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Review

Palmer Amaranth (*Amaranthus palmeri*): A Review

Sarah M. Ward, Theodore M. Webster, and Larry E. Steckel*

In little over 20 yr, Palmer amaranth has risen from relative obscurity to its current status as one of the most widespread, troublesome, and economically damaging agronomic weeds in the southeastern U.S. Numerous factors have enabled Palmer amaranth to become such a dominant and difficult-to-control weed, including its rapid growth rate, high fecundity, genetic diversity, ability to tolerate adverse conditions, and its facility for evolving herbicide resistance. It is both a serious threat to several U.S. cropping systems and a fascinating model weed. In this paper, we review the growing body of literature on Palmer amaranth to summarize the current state of knowledge on the biology, agricultural impacts, and management of this weed, and we suggest future directions for research.
Nomenclature: Palmer amaranth, *Amaranthus palmeri* S. Wats. AMAPA.
Key words: Biology, genetics, physiology, herbicide resistance, crop interference, integrated management.

En poco más de 20 años, *Amaranthus palmeri* ha salido de una relativa oscuridad a su estado actual como una de las malezas agrícolas más ampliamente distribuida, más problemática y económicamente dañina en el sureste de los Estados Unidos. Numerosos factores le han permitido a *A. palmeri* convertirse en una maleza tan dominante y difícil de controlar, incluyendo su rápida tasa de crecimiento, alta fecundidad, diversidad genética, habilidad para tolerar condiciones adversas, y su facilidad para evolucionar resistencia a herbicidas. Es una amenaza para varios sistemas de cultivos en los Estados Unidos, pero también es una maleza modelo fascinante. En este artículo, revisamos la cantidad creciente de literatura sobre *A. palmeri* para resumir el estado actual de conocimiento sobre la biología, impactos agrícolas, y manejo de esta maleza, y sugerimos futuras direcciones para su investigación.

Palmer amaranth is an annual forb native to the area encompassing northwestern Mexico and southern California to New Mexico and Texas (Sauer 1957). It has a long history of human association and use in the arid southwest; Palmer amaranth leaves cooked as greens and meal made from the ground seed were consumed by several Native American tribes including the Navajo, Pima, Yuma, and Mohave (Moerman 1998). Palmer amaranth started to spread beyond its original range in the early 20th century, probably because of human activity transporting seeds or creating new habitats through agricultural expansion; it was first reported in Virginia in 1915, Oklahoma in 1926, and South Carolina in 1957 (Culpepper et al. 2010a; Sauer 1957). Sauer (1957) observed: "Of all the dioecious amaranths, *A. palmeri* has been by far the most successful as a weedy invader of artificial habitats, whether they were prepared by primitive or modern technology."

Despite these invasive tendencies and a history of range expansion, the emergence of Palmer amaranth as a major agronomic weed is relatively recent. It was not listed among the most troublesome weeds of cotton (*Gossypium hirsutum* L.), soybean (*Glycine max* L. Merr.), or corn (*Zea mays* L.) in a 1974 survey of the southern U.S. (Buchanan 1974); its first appearance in the annual survey of the Southern Weed Science Society occurred in 1989 in South Carolina (Webster and Coble 1997). By 1995, Palmer amaranth was the most troublesome weed of cotton in both North Carolina and South Carolina, but was not listed among the top 10 troublesome weeds in any other state (Dowler 1995; Webster and Coble 1997). By 2009, Palmer amaranth was ranked as the most troublesome cotton weed in the southern U.S., occurring in nine of 10 states surveyed (Webster and Nichols 2012). Palmer amaranth is also listed among the most troublesome weeds of corn (#7 in 2009, not listed in 1994) and soybean (#2 in 2010, ranked #23 in 1995) (Webster and Nichols 2012) and has become one of the most economically damaging glyphosate-resistant weed species in the U.S. (Beckie 2006).

Taxonomy, Reproductive Biology, and Genetics

Classification and Description. The genus *Amaranthus* belongs to the family Amaranthaceae and contains approximately 75 species worldwide. Palmer amaranth is one of a distinct subgroup of 10 dioecious species within A*maranthus* that are native only to North America (Steckel 2007); all other *Amaranthus* species are monoecious. The North American dioecious amaranths are currently classified in the subgenus *Acnida*. Mosyakin and Robertson (1996) proposed that based on floral and fruit characteristics, Palmer amaranth should be placed in the section *Saueranthus* within this subgenus. However, other evidence suggests that Palmer amaranth may be more closely related to the monoecious spiny amaranth (*A. spinosus* L.). Palmer amaranth and spiny amaranth have been

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assigned as sister taxa in AFLP-based phylogenetic analyses (Wassom and Tranel 2005). These species have the same chromosome number of 2n = 34 (Gaines et al. 2012; Grant 1959a), similar genome sizes (Rayburn et al. 2005), and they share distinguishing leaf and pollen morphological characteristics (Franssen et al. 2001). A high degree of internal transcribed spacer (ITS) sequence homology between Palmer amaranth and spiny amaranth has been reported (Kirkpatrick 1995). Palmer amaranth also hybridizes more readily with spiny amaranth than with other weedy amaranth species, as discussed further below.

Palmer amaranth typically has one central reddish-green stem up to 2 m tall with many lateral branches (Sauer 1955). The alternate hairless leaves, borne on long petioles that often exceed the length of the leaf blade, are lanceolate in young plants, becoming more ovate as the plant matures, with prominent whitish veins on the underside (Sauer 1955). Often the leaves also have a darker V-shaped chevron on the upper surface, a distinguishing morphological feature that Palmer amaranth shares with its putative sister species spiny amaranth (Franssen et al. 2001). The small (2 to 3.5 mm) pistillate (female) and staminate (male) flowers occur on separate plants, but cluster together to form similar terminal cylindrical inflorescences or spikes up to 60 cm long on the central stem; flowering spikes on the lateral branches are similar in structure though somewhat shorter in length. Male and female inflorescences can be distinguished by touch; males are softer, while female inflorescences feel rougher and more prickly because of the stiff bracts. The fruit is a thin-walled utricle about 1.5 mm long; the top half of the thin-walled fruit separates at maturity to expose the single black seed within (Sauer 1955).

Reproductive Biology. As a dioecious species, Palmer amaranth is an obligate outcrosser (Franssen et al. 2001). The mechanism controlling dioecy in Palmer amaranth is unknown. Grant (1959b) noted that heteromorphic sex-determining chromosomes are not present in the karyotypes of any dioecious *Amaranthus* species, including Palmer amaranth. Apparent agamospermy has been reported in female Palmer amaranth plants pollinated by common waterhemp (*A. tuberculatus* Moq. J.D. Sauer, formerly *A. rudis* L.) (Trucco et al. 2007) and also in female Palmer amaranth plants isolated from any pollen source (Ribeiro et al. 2012). This warrants further investigation: if seed production by female plants without fertilization is a common occurrence in Palmer amaranth populations, it would have significant implications for population genetics in this species and for management of herbicide resistance.

More usually, Palmer amaranth is wind-pollinated, and male plants produce prodigious amounts of pollen. In Arizona, Palmer amaranth pollen counts in September totaled 371 pollen grains m^{-3}, among the highest contributors to autumn pollen load (Walkington 1960). While this forced outcrossing ensures a genetically variable population, it can also serve to move adaptive traits between fields and across the agricultural landscape. A field study demonstrated that the glyphosate resistance trait was transferred up to 300 m through pollen from glyphosate-resistant males to glyphosate-susceptible female plants (Sosnoskie et al. 2012a). The distance that pollen can move is affected by the aerodynamics of the pollen grain and the local atmospheric conditions. It has been estimated that Palmer amaranth pollen could travel up to 46 km from the source plant (Sosnoskie et al. 2007) although movement of viable pollen beyond 300 m from the source has not been validated. Preliminary studies determined that pollen viability was reduced within 30 min of anthesis and approached nonviability at 240 min following anthesis (Sosnoskie et al. 2007). Additional studies are needed to develop a model describing potential pollen movement in Palmer amaranth, which could influence the development and adoption of herbicide resistance management programs (Webster and Sosnoskie 2010).

Palmer amaranth seeds are small (1 to 2 mm), smooth, and round or disc-shaped (Sauer 1955). Like other *Amaranthus* species, Palmer amaranth seed are predominantly gravity-dispersed but can also be spread by irrigation and other water flow, with the movement of birds and mammals, and through agricultural management practices such as plowing, mowing, harvesting, and spreading compost, manure or gin trash (Costea et al. 2004, 2005; Norsworthy et al. 2009). Although the seeds lack specialized dispersal mechanisms, including for wind dispersal, strong winds may move them over considerable distances; a hurricane was believed to be responsible for introducing Palmer amaranth seed into a previously noninfested agricultural habitat (Menges 1987a).

