight herbicide sites of action: microtubule-, ALS-, EPSPS-, PS II-, HPPD-, PPO-, and very long-chain fatty

acid (VLCFA) inhibitors and synthetic auxins (Heap, 2020). *Amaranthus palmeri* has also been found to have multiple herbicide resistance, such as ALS- and EPSPS inhibitor resistance (Chahal et al., 2017); PS II/HPPD inhibitor resistance in Nebraska, United States (Jhala et al., 2014), as well as 2,4-D/ glyphosate/atrazine/ALS inhibitor /HPPD inhibitor resistance in Kansas, United States (Kumar et al., 2019). The evolution of herbicide-resistant *A. palmeri* populations and their widespread occurrence has made the control of this weed difficult in agronomic crops.

Amaranthus tuberculatus

Amaranthus tuberculatus, a summer annual broadleaf weed, is a native plant of North America and considered to be one of the most troublesome agricultural weeds in the midwestern United States (Waselkov et al., 2020). Historically, this weed was commonly found along the riverbanks and pond margins (Sauer, 1957), but the changing cultivation practices in the 20th century, especially the adoption of conservation tillage and intensification of agriculture are believed to promote the invasion of *A. tuberculatus* in the agricultural lands in the United States (Buhler, 1995). Research conducted in southeast Texas, United States, reported that 37-years of no-till management increased *A. tuberculatus* density by four-fold compared to the conventional-tillage system (Govindasamy et al., 2020). Since its first report in 1830 in Oklahoma, this weed is continuously moving toward the northern and eastern parts of the United States and Canada (Korres et al., 2018; Sarangi and Jhala, 2018; Schryver et al., 2017).

Seed germination

Amaranthus tuberculatus is a small-seeded weed with high initial seed viability ($>89\%$) and likely to form a persistent seedbank (Korres et al., 2018; Leon et al., 2004). Fig. 2.3 is showing the relative seed size of *A. tuberculatus* in comparison with corn and soybean. In a study conducted in Nebraska, United States, Burnside et al. (1996) reported that 3% *A. tuberculatus* seeds were recovered after 17 years of burial at 20 cm soil depth. In another study, Buhler and Hartzler (2001) reported that 12% of *A. tuberculatus* seeds persisted after 4 years of burial. The size of seedbank, persistence, and emergence of *A. tuberculatus* can be impacted by several factors including tillage, weed management practices, cropping systems, and other environmental factors. For example, a study conducted in Illinois, United States showed that tillage increased the persistence of *A. tuberculatus* seedbank in the top 6 cm soil profile (Steckel et al., 2007). Refsell and Hartzler (2009) reported that in the no-till system, the seeds of *A. tuberculatus* were concentrated near the soil surface, but the majority of the seeds were found between 9 and 15 cm in the chisel-till system.
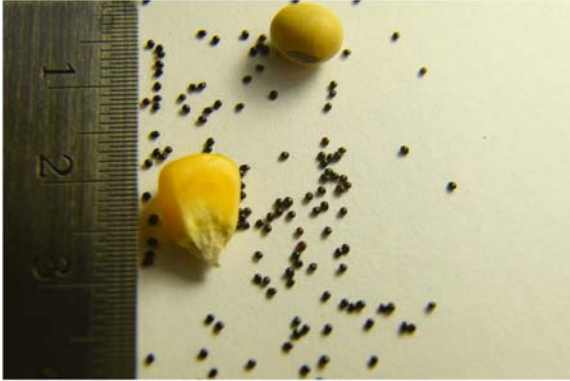
FIGURE 2.3 Relative seed size of *A. tuberculatus* in comparison with soybean and corn seeds. Provided scale is in centimeter.

Amaranthus tuberculatus is considered a late-emerging summer annual weed, and it starts emerging from mid-May in the midwestern United States (Werle et al., 2014). In a study conducted in Iowa, United States, *A. tuberculatus* continued to emerge until mid-August in no-till systems (Refsell and Hartzler, 2009). Leon and Owen (2006) reported that seedling emergence in no-till was at least four times higher than chisel and moldboard plow systems. Tillage can also promote the early emergence of *A. tuberculatus*; Govindasamy et al. (2020) reported that in conventional-tillage system, 63 GDD was required for 50% emergence of this weed, whereas 75 GDD was needed under no-till system in Texas, United States. The minimum temperature required for *A. tuberculatus* germination was 10°C, and a greater germination was observed with alternating temperatures than constant temperature (Leon et al., 2004). Similarly, Guo and Al-Khatib (2003) reported that *A. tuberculatus* germination was highest at 25/20°C day/night temperature. The dormancy of *A. tuberculatus* was phytochrome regulated and germination was promoted under continuous red light, whereas far-red light inhibited its germination (Leon and Owen, 2003).