Female Palmer amaranth plants are prolific seed producers even when late-emerging or grown under competition. In California, plants that emerged between March and June produced 200,000 to 600,000 seeds per plant when growing without plant competition (Keeley et al. 1987). Plants that emerged later, between July and October, produced fewer inflorescences and $\leq$ 80,000 seeds per plant (Keeley et al. 1987). In Missouri, Palmer amaranth plants grown from seed planted in late May and early June produced more than 250,000 seeds per plant in the absence of plant competition (Sellers et al. 2003). Palmer amaranth in South Carolina that emerged between mid-June and late-July and grown in competition with rows of soybean spaced 97 cm apart, produced 211,000 seeds m^{-2}, while those competing with rows of soybean spaced 19 cm apart produced 139,000 seeds m^{-2} (Jha et al. 2008a). Palmer amaranth seed production m^{-2} increased from 140,000 to 514,000 as weed density increased from 0.5 to 8 plants m^{-1} of row, for weeds that emerged with corn (*Zea mays* L.) in Kansas (Massinga et al. 2001). Weed seed yields were between 1,800 and 91,000 seeds m^{-2} for the same densities when Palmer amaranth emerged when corn was at the four to seven leaf stage (Massinga et al. 2001). When growing with peanut (*Arachis hypogaea* L.), there was a hyperbolic relationship between Palmer amaranth seed production per area and Palmer amaranth plant density; maximum seed production of 124,000 seed m^{-2} (1.2 billion seed ha^{-1}) occurred at the highest Palmer amaranth density of 5.2 plants m^{-2} (Burke et al. 2007).

Genetics and Cytogenetics. The basic chromosome number in the Amaranthaceae is x = 8 or x = 9 (Turner 1994). Grant (1959a) reported that Palmer amaranth chromosomes are small (2 to 3 μm) and not well differentiated. Consistent with this, Rayburn et al. (2005) reported the genome size of Palmer

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amaranth to be smaller than most of the weedy amaranths with 2C = approximately 0.95 pg. Grant (1959a) gave a chromosome count for the species of 2n = 34. Gaines et al. (2012) also gave a chromosome count of 2n = 34 for Palmer amaranth, although Rayburn et al. (2005) reported 2n = 32. Base chromosome numbers of n = 16 and n = 17 sometimes occur within the same species in *Amaranthus* (Pal et al. 1982), so it is possible that variable cytotypes of 2n = 32 and 2n = 34 occur in different populations of Palmer amaranth. Based on these chromosome counts, Palmer amaranth is probably an ancient tetraploid. Greizerstein and Poggio (1992) reported bivalent formation during meiosis in six interspecific *Amaranthus* hybrids, indicating that diploidization had occurred in the parent species, although this study did not include *A. palmeri*. Simple Mendelian patterns of inheritance in a paleopolyploid such as Palmer amaranth would depend on the extent of subsequent diploidization to produce normal chromosome pairing as bivalents at meiosis. There have been virtually no studies examining the inheritance of a known single-gene trait in Palmer amaranth, although Wetzel et al. (1999) reported 1 : 1 segregation for the acetolactate synthase (ALS) resistance gene in progeny from a susceptible Palmer amaranth x ALS-resistant common waterhemp hybrid backcrossed to Palmer amaranth, which conforms to Mendelian expectations.

Interspecific Hybridization. Hybridization among different species has been widely reported within the genus *Amaranthus* (Sauer 1950; Trucco et al. 2005). Wetzel et al. (1999) reported transfer of ALS resistance via hybridization and backcrossing between Palmer amaranth and common waterhemp, although Franssen et al. (2001), Steinau et al. (2003), and Trucco et al. (2007) found very low levels of hybridization with most hybrid progeny from this cross either nonviable or sterile. Gaines et al. (2012) also reported low levels (< 0.2%) of interspecific hybridization between Palmer amaranth and common waterhemp, with even lower levels (< 0.01%) of hybrid formation between Palmer amaranth and smooth pigweed (*A. hybridus* L.). Gaines et al. (2012) found the highest levels of successful hybridization (up to 0.4%) occurred between Palmer amaranth and spiny amaranth, with this cross producing viable and fertile F1 progeny. Attempts in this same study to hybridize Palmer amaranth with Powell's amaranth (*A. powellii* S. Wats.) and redroot pigweed (*A. retroflexus* L.) were unsuccessful. Lack of sympatry and limited overlap in flowering times even with co-occurring species may mean that hybridization in the field between Palmer amaranth and other weedy *Amaranthus* species is rare. However, the demonstrated potential for Palmer amaranth pollen movement, and for this species to transfer herbicide resistance via gene flow — both of which are discussed further below — make even occasional interspecific hybridization events a cause for concern.

Physiology

Seed Germination. In its native xeric environment, Palmer amaranth is opportunistic, rapidly germinating and completing its lifecycle in response to available moisture (Ehleringer 1985). This fast response to favorable germination conditions was characterized in a study in which seeds of nine *Amaranthus* species were subjected to alternating temperatures with a mean of 30 C; all of the viable Palmer amaranth and smooth pigweed seed germinated on the first day, while seven other *Amaranthus* species required three to eight days to achieve 50% emergence (Steckel et al. 2004).

The small size of Palmer amaranth seeds necessitates a relatively shallow position within the soil profile for successful establishment. Keeley et al. (1987) reported that Palmer amaranth seeds germinated and became established seedlings more frequently (≥ 40% emergence) at soil depths of ≤ 1.3 cm, compared to seeds initially buried at depths of ≥ 5.1 cm, which had ≤7 7% emergence. Germination of freshly harvested Palmer amaranth seeds increased with natural light compared to those in darkness, but there were no differences in germination between seeds exposed to red and far-red light sources (Jha et al. 2010a). After nine to 12 months of burial in the soil seedbank, there was a suppressive effect of far-red light and stimulant effect of red light on Palmer amaranth germination (Jha et al. 2010a). Light quantity experienced by the maternal plant also had an effect on Palmer amaranth seed germination; female plants grown in 87% shade produced viable seed, of which only 12% germinated in the absence of light, while female plants grown in full sunlight produced seed that allowed 25% germination under dark conditions (Jha et al. 2010b). In addition, seeds that matured in the middle and top third of the female Palmer amaranth plant had ≥ 67% greater germination than those viable seed that matured in the lower third of the plant (Jha et al. 2010b). These authors speculated that the growing conditions of the maternal parent, as well as position of the flowers on the female plant, could influence long-term population dynamics within the soil seedbank.

Growing degree day models developed to predict weed seed emergence define the base temperature (T_b) as the minimum temperature at which phenological development is initiated (Steinmaus et al. 2000). The base temperature for Palmer amaranth was estimated to be 16.6 C, higher than for other summer annuals tested which had a mean base temperature of 12.6 C (Steinmaus et al. 2000). Palmer amaranth germination increased with temperature, with ≤ 8% emergence at 5 C and ≥ 71% at 35 C (Steckel et al. 2004). In some instances, Palmer amaranth seed germination increased under alternating temperatures (mean temperatures of 10, 15, and 30 C) compared to constant temperatures, while there were no differences when mean temperatures were 5, 20, and 35 C (Steckel et al. 2004). Once temperatures exceeded 35 C, Palmer amaranth seed germination declined; Guo and Al-Khatib (2003) reported no germination occurring when temperatures alternated (14 h/10 h) between 50 C and 45 C. In California fields, Palmer amaranth emergence initiated at a soil temperature of 18 C, and when Palmer amaranth seeds were planted monthly between May and September, there was at least 50% emergence within 2 wk (Keeley et al. 1987). In North Carolina, maximum Palmer amaranth germination rate occurred at 26 C, with 40% lower germination rate at 14 C (Wright et al. 1999a). Palmer amaranth emergence in fields in South Carolina was favored by high diurnal fluctuations in

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soil temperature of 10 to 16 C, which characterized a safe site that was free of existing plants (Jha and Norsworthy 2009). When soybean was growing above the Palmer amaranth seeds in the soil, Palmer amaranth emergence was reduced $\geq$ 73% relative to the adjacent nonsoybean plots.

Seed Herbivory. In spite of their small size, Palmer amaranth seeds are a potential food source for various animals. Red imported fire ants (*Solenopsis invicta* Buren) and various rodents have been observed removing Palmer amaranth seeds from seed traps (Sosnoskie et al. 2011a), although it is unknown how many of the seeds were consumed by these animals. Other studies have determined that Palmer amaranth seeds are consumed by a number of birds, which in some instances may act as vectors for seed dispersal. In one study, Palmer amaranth seeds retained $>$ 60% viability after passing through intestinal tracts of killdeer (*Charadrius vociferous* L.) and various ducks (DeVlaming and Vernon 1968). Another study recovered viable Palmer amaranth seeds after 2 to 15 h inside the digestive systems of 11 different bird species (Proctor 1968).

Soil Seedbank. In a study conducted by Menges (1987a), six years of hand-weeding and herbicide use reduced the Palmer amaranth population density in the soil seedbank by 98% relative to nontreated control plots, but approximately 18 million seed ha^{-1} still persisted in the soil seedbank at the conclusion of the study. In the nontreated control plots, Palmer amaranth seedbank densities grew from 173 million seeds ha^{-1} to 1.1 billion seeds ha^{-1} between 1980 and 1985. Norsworthy (2008) reported that the Palmer amaranth seedbank in the top 5 cm of soil in a South Carolina study declined 80 to 99% during the first cropping season under both conventional tillage and herbicide-based management, and seed densities remained low at this depth for the duration of the 4-yr study. At depths of 5 to 10 cm, seed densities fluctuated but after four years were lower than at the start of the experiment. Palmer amaranth plants that establish in a field and compete with crops are likely to have emerged from the topmost fraction of the soil profile. Keeley et al. (1987) found that Palmer amaranth seedlings emerged more readily from a depth of 2.5 cm or less (36 to 44% emergence) than from depths of 5.1 cm (7.2%) or 7.6 cm (1.6%).

In seed burial studies, Palmer amaranth seeds with initial viability of 96 to 98% lost approximately 30% of their viability after six months and had less than 50% viability after a year when buried at depths of 1.0, 2.5, and 10.0 cm (Sosnoskie et al. 2011a). By 36 mo at these depths, Palmer amaranth seed had $\leq$ 15% viability (Sosnoskie et al. 2011a). When Palmer amaranth was buried at 40 cm, the reduction in viability appeared to be somewhat lessened, with 78, 61, and 22% viable seed after 6, 12, and 36 mo of burial, respectively (Sosnoskie et al. 2011a). Previous studies on burial of redroot pigweed and tall waterhemp seeds demonstrated similar findings after 36 mo, but in these studies, viable seed from both species was recovered after 17 yr of burial (Burnside et al. 1996). The long-term persistence of Palmer amaranth seed in the soil seedbank is unknown, but based on these data some seed may survive for extended periods, especially at greater depths; if brought back up to the soil surface by tillage, this seed could be a source of reinfestation.

Root System Plasticity. Palmer amaranth exhibits considerable plasticity in root : shoot ratios. Studies conducted in Death Valley, CA (within the native range of Palmer amaranth) determined that plants had a ratio of roots to shoots of 0.16 $\pm$ 0.02, which was greater than the average of both the summer and winter annuals evaluated in this xeric environment (Forseth et al. 1984). In contrast, desert perennials were found to have root : shoot ratios between 0.33 and 0.84, reflecting their need to maintain growth in times without water (Forseth et al. 1984). The relatively low root : shoot ratios suggest that in these summer annuals, carbon accumulation is used primarily for vegetative growth and reproduction, with only a small fraction used for water acquisition, and soil water is utilized only in the upper 0.5 m. Palmer amaranth has been observed to flower in response to soil moisture depletion (Forseth et al. 1984).

In contrast to the water-limited conditions of the Death Valley studies, under well-watered conditions in a greenhouse Palmer amaranth had a root to shoot ratio of 0.6 (Wiese 1968). When grown in crop production scenarios in North Carolina, Palmer amaranth partitioned a greater proportion of total biomass to root production than did soybean (Wright et al. 1999a). Palmer amaranth plants with a biomass similar to soybean had more numerous roots of greater length and smaller diameter, which likely translated into better ability to harvest limited and unevenly distributed nutrients and moisture in the soil profile (Wright et al. 1999b). In addition, compared to four soybean genotypes, roots of Palmer amaranth more effectively penetrated soil layers with high bulk densities, such as hard pans that are commonly found throughout the piedmont and coastal plain soils (Place et al. 2008). Compared with soybean and sicklepod [*Senna obtusifolia* (L.) H.S. Irwin & Barneby], Palmer amaranth roots were found to be more efficient in nitrogen uptake, with a maximum of 8 mg N g^{-1} d^{-1} of root (Place et al. 2008). These data suggest that the roots of Palmer amaranth allow it to be more competitive than other species for the two most limited resources, water and nitrogen, in the southeast U.S. (Place et al. 2008). However, while sicklepod and soybean have been shown to have mycorhizzal associations, there is no evidence that Palmer amaranth forms these associations (Wright et al. 1999b). The mycorhizzal associations in other species may temper some of the apparent competitive advantage for nutrients and water that the root system of Palmer amaranth provides.

Photosynthesis and Growth Rate. Palmer amaranth, like other *Amaranthus* species, is a C_4 plant (Wang et al. 1992). C_4 photosynthesis is more common in monocots than in dicot species; the distribution of C_4 monocot species is correlated with higher temperatures, whereas the occurrence of C_4 dicots is most strongly associated with arid environments (Ehleringer et al. 1997). Most often, C_4 dicot species are found in habitats characterized as ephemeral, disturbed, or saline (Ehleringer et al. 1997). As previously noted, Palmer amaranth has long been known as a weedy invader of such environments. In the Sonoran desert region within the native range of Palmer

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amaranth, C_4 species account for 50% of the monocot taxa while only 4% of the dicot species are C_4 plants, with an inverse relationship between relative frequency of C_4 species and rainfall amounts (Ehleringer et al. 1997).

Palmer amaranth plants are also characterized by having high rates of photosynthesis. Maximum photosynthetic rate for Palmer amaranth has been measured at 81 μmol m^{-2} s^{-1} at 42 C, which is considered high even among plants with C_4 photosynthesis (Ehleringer 1983). Net rate of photosynthesis was determined to be temperature-dependent, with the optimum range (90% of maximum) occurring between 36 and 46 C (Ehleringer 1983). Rates of photosynthesis decline rapidly outside of this optimal temperature range; photosynthesis at 25 C was approximately 50% of the maximum rate (Ehleringer 1983). This reduced photosynthesis rate at lower temperatures coupled with greater energy constraints may restrict the potential range of Palmer amaranth, or at least affect its relative competitiveness with other plants. Redroot pigweed and common waterhemp accumulated more biomass and root volume than Palmer amaranth when grown at 15/10 C (day/night temperatures); however, this was reversed at 35/30 C with Palmer amaranth accumulating more biomass and root volume that the other two species (Guo and Al-Khatib 2003). Growth of Palmer amaranth was suppressed by cool temperatures (16 C) more than growth of soybean, while higher temperatures favored growth of Palmer amaranth relative to soybean (Wright et al. 1999a). It should be noted, however, that Palmer amaranth populations have been observed as far north as Michigan, as discussed in the final section of this review.

Some desert-adapted species are capable of reducing the absorbance of solar radiation by leaves as a means of reducing photosynthesis, leaf temperatures, and water losses through transpiration. However, Palmer amaranth lacks this adaptation, as the leaf absorptance is approximately 85% of solar radiation in the 400 to 700 nm wavelength, which is more typical for plant species existing outside of hot, arid climates (Ehleringer 1981). In contrast, Palmer amaranth is capable of diaheliotropism (solar tracking), which allows the leaves to orient themselves perpendicular to the rays of the sun thus maximizing light interception and photosynthesis potential (Ehleringer and Forseth 1980). This is an adaptation that permits an ephemeral species to maximize growth and more rapidly complete its life cycle prior to the onset of detrimental environmental conditions, such as drought or high temperatures (Ehleringer and Forseth 1980). It has been suggested that heliotropism is mainly advantageous during early phenological stages, when rapid growth will provide a competitive advantage (Ehleringer and Forseth 1980; Shell and Lang 1976). Rapid growth is a characteristic of Palmer amaranth (Culpepper et al. 2010a). In a study that evaluated growth of four different *Amaranthus* species, Palmer amaranth produced 32 to 83% more dry biomass than common waterhemp, redroot pigweed, and tumble pigweed (*Amaranthus albus* L.) (Horak and Loughin 2000). Additionally, the leaf area and growth rate (in terms of height gained per growing degree day) of young Palmer amaranth plants was at least 50% greater than for the other Amaranth species early in the growing season, giving Palmer amaranth a considerable competitive advantage (Horak and Loughin 2000). These authors also noted that the rapid growth rate of Palmer amaranth provided a smaller time window for optimal control compared to other weedy amaranths.