Growth, flowering, and seed production

Amaranthus tuberculatus has an indeterminate growth habit; however, the plant morphology depends on the environmental conditions. Sarangi et al. (2016) reported that water stress can reduce plant height, number of leaves, growth index, and seed production of *A. tuberculatus* substantially. The 50% field capacity of water treatment showed 1.4- and 2.9-times less plant height and growth index, respectively, than the no water stress (100% field capacity). Guo and Al-Khatib (2003) reported that *A. tuberculatus* showed a higher heat tolerance than *A. retroflexus* and survived at 45/40°C day/night temperature for 12 days. Being a C4 weed, *A. tuberculatus* shows some

physiological characteristics, including the high photosynthetic rate at high temperature, low CO_2 compensation point, and a greater water and nitrogen use efficiency, which are proven to be beneficial for this weed to survive (Costea et al., 2005).

Similar to *A. palmeri*, *A. tuberculatus* is also a dioecious and wind-pollinated species. The shape of the pollen grains is spherical, and the pollens are very small in size (18.5 μm diameter), which has favored the long-distance travel of *A. tubeculatus* pollen by wind (Franssen et al., 2001a). Also, the pollens of this weed showed lower settling velocity (0.0185−0.021 m/s) and can remain viable for 120 hours (Costea et al., 2005; Liu et al., 2012). Sarangi et al. (2017b) estimated the pollen-mediated gene flow of *A. tuberculatus* under field conditions and concluded that 50% gene flow occurred within 3 m from the pollen source, but 10% outcrossing was recorded at 88 m from the source.

Similar to other *Amaranthus* spp., *A. tubeculatus* shows a short-day flowering response. The flowering is initiated earlier under short-day conditions (Costea et al., 2005). Shading can also negatively impact *A. tubeculatus* growth and seed production. A study conducted in Illinois, United States, showed that 40%, 68%, and 99% shading reduced the seed production by 51%, 75%, and >99%, respectively, and the trend was similar to the biomass and plant height data (Steckel et al., 2003). The fecundity of *A. tubeculatus* is highly variable and depends on many factors including competition, emergence time, management practices, soil type, and other environmental factors. *Amaranthus tubeculatus* emerging with soybean can produce 300,000 to 2.3 million seeds per female plant (Hartzler et al., 2004). Emergence timing can also impact the fecundity; Wu and Owen (2014) reported that *A. tuberculatus* plants that emerged in early-July produced 75% fewer seeds than the plants emerged in May in Iowa, United States. Seed production of *A. tuberculatus* was also reduced by 70% when the soil water content was reduced by 50% (Sarangi et al., 2016).

Amaranthus tuberculatus seeds can disperse by water, farm machinery, manure and compost, wind, birds, and other animals. In a 2-year study in the United States, the viable seeds of *A. palmeri* and *A. tuberculatus* were recovered from the digestive tracts of the migratory waterfowls (birds) after 38 hours of feeding and this study also concluded that the seeds can potentially be dispersed up to 2900 km from the source by these birds (Farmer et al., 2017). Therefore it is considered that the seed dispersal of *A. tubeculatus* played an important role in spreading herbicide-resistant populations in North America.

Competitiveness and yield reduction

Similar to *A. palmeri*, *A. tuberculatus* is also considered a competitive weed that can cause total crop loss when growing at a high density. Interference of

A. tubeculatus began at the V6 corn stage caused 4%−23% yield reduction in a study conducted in Illinois, United States (Steckel et al., 2004). The same study also reported that the season-long competition of *A. tubeculatus* at a density of 310 plants/m^2 caused 74% yield loss in corn. Allowing *A. tubeculatus* to interfere with soybean at an average density of 199 plants/m^2 for 10 weeks after emergence caused 43% yield loss (Hager et al., 2002). Bensch et al. (2003) reported that *A. tubeculatus* at a density of 0.25−4 plants/m soybean row was less competitive than *A. palmeri* but caused greater yield reduction than *A. retroflexus* at the same density.