High rates of photosynthesis, coupled with diaheliotropism, allow Palmer amaranth to accumulate biomass at faster rates than nonsolar-tracking species (Ehleringer and Forseth 1980). Studies have determined that daily interception of sunlight was 9 to 40% higher in plants with diaheliotropism relative to plants with fixed or spherical leaf distribution relative to the sun (Shell and Lang 1976). However, Palmer amaranth has also demonstrated its ability to tolerate growth within a canopy. When grown under 87% shade, Palmer amaranth leaves had 42% greater specific leaf area compared to nonshaded conditions, resulting in thinner leaves and lower light compensation points (Jha et al. 2008b). This demonstrates that Palmer amaranth is capable not only of root system plasticity – as already discussed – but also of plasticity in leaf morphology, allowing plants to adapt to low-light environments such as a crop canopy and compete for limited resources.

One of the consequences of diaheliotropism is increased leaf temperatures and greater potential for water loss (Ehleringer and Forseth 1980). In addition to C_4 photosynthesis, Palmer amaranth has the adaptive ability to increase solute concentrations in the leaves in order to maintain positive turgor and keep stomata open under droughty conditions (Ehleringer 1985). Without the change in solute concentrations, Palmer amaranth leaves would wilt and photosynthesis cease at water potentials below −1.55 MPa, while this adjustment enables the stomates to remain open and gas exchange to continue, allowing net positive photosynthesis under low water condition, down to -2.83 ± 0.11 MPa (Ehleringer 1985; Forseth et al. 1984).

The competitiveness of Palmer amaranth during the high temperatures and frequent dry conditions that characterize the coastal plain of the southern U.S. make it a formidable weed. The further benefit of herbicide resistance also removes most of the weed competition that may suppress establishment of the small seedlings.

Host to Nematodes. Palmer amaranth serves as a host to several nematode species. Relative to tobacco (*Nicotiana tabacum*), Palmer amaranth is a moderate host for two nematode species, southern root-knot nematode [*Meloidogyne incognita* (Kofoid & White) Chitwood, race 3] and peanut root-knot nematode [*Meloidogyne arenaria* (Neal) Chitwood, race 2] (Tedford and Fortnum 1988). Another study determined that *Amaranthus* species are potential though poor hosts for southern root-knot nematode (race 3) and reniform nematode (*Rotylenchulus reniformis* Linford & Oliveira) relative to cotton (Davis and Webster 2005). One of the tenets of nematode management programs is crop rotation from susceptible host crops to nonhost crops. The presence of Palmer amaranth in crop fields could compromise this management strategy for nematode species for which this weed can act as an alternate host.

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Herbicide Resistance

Palmer amaranth shows a remarkable facility for evolving herbicide resistance. Resistance to five different herbicide mechanisms of action (MOAs) has been confirmed in this species to date: ALS-inhibiting herbicides, dinitroanilines, triazines, glyphosate, and HPPD inhibitors. Some Palmer amaranth populations have been reported as resistant to more than one of these MOAs (Burgos et al. 2001; Culpepper et al. 2006; Gaeddert et al. 1997; Horak and Peterson 1995; Norsworthy et al. 2008; Sosnoskie et al. 2011b; Sprague et al. 1997; Steckel et al. 2008; Thompson et al. 2012; Wise et al. 2009).

Dinitroaniline Resistance. This was one of the first herbicide resistance traits to evolve in Palmer amaranth. Trifluralin resistance was confirmed in 1989 in Palmer amaranth populations from eight different locations in South Carolina. These populations also showed various degrees of cross-resistance to four other dinitroaniline herbicides: benefin, isopropalin, pendimethalin, and ethalfluralin (Gossett et al. 1992). The dry shoot weights of resistant and susceptible biotypes were similar, suggesting no significant fitness costs associated with resistance (Gossett et al. 1992). Trifluralin resistance in Palmer amaranth was also reported in Tennessee in 1998 (Heap 2012).

Triazine Resistance. There have been multiple reports of atrazine resistance in Palmer amaranth, starting in Texas in 1993. Atrazine resistance was reported again in Texas and also in Kansas in 1995 and in Georgia in 2008 (Heap 2012). The biological mechanisms and modes of inheritance of dinitroaniline and triazine resistance in Palmer amaranth have not been investigated.

ALS Resistance. The MOA of this class of herbicides is the inhibition of branched chain amino acid synthesis (Shaner et al. 1984). ALS inhibitors have been widely used for Palmer amaranth control since their introduction in 1982 (Gaeddert et al. 1997). Most cases of ALS resistance are because of changes in the base sequence of the ALS gene resulting in an enzyme that is less sensitive to the binding of ALS-inhibiting herbicides; this altered sequence is typically inherited as a single allele with a high degree of dominance (Saari et al. 1994; Tranel and Wright 2002). High levels of naturally-occurring variation in the ALS gene sequence have been found in some weed species such as common ragweed (*Ambrosia artemisiifolia* L.), allowing rapid and widespread selection for resistance when ALS-inhibiting herbicides are used (Tranel et al. 2004). This appears to be the basis for most ALS resistance in Palmer amaranth (Sprague et al. 1997; Burgos et al. 2001; Franssen et al. 2001), although Burgos et al. (2001) suggested that reduced absorption, translocation or enhanced metabolism could also be involved in some cases. ALS-resistant Palmer amaranth is now widespread across the southern U.S. (Bond et al. 2006); it was reported in Arkansas in 1994, North Carolina in 1995, South Carolina in 1997, Georgia in 2000, and Florida and Mississippi in 2008 (Burgos et al. 2001; Heap 2012; Horak and Peterson 1995; Vencill et al. 2002). Cross-resistance to multiple ALS-inhibiting herbicides is common in Palmer amaranth. Burgos et al. (2001) reported imazaquin-resistant Arkansas accessions that were cross-resistant to chlorimuron, diclosulam, and pyrithiobac. Wise et al. (2009) surveyed 61 accessions collected across Georgia that all showed resistance to imazipic, with 30 of these accessions also showing cross-resistance to chlorimuron, diclosulam, and pyrithiobac at the recommended field-use rate.

Glyphosate Resistance. Palmer amaranth is currently one of the most economically damaging glyphosate-resistant weeds in the U.S. (Beckie 2011). Glyphosate-resistant Palmer amaranth was first identified in Georgia in 2004 (Culpepper et al. 2006) and subsequently reported in Arkansas, North and South Carolina, and Tennessee (Norsworthy et al. 2008; Scott et al. 2007; Steckel et al. 2008; York et al. 2007). It is now widespread across the South and is spreading rapidly, with new reports from Illinois in 2010 and Michigan and Virginia in 2011 (Heap 2012; Nandula et al. 2012). Many of these glyphosate-resistant Palmer amaranth populations evolved in cropping systems exposed to repeated glyphosate use with little diversity in weed management (Beckie 2011; Culpepper et al. 2006).

Under these conditions, Palmer amaranth populations appear to have independently evolved more than one mechanism for glyphosate resistance. Resistant plants in a population from Georgia investigated by Gaines et al. (2010) were found to have amplified as many as 100 or more extra copies of the 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) gene. This gene amplification enables overexpression of the EPSPS enzyme with which glyphosate interacts, providing extra enzyme to absorb glyphosate and still leave sufficient uninhibited EPSPS to allow the plant to continue functioning (Gaines et al. 2011; Powles 2010). This unusual mechanism of herbicide resistance, which had not previously been reported in any weed population, is heritable and can be transferred via pollen from resistant males to the offspring of susceptible female Palmer amaranth plants, and to the related weedy species spiny amaranth, common waterhemp, and smooth pigweed (Gaines et al. 2012). Amplification of the EPSPS gene has also been detected in a glyphosate-resistant Palmer amaranth population from Mississippi (Ribeiro et al. 2011). It is possible that this mechanism can not only be transferred via gene flow, but also that it is evolving independently in Palmer amaranth populations in different cropping systems and geographically diverse locations in response to repeated glyphosate use.

Amplification of the EPSPS gene is not the only biological mechanism that confers glyphosate resistance in Palmer amaranth. Steckel et al. (2008) described somewhat lower – but still agronomically significant – levels of resistance in a Tennessee population where both resistant and susceptible plants accumulated shikimate when treated with glyphosate in the laboratory, indicating that the EPSPS enzyme was being inhibited in both biotypes. In contrast, glyphosate-resistant Palmer amaranth with EPSPS gene amplification does not accumulate shikimate. These authors suggested that reduced translocation of glyphosate within the plant might be the underlying resistance mechanism in this population. Resistance in a Palmer amaranth population from Mississippi also appears to involve reduced translocation, based on studies

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tracking ^{14}C-glyphosate movement within the plant (Nandula et al. 2012).