Herbicide resistance

As of 2020, the presence of herbicide-resistant *A. tuberculatus* has been reported from 19 states in the United States and Ontario, Canada (Heap 2020). Population resistant to ALS-, EPSPS-, and PS II-inhibiting herbicides are widespread in the midwestern and southern United States (Murphy et al., 2019; Rosenbaum and Bradley, 2013; Sarangi et al., 2015; Schultz et al., 2015; Singh et al., 2020; Vieira et al., 2018). Moreover, HPPD-, and PPO-inhibiting herbicide-resistant *A. tuberculatus* populations are spreading quickly across the midwestern United States (Hausman et al., 2011; Lee et al., 2008; McMullan and Green, 2011; Oliveira et al., 2017; Sarangi et al., 2019; Thinglum et al., 2011). An *A. tuberculatus* population from Missouri, United States, showed resistance to six herbicides (2,4-D, atrazine, chlorimuron, fomesafen, and mesotrione) from six different sites-of-action groups (Shergill et al., 2018). The use of soil residual herbicides from VLCFA inhibitor group was recommended for season-long control of herbicide-resistant *A. tuberculatus* population. As these herbicides interact with many primary target sites, the chance of evolving resistance to VLCFA inhibitors was low to none (Busi, 2014); however, some of the recent research reported that *A. tuberculatus* populations in the United States are also showing resistance to these herbicides (Evans et al., 2019).

Other weedy *Amaranthus* spp.

Amaranthus retroflexus, *A. spinosus*, and *A. hybridus* are the other important weedy *Amaranthus* species that can compete with the summer crops and reduce yield substantially. *Amaranthus retroflexus* is found throughout the northern, eastern, and central United States, northeastern Mexico, and southeastern Canada (Sauer, 1967). It is also present in Africa, Asia, and Europe (Brenan, 1961; Holm et al., 1991a,b; Wells et al., 1986). Moreover, it has naturalized to the newer environments of northern and southern hemispheres including a temperate climate. The tropical America is believed to be the native place for *A. spinosus*, although it was introduced later to other places in the world (Holm et al., 1991b). *Amaranthus hybridus* was historically

found on the riverbanks in the eastern North America, northern South America, and Central America (Sauer, 1967); however, due to its use as a leafy vegetable, it is now found in the south-central Asia, Africa, and Australia (Costea et al., 2001).

Seed germination

Amaranthus retroflexus, *A. spinosus*, and *A. hybridus* are monoecious plants and have both male and female flowers on the same plant (Weaver and McWilliams, 1980). On an average, they can produce 100,000−300,000 seeds per plant (Sellers et al., 2003). Similar to *A. palmeri* and *A. tuberculatus*, these three species (*A. retroflexus*, *A. spinosus*, and *A. hybridus*) have the smaller seed size and they require 350 GDD (10°C base temperature) for germination and can emerge throughout the growing season (Sellers et al., 2003). Moreover, these weeds start emerging when the soil temperature reaches 20°C (Barton, 1962), however, emergence pattern may vary depending on the species and environmental condition (Sellers et al., 2003). Studies reported that optimum temperature for *A. retroflexus* germination ranged from 25°C−40°C (Kępczyński and Bihun, 2002; Guo and Al-Khatib, 2003), whereas it was 30°C−35°C for *A. spinosus* (Steckel et al., 2004) and 32°C−34°C for *A. hybridus* (Kępczyński and Bihun, 2002).

Soil type and burial depth also impacted the seed germination of these weeds. For example, the germination of *A. retroflexus* was better in the lighter soils (sandy loam, sandy clay loam, and loamy sand) than the heavier soils (silty clay, and sandy clay) (Ghorbani et al., 1999). Burial depth below 5 cm soil can reduce the germination percentage. Ghorbani et al. (1999) observed no seed germination for *A. retroflexus* beyond 3 cm soil depth. Similarly, *A. spinosus* germinated well up to 4 cm burial depth, but no seed was germinated when placed below 6 cm depth (Chauhan and Johnson, 2009). The seedbank persistence and size can be influenced by the cropping system and tillage practice. Cardina et al. (2002) reported that in the no-till system, the size of *A. retroflexus* seedbank was two times greater than the moldboard plow. The same study also reported that the corn-oats-hay rotation had greater seed density (260−630 seeds/m^2) than the corn-soybean rotation (10−270 seeds/m^2).