HPPD Resistance. Palmer amaranth with resistance to multiple HPPD-inhibiting herbicides has recently been confirmed in Kansas, but the mechanism and mode of inheritance of this resistance is not yet known (Thompson et al. 2012).

Multiple Resistance. Increasing numbers of Palmer amaranth populations in the southern U.S. are being reported as having evolved resistance to more than one herbicide MOA. Nandula et al. (2012) described two glyphosate-resistant biotypes from a Mississippi population that also had resistance to pyrithiobac and chlorimuron. Biotypes resistant to both glyphosate and pyrithiobac have been described in a Palmer amaranth population from Georgia (Sosnoskie et al. 2011b). Additional examples of multiple resistance in Palmer amaranth include a population resistant to glyphosate and imazapic reported in 2008 in Georgia, and a population resistant to glyphosate plus pyrithiobac and chlorimuron reported in 2009 in Tennessee (Heap 2012). It is notable that to date all cases of multiple resistance in Palmer amaranth populations involve combinations of resistance to glyphosate and ALS inhibitors. This could be because ALS resistance is now so widespread in Palmer amaranth that selection for glyphosate resistance is occurring in populations where ALS resistance alleles are already present. Alternatively, populations that have already evolved glyphosate resistance may subsequently acquire ALS resistance alleles through cross-pollination.

Stacking within individual plants of different resistance mechanisms independently controlled by separate genes could readily occur in an obligate outcrosser such as Palmer amaranth. Further investigation of Palmer amaranth populations with multiple resistance is needed to determine whether gene stacking is responsible or whether a generalized resistance mechanism has evolved that is effective against more than one herbicide.

Agricultural Impacts of Palmer Amaranth

Competitive Interference. In agricultural fields, competitive success of a plant, whether it is a crop or a weed species, is a function of growth rate of the plant and relative earliness of germination (Radosevich and Holt 1984). Palmer amaranth has a rapid growth rate and ability to accumulate large quantities of biomass, even with its extended emergence pattern throughout the growing season (Jha and Norsworthy 2009). The competitiveness of Palmer amaranth has been documented in many agronomic crops in the U.S. as summarized in Table 1.

In Texas, season-long interference from Palmer amaranth densities of 1 and 10 plants 9.1 m^{-2} reduced cotton lint yields 11 and 59%, respectively (Morgan et al. 2001). In Oklahoma, each Palmer amaranth plant per 9.1 m^{-2} reduced cotton yields 6 to 11.5% (Rowland et al. 1999). There was also a relationship between lint yield and weed biomass, with 5 to 9% yield reduction for every kg of Palmer amaranth dry biomass per plot; plots were 36.4 m^2 (Rowland et al. 1999).

Any effective Palmer amaranth control system must manage a continually emerging weed population, especially as herbicides are dissipated from the emergence zone of Palmer amaranth (Culpepper et al. 2010b; Jha and Norsworthy 2009). To address the issue of season-long interference, a study was conducted to evaluate the relationship between cotton yield loss and delayed Palmer amaranth establishment by simulating inconsistent control from PRE and POST herbicides (MacRae et al. 2008). Palmer amaranth established at the three- and nine-leaf stages of cotton reduced cotton yield 0.9% for every plant per m^2 (MacRae et al. 2008). These data suggest that Palmer amaranth remains competitive with cotton even when cotton was established first. When Palmer amaranth establishment was delayed to 12- or 17-leaf stages of cotton, there was no detectable effect on cotton yield, indicating that weeds that established after POST and layby applications did not reduce cotton yields. However, plants from all establishment times were able to reproduce ($>$ 14,000 seeds $plant^{-1}$), supplying viable seed to the soil seedbank (MacRae et al. 2008).

The critical period of weed control is defined as the interval that is bounded on one end as the time at which weeds that emerged with the crop must be controlled and delimited on the other end as the time at which newly emerged weeds will not contribute to crop yield loss (Knezevic et al. 2002). MacRae et al. (2008) studied half of this interval, quantifying the cotton growth stage after which weed emergence does not affect crop yield. The other component of the critical period of weed control establishes from crop emergence the duration of weed interference that a crop can tolerate before yields are reduced. This is predicated on being able to effectively remove the weed once it is established, which is currently a challenge with Palmer amaranth with the herbicides available for control. Cotton yield losses caused by Palmer amaranth interference for the first 21 and 35 d after crop emergence were $\leq$ 5 and 20%, respectively (Fast et al. 2009). At 49 d after crop emergence, cotton yields were reduced 58%, with maximum crop yield loss (77%) occurring at the longest duration of interference (63 d after crop emergence) (Fast et al. 2009).

In addition to reducing yields, the large amounts of biomass produced by mature Palmer amaranth plants interfere with cotton harvest, compromising harvest efficiency by the frequency of work stoppages needed to dislodge thick Palmer amaranth plant stems from harvest equipment (Smith et al. 2000). The presence of Palmer amaranth increased harvest time between two- to four-fold, relative to the weed-free control (Smith et al. 2000). Morgan et al. (2001) concluded that mechanical harvest was impractical because of potential equipment damage once Palmer amaranth densities were in excess of 0.65 plants m^{-2} (six plants 9.1 m^{-1} row). Fields infested with Palmer amaranth resulted in cotton lint that contained up to 15% trash, but the residual weed matter was successfully removed using a lint cleaner, though there is an additional cost associated with this practice (Smith et al. 2000). In spite of the effect of Palmer amaranth on lint quantity, cotton fiber qualities (i.e. micronaire, length, strength, and color) were not affected by Palmer amaranth

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Table 1. Estimated yield losses caused by Palmer amaranth interference in corn, cotton, peanut, sorghum, soybean and sweet potato.

Crop	Yield loss	Emergence time	Density	Location	Reference
	%		plants m^{-2}		
Corn	11	With crop	0.66	KS	(Massinga et al. 2001)
	91	With crop	10.50	KS	(Massinga et al. 2001)
	7	4- to 7-leaf corn	0.65	KS	(Massinga et al. 2001)
	35	4- to 7-leaf corn	10.50	KS	(Massinga et al. 2001)
Cotton	11	With crop	0.11	TX	(Morgan et al. 2001)
	59	With crop	1.10	TX	(Morgan et al. 2001)
	6 – 11.5	With crop	0.11	OK	(Rowland et al. 1999)
	41 – 65	With crop	0.66	OK	(Rowland et al. 1999)
	6	3- to 9-leaf cotton	0.18	GA	(MacRae et al. 2008)
Peanut	28	With crop	1.10	NC	(Burke et al. 2007)
	68	With crop	6.00	NC	(Burke et al. 2007)
Sorghum	13	With crop	0.35	OK	(Moore et al. 2004)
	50	With crop	1.58	OK	(Moore et al. 2004)
Soybean	17	With crop	0.33	AR	(Klingaman and Oliver 1994)
	64	With crop	3.33	AR	(Klingaman and Oliver 1994)
	68	With crop	10.00	AR	(Klingaman and Oliver 1994)
	79	With crop	10.50	KS	(Bensch et al. 2003)
Sweetpotato	56	With crop	0.47	NC	(Meyers et al. 2010)
	94	With crop	6.13	NC	(Meyers et al. 2010)

weed density (Morgan et al. 2001; Rowland et al. 1999; Smith et al. 2000).

Relative to cotton, soybean is an aggressive plant that establishes more rapidly and is generally more tolerant of weed presence (Zimdahl 1980). At 12 wk after crop emergence, soybean canopy width was reduced 55% by 10 Palmer amaranth plants m^{-1} of row relative to the weed-free control (Klingaman and Oliver 1994). Palmer amaranth densities of 0.33, 3.33 and 10 plants m^{-1} reduced soybean yields 17, 64, and 68%, respectively (Klingaman and Oliver 1994). In a comparison of *Amaranthus* species at densities of 0.25 to 4 plants m^{-1} of row, Palmer amaranth accumulated greater plant biomass, produced more seed, and caused more soybean yield loss than redroot pigweed and common waterhemp (Bensch et al. 2003). At a density of eight plants m^{-1} of row, soybean yield loss was 79% from season-long Palmer amaranth interference (Bensch et al. 2003).

Unlike cotton and soybean, peanut is a low-growing crop. Peanut yield loss from season-long interference of 1 and 5.5 Palmer amaranth plants m^{-1} of row was predicted to be 28 and 68%, respectively (Burke et al. 2007). As with other crops, Palmer amaranth would likely reduce harvest efficiency and could cause equipment issues with digging and harvesting that are not accounted for in these estimates. While there have been no studies that have directly compared Palmer amaranth competitiveness among other weed species in peanut, Burke et al. (2007) found that parameter estimates of competitiveness across studies indicated Palmer amaranth to be more competitive than broadleaf signalgrass (*Urochloa platyphylla* (Munro ex C. Wright) R. D. Webster), bristly starbur (*Acanthospermum hispidum* DC), tropic croton (*Croton glandulosus* L. var. *septentrionalis* Müll. Arg), horsenettle (*Solanum carolinense* L.), wild poinsettia (*Euphorbia heterophylla* L.), and jimsonweed (*Datura stramonium* L.). However, Palmer amaranth was less competitive than common ragweed, fall panicum (*Panicum dichotomiflorum* Michx.), and common cocklebur (*Xanthium strumarium* L.) in peanut (Burke et al. 2007).

In Kansas, Palmer amaranth that emerged with the crop reduced corn yields 11 to 91% at densities of 0.5 to 8 plants m^{-1} (rows spaced 76 cm apart) (Massinga et al. 2001). When Palmer amaranth emergence occurred at the four- to seven-leaf stage of corn, Palmer amaranth interference resulted in corn yield reductions of 7 to 35% at 0.5 to 8 plants m^{-1} (Massinga et al. 2001). Regardless of the timing of Palmer emergence relative to corn, the economic threshold (i.e. the population density of Palmer amaranth at which weed control is economically justified) was exceeded even at the lowest tested Palmer amaranth density.

There was an inverse linear relationship between Palmer amaranth density and grain sorghum (*Sorghum bicolor* L.) yield, with maximum sorghum yield loss of 38 to 63% at the highest tested Palmer amaranth density of 1.58 plants m^{-2} (Moore et al. 2004). One consequence of Palmer amaranth interference was the linear relationship between grain moisture and Palmer amaranth density; the weed affected the drying of the crop, which could delay harvest (Moore et al. 2004).

Sweet potato [*Ipomoea batatas* (L.) Lam.] is also a low-growing crop in which Palmer amaranth interference reduces yield quantity and quality (Meyers et al. 2010). The highest grade of sweet potatoes, 'Jumbo', is reduced 56 and 94% from Palmer amaranth densities of 0.47 and 6.13 plants m^{-2}, respectively, with 'marketable' grade reduced 36 and 81% at these densities (Meyers et al. 2010). The threshold density of Palmer amaranth that is equivalent to 10% yield loss is 0.08 plants m^{-2}, or one plant every 12.5 m^2. The upright growth of Palmer amaranth shades the sweet potato canopy, intercepting more than 65% of available light beginning at 6 WAP. There was a linear relationship between level of light interception and yield loss, with a 1.1 to 1.35% yield loss for each percentage of light intercepted by Palmer amaranth (Meyers et al. 2010).

Noncompetitive Interference. Palmer amaranth plants may also affect crop growth through noncompetitive interference (i.e. allelopathy). Soil amended with Palmer amaranth

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residues resulted in reduced fresh weights of both carrot (*Daucus carota* L.) and onion (*Allium cepa* L.) and affected carrot seedling establishment (Bradow and Connick 1987; Menges 1987b). Greater inhibition of seedling growth occurred in response to leaf and reproductive tissue compared to tissues from stem and root (Menges 1987b). Plant tissue from the aerial parts of Palmer amaranth and five other *Amaranthus* species have been found to contain volatile organic compounds which reduce germination of carrot, onion, and tomato (*Lycopersicon esculentum* Mill.) (Connick et al.1987).

Conservation Tillage. The development and wide use of glyphosate-resistant crops has facilitated the adoption of conservation tillage practices in the southeast U.S. (Givens et al. 2009; Price et al. 2011) providing advantages that include fewer trips across the field, reduced soil erosion, greater water infiltration, reduced herbicide loss through runoff and greater carbon accretion (Causarano et al. 2006; Potter et al. 2004; Triplett and Dick 2008). Between 1994 and 2008, conservation tillage increased 49% for soybean and 85% for cotton (Price et al. 2011). However, conservation tillage eliminated the ability to use cultivation as a weed management tool, resulting in a greater reliance on herbicides for weed control. Whereas cotton production typically used five herbicides and multiple in-crop cultivations prior to the introduction of glyphosate-resistant cotton, early adopters of glyphosate-resistant crops often eliminated use of PRE-applied herbicides and relied on near-exclusive use of glyphosate for weed control (Chandler 1984; Price et al. 2011). As a result, the evolution of glyphosate-resistant Palmer amaranth poses a significant threat to conservation tillage, as deep turning with a moldboard plow and in-crop cultivation are two potential solutions to reduce the germinable soil seedbank and control emerged seedlings in resistant populations (Price et al. 2011).

Management of Palmer Amaranth

The spread of glyphosate-resistant Palmer amaranth has stimulated increased research on management of this weed. Much of this recent research has been conducted in cotton, soybean, and peanut cropping systems where Palmer amaranth has become a serious threat to production. Research on herbicidal management of Palmer amaranth management initially focused on glyphosate-based weed control, but more recently the focus has shifted to glufosinate-based systems, reflecting the increased occurrence of glyphosate-resistant Palmer amaranth populations. In this section we summarize recent published studies on herbicide-based management of Palmer amaranth in cotton, corn, soybean, and peanut and consider the potential impact of new herbicide-resistant crop technology, before reviewing research on nonchemical management.

Cotton. Glyphosate-resistant Palmer amaranth management is a serious concern for cotton growers (Culpepper et al. 2006; Norsworthy et al. 2008; Norsworthy et al. 2012a; Sosnoskie and Culpepper 2012; Steckel et al. 2008). A major issue is that in much of the Midsouth and Southeast U.S. Palmer amaranth is not only resistant to glyphosate but also to ALS-inhibiting herbicides (Heap 2012). This leaves no topical herbicide control options in Roundup Ready Flex® (RRF) or conventional cotton (Culpepper et al. 2006; Norsworthy et al. 2008; Steckel et al. 2008). Overlapping residual herbicides and activating them with irrigation or timely rainfall after application has become the only practical way to grow RRF cotton in a Palmer amaranth infested field using chemical weed control (Culpepper 2009; Culpepper et al. 2007; Whitaker et al. 2008). Norsworthy et al. (2010) quantified the amount of precipitation needed to move herbicides into the soil solution so they are active on the weeds. These authors reported that flumioxazin and fomesafen needed the least amount of precipitation (0.5 cm) to become active, while *S*-metolachlor, pendimethalin, and diuron required more precipitation (1.3 cm) to achieve the same level of residual Palmer amaranth control. Kichler et al. (2010) noted that trifluralin, pendimethalin, and fomesafen applied preplant incorporated (PPI) provided better control and less cotton injury than when applied PRE without incorporation. However, in a subsequent study, fomesafen applied PRE provided better Palmer amaranth control (Kichler et al. 2011). Riar et al. (2012) showed that for consistent control within the cotton row middles the final herbicide pass should contain a residual herbicide effective on Palmer amaranth such as linuron, diuron, or flumioxazin. The overlapping residual method utilized in a RRF cotton system allows growers to plant varieties most adapted to the Midsouth and Southeast (Bullington et al. 2011), and Riar et al. (2011) reported that utilizing overlapping residual applications in a RRF system resulted in Palmer amaranth control similar to that in a glufosinate-resistant (LibertyLink®, LL) system, provided the residual herbicides were activated through precipitation or irrigation. Several studies found that overlapping residual herbicides in cotton without precipitation or irrigation resulted in inconsistent Palmer amaranth control (Bond et al. 2010; Kichler et al. 2010; Steckel 2012b; Wilson et al. 2011). This is a major concern for growers that do not have irrigated row-crop production (Culpepper et al. 2012; Steckel 2012a,b). However, in states such as Arkansas where irrigation is more available, the overlapping residual method is widely utilized (Anonymous 2012; Norsworthy et al. 2012a).