Herbicide resistance

Amaranthus retroflexus, *A. spinosus*, and *A. hybridus* have developed resistance to multiple herbicide sites-of-action, causing their management difficult. *Amaranthus retroflexus* has evolved resistance to ALS-, PS II-, and PPO-inhibiting herbicides (Heap, 2020; Wang et al., 2017; Woodyard et al., 2009). Likewise, *A. hybridus* has evolved resistance to ALS-, EPSPS-, PS II-, and PPO-inhibiting herbicides and synthetic auxins (Fuerst et al., 1986; Heap, 2020; Manley et al., 1999; Nie et al., 2019).

Competitiveness and yield loss

Amaranthus retroflexus, *A. spinosus*, and *A. hybridus* are troublesome weeds in more than 25 crops worldwide (Berry et al., 2006; Holm et al., 1991b). These weeds can emerge before or at the same time of the crop emergence and compete for resources such as space, water, and nutrients. Depending on the crop, weed density, emergence time, and duration of competition, these weeds can cause 5%−100% yield loss. *Amaranthus hybridus* at 6 plants/m^2 density caused 100% yield reduction in watermelon (*Citrullus vulgaris* Schrad.) and muskmelon (*Cucumis melo* L.) when allowed to compete for the whole season (Terry et al., 1997). In another study, Stuart et al. (1984) observed 43% cotton yield loss when the density of *A. hybridus* was 0.7 plants/m^2. Morales-Payan and Stall (2002a, 2002b) reported 30% and 61% yield loss in bell pepper (*Capsicum annuum* L.) at 1 and 6 plants/m^2 of *A. hybridus* density, respectively. A study conducted in Kansas, United States, reported that *A. retroflexus* at 12 plants/m^2 density caused 40% yield loss in sorghum (Knezevic et al., 1997). Dielman et al. (1995) also reported a 12.3% yield loss of soybean with two *A. retroflexus* plants/m^2. Depending on the weed density and emergence timing, *A. retroflexus* reduced corn yield up to 34% in a study conducted in Ontario, Canada (Knezevic et al., 1994).

Management of weedy *Amaranthus*

Chemical control of *Amaranthus* weeds

Due to having a wide window of emergence, a single herbicide application would not provide season-long control of *Amaranthus* spp. including *A. palmeri* and *A. tuberculatus*. Therefore management programs in agronomic crops should focus on clean start of the growing season with the application of a PRE residual herbicide with multiple sites of action followed by an effective postemergence (POST) herbicide application. Sarangi et al. (2017a) in a field experiment conducted in Nebraska, United States, reported that PRE followed by POST herbicide programs that include saflufenacil plus imazethapyr plus dimethenamid-P, sulfentrazone plus cloransulam, or *S*-metolachlor plus metribuzin as PRE, followed by fomesafen plus glyphosate, *S*-metolachlor plus fomesafen, or acifluorfen plus glyphosate as POST resulted in more than 90% control of glyphosate-resistant *A. tuberculatus* throughout the growing season, whereas, POST-only herbicide treatments had less than 70% control of glyphosate-resistant *A. tuberculatus*.

Mixing foliar-active POST herbicides with a residual herbicide would provide an overlapping residual activity to prevent *Amaranthus* spp. emergence later in the growing season; however, the presence of sufficient soil moisture is critical for the activity of soil residual herbicides. Sarangi and Jhala (2019) conducted a field experiment to compare PRE, PRE followed by POST, and PRE followed by POST plus residual herbicide

programs for *A. palmeri* control and soybean yield, and reported that PRE herbicide showed 66% control of *A. palmeri*, whereas 86% and 97% control was obtained with the PRE followed by POST, and PRE followed by POST plus residual herbicide programs, respectively, at 28 days after POST herbicide application, and PRE followed by POST plus residual herbicide program resulted in higher soybean yield than other treatments. Aulakh and Jhala (2015) reported similar results with PRE followed by POST herbicide programs, where POST program includes foliar-active herbicides tank-mixed with acetochlor, pyroxasulfone, or *S*-metolachlor in glufosinate-resistant soybean. Multiple herbicide-tolerant corn, soybean, and cotton were launched recently, and they will provide additional herbicide choices for controlling the glyphosate-resistant *Amaranthus* species; however, growers should not rely only on 2,4-D choline, dicamba, or glufosinate or their sequential applications for POST weed control program (Shyam et al., 2021).