An alternative management strategy is to plant LL cotton and utilize a glufosinate-based Palmer amaranth management system (MacRae et al. 2007). This system utilizes preplant, PRE and in-crop residual herbicides - as with the overlapping residuals method - in combination with glufosinate POST and POST-directed applications (Culpepper et al. 2009). The ability to control emerged Palmer amaranth with glufosinate makes this system more consistent in nonirrigated production systems (Culpepper 2009; MacRae et al. 2007; Riar et al. 2011; Steckel 2012a; Whitaker et al. 2011). Bond and Eubank (2011) found that a PRE application of fluometuron followed by two sequential glufosinate applications applied POST controlled Palmer amaranth more effectively than sequential POST applications alone. These authors also noted that control with glufosinate was better on smaller Palmer amaranth plants (13 cm tall) than on larger (26 cm tall)

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plants. Whitaker et al. (2011) also determined that utilizing a PRE-applied herbicide with good activity against Palmer amaranth followed by a timely glufosinate application POST resulted in consistent control. Other researchers reported that glufosinate application techniques resulting in reduced coverage, such as utilizing air induction nozzles or lowering application rates by at least 20%, reduced Palmer control in LL cotton (Doherty et al. 2011).

Because of the performance issues of LL cotton in the Midsouth and Southeast U.S., most growers have used WideStrike® cotton varieties, which historically have performed better than LL cotton varieties (Main 2011; Steckel et al. 2012c; Whitaker et al. 2011). Although WideStrike® cotton varieties have lower tolerance to glufosinate compared with LL (Tan et al. 2006), they allow growers to apply both glyphosate and glufosinate as part of their weed control program without reducing yields (Culpepper et al. 2009). This particular management system has become widely used by farmers in the states of Tennessee, North Carolina and Georgia (Anonymous 2012; Norsworthy et al. 2012a; Sosnoskie and Culpepper 2012; Steckel et al. 2012a). The wide adoption is interesting as there is no compensation for a grower who uses glufosinate POST on WideStrike® cotton and has herbicide injury. Neither university researchers, Bayer CropScience, the manufacturers of glufosinate, nor PhytoGen®, who market 'PHY 375 WRF®' and 'PHY 485 WRF®', recommend glufosinate applications to WideStrike® cotton.

The increased use of PPI- and PRE-applied herbicides to provide residual control in glyphosate- and glufosinate-based Palmer amaranth management systems has increased loss of cotton stand (Culpepper et al. 2012; Steckel 2012b). Culpepper et al. (2012) and Kichler and Culpepper (2012) reported that timing of precipitation around the PRE herbicide coupled with planting depth, soil temperature, and soil type all impact the effect of these herbicides on the establishing cotton stands. They found that planting cotton into dry soil and then irrigating overhead following a PRE application of fomesafen or fomesafen plus pyrithiobac, caused serious injury to emerging cotton and stand establishment problems. However, when those same applications were made to moist soil and then overhead irrigated, little injury was observed.

Corn. Good control of Palmer amaranth in corn can be achieved when mixtures of two herbicides effective on the weed are applied POST. Jones et al. (1998) found that a mixture of glufosinate with atrazine enhanced Palmer amaranth control over glufosinate alone. Bararpour et al. (2011) reported that two HPPD-inhibiting herbicides can provide good control of Palmer when mixed with atrazine. Corn yields were increased from 11,340 kg ha^{-1} to 11,970 kg ha^{-1} and 11,460 to 11,970 kg ha^{-1} when atrazine was tank-mixed with isoxaflutole and tembotrione, respectively, in a study site infested with Palmer amaranth. A separate study showed that atrazine plus isoxaflutole plus thiencarbazone-methyl provided 91% control of Palmer amaranth 8 wk after PRE application compared to 81% control with atrazine removed from the mixture (Stephenson and Bond 2012).

Soybean. Management of glyphosate-resistant Palmer amaranth is also a serious concern for soybean growers (Jordan et al. 2011; Prostko 2011; Scott et al. 2011; Steckel et al. 2012a,b). A major issue is that herbicides used in place of glyphosate to control emerged Palmer amaranth in soybean, such as fomesafen and lactofen, must be applied before Palmer amaranth is 8 cm tall to be effective (Prostko 2011; Steckel et al. 2012b). If that window is missed, soybean crops are often tilled up and replanted in the southern U.S. (Norsworthy et al. 2012a; Steckel et al. 2012b). As with cotton, PRE-applied residual herbicides are the pillar of managing glyphosate-resistant Palmer amaranth in soybean (Norsworthy et al. 2012b; Scott et al. 2011). In both glyphosate-resistant and conventional soybean, the most consistent herbicide program is PRE application of herbicides with good activity on Palmer amaranth, such as *S*-metolachlor plus flumioxazin or flumioxazin plus pyroxasulfone, followed by fomesafen when Palmer amaranth plants are less than 7 cm tall (Dillon et al. 2011). Jordan et al. (2011) reported 55 to 70% control with PRE-applied flumioxazin, sulfentrazone, *S*-metolachlor, fomesafen plus *S*-metolachlor, and chlorimuron plus metribuzin by early August. These authors also reported that sequential glufosinate applications provided 83% Palmer amaranth control. Holshouser and Ahmed (2011) also reported good Palmer amaranth control (95%) three weeks after treatment with glufosinate applications in LL soybean.

Peanut. Glyphosate-resistant Palmer amaranth is also a threat to peanut production (Prostko 2012). A regimen of pendimethalin applied PPI followed by flumioxazin or sulfentrazone PRE and paraquat plus *S*-metolachlor applied early-POST, followed by lactofen or acifluorfen late-POST to small (< 7 cm tall) Palmer amaranth is necessary to produce peanut in fields infested with glyphosate- and ALS-resistant Palmer amaranth (Prostko 2011). Prostko (2011) evaluated applicators for nonselective herbicides for control of Palmer amaranth in peanut production systems. He found that a 50% solution of paraquat applied in one direction with Grass-Works Weed Wiper® (Grass Works Weed Wiper, LLC, Lincoln, AR), TopCrop Super Sponge Weed Wiper® (Smucker Mfg., Harrisburg, OR), and the LMC-Cross Wick Bar® (Cross Application Equipment Company, Albany, GA), when the Palmer amaranth was 115 cm tall provided 85% control. This research laid the foundation for a 24C label in Georgia, Florida, and South Carolina for this practice in peanut.

Palmer Amaranth Management with New Herbicide-Resistant Trait Technologies. In the future, rapid adoption of cotton varieties with excellent tolerance to glyphosate and glufosinate (Glytol® + LL) is likely. Reed et al. (2011) reported good Palmer amaranth control and no crop injury when utilizing a glufosinate-based system that utilized PPI, PRE, and residual herbicides tank-mixed with glufosinate in Glytol® + LL cotton. The next generation of herbicide-resistant crops will provide tolerance to either dicamba, 2,4-D, or the HPPD herbicides (Castle et al. 2006; Chafin et al. 2010; Norsworthy 2011a; Steckel et al. 2012a; York et al. 2012). Many of these varieties will also have stacked tolerance to glufosinate and glyphosate (Chafin et al. 2010; Steckel et al.

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2012a; York et al. 2012). Initial research evaluating weed management systems utilizing herbicides that will be used with these traits indicates that all of them can be effective tools in a system to manage Palmer amaranth (Chafin et al. 2010; Culpepper et al. 2011; Marshall 2012; Merchant et al. 2011; Norsworthy 2011a; Steckel et al. 2012a,b; York et al. 2012). Stephenson et al. (2011) reported that 2,4-D mixed with glyphosate enhanced control of glyphosate-resistant Palmer amaranth but provided no additional control when applied to glyphosate-susceptible populations. Marshall (2012) evaluated Palmer amaranth control in cotton resistant to dicamba, glufosinate, and glyphosate and determined that dicamba alone could control Palmer amaranth up to 12 cm. Steckel et al. (2012b) reported that flumioxazin applied PRE followed by dicamba and glyphosate applied POST to Palmer amaranth before it reached a height of 12 cm provided good control in soybean resistant to dicamba and glyphosate. Palmer amaranth that reached heights of 13 to 36 cm could be controlled with tank mixes of glufosinate plus 2,4-D or dicamba in a noncrop experiment (Norsworthy 2011a). Chafin et al. (2010), Merchant et al. (2011), and York et al. (2012) also reported good control of Palmer amaranth 15 to 20 cm tall at application with a mixture of glufosinate and 2,4-D or dicamba.

Nonherbicidal Management of Palmer Amaranth. As Palmer amaranth has already demonstrated considerable ability for evolving herbicide resistance, it is likely that this weed will in the future become resistant to other herbicides (e.g. glufosinate, fomesafen, dicamba, and 2,4-D) if these are relied upon too heavily as was done with glyphosate (Norsworthy et al. 2012c; Prostko 2011; Steckel 2012a). For example, multiple applications of PPO-inhibiting herbicides within a single growing season are cause for concern. Cultural practices that row-crop producers have largely abandoned in recent years, such as cover crops, cultivation, hand-weeding, and crop rotation should be incorporated into integrated management strategies to reduce selection pressure for resistance to the few herbicides that still remain active on Palmer amaranth (Culpepper et al. 2010b; DeVore et al. 2010, 2011; Norsworthy et al. 2012c; Prostko 2011). This is supported by simulation modeling of Neve et al. (2011a) that showed rotating glyphosate-resistant cotton with corn or cotton resistant to other herbicides would delay resistance evolution by 2 to 3 yr compared to a glyphosate-resistant cotton monoculture; combining glyphosate application with the use of PRE and POST residual herbicides reduced the risk of herbicide resistance to a projected 12% of Palmer amaranth populations. In contrast, five annual glyphosate applications with no other herbicide use was predicted to result in evolution of resistance in 39% of Palmer amaranth populations after 5 years and 60% of populations after 10 yr (Neve et al. 2011b).

The two cultural practices most comprehensively investigated for managing Palmer amaranth are tillage and the use of cover crops. As noted in an earlier section of this review, Palmer amaranth germination and seedling establishment is significantly reduced when seed is buried at depths of 5 cm or more in the soil profile; hence, cultivation that achieves this can be a useful management tool. Price et al. (2011) reported that sweep cultivators can augment PRE herbicides in controlling Palmer amaranth in cotton, and Prostko (2012) reported that using a moldboard plow to bury Palmer amaranth seed at least 10 cm deep will provide 50% control in peanut. Culpepper et al. (2010b) showed that deep tillage in the autumn followed by a cereal rye (*Secale cereal* L.) cover crop increased Palmer control 18% when used in conjunction with a glufosinate-based cotton herbicide program, while Webster et al. (2011) reported that a winter cover crop of cereal rye plus Austrian winter pea (*Pisum sativum* L.) reduced Palmer amaranth populations the following June by 80%. This is supported by results from Sosnoskie et al. (2012b) and Burgos and Talbert (2000) who found that allelopathic chemicals produced by cereal rye inhibit Palmer amaranth germination and seedling growth. Earlier studies have also shown that establishment of small-seeded weeds (of similar size to those of Palmer amaranth) is reduced by mulch residues (Mohler and Teasdale 1993; Teasdale and Mohler 2000). In the absence of PRE herbicides, early-season Palmer amaranth populations were reduced when cotton was planted into a strip-tillage rolled rye winter cover crop system, relative to the strip tillage winter fallow system (Timper et al. 2011). The costs and benefits of strip tillage of summer crops into high-residue winter cover crops are still under investigation, but some studies have examined the effectiveness of combining cultural practices with a cover crop. Culpepper et al. (2010b) reported 98% control of Palmer amaranth with deep tillage in the autumn followed by a cover crop of rye that year, while Culpepper et al. (2007) found that planting cotton in strip-tillage production of a cereal rye cover crop provided good Palmer amaranth control between the rows. Aulakh et al. (2011) reported that a cover crop of crimson clover (*Trifolium incarnatum* L.) provided more biomass and better Palmer amaranth control than cereal rye, and noted that in LL cotton use of a cover crop and deep tillage resulted in yields similar to those obtained with PRE and POST applications of glufosinate for Palmer amaranth control. DeVore et al. (2011) described an 85% reduction in Palmer amaranth emergence after deep tillage in the autumn followed by a cereal rye cover crop.

As with any weed species, controlling the seed bank is an essential component of integrated management of Palmer amaranth. Norsworthy (2011b) and Prostko (2012) reported that cultural practices such as hand-weeding and improved sanitation to avoid spreading weed seed in cotton gin trash need to be employed along with herbicides for consistent control of Palmer amaranth. However, hand weeding needs to be employed with care; Sosnoskie et al. (2012c) reported that hand-pulled Palmer amaranth can reroot and produce seed if left lying in the field. Flowering Palmer amaranth with stems severed using a hoe at 15 cm, 3 cm, and at the soil surface resprouted and produced 129,000, 36,000 and 22,000 seeds plant^{-1} , respectively (Sosnoskie et al. 2012c). Although the amount of seed produced from the chopped plants was much less than the 400,000 seeds plant^{-1} produced by Palmer amaranth that was not hoed, this research demonstrated that hand-weeding can help reduce the Palmer amaranth seed bank but used alone cannot eliminate it. Gin trash collected at cotton gins and then spread on fields can also spread Palmer

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amaranth. Norsworthy et al. (2009) reported that viable Palmer amaranth seed was found in the top 25 cm of gin trash piles, even after two years of composting, and proposed that additional technologies are needed to ensure disposal of a gin-trash product free of viable weed seed. Crop rotation can also be used as a tool to control the seed bank; Norsworthy (2011b) and Steckel (2012a) reported that rotating from cotton to corn, thereby applying herbicides labeled for use in corn, can reduce the Palmer amaranth seed bank but only if Palmer is controlled after corn harvest, which in much of the southern U.S. runs from July through August. Palmer amaranth that emerges in late July or early August can still add significant seed to the soil seed bank (Norsworthy et al. 2012b). Prostko (2012) reported that mowing or tilling Palmer amaranth less than 15 cm in height is an effective control measure after corn harvest in Georgia.

A frequently overlooked cultural practice is Palmer amaranth management in field borders, roadsides and railroad rights-of-way (Bond 2012; Norsworthy et al. 2012c). Vegetation in these areas is often sprayed with glyphosate, either inadvertently as fields are being treated or as targeted application for right-of-way weed management. With the resulting loss of other vegetation, glyphosate-resistant weeds, particularly Palmer amaranth, flourish and produce significant seed numbers that readily wash into fields (Bond 2012). The author went on to note, that the best management practice for these situations is to reestablish the perennial grass cover which will greatly reduce Palmer amaranth establishment.

The emerging picture for management of glyphosate-resistant Palmer amaranth is that no single herbicide will successfully control this weed for more than a four- to five-year period (Culpepper 2006; Heap 2012), and that nonchemical approaches to management can also be inconsistent (Sosnoskie et al. 2012c). To be sustainable, future management will require an integrated approach that combines diverse crop- and site-appropriate cultural practices with timely application of herbicides utilizing more than one MOA effective on Palmer amaranth.

Summary and Future Research

Various factors have contributed to the emergence of Palmer amaranth as a major weed in cropping systems across the southern U.S. Some of these factors are associated with changing weed management practices. For example, adoption of conservation tillage and abandonment of deep cultivation favors Palmer amaranth with its small seeds that germinate at shallow soil depths. Increased dependence on herbicides with a limited array of MOAs, especially sole reliance on glyphosate in glyphosate-resistant crops, also contributes to a favorable environment for a weed such as Palmer amaranth that has large genetically diverse populations and the potential for rapid evolution of resistance. Palmer amaranth is an opportunistic and competitive weedy species *par excellence* with high fecundity, rapid germination and growth, and a capacity for phenotypic and phenological plasticity that enables seed production under different conditions until late in the growing season. As a desert-adapted C_4 plant, its U.S. range to date appears to have been limited to the southern tier of states in part by temperature requirements for germination. The high optimal temperature range for maximum photosynthesis previously discussed - between 36 and 46 C according to Ehleringer (1983) - may also place Palmer amaranth at a competitive disadvantage with other weedy species, including other *Amaranthus* spp., in higher latitudes and cooler environments. However, Palmer amaranth populations have recently been observed in Illinois and Michigan (C. Sprague, personal communication) and in Colorado (D. Giacomini, personal communication). The extent to which Palmer amaranth might expand its range northward in response to climate change and warmer temperatures is unknown, and should be investigated.

Another unexplored area of research is the potential for genomic plasticity and epigenetic adaptive response in this species. The rapid evolution in Palmer amaranth of a novel form of glyphosate resistance because of multiple copies of the EPSPS gene suggests the genome of this weed may also be capable of other forms of rearrangement. Epigenetic responses to changing environments, based on alterations in genome architecture and gene expression rather than changes in the underlying DNA base sequence, could explain at least some of Palmer amaranth's capacity for rapid adaptation.

Further research on long-term management strategies for herbicide-resistant Palmer amaranth is also needed. The introduction of stacked trait crop varieties with multiple herbicide resistances will provide growers with more flexible options for chemical control in the short term. However, Palmer amaranth populations with resistance to more than one herbicide MOA are already being reported, as described earlier in this review. Given the adaptive capacity this weed has already demonstrated, the further evolution of multiple herbicide resistance in Palmer amaranth is highly likely. The development and implementation of management practices that integrate sustainable herbicide use with appropriate nonchemical methods for cropping systems impacted by Palmer amaranth should therefore be a priority.

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