Need for integrated weed management

> *"If herbicide-resistant-weed problems are addressed only with herbicides, evolution will most likely win"*
>
> by Mortensen et al. (2012)

Overreliance on a single herbicide site of action selected the resistant populations of *Amaranthus*. The introduction of the genetically modified glyphosate-tolerant crops promoted the rapid spread of glyphosate-resistant weed populations in the world. Biotechnology companies are currently promoting multiple herbicide-tolerant crops as the solution to glyphosate-resistant weed issues; however, this can create new herbicide-resistant weed challenges if proper precautions are not taken. Herbicide-resistant weeds are not only a threat to global food security but also can negatively impact environmental quality by increasing the herbicide application. Therefore the integrated weed management approach should be taken to reduce the selection pressure, decrease herbicide use, and preserve the finite herbicide choices.

Herbicide-dependent weed control treatments sometime fall short of providing satisfactory control of *Amaranthus* spp. A late-season survey of cotton fields in Texas, United States, revealed that *A. palmeri* and *A. tuberculatus* that escaped the standard herbicide programs could add up to 14 million seeds/ha to seedbank (Werner et al., 2020). Therefore the successful adoption of a multitactic weed management approach that includes physical, mechanical, and biological control of weeds along with the herbicides is the need for better weed management (Bagavathiannan and Davis, 2018). For example, Price et al. (2016) concluded that *A. palmeri* density reduced exponentially as a function of cover crop biomass, and a deep tillage along with cover crops increased *A. palmeri* control substantially. Similarly, a study conducted in Georgia, United States, showed that winter cover crops with high biomass

production ability suppressed *A. palmeri* germination early in the season, providing a slightly longer window for POST herbicide application (Webster et al., 2013).

Harvest weed seed control (HWSC) comprises a set of nonchemical weed management tactics that can destroy or remove weed seeds at crop harvest and prevent the addition of seeds to the seedbank. Some of these HWSC tactics are proven to be effective in depleting the *Amaranthus* spp. seedbank (Shergill et al., 2020b). Studies conducted in the United States reported that the impact mill can destroy 96.2% and 92.4% *A. tuberculatus* and *A. hybridus* seeds, respectively (Shergill et al., 2020a). Another research conducted in Arkansas, United States, showed that a heat index of 22,600 in narrow-windrow burning was enough to kill *A. palmeri* seeds by 100% and narrow-windrow burning or chaff removal integrated with an effective herbicide program reduced *A. palmeri* density and seedbank size significantly (Norsworthy et al., 2016, 2020).

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Biology and Management of Problematic Crop Weed Species

Edited by
Bhagirath S. Chauhan

Weeds are the main biological constraint to crop production throughout the year. Uncontrolled weeds could cause 100% yield loss. In Australia the overall cost of weeds to Australian grain growers was estimated at AU$ 3.3 billion annually. In terms of yield losses, weeds amounted to 2.7 million tons of grains at a national level. In the United States weeds cost US$ 33 billion in lost crop production annually. In India these costs were estimated to be much higher (US$ 11 billion). These studies from different economies suggest that weeds cause substantial yield and economic loss.

Biology and Management of Problematic Crop Weed Species details the biology of key weed species, providing vital information on factors affecting seed germination and plant growth. These species include *Avena* species, *Chenopodium album*, *Chloris virgata*, *Conyza bonariensis*, *Cyperus rotundus*, and *Lolium rigidum*. This information is crucial for researchers and growers to develop integrated weed management strategies.

Written by leading experts across the globe, this book is an essential read to plant biologists and ecologists, crop scientists, and students and researchers interested in weed science.

Key features

- Provides detailed information on the biology of different key weed species
- Covers weed seed germination and seedling emergence
- Presents the factors affecting weed growth and seed production
- Provides different management strategies

About the editor

Professor Chauhan received his PhD in Weed Science from the University of Adelaide, South Australia, in 2007. He is on the editorial board for several highly regarded journals, including *Frontiers in Agronomy*, *Weed Science (WSSA)*, and *Indian Journal of Weed Science*. He has published over 400 articles and edited several books, including "Non-chemical Weed Control."

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